Characteristics of Simian Adaptation Fields Produced by Behavioral Changes in Saccade Size and Direction

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The gain of saccadic eye movements can be altered gradually by moving targets either forward or backward during targeting saccades. If the gain of saccades to targets of only one size is adapted, the gain change generalizes or transfers only to saccades with similar vectors. In this study, we examined the spatial extent of such saccadic size adaptation, i.e., the gain adaptation field. We also attempted to adapt saccade direction by moving the target orthogonally during the targeting saccade to document the extent of a direction or cross-axis adaptation field. After adaptive gain decreases of horizontal saccades to 15° target steps, >82% of the gain reduction transferred to saccades to 25° horizontal target steps but only ~30% transferred to saccades to 5° steps. For the horizontal component of oblique saccades to target steps with 15° horizontal components and 10° upward or downward vertical components, the transfer was similar at 51 and 60%, respectively. Thus the gain decrease adaptation field was quite asymmetric in the horizontal dimension but symmetric in the vertical dimension. Although gain increase adaptation produced a smaller gain change (13% increase for a 30° forward adapting target step) than did gain decrease adaptation (20% decrease for a 30° backward adapting target step), the spatial extent of gain transfer was quite similar. In particular, the gain increase adaptation field displayed asymmetry in the horizontal dimension (58% transfer to 25° saccades but only 32% transfer to 5° saccades) and symmetry in the vertical direction (50% transfer to the horizontal component of 10° upward and 40% transfer to 10° downward oblique saccades). When a 5° vertical target movement was made to occur during a saccade to a horizontal 10° target step, a vertical component gradually appeared in saccades to horizontal targets. More than 88% of the cross-axis change in the vertical component produced in 10° saccades transferred to 20° saccades but only 12% transferred to 4° saccades. The transfer was similar to the vertical component of oblique saccades to target steps with either 10° upward (46%) or 10° downward (46%) vertical components. Therefore both gain and cross-axis adaptation fields have similar spatial profiles. These profiles resemble those of movement fields of neurons in the frontal eye fields and superior colliculus. How those structures might participate in the adaptation process is considered in the DISCUSSION.

RESULTS

Introduction

When the rapid eye movements known as saccades are made to targets within ± 15° of straight ahead, they are quite accurate in both human and nonhuman primates. This accuracy persists throughout life (Warabi et al. 1984) even though neurons in the saccadic control system may die and the extraocular muscles may weaken. How the brain overcomes these difficulties to allow the eyes to fall on target has become an area of increasing interest. For rapid somatic movements of the limbs and head, visual and other feedback may be used to compensate for such impairments. Saccades, however, are so rapid that visual feedback is too slow to influence their trajectories. Therefore there must be some other mechanism that adjusts the efficacy of neuronal elements and compensates for their deterioration due to aging or disease.

Recent investigations of this mechanism have been based on a behavioral paradigm pioneered by McLaughlin (1967). In this paradigm, the gain (G) of saccades, i.e., the ratio of the amplitude of the eye saccade (E) to the amplitude of the target displacement (T) that elicited it, can be altered reversibly. After the target jumps, the onset of a saccade toward the target is detected, and the target is stepped backward during the saccade by a certain percentage of the initial target step so that the eye lands beyond the target as though the saccade had been too large. Consequently, the eye must make a backward corrective saccade to acquire the target. The amplitudes of the initial and corrective saccades gradually become smaller, and the eye often goes directly to the back-stepped target location rather than to the initial target location. This process of adaptation can occur within <100 trials in humans (Deubel et al. 1986; McLaughlin 1967; Miller et al. 1981) and ~1,000 trials in monkeys (Straube et al. 1997). After adaptation, if a subject is presented with an ordinary target step that is not accompanied by an intrasaccadic backward step, the eye falls short of the target, i.e., saccadic gain (E/T) has been reduced. Gain reductions largely persist after an adapted monkey has been in the dark for 20 h, suggesting that adaptation is the result of a true neuronal plasticity (Straube et al. 1997). A similar paradigm with forward intrasaccadic steps can cause a gain increase in both humans (Miller et al. 1981; Semmlow et al. 1989) and monkeys (Straube et al. 1997).

Saccadic gain changes produced by the McLaughlin paradigm are not parametric, i.e., they do not generalize completely to saccades with other vectors. For example, gain changes for saccades to targets in one direction do not generalize to saccades in the opposite direction in either humans (Deubel et al. 1986; Miller et al. 1981; Semmlow et al. 1989; Weisfeld 1972) or monkeys (Straube et al. 1997). Adaptation of saccades to target steps of one size does not transfer completely to saccades to target steps of other sizes in either humans (Frens and Van Opstal 1994; Semmlow et al. 1989) or monkeys. In previous experiments, we found that behavioral gain reduction of hori-
horizontal saccades to target steps of only one size causes only a partial gain reduction of horizontal saccades to target steps of other sizes (Straube et al. 1997) and also produces gain reductions in the horizontal component of oblique saccades to target steps with the same horizontal component (Wallman et al. 1996; Wallman and Fuchs, 1998). In both of these studies, the transfer of gain reduction decreased as the tested saccades differed increasingly in either amplitude or direction from the adapted saccade.

Taken together, these data suggest that there is a limited “adaptation field” within which a gain change produced by a specific adaptation paradigm is expressed (Frens and Van Opstal 1994). However, it is impossible to construct a complete adaptation field from our previous two sets of data or from those in the literature because the data were drawn from different animals under different conditions. Therefore we performed gain adaptation experiments using the same animal in the same session under the same conditions. We also attempted to adapt saccade direction by jumping the target orthogonally during a targeting saccade, and we determined the extent of the transfer of this cross-axis adaptation on saccades with different vectors. Our objective was to determine whether such gain and direction adaptation fields resemble the movement fields exhibited by neurons in saccadic structures such as the frontal eye fields (FEFs) and the superior colliculus (SC) (Melis and Van Gisbergen 1996). We reasoned that if adaptation fields had characteristics that were similar to movement fields in the FEFs or SC, those structures might be molding the characteristics of the adaptation process. For example, they might contribute an error signal that drives adaptation. Although the SC, the caudal fastigial nucleus of the cerebellum, and the saccadic brain stem burst generator have been proposed as elements in several models of saccade adaptation (e.g., Dean et al. 1994), very little, if any, data are available about their behavior during adaptation. Therefore although we will show here that adaptation and movement fields are similar in many respects, we will only be able to speculate about the significance of the similarities.

METHODS

The subjects were three rhesus macaques that exhibited robust, saccadic gain adaptations when subjected to the McLaughlin paradigm. The animals were trained to follow a target as it moved on a screen facing them. Target motion was produced by controlling the position of a red laser light spot, which subtended angles of either 0.25 or 0.4° in two different test situations. Before the image of the red spot reached the screen, two mirror galvanometers situated orthogonal to each other intercepted it. Voltages specified by a Macintosh IIIX computer equipped with M1 and MIO boards drove the galvanometers to deflect the target and thereby produced target motion in two dimensions.

Eye movements were measured by the electromagnetic search coil technique (Fuchs and Robinson 1966; Robinson 1963). The animal’s head was held stationary within the magnetic fields by means of three dental acrylic lugs attached to the skull. These, along with the eye coil, were implanted in an aseptic surgical procedure while the animal was under general anesthesia. The monkeys were rewarded with fortified applesauce for keeping their eyes within ±2° of the target for 1–4 s. After an animal was trained, we could determine eye position to within 0.5° of arc over a range of eye movements between ±20° of straight ahead. Once the animals had learned to make saccades reliably, we did experiments to characterize the size and shape of saccadic gain adaptation fields or cross-axis adaptation fields.

The surgical and behavioral training procedures used in our laboratory are well documented (e.g., Fuchs et al. 1993) and 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 (NIH publication 85–23) and with recommendations from the Institute of Laboratory Animal Resources and the American Association for Accreditation of Laboratory Animal Care.

Gain adaptation fields

In these experiments we produced either increases or decreases in the gain of horizontal saccades and tested the effects of this adaptation on saccades of similar amplitudes and directions. Each saccade elicited by an initial horizontal target step of a fixed size (most often 15° in these experiments) was detected when its velocity exceeded ~50°/s. This triggered an intrasaccadic adapting target step either in the same direction as the initial step (forward adaptation), thereby producing a gain increase, or in the opposite direction from the initial target step (backward adaptation), resulting in a gain decrease. The computer program that generated target motion caused the target to jump by 30% of the initial step amplitude. In this experiment and those that followed, the computer did not allow the target to land >20° away from the primary direction of gaze on either the initial or subsequent intrasaccadic step. Because targets could step to either the right or the left and the next trial commenced from where the previous one had ended, saccades started at many different positions between ±20°; therefore, the animal could not predict where the target would land after the intrasaccadic target jump.

As we and others have shown previously, such surreptitious intrasaccadic target steps reliably produce either reductions or increases in gain within ~1,000 trials (Straube et al. 1997). In these experiments, therefore, we subjected the monkeys to ≥1,000 saccades in each adapted direction. After adaptation, we collected horizontal saccades to a variety of target step amplitudes, including those used during the adaptation trials, to evaluate the spatial extent of adaptation along the adapted axis. To evaluate the degree of adaptation along an axis orthogonal to the adapted axis, we collected oblique saccades to targets with the same horizontal component as that adapted but with a variety of vertical components. In this experiment and all those described in the following text, 10–30 saccades were collected for each target step before and after adaptation and were averaged separately.

To produce a gain adaptation field, we first determined the percentage of change in saccadic gain (G = E/T) as Percentage of Gain Change = (Gpost - Gpre)/Gpre, which, because target amplitude was constant, reduced to Percentage of Gain Change = (Epost - Epre)/Epre.

The amount by which the percentage of gain change produced for saccades to the adapted target amplitude generalized (i.e., transferred) to saccades made to targets of other, nonadapted amplitudes was simply Percentage of Gain Transfer = [% Gain Change at Non-adapted Amplitudes]/[% Gain Change at Adapted Amplitudes].

For example, if adaptation produced a direct gain change of 20% in the adapted saccades to 10° horizontal targets but caused a 5% gain reduction in saccades to 5° horizontal targets, the percentage of gain transfer from the adapted to the nearby saccade would be 5/20 or 25%.

To determine the gain transfer in the direction orthogonal to that adapted, we determined the percentage of gain change in the adapted horizontal saccade and compared it with the percentage of gain change in the horizontal component of oblique saccades to targets whose horizontal component amplitudes were the same as the target amplitude that elicited the adapted saccade.

On different days the same monkey can exhibit quite different
amounts of adaptation under identical conditions (Straube et al. 1997).
To optimize our chances of seeing transfer from adapted saccades to nonadapted saccades of other sizes and directions, we considered data only from experiments in which the animal exhibited a gain change of ≥10% in saccades to the adapted target size.

**Cross-axis adaptation fields**

To attempt to induce an orthogonal component into purely horizontal saccades, we jumped the target vertically when a saccade to a horizontal target step exceeded a velocity of ~50°/s. The target was stepped only during saccades to horizontal steps of 10°; it was stepped upward by 5° for horizontal saccades in one direction and downward by 5° for saccades in the opposite direction. After each monkey had been exposed to ≥2,600 adapting trials (~1,300 in each direction), we collected saccades to horizontal steps of different sizes and to oblique target steps with the same horizontal component as that adapted. As data were collected before and after adaptation, the target was turned off briefly (~100–200 ms) as the targeting saccades reached velocities of 50°/s so that the monkey received no postsaccadic error signal. If it was present, such a signal would act to readapt the monkey’s saccades to a normal gain (Straube et al. 1997). Because we had no experience with the range of changes that could be produced in these cross-axis adaptations, we included the data from every experiment.

The percentage of cross-axis adaptation was determined as the average change of the vertical component of a saccade divided by the imposed intrasaccadic vertical target step of 5°. We could not use a measure similar to that used to describe gain adaptation because the average preadapted vertical component was always near zero. Similar to gain transfer, the percentage of cross-axis transfer was determined as Percentage of Cross-Axis Transfer = [% Vertical Component Change in Nonadapted Direction]/[% Vertical Component Change in Adapted Direction].

For example, if a vertical 5° intrasaccadic jump induced a 2° vertical component in adapted saccades to a 10° horizontal step, the percentage of cross-axis adaptation would be 40%. If, after adaptation, saccades made to a 20° horizontal target step had acquired a 1° vertical component, the percentage of cross-axis adaptation would be 20%, and the percentage of cross-axis transfer from the adapted saccade to the 10° target step to the nonadapted saccade to the 20° target step would amount to 50%.

**Data analysis**

To analyze the data, we digitized the pre- and postadaptation saccades on-line by sampling horizontal and vertical eye and target positions at 1 kHz. An analysis program calculated the horizontal and vertical eye velocities and scrolled the target signal and the eye position and velocity signals across a computer monitor. When saccadic eye velocity reached 75°/s, the program stopped scrolling and marked the target step and the onset and offset of the horizontal and vertical components of the saccade on the basis of an adjustable velocity criterion, which was set to 5°/s. These markings, which could be modified by the investigator, allowed a second program to calculate the saccade metrics, e.g., the size, duration, and peak velocity of the saccade and the size of the target step. On the basis of the saccade and target metrics, the program also determined the horizontal saccadic gain as (horizontal eye movement amplitude)/(target movement amplitude) for each targeting saccade. For some of the analysis, the data were exported to commercial programs [Excel (Microsoft), Cricket Graph (Computer Associates International), IGOR (Wavemetrics), and Canvas (Deneba Systems)] for further manipulation. Statistical comparisons were done using a t-test for two samples assuming equal variance.

**RESULTS**

**Saccadic gain adaptation fields**

**GAIN DECREASE ADAPTATION FIELDS.** After saccades to horizontal target steps had undergone a behavioral gain reduction, the horizontal components of saccades with similar vectors also experienced a decrease in gain. In the representative experiment illustrated in Fig. 1, we caused saccades to 15° horizontal target steps to undergo a gain increase and then tested the gain of both larger (20 and 25°) and smaller (5 and 10°) horizontal saccades. We also tested oblique saccades with 15° preadapted horizontal components and various vertical components (5 and 10°, up and down). The saccades to larger and smaller target steps were smaller, on average, than before adaptation (Fig. 1: saccades to 10° and 20° not shown for ease of viewing), as were the horizontal components of oblique saccades to target steps with similar horizontal amplitudes.

From the raw data in Fig. 1, we calculated the average gain before and after adaptation for horizontal saccades (Fig. 2, top left) and for the horizontal components of oblique saccades (Fig. 2, top middle). From these averages, we determined the average percentage of gain decrease for saccades of different sizes and directions (Fig. 2, top right). Similar calculations for a representative experiment with monkey BW are shown in Fig. 2, bottom. Finally, from the average percentage of gain decreases, we determined the mean percentage of gain transfer from the adapted 15° saccade (taken as 100% transfer) to other horizontal saccades and to the horizontal component of oblique saccades (Table 1). We then constructed gain decrease adaptation fields by averaging data from at least two experiments with each monkey (Fig. 3).

Gain decrease adaptation fields were not symmetric in all dimensions. Gain reductions transferred more completely to
saccades made to larger target steps than to saccades made to smaller ones (Fig. 3). The average gain transfer to horizontal saccades made to 25° target steps was 77% for monkey BW and 88% for monkey TO, but only 30 and 28%, respectively, for saccades to 5° target steps (Table 1). In contrast to this asymmetric gain reduction along the horizontal adapted direction, the decrement of horizontal gain as a function of how much an oblique saccade differed from the adapted horizontal direction was more symmetric (plotted as up/down components in Fig. 3). Average gain transfer to the horizontal component of saccades with a 10° upward component was 52% for monkey BW and 49% for monkey TO; for saccades with a 10° downward component, average gain transfer was 50% for monkey BW and 69% for monkey TO (Table 1). For both upward and downward oblique saccades, the transfer was less than that for large horizontal saccades but more than that for small horizontal saccades. In summary, saccadic gain changes are transferred quite asymmetrically in the adapted direction and more symmetrically in the direction orthogonal to it.

GAIN INCREASE ADAPTATION FIELDS. After saccades to horizontal target steps underwent behavioral gain increases, the horizontal components of saccades with similar vectors also experienced gain increases (Fig. 4). Average percentages of gain increase of the data in Fig. 4 from monkey TO and averages from a representative experiment with monkey BW are shown in Fig. 5. As seen in these two experiments (Fig. 5, right) and in the average of all experiments in each monkey (Fig. 6), asymmetries also occurred in the gain increase adaptation fields. Like gain decrease adaptation fields, gain increases tend to transfer better to saccades that are larger than the adapted one than to those that are smaller. For monkey BW, the average gain transfer was 74% to horizontal saccades made to 25° target steps but only 39% to saccades made to 5° targets.
(Fig. 6, Table 1). The asymmetry was less marked in monkey TO, which had an average gain transfer of 41% to saccades made to 25° target steps and 25% to saccades to 5° steps. As with gain reduction adaptation fields, the transfer to the horizontal component of saccades with oblique vectors was more symmetric than the transfer to horizontal saccades of different sizes. The average gain transfer to the horizontal component of saccades with a 10° upward component was 55% in monkey TO, which had an average gain transfer of 41% to saccades made to 25° target steps and 25% to saccades to 5° steps. As with gain reduction adaptation fields, the transfer to the horizontal component of saccades with oblique vectors was more symmetric than the transfer to horizontal saccades of different sizes. The average gain transfer to the horizontal component of saccades with a 10° upward component was 55% in monkey TO, which had an average gain transfer of 41% to saccades made to 25° target steps and 25% to saccades to 5° steps. As with gain reduction adaptation fields, the transfer to the horizontal component of saccades with oblique vectors was more symmetric than the transfer to horizontal saccades of different sizes. The average gain transfer to the horizontal component of saccades with a 10° upward component was 55% in monkey TO.

![Fig. 3](http://jn.physiology.org/)

**FIG. 3.** Transfer of behavioral gain decreases of saccades made to 15° horizontal target steps (taken as 100%) to horizontal saccades of other sizes and the horizontal component of oblique saccades with the same horizontal component target step. H\text{comp} and V\text{comp} refer to the horizontal and vertical components of preadapted saccades averaged for each different target step. Data averaged from 2 experiments with monkey BW and 4 with monkey TO.
many saccades were required to produce an increase.

In the experiment with *monkey TO*, saccades to 10° target steps to the right and left in the adapted hemifield exhibited robust gain reductions (Fig. 8, left), which transferred, in part, to neighboring horizontal saccades of 5, 15, and 20°. Similar gain changes occurred for rightward and leftward saccades in the nonadapted hemifield (Fig. 8, middle). The shapes of the adaptation fields along the horizontal axis (Fig. 8, right) for rightward and leftward saccades in the adapted hemifield were quite similar to the adaptation fields that transferred to the nonadapted hemifield: only the gain decreases for 15 and 20° rightward saccades were significantly less than those in the adapted hemifield (*P* ≤ 0.05). Similar transfer from the adapted to the nonadapted hemifield was seen in the average of the two experiments with *monkey CR* (Fig. 8, right insets). Again, the shapes of the adaptation fields were qualitatively similar and only the data for 10° rightward and 15° leftward saccades differed significantly between the adapted and nonadapted hemifields. Therefore we conclude that the adaptation field is specific to the vector of the target step that is adapted and that the adaptation field is expressed even if the adapted target step occurs at different loci within the animal’s oculomotor range.

**Cross-axis adaptation fields**

In the foregoing experiments, we adapted horizontal saccade gain alone and assessed the transfer to saccades with other vectors. In the experiments described in this section, we investigated whether the direction of a pure horizontal saccade could be altered by application of a vertical intrasaccadic adapting step. To study the characteristics of such cross-axis adaptation and to determine whether they differ from those of gain adaptation, we adapted saccade direction by stepping the target either upward or downward during a horizontal saccade. Figure 9 shows the amplitudes of saccades to horizontal and oblique target steps before and after a cross-axis adaptation in which saccades to 10° leftward target steps displaced the target downward by 5° and those to rightward steps displaced it upward by 5°. Both horizontal and oblique saccades acquired substantial vertical components specific to the adapting conditions: 10°
saccades to leftward targets acquired downward components, whereas 10° saccades to the right acquired upward components. Furthermore this adaptation transferred, at least in part, to horizontal saccades made to other target step sizes (5°, 10°, 20°, and 25°) and to oblique saccades with 15° horizontal components and ±5° and ±10° vertical components. Percentage of gain increase for horizontal and oblique saccades as determined from data left and middle. Adapting, intrasaccadic step for 15° saccades was forward by 30% of the target step. Details of this figure are like those of Fig. 2.

Although the saccades in the experiment shown in Fig. 9 acquired clear vertical components, they exhibited little, if any, alteration in the gain of their horizontal components; only the horizontal gains of leftward 14° and 20° saccades and rightward 7° saccades were altered by the cross-axis adaptation (P < 0.05). In other experiments with this monkey (BW), horizontal saccade gains also showed significant differences for some saccade sizes but the same saccade sizes were not affected consistently from one experiment to another. In monkey TO, 50% of the experiments produced data similar to those from monkey BW in that the horizontal gains of many more of the tested saccades were unaffected than affected during cross-axis adaptation. In the other 50%, however, the horizontal gains at more than half of the tested saccade sizes in each experiment were different after cross-axis adaptation. Therefore although most of our data suggest that the cross-axis paradigm primarily affects saccade direction while producing little effect on saccade size, further experiments would be necessary to establish this suggestion conclusively.

Taking the raw data in Fig. 9B as an example, we calculated the average vertical component before and after adaptation for horizontal saccades that were both larger and smaller than that adapted (Fig. 10; top left) and for different-sized oblique saccades with the same size horizontal component as the adapted saccade (Fig. 10; top middle). From these averages, we determined the average change in vertical component amplitude for saccades of different sizes and directions (Fig. 10; top right) and the average percentage of cross-axis adaptation (see METHODS). Figure 10, bottom, shows data from a representative experiment on monkey TO in which rightward saccades were accompanied by downward steps.

Table 2 shows similar data for all 14 experiments in the two
monkeys. At the adapted saccade size of 10°, there was no significant difference (P > 0.05) in the percentage of change in the vertical component whether an upward cross-axis signal was launched during rightward or leftward saccades; nor was there a difference whether a downward cross-axis signal occurred during left- or rightward saccades. This conclusion is based on a comparison of data obtained during saccades to the left and to the right during the same experimental session (experiments with the same date in Table 2). Therefore we averaged all the data obtained with upward adapting steps and all the data obtained with downward adapting steps separately for each monkey. From these averages, we determined the percentage of cross-axis transfer from the adapted 10° saccade (taken as 100% transfer) to other horizontal saccades and to the horizontal component of oblique saccades (Table 2).

At the adapted target size of 10°, monkey BW exhibited a greater average change in the vertical saccadic component (40.6% for upward steps, 39.2% for downward) than did monkey TO (33.4 and 30.6%, respectively). Figure 11 shows how this cross-axis adaptation transferred to other saccades. As with saccadic gain adaptation, cross-axis adaptation had less influence on small horizontal saccades than on large ones. For both monkeys, the amount of transfer was qualitatively similar whether the intrasaccadic target steps had been upward or downward (Fig. 11, horizontal target steps). Whenever there was a significant difference in the percentage transfer (Fig. 11,
Both upward and downward cross-axis adaptation produced a relatively symmetrical transfer to the upward and downward vertical components of oblique saccades for both monkeys (Figs. 10, and 11). Although the transfer was symmetrical, the amount of transfer for some vertical target components depended on whether the saccades had been adapted with upward or downward target steps; whenever there was a significant difference in the percentage transfer, it was greater for upward adaptation (Fig. 11). In all panels, horizontal saccade amplitude refers to the size of the preadapted saccade.

In Fig. 11 (average), we plotted the cross-axis adaptation fields by averaging the percentage of cross-axis transfer with or without regard for whether the direction of adaptation was upward or downward. Only 63% (monkey TO) and 45% (monkey BW) of the cross-axis adaptation at 10° transferred to horizontal saccades to target steps that were 3° smaller, i.e., 7° in size. Horizontal saccades to target steps that were 6° smaller than that adapted, i.e., 4° in size, experienced average transfers of just 16% (monkey TO) and 8% (monkey BW) in two experiments with each monkey. In contrast, saccades that were larger than the adapted saccade experienced considerable cross-axis transfer. The amount of transfer to horizontal saccades made to target steps that were 10° larger, i.e., 20° in size, averaged 95% in monkey TO and 80% in monkey BW. In contrast, the percentage of cross-axis transfer to the vertical component of saccades to oblique target steps averaged 48 and 44% in both the upward and downward directions for monkeys BW and TO, respectively. Therefore, cross-axis adaptation has a more symmetrical influence on the vertical component of oblique saccades than it does on the acquired vertical component of horizontal saccades. All in all, the shapes of the adaptation fields after behavioral acquisition of a saccadic component orthogonal to the adapted saccade (Fig. 11) resemble those that follow a saccadic gain change (Figs. 3 and 6).

Further properties of directional and gain adaptation

TIME COURSES OF CROSS-AXIS AND GAIN DECREASE ADAPTATION. In addition to the similarities in the shapes of their adaptation fields, gain decrease and directional adaptations also had similar time courses. To chart their time courses, we plotted either saccade gain or the vertical component of the saccade for cross-axis adaptation as a function of the number of the adapted saccade and fitted the relations with exponential curves.
from which we could determine the rate constant (see Straube et al. 1997 for examples). In two cross-axis adaptations and four gain-reduction adaptations each with the two monkeys, the average rate constants of exponential fits to direction and gain reduction adaptation were 364 and 474 saccades, respectively, for monkey BW and 733 and 627 saccades for monkey TO. Although adaptations of both direction and gain were slower in monkey TO than in monkey BW, the former showed slower adaptations for gain than for direction, whereas the latter showed slower adaptations for direction than for gain. Furthermore for both monkeys, the difference in rate constants for the two adaptations was only 100 saccades. Therefore we conclude that cross-axis and gain decrease adaptations have similar rate constants.

RETENTION OF SACCADIC GAIN AND DIRECTIONAL CHANGES. The day after adaptation, we often noticed that the monkeys had retained some of a gain reduction but usually little, if any, of a gain increase. To quantify this apparent difference, we increased the gain of rightward 13.5° saccades and decreased the gain of leftward 13.5° saccades in both monkeys and measured the gain again after they had spent 24 h in their cages under normal illumination conditions. Monkeys TO and BW retained 45 and 71%, respectively, of their gain decreases but only 13 and 17% of their gain increases. Although these were only single experiments with each animal, the results confirm our qualitative impressions that saccadic gain reductions are more enduring than gain increases.

We also tested whether the adaptations produced by gain reductions and cross-axis adaptation had comparable retention. In two experiments on each animal, we either adapted the direction or reduced the gain of horizontal saccades and then evaluated saccadic performance after the animals had been in their cages for ~16 h (monkey TO) or ~24 h (monkey BW). After cross-axis adaptation, an average of 25% of the adaptation was retained in monkey TO and 18% in monkey BW. After gain reduction, on the other hand, an average of 45% was retained in monkey TO and 71% in monkey BW. Although these too were only single experiments with each animal, the results tentatively suggest that adapted changes in gain reduction are retained better than adapted changes in direction.

DISCUSSION

Our study makes several points. First, we have confirmed the findings of other investigators (Frens and Van Opstal 1994; Semmlow et al. 1989) that intrasaccadic target displacements do not produce the same gain adjustment for all saccades; rather, the strongest influence is on saccades whose amplitudes and directions are nearest to those of the adapted saccade. Our contribution has been to describe the region of influence (i.e., the adaptation field) of saccades with specific vectors whose gain has been either increased or decreased. Second, we have shown that cross-axis adaptation can induce an orthogonal component in a previously purely horizontal saccade and that cross-axis adaptation, like saccade gain adaptation, is local. Third, we have shown that gain reduction adaptation and direction adaptation have similar time courses but apparently differ in their ability to retain adaptation, whereas gain increase adaptation appears to have both a slower time course and a poorer retention than gain decrease adaptation. We will speculate on the significance of these differences later in the discussion. Fourth, we have shown that the adaptation fields for gain and cross-axis adaptation have rather similar shapes. We will consider possible reasons for the shapes of adaptation fields, explore their similarity to movement fields in the SC and FEFs, and discuss whether the similarity implies involvement of those two structures in saccadic adaptation.

Saccade adaptation fields

Our data show that horizontal saccades can be forced to adapt their size and to acquire an orthogonal component and
that these gain and cross-axis adaptations generalize best to saccades with similar vectors. The more a saccade differs in amplitude and direction from the adapted saccade, the less it is adapted (Figs. 3, 6, and 11). However, the decrement in the transfer of adaptation depends on the vector of the tested saccade. For both gain and cross-axis adaptation, the average percentage of transfer falls sharply for horizontal saccades that are smaller than the adapted saccade but more gradually for larger horizontal saccades and the horizontal component of saccades with a vertical component (Figs. 3, 6, and 11). The shapes of gain (both increase and decrease) and cross-axis adaptation fields are quite similar, with asymmetric contours along the adapted axis (always horizontal in our study) but relatively symmetric contours along the orthogonal axis.

A salient property of adaptation fields is that gain transfer is poor to saccades smaller than those adapted and much better to larger saccades. On the basis of behavioral considerations, poor transfer to small saccades might be expected. As saccades become smaller, the target step that elicits them falls closer to the fovea so less adaptation is necessary. For example, if 10° saccades undergo a gain reduction of 20%, there is a dysmetria of 2°. If gain transfer is perfect, a 5° saccade would experience a 1° hypometria. However, if the effective fovea is 0.5° in diameter, a 5° saccade wouldn’t need to adapt by 20% because a 10% adaptation would place the target within the fovea.

**Cross-axis adaptation.** Others have adapted saccade direction in both humans (Deubel 1987; Frens and Van Opstal 1994; Mack et al. 1978) and monkeys (Deubel 1987; Melis and Van Gisbergen 1996). The average 36% cross-axis adaptation that we obtained with 5° vertical target steps during 10° horizontal saccades in monkeys BW and TO is similar to the average 32% adaptation obtained with 1.5° vertical target steps during 3° saccades with humans (Mack et al. 1978). As in the case of...
either upward (1) or downward (2) produced by cross-axis adaptation of 10° horizontal saccades with 5° vertical target steps. Cross-axis adaptations were performed on saccades to the right (R) and left (L) and with saccadic gain, which may be either increased or decreased, it is also possible to cause a previously horizontal saccade to acquire either an upward or a downward orthogonal component. It could be argued that we chose an inappropriate metric to evaluate the extent of cross-axis adaptation. Instead of considering a change in the vertical component of the saccade, perhaps we should have considered the change in the angle of the adapted saccade vector. However, we already have demonstrated that the horizontal component does not show a consistent, significant change during adaptation of the vertical component, from which we conclude that the tangent of the angle of the adapted saccade vector is proportional to the vertical saccade component alone. Therefore we would expect that the cross-axis adaptation field profiles would be similar whether we use the change in the vertical component, as we did in this study, or the change in the angle of the saccade as the metric with which to evaluate the amount of cross-axis adaptation. Indeed, when we plotted adaptation fields on the basis of...
saccade angle rather than the size of the vertical component in two experiments with monkey BW (07/05/97 and 11/1/97) and with monkey TO (08/08/97 and 09/11/97), there were only subtle differences in the profiles of the adaptation fields. In particular, the salient features, i.e., a more rapid decrement for smaller than larger saccades and a symmetric decrement for saccades to targets orthogonal to that adapted, were preserved. The difference in the details of the adaptation fields probably can be attributed to the fact that inverse trigonometric functions are not linear functions of larger angles.

DIFFERENCES IN THE CHARACTERISTICS OF GAIN AND CROSS-AXIS ADAPTATION. Although their adaptation fields seem rather similar, there are differences between gain and cross-axis adaptation. First, more saccades are required to produce gain increases than either gain decreases or cross-axis adaptation, both of which have similar rate constants for each of our monkeys. Our finding that the rate constants for cross-axis and gain decrease adaptation exhibited no consistent differences seems to be at odds with Deubel's (1987) findings in monkeys, which showed rate constants for gain decrease adaptation (>400 saccades) (Fig. 3 in Deubel 1987) that were more than double those for direction adaptation (~200 saccades). However, in Deubel's study pure direction adaptation was elicited because the intrasaccadic, adapting target jump had the same vector but not, as in our study, the same horizontal component. We have no explanation for how this difference in the intrasaccadic target step could account for the disparity between the results of these two studies.

Also, the cross-axis paradigm might have produced a pure rotation of the adapted saccade vector. Instead we found a specific alteration of the vertical saccade component. This finding seems to suggest that cross-axis adaptation is not expressed in polar coordinates. However, others have shown that it is possible to achieve selective adaptation of saccade direction (Deubel 1987).

Second, we have demonstrated that gain decrease adaptations...
are better retained after an adapted monkey spends the night in its cage than are gain increase or cross-axis adaptations. Therefore despite the similarities in the shapes of their adaptation fields, gain decrease adaptation seems different from both gain increase and cross-axis adaptation in several ways.

These data are consistent with our earlier observation that saccadic gain increases could be served by a mechanism with different dynamics than that subserving gain decreases (Straube et al. 1997). In most natural disorders such as muscle weakness and cell death, hypometric saccades are to be expected. Therefore it seems paradoxical that the saccadic adaptation mechanism that apparently is most useful, i.e., that producing a gain increase, would be relatively slower and less efficient and would not retain adaptation as well as the mechanism producing gain reduction.

**Neuronal participants in saccade adaptation**

SIMILARITY OF ADAPTATION AND MOVEMENT FIELDS. Gain and cross-axis adaptation fields show a qualitative similarity to the movement fields of neurons in the SC (Freedman and Sparks 1997; Figs. 1–3 in Sparks et al. 1976) and the FEFs (Fig. 3 in Bruce et al. 1985; Fig. 19 in Bruce and Goldberg 1985; Goldberg and Seagraves 1989). Figure 12 shows representative movement fields of neurons with preferred sizes of −5°, intermediate (−10°), and large (−15°) preferred vectors are illustrated.
peaked, and for larger target steps they appear to be quite broadly tuned. Although they are not always identical, the similarity of movement and adaptation fields is rather striking, considering the variability of the saccadic adaptation process from day to day and from monkey to monkey.

Not only are gain reduction adaptation and movement fields qualitatively similar in shape, both are relatively independent of eye position. We already have mentioned that saccade-related burst neurons in the SC (Wurtz and Goldberg 1971) and probably the FEFs (M. E. Goldberg, personal communication) discharge similar bursts no matter where the eye movement is initiated. Gain reduction adaptation also does not depend on eye position because gain changes for saccades adapted to target steps in one oculomotor hemifield transfer well to saccades to the same target steps in the other hemifield (Fig. 8). The generalization of gain reduction adaptation across different eye positions also has been demonstrated in humans (Albano 1996), although in that study the ipsilateral and contralateral saccadic end positions differed by only 6°. Therefore many of the salient features of adaptation fields are reflected in the movement fields of neurons in the SC and also the FEFs.

Adaptation and Movement Field Similarities: A Clue About Function? Does the similarity of adaptation fields and saccadic movement fields implicate topographically organized areas such as the FEFs and the SC in saccade plasticity, and if so, how? One possibility is that movement fields in the SC or FEFs are themselves altered during saccade adaptation. Several labs have addressed this possibility in the SC by probing its activity through either single-unit recording or electrical stimulation before and after monkeys underwent behavioral gain decreases (Fitzgibbon et al. 1986; Frens and Van Opstal 1997; Goldberg et al. 1993; Melis and Van Gisbergen 1996). After adaptation, the activity of some saccade-related burst neurons continued to discharge with the same vigor as before adaptation even though the saccade was reduced in size. For example, a 10° target step after adaptation might elicit a 7° saccade at a 10° site in the SC, but the saccadic burst would be similar to that occurring before adaptation, suggesting that activity in the SC was best related to the desired rather than the actual saccade vector. In contrast, stimulation of a collicular site after behavioral adaptation produced saccades that had not been altered by the adaptation. Unfortunately the recording data suggest that the saccadic gain adaptation acts downstream of the SC, whereas the stimulation data lead to the opposite conclusion. Neither set of data suggests that the movement fields of the SC itself change during the adaptation process. Similar experiments have not yet been done on the FEFs.

How then might the SC or FEFs participate in saccadic gain adaptation? Most of the crucial data required to address this question are not yet available, so the following scenario must be viewed as highly speculative. We do know that there are two major inputs to the brain-stem burst generator that produces saccades. One, which arises from the SC (Moschovakis et al. 1996), has been established by anatomic and electrophysiological studies. A second, which arises from the caudal fastigial nucleus (CFN) of the cerebellum, is supported by anatomic (Noda et al. 1990) and electrophysiological (Scudder 1997) studies and by the effects of CFN inactivation, which causes saccadic eye movements to become very dysmetric (Robinson et al. 1993). If adaptation is not associated with a change in the activity of the SC input, a change must occur in CFN discharge. Under normal, i.e., nonadapted, circumstances, CFN neurons discharge nearly equal bursts for saccades of all sizes, but the timing of the burst varies with saccade size and direction (Fuchs et al. 1993). Therefore during adaptation, CFN neurons must change their discharge patterns, probably both in magnitude and timing, but only for saccades to the adapted target step and its vector neighbors. Recent studies indicate that changes in both burst timing (Scudder 1998) and magnitude (F. Robinson, unpublished data) do occur during saccadic gain adaptation, although it is not clear whether they are specific for the adapted saccade.

During saccadic gain changes, therefore, the CFN must acquire an altered discharge pattern with an activity profile (e.g., overall number of spikes as a function of saccade amplitude) that resembles the developing adaptation field. Because the adaptation field resembles a SC movement field, such a signal could be supplied by the SC. However, the altered input signal associated with the adapted saccade and its vector neighbors would have to be extracted from the overall collicular map, which has movement fields for saccades of all sizes and directions. The “highlighting” of a particular locus of SC activity could occur in the nucleus tegmenti pontis (NRTP), which receives a heavy input from the SC and sends a strong projection to the oculomotor vermis, a source of CFN afferents. NRTP neurons, like those of the SC, have movement fields (Crandall and Keller 1985). During adaptation, another input, possibly from the FEFs, gradually would highlight only those NRTP signals associated with the adapted saccade. These, in turn, would alter only that cerebellar activity necessary to produce the local changes characteristic of an adaptation field. Of course, it also is possible that saccadic gain adaptation actually is accomplished by a completely different mechanism.

Finally, it might be argued that the similarity of adaptation and movement fields, while striking at first glance, is only qualitative and that a quantitative comparison of Figs. 3, 6, and 11 with Fig. 12 reveals that movement fields of SC neurons actually are narrower in width than those of adaptation fields. However, the characteristics of adaptation surely must result from a population of cells whose net influence would be broader than that of its individual constituents. Clearly, documenting the discharge patterns of the various elements of the adaptation network, in particular, the changes of the movement fields of neurons in the NRTP and possibly the caudal fastigial nucleus, during saccadic gain changes will be necessary before we can construct a realistic model of the adaptation process.

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