



Saccades to remembered targets exhibit enhanced orbital position effects in monkeys

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Abstract

Remembered saccades of rhesus monkeys are markedly influenced by starting eye position. Altering the initial position systematically affects the direction or amplitude of the movements to a striking degree. In general, changes in the horizontal or vertical starting position primarily produce changes in the horizontal or vertical component, respectively, regardless of whether the target displacement occurs in the horizontal or vertical direction. For some monkeys, a similar pattern of initial position influence on movement direction can be seen in the curvature of visually guided saccades. Starting position also modulates the upward offset in fixation, which monkeys display in the dark. © 2001 Elsevier Science Ltd. All rights reserved.

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1. Introduction

The saccadic system produces high-velocity, conjugate movements that rapidly shift the line of sight from one region of the visual field to another. Saccades to targets that are continuously available, *visually guided saccades*, are more accurate and faster than saccades to remembered target locations, *remembered saccades* (Becker & Fuchs, 1969; White & Sparks, 1986). The amplitude and direction of visually guided saccades is relatively independent of the initial orbital position within the range of $\pm 20^\circ$. In this study, we examined the orbital dependence of remembered saccades in the dark. A wholly unexpected and striking orbital dependence appeared for this saccade type.

The error of remembered saccades, initiated from the primary position, has been shown to comprise both a variable and a systematic component (Gnadt, Bracewell, & Anderson, 1991; White, Sparks, & Stanford, 1994). The variable error consists of a greater inter-trial variability in the endpoint of the movement, producing a larger range of scatter than for visually guided saccades. The systematic error alters the vertical

and/or the horizontal component of the saccade in a consistent manner. The systematic error of the vertical component of remembered saccades for monkeys has been described as an upward bias: movements to targets in any direction end above the target location. The systematic error of the horizontal component of monkeys has been reported as usually hypometria (White et al., 1994). We found that monkeys display two, perhaps independent, horizontal systematic errors: a horizontal dysmetria for remembered saccades to targets with a horizontal component and a horizontal deviation of movements to vertical target displacements.

The major goal of the experiments described in this paper was to examine, in rhesus monkeys, the orbital dependence of the systematic errors of remembered saccades. For comparison, effects of orbital position on visually guided saccades were also analyzed. We report that starting eye position markedly modulates the horizontal and the vertical systematic errors of remembered saccades. For some monkeys, the effect of starting position on movement direction that appeared for remembered saccades could be seen to a lesser degree in the curvature and/or endpoints of visually guided saccades. Our results show that a lack of compensation for the elastic restoring forces of the extraocular muscles

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and orbital tissues cannot account for all the orbital effects seen, but may participate in causing a subset. By deduction, we conclude that neural processes are involved in directly producing the errors.

Monkeys exhibit an upward offset when fixating in the dark (Snodderly, 1987; Barash, Melikyan, Sivakov, & Tauber, 1998). While studying the effect of orbital position on remembered saccades, an influence of vertical starting position on the upward offset became apparent. This additional influence of orbital position magnifies the error of remembered saccades, which were examined in the dark, and so an analysis of this effect is included.

A preliminary report of part of this study was presented previously (Barton & Sparks, 1992).

2. Methods

2.1. Subjects and eye movement recordings

Five rhesus monkeys (*Macaca mulatta*) served as subjects. Eye position signals were recorded by the scleral search coil technique (Robinson, 1963; Fuchs & Robinson, 1966; Judge, Richmond, & Chu, 1980). For the monkeys, the search coils were surgically implanted under the conjunctiva (GE—left eye, NE—right eye, later both eyes, CS—left eye, SB—both eyes, SA—left eye). The horizontal and vertical eye position signals were digitized (500 Hz) during the experiment and stored for later analysis. To allow head restraint for the monkeys, a steel post receiver was attached to the skull using stainless steel bone screws and bone cement. When immobilizing the monkey's head, the experimenter visually aligned it in the straight-ahead position. For one monkey, SA, the head was free to move. The head position of this animal was recorded with a search coil that was attached to the head for the duration of the experiment. All animal experimental and care procedures were in accordance with the NIH Guide for the Care and Use of Laboratory Animals.

2.2. Behavioral tasks

All five monkeys were well trained on visually guided saccade tasks before being trained to perform remembered saccades. Each monkey had at least 2 months of training (usually 5 days a week) with remembered saccades before data collection. The remembered saccades were performed in darkness and the visually guided with dim background illumination.

For visually guided trials, monkeys were allowed 1 s to acquire the initial fixation stimulus (F). After fixating for a variable interval (300–500 ms), target (T) appeared concurrently with the fixation light. The monkey was required to fixate F until it was extinguished (300–

500 ms). The offset of F was the cue for the monkey to look to T and maintain fixation of T for 500 ms.

The remembered saccade task was the same as the visually guided task for the initial fixation period. However, after the concurrent display of stimuli F and T, target T was extinguished, instead of F. The monkey was required to maintain fixation of F for another 500 ms, at which point, it was extinguished. The offset of F was the cue for the monkey to look to the remembered location of T. The target T never reappeared. Darkness was introduced just before the remembered trials began and remained throughout the data collection for this trial type.

For both trial types, the monkeys were rewarded with a drop of water if the saccade directed gaze to an electronic window around the target. For some of the origin–target combinations, the systematic error of the remembered saccades was of such a high magnitude that it was necessary to extend the window 20° from the target.

For three monkeys (NE, CS, GE), both remembered and visually guided trials were presented for target displacements in the four cardinal directions of amplitude 10°, 18° and 26°. The position of the fixation stimulus (F) was varied in the horizontal and vertical directions. For both rightward and leftward target displacements, the position of the fixation stimulus varied between nine positions [(rightward: $V_{origin} = 18, 0, -18$ and $H_{origin} = 10, 0, -18$) (leftward: $V_{origin} = 18, 0, -18$ and $H_{origin} = -10, 0, 18$)]. For both upward and downward target displacements, the position of the fixation stimulus varied between 11 positions for CS and 13 positions for NE and GE [(upward: $V_{origin} = 10, 0, -18$ and $H_{origin} = 18, 0, -18$, also $(-10, 0)$ $(10, 0)$) (downward: $V_{origin} = -10, 0, 18$ and $H_{origin} = 18, 0, -18$ also $(-10, 0)$ $(10, 0)$) (plus $(28, 0)$ $(-28, 0)$ for NE and GE)]. To ensure that the findings were robust, each target and origin combination was generally presented in two sessions (different days) for the three monkeys. The results illustrated in the figures are for one of the sessions, which is similar to the other session, unless stated otherwise.

For monkey NE, some data collection occurred 1 year before the comprehensive data collection described above. These data sessions examined visually guided and remembered saccades to vertical target displacements, both upward and downward. The starting position varied along the horizontal meridian, and the targets were of amplitude 22°, 24°, 26°. Both sets of data are presented for reasons described in Section 3.2.2.

In a fourth monkey (SB), both remembered and visually guided trials were presented for target displacements of amplitude 26° in the four cardinal directions. For this monkey, the fixation stimulus was shifted only along the horizontal and vertical meridians. Each target

and origin combination was usually presented in a single session.

2.3. Data analysis

Visual targets consisted of light-emitting diodes (LED), embedded in a board at one-inch intervals. Each inch corresponded to 2° of target space, with the board placed approximately 72.9 cm (28.7 inches) from the eyes. Because the board on which the LEDs were placed was flat, target displacements of equal distance on the board did not correspond to equal angular rotations of the eye in the orbit. Therefore, a ‘tangent correction’ was done to best determine the angular distance through which the eyes rotated to reach the target. The following equations were used to convert the tangential display into circumferential coordinates.

$$x' = \arctan(x/dpr)*dpr$$

$$y' = \arctan((y* \cos(x/dpr))/dpr)*dpr$$

where (x,y) is the target location in degrees in tangential coordinates, (x',y') is the equivalent position in degrees in circumferential dimensions, and dpr is degrees per radians (180/pi). For example, the 18° programmed displacements along the cardinal axis were calculated to be 16.14°, 17.44°, 17.44° for the three origins, going from the most eccentric displacements (Vorigin = ±10) to those ending closest to straight-ahead (Vorigin = ±18). In order to compare the errors in movement amplitude between the origins and trial types, these calculated values of target displacement amplitude were subtracted from the movement amplitude and the horizontal or vertical displacement error determined. Absolute values were used when necessary so that positive values of the displacement error represent overshoot and negative undershoot, regardless of the direction. In Section 3, the target displacements will be referred to by the programmed displacement and not the actual displacement, which differed only slightly.

Monkeys GE and NE exhibited an asymmetry in their eye coil signals such that displacements of the eye along the horizontal axis appeared larger in one hemifield than equal displacements in the opposite hemifield. With GE, movements in the right hemifield appeared larger than equal displacements in the left hemifield. With NE, movements in the left hemifield appeared larger than movements in the right hemifield. For example, for the data of monkey NE, a 26° eye position signal was obtained for fixations of the rightward 26° target but eye position signals of 19° or 20° were obtained when the animal was fixating the 18° leftward target. Frequently, small vertical asymmetries were also obtained for sessions. Since the inaccuracies produced by these asymmetries in eye position signals were small compared to the magnitude of the direction

and amplitude biases, and because we could not devise a method of correcting the data obtained on memory trials that was free of experimenter bias, the data presented in the figures and tables have not been corrected for these asymmetries.

The tests of statistical significance were performed with the STATISTICA program. The null hypothesis that trial type did not influence the effect of the initial fixation position on displacement error was tested with an ANOVA two-way interaction between trial type and origin, with error as the dependent variable. The ANOVAs were done separately for each size of target displacement and only one data collection session at a time. The displacement error as a function of starting position was plotted for both trial types to examine the significance and the direction of the slopes. Comparisons between group means were done with the *t*-test when the assumption of homogeneity of variance in the two groups was met. When the variances in the two groups were reliably different, the Mann–Whitney *U*-test was used instead.

In order to analyze the upward offset in fixation, the data from the visually guided and remembered trials were used to compare the fixation positions in the light and the dark, respectively. The null hypothesis that the level of background illumination (light vs. dark) did not influence the effect of the initial fixation position on vertical starting eye position was tested with an ANOVA two-way interaction between trial type and origin, with vertical starting eye position as the dependent variable.

To obtain an index of the magnitude of the curvature during the saccade, the endpoints of the movement were connected with a straight line. The area between the curve traced by the saccade trajectory and the straight line was divided by the length of the line and this value equaled the index of curvature (IC).

3. Results

3.1. Horizontal target displacements

The amplitude and direction of remembered saccades to horizontal target displacements changed considerably as the initial orbital position changed. Fig. 1 shows visually guided and remembered saccades to leftward 18° target displacements from different initial eye positions. As shown in Fig. 1B, the upward bias, characteristic of remembered saccades in monkey, increased for downward initial eye positions and diminished for upward. These changes in direction along the vertical axis for remembered saccades to horizontal targets are referred to as the *vertical direction bias*. As also seen in Fig. 1B, the horizontal component of the remembered saccades decreased as the starting position shifted left-

ward. These shifts in the horizontal component of the movements to horizontal targets will be referred to as the *horizontal amplitude bias*.

Rhesus monkeys have an upward offset for fixations in the dark, i.e. the position of fixation is above that in the light. Hence, when darkness was introduced for the remembered trials, an upward offset appeared for the fixation of F. In effect, the monkeys behaved as if the fixation target were higher than it really was. Therefore, their saccades to the fixation target landed above that point, and this erroneous position was maintained for the rest of the fixation period, without drift. This offset varied as a function of the vertical starting position. As seen in Fig. 1B, when F was presented at 18° down in the orbit, the saccades originated above this point, whereas when F was presented at 18° up in the orbit, the saccades originated close to this location. The vertical displacement error (the difference between the target

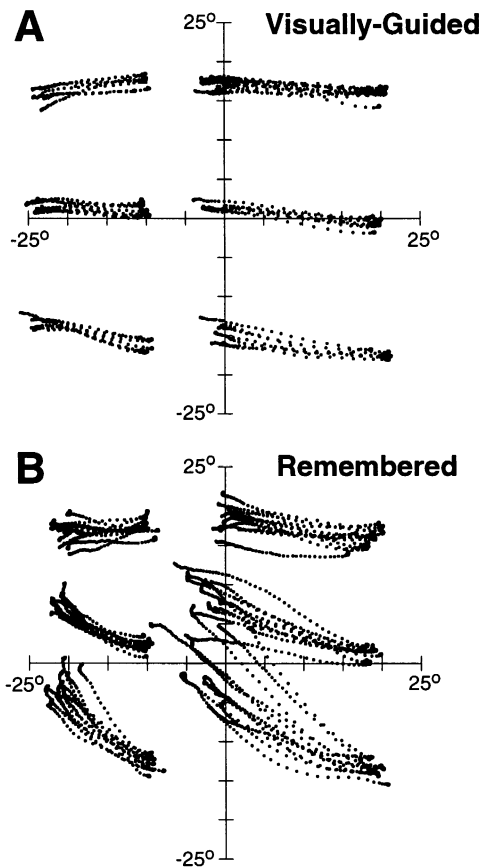


Fig. 1. Plots of visually guided (A) and remembered saccades (B) to 18° leftward target displacements for monkey GE. Traces of at least five saccades are superimposed at each of the six starting positions [(18,18) (18,0) (18,-18) (-10,18) (-10,0) (-10,-18)]. Each dot in the trace corresponds to the sampled eye position, which was taken every 2 ms. Most of the visually guided saccades initiated from the 18° eccentric vertical location exhibit a slight vertical deviation towards the center of the orbit. This vertical component can, in part, be attributed to the tangent error (see Section 2), which comprised a calculated 0.8° vertical component towards the center of the orbit.

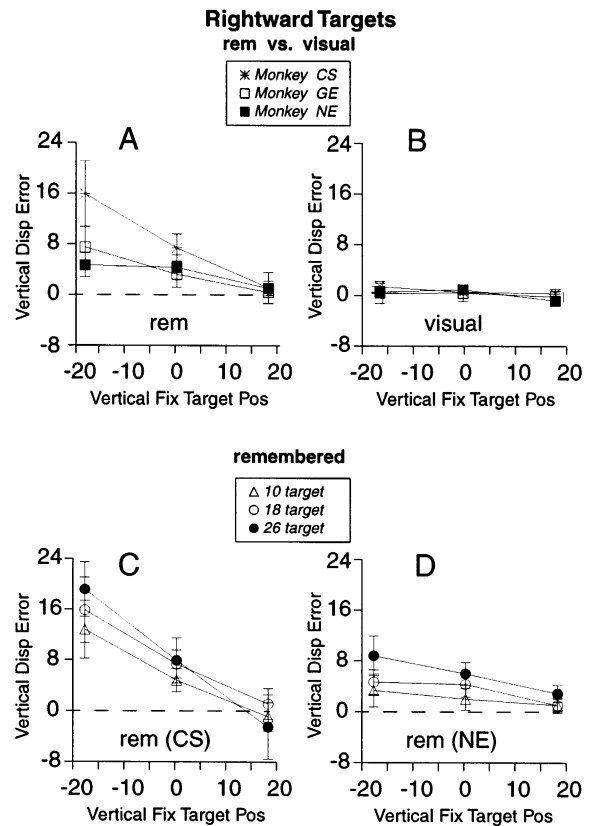


Fig. 2. Vertical direction bias. Mean amplitude of the vertical displacement error as a function of the vertical position of the fixation stimulus for rightward target displacements. Positive values of the error represent upward movements and negative downward movements. The dashed lines correspond to the lines of zero error. The three fixation positions shown are [(0,-18) (0,0) (0,18)]. (A, B) Rightward remembered (A) and visually guided (B) saccades to 18° target displacements are presented for three monkeys (CS, GE, NE). (C, D) Rightward remembered saccades to three sizes of target displacements (10°, 18°, 26°) are shown for monkeys CS (C) and NE (D).

and eye displacement) was examined instead of the vertical final eye position error (the sum of the vertical displacement error and the upward offset) because the mechanisms producing the vertical displacement error and the upward offset may be separate and because this study focuses on the saccade generating processes.

3.1.1. Vertical direction bias

The initial orbital position markedly influenced the vertical direction bias, which increased with downward initial eye positions (decreased with upward). In Fig. 1B, the downward initial eye positions resulted in remembered saccades with an erroneous upward component of as much as 15°. This bias changed to an average of 2.4° downward when the initial fixation position was 18° up in the orbit (Horigin = 0, not shown). Fig. 2A and B plot the mean amplitude of the vertical displacement error as a function of the vertical position of the

fixation target for three monkeys. This is shown for movements to 18° target displacements. Positive values correspond to upward errors and negative to downward. All three monkeys exhibited the same pattern: the vertical component of remembered saccades increased as the starting position moved downward and decreased as it moved upward. This occurred in a similar manner for leftward movements (as seen in Fig. 1). For both rightward and leftward remembered saccades, the monkeys did not make secondary, corrective saccades to the actual location of the extinguished target.

The influence of vertical starting position on the vertical component of remembered saccades to horizontal targets occurred for the full range of target displacements, with the largest target displacement (26°) producing the greatest bias. Fig. 2C and D summarize the vertical direction bias that occurred during remembered saccades to three different size target displacements. The remembered saccades of monkeys CS and NE are shown, which generally represent the largest and smallest magnitude of bias for the monkeys sampled. The bias of CS was so pronounced that remembered saccades from the downward starting position looked like movements to targets that were more vertical than horizontal.

For all the data sets examined (28), [three monkeys (NE (10), GE (6), CS (12)), three targets (10, 18, 26)], the effect of vertical starting position was significantly

different for remembered and visually guided saccades to rightward and leftward target displacements (two-way ANOVA: $P < 0.0001$ (22), $P < 0.001$ (2), $P < 0.01$ (2), $P < 0.05$ (2)). Monkey SB also exhibited the vertical direction bias (not shown).

Visually guided saccades in ambient light exhibited some traces of the same pattern of vertical component modulation with orbital position (Fig. 2B). For 16 of the 28 data sets examined, the slope of the line describing the vertical error as a function of vertical fixation target position was significantly different from zero ($P < 0.05$) and in the direction consistent with the vertical direction bias. For 11/28 data sets, the slopes were not significantly different from zero, and for only 1/28 was the effect in the opposite direction. Monkey NE showed the smallest bias during remembered saccades and displayed the bias least frequently (3/10 data sets) during visually guided saccades, whereas CS exhibited the largest vertical direction bias during remembered saccades and displayed the bias most frequently during visually guided saccades (9/12 data sets). For the visually guided data sets of CS that did show the bias, the magnitude (slopes) were, on average, 10% of those for remembered saccades. For both visually guided and remembered saccades, the amplitude of the modulation increased as the background illumination decreased (not illustrated).

The visually guided movements of CS were greatly curved. The initial direction and the amount of the curvature seemed to reflect the vertical direction bias of remembered saccades. Fig. 3 shows traces of visually guided saccades to 26° displacements of the target. The saccades initiated from down in the orbit initially moved upward before the trajectory reversed and brought the movement back towards the target (average Index of Curvature (IC) = 5.1). The upward curvature, similar to the vertical direction bias of remembered saccades, decreased as the starting position moved up in the orbit (for $V_{origin} = 0$, IC = 1.5) and as the size of the target displacement decreased.

The influence of horizontal starting position on the vertical bias of remembered saccades to horizontal target displacements was examined in two monkeys. For both leftward and rightward movements to 18° target displacements, movements away from the center of the orbit ($H_{origin} = \pm 10$) resulted in a significantly larger vertical component than centripetal movements ($H_{origin} = \pm 18$) in 4/5 data sets ($V_{origin} = 0$) [2/2 NE (t -test, $P < 0.000001$), 2/3 CS; (1 t -test, $P < 0.01$; 1 U -test, $P < 0.001$)]. Hence, changing the starting position along the horizontal meridian could also produce changes in the direction of the saccade to horizontal target displacements. Often, the effect was easily seen by eye; however, usually, this influence on the vertical component was considerably smaller than that of changing the starting position along the vertical meridian.

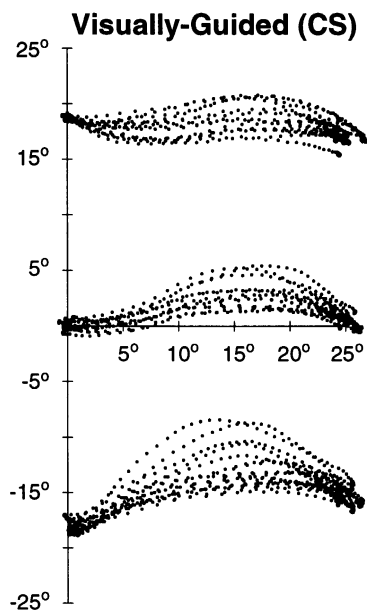


Fig. 3. Plot of visually guided saccades to 26° rightward target displacements for CS. Multiple traces of saccades are superimposed at each of the three starting positions [(0, -18) (0,0) (0,18)]. The movements displayed an average index of curvature of 5.1 and 1.5 for the starting positions of 18° down and the primary position, respectively.

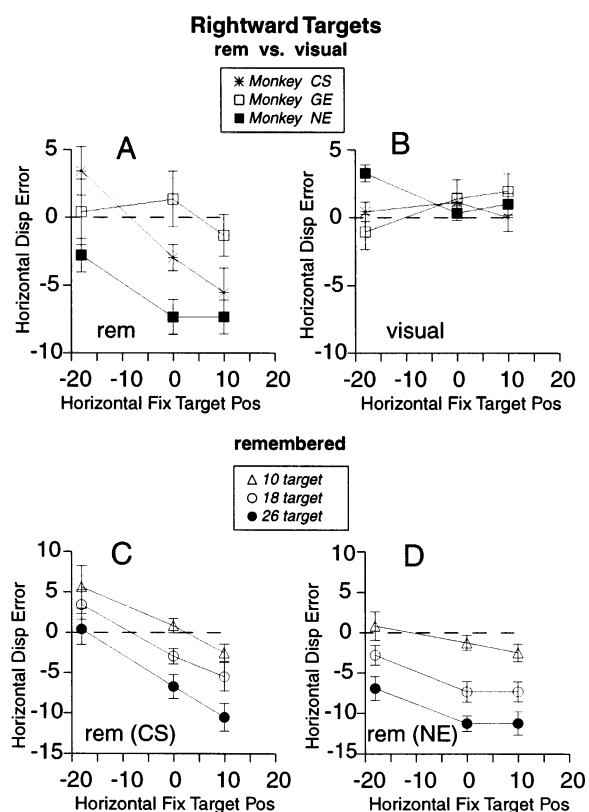


Fig. 4. Horizontal amplitude bias. Mean amplitude of the horizontal displacement error as a function of the horizontal position of the fixation target. Positive values of the error represent overshoot and negative values undershoot, with the dashed line indicating the line of zero error. The three fixation positions shown are $[(-18,0) (0,0) (10,0)]$. (A, B) Remembered (A) and visually guided (B) saccades to 18° rightward target displacements are presented for three monkeys (CS, GE, NE). (C, D) Rightward remembered saccades to three sizes of target displacements (10° , 18° , 26°) are shown for monkeys CS (C) and NE (D).

To determine if the vertical direction bias occurs in an animal with an unrestrained head, the remembered saccades of a 'head-free' monkey were examined. Horizontal target displacements (between 20° and 70°) were presented to monkey SA, while the vertical starting position varied between 20° down, 0° and 20° up. The vertical gaze (head + eye) amplitude of the remembered movements increased monotonically as the starting position moved down and decreased as it moved up. The vertical amplitude of the head movements for remembered movements was not significantly influenced by the vertical starting position (one-way ANOVA, $P = 0.96$). Hence, the vertical direction bias of the remembered saccades resulted from a bias of the eye movements, without a bias in the head movements. In general, for both visually guided and remembered saccades, the head makes only a small contribution to vertical gaze displacements (Freedman & Sparks, 1997). Accordingly, the head movement is not expected to be a substantive component of the vertical direction bias.

Therefore, this experiment does not examine whether circuits influencing both the head and eyes code the bias, but whether the bias results from an abnormality of the head restrained situation. The head did contribute to the gaze shift in the horizontal direction, between -3° (moved opposite to target) and 46° , with an average of 18.4° . Consequently, the head-restrained situation does not cause the vertical direction bias.

3.1.2. Horizontal amplitude bias

The influence of horizontal starting position on the amplitude of the horizontal component for horizontal target displacements was examined in the same monkeys. Fig. 4A and B plots the horizontal amplitude bias for 18° rightward target displacements. In general, the amplitude of the horizontal component of remembered saccades decreased as the starting position shifted in the direction of the target. This is shown in Fig. 4A, where the error usually moves in the negative direction as the origin shifts to the right. Therefore, centrifugal saccades tended to display a shorter horizontal component than centripetal. The decrease in the amplitude of the horizontal component as the starting position shifted in the direction of the target occurred for leftward remembered saccades, also. As with the vertical direction bias and the other biases described in this paper, the monkeys did not make secondary saccades to the actual location of the extinguished target.

In general, the pattern of horizontal amplitude bias occurred for all three sizes of target displacements. Fig. 4C and D summarize the bias for two monkeys. For all three targets, the horizontal component amplitude decreased as the origin shifted in the direction of the target. The effect usually increased with the size of the target displacement (steeper slopes). Note the marked modulation in movement amplitude as the starting position shifted, especially for CS (C). For the 26° target displacements, the amplitude of this monkey's saccades changed by more than 10° . In the data for the three monkeys, the horizontal components of the saccades initiated from the straight-ahead position were usually hypometric regardless of target size. The effect of horizontal orbital starting position was significantly different for the two trial types in 28/33 data sets examined [(three monkeys) (two-way ANOVA: $P < 0.0001$ (22), $P < 0.001$ (2), $P < 0.01$ (2))]. Four of the five data sets that did not show a significant interaction were for 10° target displacements of monkey GE. Monkey SB exhibited the same pattern of horizontal amplitude bias as the other three monkeys (not shown).

The horizontal amplitude bias of remembered saccades did not appear as consistently during visually guided movements. In 13/31 of the data sets for visually guided saccades examined, the displacement error shifted in the positive direction as the starting position shifted in the direction of the target (see Fig. 4B). This

shift in the opposite direction for visually guided saccades occurred primarily in 2/3 monkeys and only for visually guided saccades in one direction (NE-leftward, GE-rightward).

As mentioned in Section 2, Monkeys NE and GE had asymmetries in their eye coil signals, such that movements in one hemifield appeared larger than the other (NE-leftward, GE-rightward). Accordingly, in the data of GE, the effect of a decrease in amplitude as the origin shifted in the direction of the target was diminished for rightward movements and magnified for leftward movements by the asymmetry. Similarly, in the data of NE, the asymmetry in the opposite direction magnified the bias for rightward movements and diminished it for leftward movements. Therefore, the asymmetries in the eye-coils of NE and GE appear to be involved when the shift occurred in the opposite direction during visually guided saccades.

3.1.3. Initial vertical position offset

Rhesus monkeys are known to demonstrate an upward offset when fixating in the dark. For the same three monkeys, the vertical offsets associated with $V_{origin} = -18, 0, 18$ were examined in both the light and the dark (four data sets for each monkey, $H_{origin} = 0$). These data were taken from the remembered (dark) and visually guided (light) trials to horizontal target displacements. The vertical offset for any origin was considered the difference between the average, vertical initial eye position for the saccades in the light and the dark. As stated previously, the upward offset exhibited in darkness decreased as the starting position moved from downward to upward (see Fig. 1). At the fixation target of $V_{origin} = -18^\circ$, the vertical starting position was significantly higher for the trials in the dark than in the light for all 12 data sets ($P < 0.0001$). The magnitude and the variation of the upward offset depended on the monkey, with averages of $4.8^\circ, 2.9^\circ, 2.2^\circ$ for monkeys GE, NE and CS, respectively.

For the straight-ahead position, there remained a significant difference for all data sets ($P < 0.0001(10)$, $P < 0.001(2)$), although the magnitude of the offset had decreased. At this position, it averaged $2.9^\circ, 1.6^\circ$ and 0.9° for the same monkeys. At the highest starting position, the offset diminished further with averages $1.0^\circ, 0.6^\circ, 0.5^\circ$ and four of the 12 data sets showing no significant offset ($P > 0.05$). For all origins examined, the starting position was never significantly higher in the light than in the dark. The effect of the vertical fixation target position on the vertical starting eye position was significantly different for trials in the dark versus the light in all 12 data sets (two-way ANOVA: $P < 0.0001$). In general, there was more scatter in initial orbital position around the lower starting positions for fixations in the dark than in the light.

As mentioned in Section 2, some initial data collection occurred 1 year before the comprehensive data collection for monkey NE. During this time, the upward offset diminished. The upward offset that occurred during the first year for remembered trials in the dark ($V_{origin} = -20$) was 11.8° above (average two data sets) where the monkey fixated for visually guided saccades in the light, 6.1° above for $V_{origin} = 0$ (average three data sets) and 4.3° above at $V_{origin} = 20$ (one data set). Whereas, for the later sessions, the average offset fell at $2.9^\circ, 1.6^\circ, 0.9^\circ$ for the $V_{origin} = -18, 0, 18$, respectively. It was not a goal of this study to thoroughly analyze the upward offset over time, but it seems possible that experience assisted in diminishing the offset, even though NE was well trained to make the saccadic eye movements of the earlier experiments.

The vertical offset of CS was not larger than the offset that NE displayed in the later sessions, yet the vertical direction bias of CS was notably larger than the bias of NE. Therefore, the effect of starting position on the vertical offset did not appear to increase with the effect on the vertical direction bias.

For saccades originating from starting positions with an upward offset, the vertical direction bias, which reflects the vertical displacement error, does not describe the entire vertical error between the final eye position and the target location. The upward offset must be added to the vertical displacement error to determine the entire vertical error. It follows that because of the upward offset, oblique saccades with a downward component would be required to accurately achieve the horizontal target displacements, instead of the upwardly directed oblique saccades that occurred.

3.2. Vertical target displacements

Remembered saccades to vertical target displacements were also greatly altered by changes in the initial orbital position. Fig. 5 shows visually guided and remembered saccades to 26° downward target displacements. Similar to the biases for horizontal target displacements, primarily two biases are described that occur for remembered saccades to vertical target displacements: the *horizontal direction bias* and the *vertical amplitude bias*. As seen in Fig. 5B, the horizontal component of the remembered saccades became increasingly leftward as the initial eye position shifted to the right. These changes in the movement direction along the horizontal axis for remembered saccades to vertical target displacements are referred to as the *horizontal direction bias*. In addition, the vertical component of the remembered saccades diminished as the initial eye position moved down. These shifts in the vertical component of the remembered saccades to vertical target displacements will be referred to as the *vertical amplitude bias*.

3.2.1. Horizontal direction bias

Saccades to downward remembered target locations exhibited a horizontal bias. The bias disappeared at a particular position along the horizontal meridian. This position of zero horizontal component will be referred to as the null position. As the starting position deviated horizontally from the null position, a horizontal component was introduced in the direction of this point. The greater the horizontal deviation of the starting position from the null position, the greater the horizontal bias. As seen in Fig. 5B, the remembered saccades initiated from the right displayed a striking leftward component of as much as 14° when there was no horizontal component to the target displacement. This leftward component gradually decreased as the origin shifted left and eventually became slightly rightward for movements initiated

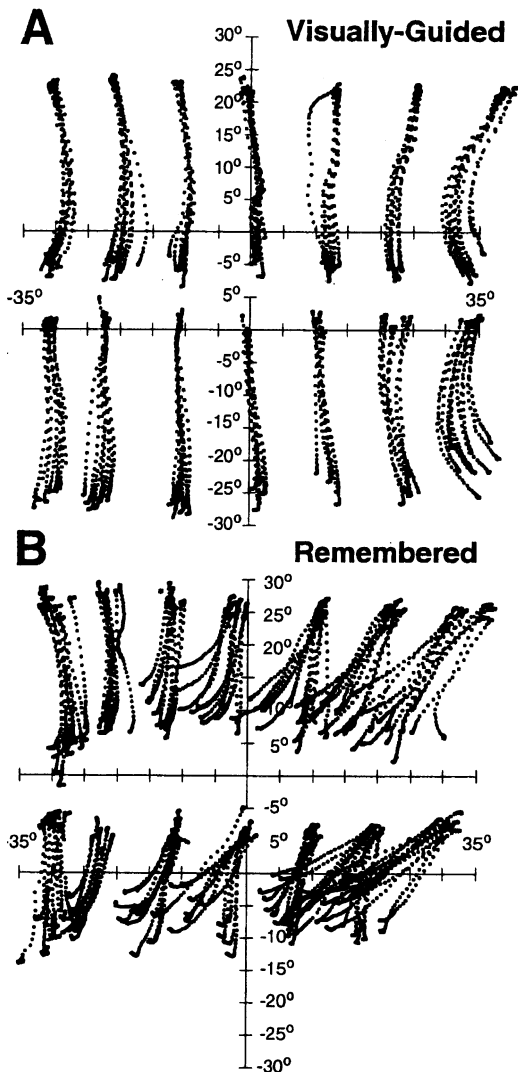


Fig. 5. Plots of visually guided (A) and remembered saccades (B) to 26° downward target displacements for monkey NE. To prevent overlap of the saccades initiated from the two vertical starting positions, a gap interrupts the vertical axis. The remembered saccades started higher in the orbit due to the upward offset.

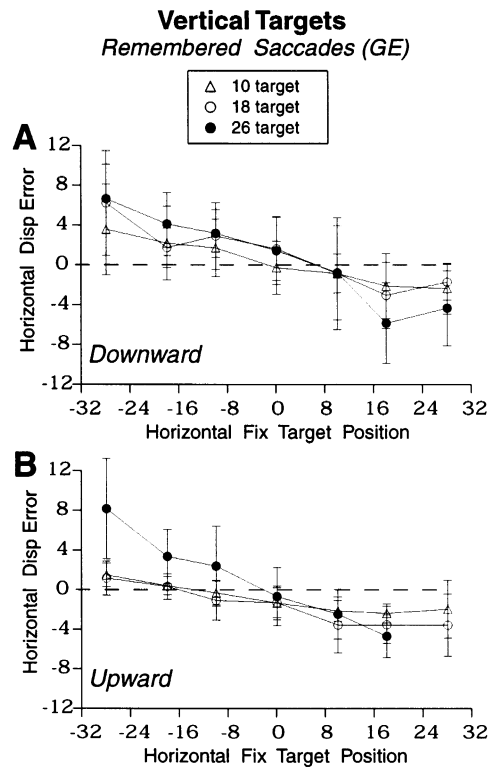


Fig. 6. Horizontal direction bias. The horizontal displacement error of remembered saccades to vertical target displacements as a function of the horizontal fixation position for monkey GE. Movements to three sizes (10°, 18°, 26°) of downward (A) and upward (B) target displacements are shown. Negative values of the horizontal component correspond to leftward movements and positive values to rightward.

from 30° to the left. These data were taken from the earlier collection sessions and the effect occurred for the three sizes of target displacements, 22°, 24°, and 26°. The location of the null position was found by determining the fixation position that corresponded to a saccade with zero horizontal component. This was done by plotting the horizontal fixation position against the horizontal component and then determining the fixation position that intersected the line at the zero horizontal component position. For NE, the null position occurred at approximately 22° left. SB exhibited a similar increase in the horizontal component as the starting position moved away from the null position, which occurred at approximately 16° left. After the horizontal direction bias of SB was noted, an eye coil was added to the second eye to determine if the eyes moved conjugately. No noticeable changes in the null point occurred after the operation, and the eyes did move conjugately. The remembered saccades of GE displayed a similar trend of an increase in the horizontal bias as the starting position deviated from the null position (see Fig. 6). This monkey displayed a less pronounced horizontal bias than NE or SB, with a null position closer to zero (approximately 6° for $T = 26^\circ$).

The effect of horizontal starting position on the horizontal displacement error of downward remembered saccades was significantly different for the two trial types in 9/9 data sets examined [(three monkeys: CS, NE, GE) (two-way ANOVA: $P < 0.00001$)].

Saccades to *upward* remembered target displacements demonstrated a horizontal bias in the three of the four monkeys examined. Similar to the movements for downward target displacements, the upward saccades of GE (Fig. 6B) and CS (not shown) exhibited a bias that increased as the starting position deviated from a null position, although the location of the null position for upward and for downward saccades was not the same (compare Fig. 6A and B). NE displayed a horizontal bias during upward remembered saccades that diminished for movements initiated from the eccentric starting positions and increased as the starting position moved towards the center. Fig. 7A plots the horizontal bias of NE for both upward and downward remembered target locations. The data for downward movements in Fig. 7A are the same saccades presented in Fig. 5. Note the difference in the pattern of the bias for upward saccades from that for downward saccades.

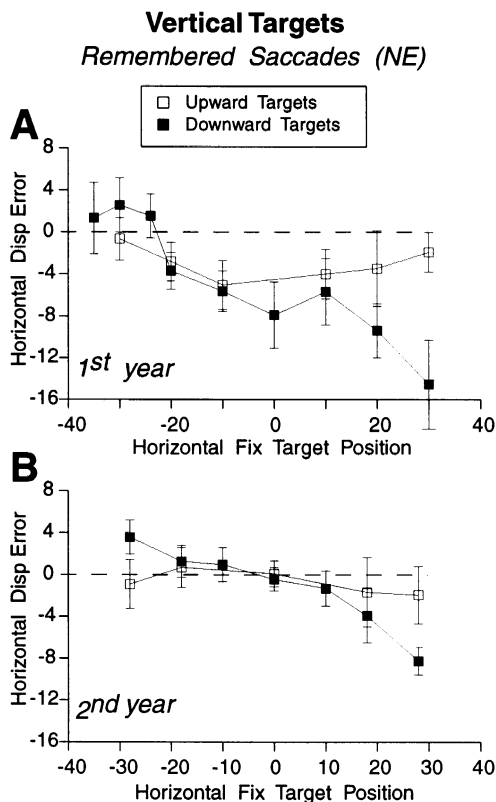


Fig. 7. The horizontal displacement error of remembered saccades to vertical target displacements as a function of the horizontal fixation position for monkey NE ($V_{origin} = 0$). All target displacements are 26° in amplitude. (A) The horizontal error of saccades to both upward and downward targets are shown for both the 1st (A) and 2nd (B) years. Negative values of the horizontal component correspond to leftward movements and positive to rightward.

Moreover, the bias for upward movements did not become as large as that for downward movements. SB did not exhibit a horizontal bias for upward remembered target displacements.

The effect of horizontal starting position for saccades to upward target displacements was significantly different for the two trial types in all the data sets examined (9) [(three monkeys: CS, NE, GE) (two-way ANOVA: $P < 0.00001$ (8), $P < 0.001$ (1))]. For both upward and downward remembered saccades, the *horizontal direction bias* showed no consistent differences in magnitude for the different size target displacements.

The effect on movement trajectory as the starting position shifted horizontally was largely in the horizontal direction. In most cases, either no noticeable or relatively small changes in the vertical component of the remembered saccades occurred.

3.2.2. Time-dependent changes in the horizontal direction bias

While there were no discernible changes in the *horizontal direction bias* of remembered saccades during any single data collection session, shifts did occur over the course of time. Fig. 7 compares the bias of NE for data sessions collected approximately 1 year apart. In the later data, the null position for downward remembered saccades occurred at roughly 2° right, which was a striking shift from the previous 22° left null position. In addition, the horizontal component of upward remembered saccades diminished from the previous year, reaching an average of only 0.7° at the starting position producing the maximum horizontal deviation. Two eye coil operations were performed during this time, one to implant a coil in the left eye and the other, unfortunately, to replace an existing coil in the right eye. While these operations may have influenced the location of the null position, they did not influence the accuracy of the visually guided saccades in any noticeable manner.

3.2.3. Curvature of visually guided saccades

No consistent *horizontal direction bias* was apparent in the visually guided saccades. However, the visually guided movements of monkey SB exhibited a curvature that reflected the pronounced horizontal bias of her remembered saccades. This monkey showed an increase in the leftward curvature (visually guided) and leftward component (remembered) of downward saccades as the origin shifted rightward ($H_{origin} = 20^\circ$, $IC = 1.26$; $H_{origin} = 30^\circ$, $IC = 1.97$). The upward remembered saccades of SB did not exhibit a horizontal bias and the upward visually guided saccades that were initiated from origins 20° to the right did not curve leftward (average index of curvature at $H_{origin} = 20^\circ$, $IC = 0.34$). Unfortunately, the upward visually guided saccades from 30° to the right were not collected at this time.

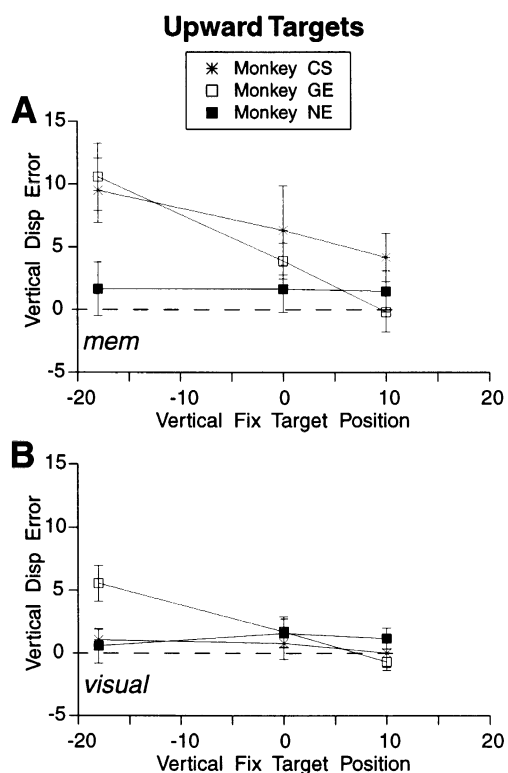


Fig. 8. Vertical amplitude bias. Mean amplitude of the vertical displacement error as a function of the vertical position of the fixation stimulus for 18° upward target displacements. Remembered (A) and visually guided (B) saccades are presented for three monkeys (CS, GE, NE). The three fixation positions shown are [(0, -18) (0,0) (0,10)].

Monkey NE also showed curvature in his downward visually guided saccades. Fig. 5A shows an XY plot of downward visually guided saccades of NE to 26° target displacements. When the saccades were initiated from 20° to the right, a leftward curvature appeared, which increased as the origin shifted farther rightward ($H_{\text{origin}} = 20$, $IC = 1.21$, $H_{\text{origin}} = 30$, $IC = 1.87$). These saccades were recorded during the same session as the downward remembered saccades in Fig. 5B, which show an increase in the leftward component as the origin shifted rightward. The changes in the horizontal bias of the remembered saccades of NE occurred in parallel with changes in the curvature of the visually guided movements. After the null position of the downward remembered saccades of NE had shifted towards the straight-ahead position, the leftward curvature of the downward visually guided movements decreased (t -test, $P < 0.01$).

3.2.4. Vertical amplitude bias

As has been reported previously (White et al., 1994), the upward bias observed during remembered saccades to horizontal target displacements also occurred for vertical target displacements ($V_{\text{origin}} = 0$). In general,

upward remembered saccades were hypermetric for two of the three monkeys (CS, GE) and downward remembered saccades were hypometric for all three monkeys. Fig. 8 shows the effect of orbital position on the vertical displacement error for upward saccades. In the two monkeys that displayed overshoot for upward remembered saccades, the amplitude of the vertical component increased as the origin shifted downward and decreased as it shifted upward. There was a similar and less pronounced pattern of change in vertical amplitude with origin for visually guided movements. This was indicated by significantly negative slopes for 7/8 data sets. The slopes of the visually guided trials that demonstrated the bias were on average 19% and 64% those of the remembered trials, for CS and GE, respectively. For the third monkey (NE), there was no consistent influence of vertical starting position on the amplitude of the upward remembered or visually guided saccades. For the downward remembered saccades of all three monkeys, the vertical amplitude increased as the starting position shifted upward and decreased as it shifted downward. A similar, but less pronounced, influence of initial eye position on amplitude occurred for visually guided saccades of monkeys CS and GE. The slopes of the data for visually guided trials were 50% and 37% those of remembered trials for CS and GE, respectively. There was no consistent difference between the two trial types for monkey NE.

For monkeys CS and GE, 14/15 data sets showed that the effect of vertical starting position was significantly different for the two trial types (three targets, two-way ANOVA: $P < 0.0001$ (10), $P < 0.001$ (1), $P < 0.01$ (3)). For NE only 3/8 data sets showed the effect of origin to be modified by trial type ($P < 0.0001$ (2), $P < 0.05$ (1)).

4. Discussion

To summarize, varying the initial orbital position of remembered saccades in the dark results in a large and unexpected influence on the trajectory of the movement for rhesus monkeys. The upward bias for remembered saccades to horizontal targets, characteristic of rhesus monkeys, was markedly modulated by the vertical starting position, *vertical direction bias*. It increased with downward starting positions and decreased, sometimes moving downwards, with upward starting positions. The monkeys also displayed a systematic shift in the horizontal component of remembered saccades to vertical target displacements when the starting position shifted along the horizontal axis, *horizontal direction bias*. This bias appeared as a pull towards a null position along the horizontal axis.

When the starting position shifted in the direction of the target displacement, this caused a change in the

component amplitude of the remembered saccades along the axis of the target displacement, the *horizontal and vertical amplitude biases*. In general, the amplitude biases caused the component amplitude to become smaller for changes in starting position in the direction of the target displacement. Accordingly, centrifugal remembered saccades were usually shorter than centripetal. In short, for either the direction or amplitude biases, the direction of the change in movement trajectory primarily depended on the direction of the change in initial eye position.

Once the direction biases of the monkeys were noted, a similar pattern of orbital modulation became apparent in the curvature of the visually guided saccades for some monkeys, although to a lesser degree. This suggests that during visually guided saccades in ambient light, an additional mechanism sends a signal that compensates for the direction biases.

4.1. Source of biases

There is not sufficient evidence to establish the source(s) of the biases. The data indicate that multiple mechanisms are involved in producing the biases. The horizontal and vertical direction biases could be one direction bias ‘pulling’ the eyes to a point up and lateral. However, the results of introducing monocular vision (Barton, 2000), not described in this paper, are incompatible with the hypothesis of a single mechanism for the direction biases. Patching one eye caused quite different effects on the horizontal and vertical direction biases: the vertical errors diminished immediately, while the null point of the horizontal direction bias gradually shifted in the direction contralateral to the patched eye. These disparate effects suggest separate mechanisms. Since the horizontal direction bias can shift over time, either with or without patching, this indicates that the mechanism of compensation for this bias can plastically adjust the signal.

4.1.1. Visual cues

Since the errors increase with the decrease in ambient light, this suggests that the general quality of visual cues affects the development of the errors. Requiring a subject in darkness to look to the remembered target location further degrades the quality of visual cues and, therefore, augments the dysmetria. While the errors may increase with diminishing visual information, there are clearly other factors involved. This is demonstrated by the observation that orbital starting position affects the biases and that the biases appear to a lesser degree for visually guided saccades in the light. That the horizontal direction bias changed over the course of time for one monkey without any changes in the visual cues also points to other causes.

4.1.2. Muscle mechanics

Saccadic eye movements are produced by a pulse and step of motoneuron activity. The pulse, or burst, overcomes orbital viscosities and generates the high-velocity saccade. The neural integration of the pulse by pre-motor nuclei forms the step, or tonic, component of the activity (reviewed in Hepp, Henn, Vilis, & Cohen, 1989). The step opposes the restoring forces of the extraocular muscles and globe restraining tissues to hold the eye in the new position. These restoring forces increase non-linearly as the eye deviates to an eccentric position (Robinson, 1964; Collins, 1971; Collins, O’Meara, & Scott, 1975). At some point in the saccade-generating system, neural mechanisms must compensate for the restoring forces in order to prevent any shortening of centrifugal movements (beginning near the primary position) and any lengthening of centripetal movements (ending near the primary position). The signal transforms compensating for the elastic restoring forces of the muscles and orbital tissue are thought to be added late in the saccade generating process (Ritchie, 1976; Optican & Robinson, 1980). If this mechanism(s) malfunctions, erroneous saccades will occur, and the errors will vary as the initial orbital position shifts. Therefore, one possible explanation for the orbitally dependent dysmetria of remembered saccades is a failure to compensate for the restoring forces.

The data presented herein strongly suggest that the mechanical properties of the muscles and orbital tissue cannot account for the orbitally dependent modulation seen in the direction biases of the monkeys. The null point of the horizontal direction bias and the magnitude of the vertical direction bias were quite idiosyncratic. This difference does not reflect the obvious similarity in muscle structure between monkeys. If the horizontal direction bias were due to the equilibrium point of the horizontal recti muscles not being straight-ahead but offset laterally or medially, so that uncompensated restoring forces would pull each eye to the offset position, then both eyes would move laterally or both move medially. Therefore, the eyes would move disjunctively. However, in one monkey (SB), the movements of both eyes were monitored and found to move conjugately. In addition, if the medial and lateral rectus restoring forces caused the horizontal direction bias, it should look similar for upward and downward movements. Yet the two monkeys who had a pronounced leftward bias for downward movements displayed little if any for upward saccades.

The amplitude biases generally resulted in the centripetal remembered saccades being of greater amplitude than the centrifugal. This pattern is consistent with the pulling forces of the extraocular muscles. Therefore, while a lack of compensation for the elastic restoring forces does not seem to account for the direction biases, it may still produce the amplitude biases. If the restor-

ing forces are involved in generating the amplitude biases, they still do not appear to completely account for biases. As with the direction biases, the magnitude of the amplitude biases varied considerably across subjects unlike the obvious similarity in muscle structure. Single-unit experiments could discern if the orbitally dependent changes in amplitude are a function of a direct neural command or a lack of a compensatory signal for the restoring forces.

4.1.3. Neural coding of biases

The deviation of the remembered saccades, associated with the direction and the amplitude biases, exhibited no noticeable postsaccadic drift. If a mismatch arises between the burst and the step that produce and maintain saccadic eye movements, postsaccadic drift will occur. Therefore, the biases evidently occur before or at the sites of neural integration, which produce the appropriate step. Similarly, if the amplitude biases are a function of a direct neural command and not the result of a lack of a muscle compensatory signal, these errors also occur before or at the site of neural integration. Evidence points to the interstitial nucleus of Cajal (INC) as having an important role in the integration process for vertical and torsional eye movements (Fukushima, 1987; Helmchen, Rambold, Fuhry, & Butner, 1998). The nucleus prepositus hypoglossi (NPH) and the medial vestibular nuclei (MVN) are critical for the integration of horizontal eye signals (Cannon & Robinson, 1987; Cheron & Godaux, 1987; Mettens, Godaux, Cheron, & Galiana, 1994; Arnold, Robinson, & Leigh, 1999). This suggests that any neural coding of vertical or horizontal biases occur before or at the level of the INC and the NPH-MVN, respectively. This hypothesis is supported by a study that examined the tonic activity in the MVN and found it to reflect the erroneous endpoints of the direction biases (Barton & Sparks, 1993; Barton, 2000).

The experiments by Stanford and Sparks (1994) compared monkey superior colliculus (SC) activity during remembered and visually guided saccades initiated from the straight-ahead position. They found that the collicular activity did not reflect the upward bias. The cells fired similarly for the accurate visually guided movements as for upwardly distorted remembered movements. In addition, a remembered saccade to a target below the cell's movement field that erroneously landed within the cell's movement field did not produce a discharge. Barton and Sparks modified the methods of Stanford and Sparks to examine the correlation between SC discharge and movement for remembered saccades initiated from different vertical starting positions (Barton, 2000). Since the SC movement fields were usually oblique, and not only horizontal or vertical, the vertical errors were probably caused by a combination of the vertical amplitude and the vertical

direction biases. The results of these experiments indicated that the SC does not code the systematic errors of remembered saccades produced as the starting position shifts along the vertical axis.

The cerebellum is a promising candidate for either producing or compensating for the biases. Recordings in the posterior vermis revealed cells where the initial orbital position influenced the activity associated with saccades (McElligott & Keller, 1982). After ablations that included the vermal lobuli VI–VII (Ritchie, 1976) and after temporary inactivation of the FN with muscimol (Robinson, Straube, & Fuchs, 1993), a saccadic dysmetria developed, which resulted in centripetal saccades having a larger amplitude than centrifugal. Temporary lesions of the FN also caused a greater inter-trial variability in size, course and velocity profiles (Robinson et al., 1993), while ablations in the region of the oculomotor vermis increased the variability in size and latency (Takagi, Zee, & Tamargo, 1998). This suggests that the cerebellum participates in producing accurate, stereotyped movements. Because remembered saccades are neither accurate nor stereotyped, the cerebellum may function improperly during remembered saccades. After unilateral inactivation of the FN in the head-free cat (Goffart & Pelisson, 1994, 1998), saccades towards the side of the lesion appeared systematically biased in the direction of an erroneous goal, similar to the direction biases of the remembered saccades, which caused deviation towards a null position.

Temporary lesions in the posterior interpositus nucleus caused an upward bias for visually guided saccades to both horizontal and vertical targets (Robinson, 2000). The upward bias was quite striking. For one monkey (monkey 2), saccades to horizontal target displacements of 10° had vertical components of more than 10° for both rightward and leftward targets. The saccades to vertical targets undershot for downward saccades and overshot for upward, with one monkey's upward saccades to 10° target displacements increasing to 17° . This is obviously reminiscent of remembered saccades. Some effects on the horizontal component of saccades to vertical target displacements occurred but were neither as pronounced nor as consistent as the influence on the vertical component. The author did not report varying the vertical starting position for saccades to horizontal targets or the horizontal starting position for saccades to vertical targets. Accordingly, it is not possible to discern the role of this region with respect to the direction biases, although the data suggest that it may compensate for the vertical direction bias. The effect of the lesions on the gain of centripetal versus centrifugal saccades was examined, with no difference noticed. Therefore, this region does not seem involved in producing or compensating for the amplitude biases. Perhaps the cerebellar nuclei work in concert to correct for the influence of the restoring forces and the direction biases.

4.2. Upward offset in fixation

Rhesus monkeys demonstrate an upward offset when fixating in the dark. The offset was found to diminish as the starting eye position moved from downward to upward. This pattern resembles the vertical direction bias. Furthermore, these offsets remained uncorrected, similar to the vertical direction bias. One would think that if the same source caused the vertical direction bias and the vertical offset, then a correlation would exist between the magnitude of the offset and the vertical direction bias across monkeys, i.e. the monkey displaying the largest vertical direction bias would have the largest offset. However, no such correlation appeared, which cast some doubt on whether the two types of errors come from the same source.

A study by Barash et al. (1998) examined the upward shift in fixation caused by darkness in *Macaca fascicularis*. They reported a small effect of vertical orbital position, with upward fixations producing a smaller offset. Their results show a similar pattern of influence, although not to the same degree, as occurred in the present study on *Macaca mulatta*. In one monkey, they reported an approximately 1.7° increase in the upward offset from when the monkey had only 1 week of training to after 8 months of training. They concluded that training makes the offset more prominent. We did not examine the offset of an untrained monkey. However, one monkey showed a clearly larger bias during the earlier session, when he had received training, than a year later with more experience. It seems that ascertaining the influence of training on the offset requires a more thorough investigation of the vertical offset over time for multiple monkeys.

4.3. Consideration of biases for future experiments

The systematic errors of rhesus monkeys described herein represent a significant perturbation to the saccadic system. Studies that involve changes in orbital starting position or remembered saccades need to take these biases into account. For example, neural studies that compare stimulation evoked saccades and the remembered saccades that produce optimum discharge for a particular site should consider that a disparity between the two could be unrelated to that site's activity, especially for eccentric starting positions. The models of the saccadic system do not address the issue of the effects of starting position; however, any models that do incorporate this issue clearly need to address the biases described herein. Finally, the phenomenon described may offer a window of insight into certain issues in the study of saccadic generation, such as the on-line correction of saccade metrics, the compensation for the elastic restoring forces, and the alteration of the SC command.

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