Properties of Horizontal Saccades Accompanied by Blinks

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Rottach, Klaus G., Vallabh E. Das, Walter Wohlgemuth, Ari Z. Zivotofsky, and R. John Leigh. Properties of horizontal saccades accompanied by blinks. J. Neurophysiol. 79: 2895–2902, 1998. Using the magnetic search coil technique to record eye and lid movements, we investigated the effect of voluntary blinks on horizontal saccades in five normal human subjects. The main goal of the study was to determine whether changes in the dynamics of saccades with blinks could be accounted for by a superposition of the eye movements induced by blinks as subjects fixated a stationary target and saccadic movements made without a blink. First, subjects made voluntary blinks as they fixated on stationary targets located straight ahead or 20° to the right or left. They then made saccades between two continuously visible targets 20 or 40° apart, while either attempting not to blink, or voluntarily blinking, with each saccade. During fixation of a target located straight ahead, blinks induced brief downward and nasalward deflections of eye position. When subjects looked at targets located at right or left 20°, similar initial movements were made by four of the subjects, but the amplitude of the adducted eye was reduced by 65% and was followed by a larger temporalward movement. Blinks caused substantial changes in the dynamic properties of saccades. For 20° saccades made with blinks, peak velocity and peak acceleration were decreased by ~20% in all subjects compared with saccades made without blinks. Blinks caused the duration of 20° saccades to increase, on average, by 36%. On the other hand, blinks had only small effects on the gain of saccades. Blinks had little influence on the relative velocities of centrifugal versus centripetal saccades, and abducting versus adducting saccades. Three of five subjects showed a significantly increased incidence of dynamic overshoot in saccades accompanied by blinks, especially for 20° movements. Taken with other evidence, this finding suggests that saccadic omnipause neurons are inhibited by blinks, which have longer duration than the saccades that company them. In conclusion, the changes in dynamic properties of saccades brought about by blinks cannot be accounted for simply by a summation of gaze perturbations produced by blinks during fixation and saccadic eye movements made without blinks. Our findings, especially the appearance of dynamic overshoots, suggest that blinks affect the central programing of saccades. These effects of blinks need to be taken into account during studies of the dynamic properties of saccades.

INTRODUCTION

Saccadic gaze shifts are often accompanied by blinks. The probability of a blink occurring increases with the size of the gaze shift (von Cranach et al. 1969; Evinger et al. 1991, 1994; Watanabe et al. 1980). This concerns saccades without head movements as well as combined eye-head gaze shifts (Evinger et al. 1994; Tinuper et al. 1989). During a blink, a burst of activity occurs in the normally quiescent orbicularis oculi muscle, and time-linked activity ceases in the levator palpebrae muscle, which provides lid elevation by tonic contraction (Evinger and Manning 1993; Schmidtke and Büttner-Ennever 1992). There is evidence for a linkage between the circuitry producing saccades and the neural circuits subserving blinks (Evinger et al. 1994). The concurrence of a blink and its size depends not only on the size of the saccade but also on visual requirements (Beideman and Stern 1977; Fogarty and Stern 1989). Both saccades and blinks interfere with vision, and are time locked.

Blinks induce eye movements even if no attempt is made to shift gaze. Using the magnetic search-coil technique, Collewijn and colleagues (1985) demonstrated that during attempted fixation of a target straight ahead, blinks cause transient downward and nasalward eye movements. These blink-induced movements have amplitudes of up to 5° in both the horizontal and vertical direction. They are slower than saccadic eye movements of the same size. The duration and shape of the spatial trajectories of lid and eye movement are different. However, the blink-associated movements in an eye passively opened or closed during an attempted blink are almost identical. Thus these movements are induced by the extraocular muscles and not by a mechanical interaction of lid and eye (Collewijn et al. 1985). It has been shown in rabbits and guinea pigs that these movements are due to a cocontraction of all extraocular muscles with the exception of the superior oblique muscle (Evinger and Manning 1993; Evinger et al. 1984).

The effect of an eccentric eye position in the orbit on the blink-induced eye movement is not settled. Thus Collewijn et al. (1985) still found eye movements directed inward and downward, although they were somewhat modified by an apparent pull toward the center. In contrast, Evinger et al. (1984) and Riggs et al. (1987) suggest that the eye always rotates toward a central position, resulting in changing directions of the eye movements for different eccentric gaze positions.

How blinks made with saccades affect the metrics of the gaze shift has, to our knowledge, not received systematic study. We set out to compare the dynamic properties of saccades made while subjects either deliberately made or withheld a concurrent blink. We wondered whether such changes could be ascribed to a cocontraction of the extraocular muscles, produced by blinks, that was simply superimposed on the saccade. We found some changes that could be accounted for by such a mechanism, but also discovered other effects (brief saccadic oscillations) that suggested an effect of blinks on the saccade-generating mechanism itself.
METHODS

Subjects

Five normal subjects (S1–S5, age 22–48, 1 female, 4 males) participated in the experiment; all gave informed consent. All had previous experience with eye movement recordings. Only one subject (S4) was informed about the goals of this study. Two subjects (S3 and S4) were myopic. They did not wear glasses during the experiment but were easily able to see the visual targets.

Eye movement measurements

Horizontal and vertical movements of both eyes were recorded using the magnetic search coil technique (Seidman et al. 1995), in which a scleral induction coil is embedded in a silicone annulus. A properly mounted annulus adheres firmly to the limbus and its position is not affected by lid movements (Collewijn et al. 1985). Vertical movements of one lid were recorded using a lid coil that was 4 mm diam and contained five turns of wire. The weight of the lid coil was slight (<0.5 g), and subjects did not note the presence of the coil after a few minutes. It was taped close to the margin of the upper lid above the center of the pupil when gaze was directed straight ahead. The scleral search coils were calibrated before each experimental session using a protractor device. The experimental trials lasted ~30 min per subject. Coil signals were filtered (bandwidth 0–90 Hz) before digitization at 250 Hz. During testing, subjects braced their heads stationary against a firm support.

Experimental stimuli and paradigms

The visual stimuli consisted of three light-emitting diodes that were mounted on a tangent screen 1.2 m in front of the subjects. They were located 20° left, 0°, and 20° right with respect to the subject. The room lights were dimmed. First, subjects performed several blinks while fixating each of the three different targets in turn (without saccadic gaze changes). Then the subjects made voluntary saccades between two of the diodes, the other being switched off. Thus saccades were made between two continuously visible targets, located at 0° and 20° right, 0° and 20° left, or 20° right and 20° left. Individual trials lasted 20 s. At the beginning of each trial, subjects were instructed to make saccades between the two visible targets either without blinks or deliberately making a blink with each saccade. Subjects were asked to perform saccades at a convenient frequency, which was usually at ~1–2 Hz. Before collecting data, subjects were familiarized with the task during a short period of training. We collected 40–80 saccades for each of the 6 test conditions; the total number of recorded saccades was 1,646.

Data analysis

Velocity and acceleration signals were obtained by differentiation of the eye position signal. Analysis was performed interactively, but with the use of preset criteria.

SACCADeS. The beginning and end of horizontal components of each saccade was detected by the program automatically. Because blinks often began shortly before the saccade, adduction (induced by the blink) overlapped the beginning of the saccade. Thus we used a direction and a velocity (40°/s threshold) criterion to determine the onset of the saccade. With the use of this approach, the onset of the saccade was reliably detected at a very similar time in both eyes. The end of the saccade was defined as where eye velocity fell below 25°/s. At the end of some saccades, a small, oppositely directed saccade (a dynamic overshoot) occurred (Bahill et al. 1975). To detect these dynamic overshoots, we used a velocity criterion of 25°/s combined with a change in direction of the eye movement. The end of the dynamic overshoot was set where the velocity of the eye fell below 25°/s. When a saccade was accepted, the program determined peak velocity, peak acceleration, and deceleration, the timing of these events, the “pulse” amplitude (corresponding to where eye velocity dropped below 25°/s), pulse gain (saccadic amplitude/required amplitude to foveate the target), and duration of the saccade. Because the eyes behaved similarly, statistical evaluation of the saccadic gain, peak velocity, peak acceleration, peak deceleration, and duration was restricted to the dominant eye.

Blinks. Blinks were analyzed semiquantitatively. The subject was asked to make a few blinks with complete closure of the eye. The amplitude of these blinks detected by the coil signal was set equal to 1. During the trials with blinks, a saccade was regarded to be accompanied by a blink if the blink signal was at least 0.5. This was done to register only saccades that were accompanied by large blinks. However, it should be mentioned that most of the blinks reached relative sizes of at least 0.8. During saccades made without blinks, the lid signal was typically below 0.1. If a blink was detected, the lid velocity signal (obtained by differentiation of the lid position signal) was used to determine onset and end of the blink. These points were set where the lid velocity signal respectively rose above, or fell below, a threshold of three standard deviations of the lid velocity signal obtained during a period with no detectable lid movement. This approach was selected because the lid signal was not calibrated and was similar to the method previously employed for the determination of smooth pursuit onset (Carl and Gellman 1987; Morrow and Sharpe 1993; Rottach et al. 1996).

STATISTICS. The χ² test was used to compare the frequency of dynamic overshoot in saccades with and without blinks. For all other comparisons, the Mann-Whitney rank sum test was used, with a P value of <0.05 applied to determine statistical significance, unless otherwise stated.

RESULTS

Blinks during fixation

In all of our subjects, during viewing of a stationary target located straight ahead, blinks elicited brief downward and nasalward deflections of the eye position, as previously reported (Collewijn et al. 1985). The amplitudes of the horizontal components of these movements for all subjects ranged between 0.8 and 5.0° (range of subject means, 1.1–4.1°), and of the vertical components ranged between 0.5 and 4.8° (range of subject means, 0.7–4.2°). The eyelid movement consistently outlasted the blink-induced eye movement. During fixation at 0°, the mean duration of blinks for all subjects was found to be 369 ms, whereas the mean duration of blink-associated eye movements was only 248 ms. A typical example is shown in Fig. 1 (left). There was a high variability of the amplitudes of these movements, both between subjects and for different blinks made by individual subjects. However, the pattern of downward and nasalward deflection remained consistent for all recorded blinks. Further analysis of the trajectories of such eye movements induced by blinks showed that the eyes described loops: counterclockwise in the left eye and clockwise in the right eye, from the viewpoint of the subject (Fig. 2).

When subjects performed blinks while fixating the targets located at 20° right and left, four subjects continued to show a nasalward direction to the initial horizontal movement.
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higher for eye movements with blinks (see Table 1), but for 40° saccades there was no clear trend. Because our determinations of saccadic gain depended on measurement of eye position when velocity fell below 25°/s, the presence of a dynamic overshoot would be expected to cause an increase in the value of saccade amplitude because the eye transiently overshot the target. To control for this, we also determined the amplitude of the saccade at the end of the dynamic overshoot (if present). This analysis showed that at least a part of the increase in gain was due to the higher incidence of dynamic overshoot in saccades with blinks (Table 1).

Because blinks had a surprisingly small effect on the accuracy of saccades, we wondered whether the nasal-downward deflection of the eyes was still present when blinks coincided with saccades. That this is the case, at least in the vertical direction, is clearly shown by the trajectories of saccades with blinks (Fig. 3). During the first part of a saccade, the eyes move downward. Toward the end of the saccade, they return close to the appropriate vertical position, so that no or only a small vertical corrective saccade is required. This yields a curved biphasic saccadic trajectory. The mean amplitude of vertical deflections for 20° saccades ranged 0.41 ± 2.46° for the initial downward component and 0.25 ± 0.73° for the upward corrective component. Similarly, for 40° saccades, mean amplitude of vertical deflections ranged 0.42–2.55° for the initial downward component and 1.01–1.48° for the corrective upward component. Therefore our data show that the magnitude of vertical deflections was smaller during blink-associated saccades as compared with magnitude of vertical deflections during fixation. Also, the biphasic trajectory was more pronounced during larger magnitude saccades.

The presence of the horizontal component of the blink-induced eye movement was harder to determine in our paradigm because we only studied horizontal saccades. A representative set of data is shown in Fig. 4. The small deflections at the beginning of each saccade (indicated by asterisks in

FIG. 1. Effect of blinks on the metrics of saccades during fixation of the center of the screen (S5). Left part of the figure: looking at the center of the screen; middle: looking to the right side (20°); right: looking to the left side (20°). The initial horizontal component of the blink-induced eye movement is always nasalward. However, during eccentric fixation, the amplitude of this initial component is notable decreased in the adducted eye. The blink-induced eye movement in the adducted eye tends to become biphasic. In the example shown, this can be seen with the blinks occurring during fixation at 20° left. The secondary (temporalward) component of the right eye often has a larger amplitude than the primary nasalward component. Furthermore, both eyes always move downward. In this and all further plots, up deflections specify upward/rightward eye movements, whereas downward deflections specify downward/leftward eye movements. LH, horizontal position of left eye; RH, horizontal position of right eye; LV, vertical position of left eye; RV, vertical position of right eye; LID, position of the right eyelid.

Only S2 showed a reversal of the horizontal movement in the left eye during fixation at 20° right: in this condition, both eyes moved leftward. However, in all subjects, during eccentric fixation, the amplitude of the initial horizontal component was decreased in the adducted eye, on average by 65%. The blink-induced eye movement in the adducted eye tended to become biphasic. As a result, the secondary (temporalward) component often had a larger amplitude than the primary nasalward component (Fig. 1). In the adducted eye, the frequency of this secondary direction reversal ranged 19–85% with a mean frequency of 62%.

There was no consistent effect of eccentric gaze on the vertical component of the blink-induced movements. The vertical movement of the upper eyelid during blinks invariably showed a fast downward and a much slower upward component, in agreement with earlier descriptions (Becker and Fuchs 1988; Evinger et al. 1991; Fuchs et al. 1992; Guitton et al. 1991).

**Effect of blinks on the metrics of saccades**

When we compared the *gain* of saccades made with or without a blink to the 20° stimuli, the gain tended to be

FIG. 2. Trajectories of the blink-induced eye movements (S5, blinks during fixation of the center of the screen). Circles indicate starting region for each saccade. Both eyes initially move nasalward and downward. In addition, the eyes describe loops: counterclockwise in the left eye and clockwise in the right eye, as seen by the subject.
TABLE 1. Influence of blinks on the gains of saccades

<table>
<thead>
<tr>
<th>Subject</th>
<th>Gain of 20° Saccades</th>
<th>Gain of 40° Saccades*</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>No DO correction</td>
<td>With DO correction</td>
</tr>
<tr>
<td></td>
<td>Without</td>
<td>With</td>
</tr>
<tr>
<td>S1</td>
<td>0.99</td>
<td>1.00</td>
</tr>
<tr>
<td>S2</td>
<td>0.95</td>
<td>0.99†</td>
</tr>
<tr>
<td>S3</td>
<td>0.96</td>
<td>0.99†</td>
</tr>
<tr>
<td>S4</td>
<td>1.00</td>
<td>1.01</td>
</tr>
<tr>
<td>S5</td>
<td>0.98</td>
<td>1.06†</td>
</tr>
</tbody>
</table>

DO, dynamic overshoot. * Not statistically significant. † Statistical significance, $P < 0.001$.

Effects of blinks on the dynamic properties of saccades

Results for all subjects and conditions are summarized in Fig. 5. For the 20° stimulus, all subjects showed a significant decrease of peak velocity (average 19%) when saccades were accompanied by blinks. There was also a decrease in peak acceleration and peak deceleration. On the other hand, the duration of those saccades made with blinks was consistently increased (Fig. 4). This effect of blinks was similar, but somewhat smaller, for 40° saccades. In this condition, the saccades of one subject (S1) remained almost unaffected. Nonetheless, the duration of the blink was consistently longer than the associated saccade. Thus, during 20° saccades, the mean duration of blinks for all subjects was found to be 331 ms, whereas the mean duration of associated saccades was 115 ms. Similarly, during 40° saccades, the mean duration of blinks for all subjects was found to be 363 ms, whereas the mean duration of associated saccades was 181 ms.

Comparison of the effect of blinks on centripetal and centrifugal saccades

In saccades without blinks, the peak velocity for saccades toward the central position (centripetal) is higher than the peak velocity of centrifugal saccades of similar size (Collewijn et al. 1988). We found that this difference persisted for saccades accompanied by blinks, but was of smaller magnitude. In one subject (S1) centrifugal saccades with blinks were faster than centripetal saccades. These data are summarized in Table 2.

Comparison of the effects of blinks on the abducting and adducting eye

For saccades made without blinks, the peak velocity of the abducting eye was greater than that of the adducting eye, in most subjects, for 20° saccades; effects on 40° saccades were less consistent. However, for saccades accompanied by blinks, abducting saccades were more consistently faster. It should be noted that this finding cannot simply be explained by a superimposition of the blink-induced eye movement on the saccades, because this would be expected to speed up the adducting eye. These differences in velocity for similar amplitude saccades are summarized in Table 3.

Postsaccadic oscillations

An unexpected finding was the occurrence of dynamic overshoots following saccades made with blinks (Fig. 4). In saccades made without blinks, dynamic overshoots were uncommon. For 20° saccades accompanied by blinks, the incidence of dynamic overshoot increased significantly in three subjects. Two subjects showed greater proportion of dynamic overshoots during 40° blink-associated saccades as compared with 40° saccades without blinks, whereas one subject showed the reverse (Fig. 6).

It was not possible to make a meaningful comparison concerning the amplitude of dynamic overshoot because, for saccades made without blinks, very few dynamic overshoots...
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FIG. 4. Top panel: time plot of 4 representative 20° centrifugal saccades of S5 without (left) and with (right) blinks. Thick line represents the lid position signal. Bottom panel: velocity profile of these saccades. Asterisks indicate the initial convergent movement of the eyes at the beginning of the saccade. Note the dynamic overshoots (DO) frequently occur at the end of the saccades with blinks. This usually occurs in both eyes and therefore cannot be explained by a superposition of the blink-induced eye movement (which is nasallyward in both eyes). The velocity profile gives an estimate of the decreased peak velocity and increased duration of saccades accompanied by blinks. LH, horizontal position of left eye; RH, horizontal position of right eye; LID, position of the right eyelid; LHV, horizontal velocity of the left eye; RHV, horizontal velocity of the right eye.

occurred. For saccades accompanied by blinks, the average amplitude of the dynamic overshoot was 0.5° (S1), 1.2° (S2), 1.3° (S3 and S4), and 2.6° (S5). These amplitudes of dynamic overshoot appear to be larger than those previously reported (<1.0°) in studies that did not consider the effects of blinks (Bahill et al. 1975; Boettzel et al. 1993; Kapoula et al. 1986).

Furthermore, we found that during blink-associated saccades, the peak velocity of saccades with dynamic overshoots was greater than those without dynamic overshoots. For example, in subject 5 (see Fig. 4), who most frequently showed dynamic overshoots during blink-associated saccades, we found that his mean peak velocity for 20° saccades with dynamic overshoot was 403°/s, whereas his mean peak velocity for 20° saccades without dynamic overshoot was only 317°/s. This difference was significant (P < 0.0001).

Discussion

In this study, we investigated the effects of voluntary blinks on the properties of horizontal saccades. Even for the predictable stimuli that we used, saccadic velocity and duration were substantially affected, although gain was not. To our knowledge, this effect of blinks has not been previously reported in humans and has implications both for concepts concerning the generation of saccades and also analysis of their dynamic properties. Our primary goal in this study was to determine whether these changes in saccadic dynamics could be solely ascribed to the effects of voluntary blinks when subjects attempt steady fixation.

Effects of blinks on gaze during fixation of stationary targets

Our results confirm that blinking while looking straight ahead causes a downward and nasallyward movement of both eyes. (Collewijn et al. 1985; Evinger et al. 1984; Ginsborg and Maurice 1959; Riggs et al. 1987). An eccentric gaze position modified these eye movements, most notably by a reduction of the initial movement of the adducted eye, which was followed by a larger temporallyward movement for 62% of blinks. This finding suggests that, under such circumstances, the eye is not only pulled nasallyward but also toward the central position. Blink-induced eye movements may be the result of cocontraction of the extraocular muscles that occur time locked to the blink. One possible explanation for nasallyward movements of the eyes is that, during this cocontraction, activation of the horizontal rectus muscles is not simultaneous: in the rabbit, the electromyographic activity in the medial rectus started 13 ms earlier than in the lateral rectus (Evinger and Manning 1993). The modification of this pattern when the eyes are in eccentric positions in the orbit might be due to passive elastic forces due to the orbital tissue, which tend to return the eye to a more central position (Robinson 1964).

Effects of voluntary blinks on horizontal saccades

Our analysis suggests that these blink-induced eye movements are also present during a saccade that occurs together with a blink, resulting in a curved trajectory of the eye movement (Fig. 3). Although saccadic gain was hardly affected by blinks, there was a strong effect on the dynamic
properties. Peak velocity, acceleration, and deceleration were significantly decreased, and duration was increased. Could these changes be explained by a superposition of blink-induced eye movements?

The cocontraction of the extraocular muscles caused by a blink would be expected to slow down a saccade if it was superimposed on and synchronized with normal muscle activation for the saccade. We confirmed (Table 2) that, for saccades without blinks, a consistent difference exists between centripetal and centrifugal saccades: the peak velocity for saccades toward the central position is \( \approx 10\% \) greater than the peak velocity of centrifugal saccades of the same size (Collewijn et al. 1988). If the eye is always pulled toward its central position by a blink (Evinger et al. 1984; Riggs et al. 1987), this centripetal/centrifugal velocity difference should be enhanced in saccades accompanied by blinks. However, our data do not support this hypothesis (Table 2); in saccades accompanied by blinks, the centripetal/centrifugal velocity difference was not increased. The relationship between the peak velocities was either unchanged or diminished. Thus a modification of the centripetal/centrifugal velocity difference of saccades

### Table 2. Comparison of peak velocities of centripetal versus centrifugal saccades

<table>
<thead>
<tr>
<th>Subject</th>
<th>( V_{\text{max}} ) in 20° Saccades Without Blinks, deg/s</th>
<th>( V_{\text{max}} ) in 20° Saccades With Blinks, deg/s</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Centripetal</td>
<td>Centrifugal</td>
</tr>
<tr>
<td>S1</td>
<td>371</td>
<td>326</td>
</tr>
<tr>
<td>S2</td>
<td>362</td>
<td>331</td>
</tr>
<tr>
<td>S3</td>
<td>360</td>
<td>278</td>
</tr>
<tr>
<td>S4</td>
<td>408</td>
<td>361</td>
</tr>
<tr>
<td>S5</td>
<td>464</td>
<td>425</td>
</tr>
<tr>
<td>Average</td>
<td>393</td>
<td>344</td>
</tr>
</tbody>
</table>

* Values were calculated as peak velocity of centripetal saccades minus peak velocity of centrifugal saccades. Abducting and adducting saccades were pooled for this analysis. † “Difference” was significant with \( P < 0.01 \).
TABLE 3. Comparison of peak velocities of abducting and adducting saccades

<table>
<thead>
<tr>
<th>Subject</th>
<th>V_{max} Abducting Eye Minus V_{max} Adducting Eye, 20°</th>
<th>V_{max} Abducting Eye Minus Adducting Eye, 40°</th>
</tr>
</thead>
<tbody>
<tr>
<td>S1</td>
<td>No blinks -5 With blinks 26* No blinks -4 With blinks 43*</td>
<td></td>
</tr>
<tr>
<td>S2</td>
<td>7 45* 7 45*</td>
<td></td>
</tr>
<tr>
<td>S3</td>
<td>26 -18* 44* -22*</td>
<td></td>
</tr>
<tr>
<td>S4</td>
<td>1 11 -36* -31*</td>
<td></td>
</tr>
<tr>
<td>S5</td>
<td>5 46* -16* 23*</td>
<td></td>
</tr>
<tr>
<td>Average</td>
<td>6.8 22.0 -1.0 11.6</td>
<td></td>
</tr>
</tbody>
</table>

Data were calculated from the peak velocity (V_{max}) of the abducting eye minus V_{max} of the adducting eye. Thus a positive number indicates that the abducting eye was faster. Centrifugal and centripetal saccades were pooled for analysis of 20° saccades; 40° saccades were symmetrical. * “Difference” was significant with P < 0.05.

Evoked and hypotheses for the effect of blinks on central saccadic programming

How could blinks influence the generation of saccades? Although visual inputs are available when saccades are made without blinks, but not with blinks, the brief nature of saccades prevents any effect of visual feedback on their dynamic properties. Thus blinks appear to have a direct effect on saccadic programming. It is presently thought that the oculomotor nuclei receive the command for horizontal saccades from burst neurons in the paramedian pontine reticular formation (PPRF) and the command for vertical saccades from burst neurons in the rostral interstitial nucleus of the medial longitudinal fasciculus (riMLF), which lies in the prerubral fields of the rostral midbrain (see Büttner-Ennever 1988; Leigh and Zee 1991 for reviews). Both sets of saccadic burst neurons are held in check by omnipause neurons (OPN) that lie in the nucleus raphe interpositus (rip) of the pons (Büttner-Ennever et al. 1988; Langer and Kaneko 1990). The OPN are so-called because they pause their inhibitory discharge for all saccades, and also for blinks (Hepp et al. 1989; Mays and Morrisse 1993). Although the cessation of OPN activity that occurs during blinks could allow the saccadic burst neurons to discharge, it is not clear why the resulting eye movements should be disjunctive. One possible explanation is that the latter is due to the recently demonstrated influence of OPN on vergence neurons (Mays and Gamlin 1995). In addition, blinks reduce the discharge of short-lead burst neurons in the PPRF (Mays and Morrisse 1995) and also saccade-related burst neurons in the deep layers of the superior colliculus (Goossens et al. 1996).

Additional evidence for the proposal that blinks affect the central programming of saccades comes from the finding of brief saccadic oscillations [dynamic overshoots (Bahill et al. 1975)] immediately after saccades made in conjunction with blinks. A model developed by Zee and Robinson (1979) was able to simulate dynamic overshoots in normal subjects and pathological saccadic oscillations such as shown by patients with a variety of neurological disorders (Ashe et al. 1991; Hain et al. 1986; Leigh and Zee 1991). In this model, dynamic overshoot occurs if the OPN do not immediately resume discharging at the end of a saccade. In saccades accompanied by blinks, the OPN could be prevented from resuming discharge at the end of the eye movement. The duration of blinks accompanying 20 and 40° saccades is similar, but the duration of a saccade depends on its amplitude. Thus a higher incidence of postsaccadic oscil-

FIG. 6. Comparison of the frequency of dynamic overshoots in saccades without and with blinks. Bars show how many percent of the saccades were followed by a dynamic overshoot in 1 or both eyes. In 20° saccades, dynamic overshoot is more likely to occur in saccades accompanied by blinks; in 40° saccades there is no clear trend. White bars represent the saccades without blinks, hatched bars the saccades accompanied by blinks. Asterisks indicate a significant difference between the 2 conditions (P < 0.0001).
lations would be expected for 20° saccades, for which the difference between the duration of blink and saccades was greater, and this was true for our results. In accordance with this hypothesis, recent data show that in patients with prolonged vertical components of oblique saccades, the eyes oscillate in the horizontal plane until the vertical component of the saccades is complete (Rottach et al. 1997). In such patients, it is postulated that the OPN are still silent during the ongoing vertical component of the saccades and promote instability in the horizontal plane. In our present study, the subject with the fastest saccades had most dynamic overshoots. The high saccadic velocity may reflect a high burst-cell gain, which would explain the greater tendency for oscillations in this subject.

Conclusions
The results of this study indicate that blinks clearly affect the dynamic properties of accompanying saccades, but accuracy is almost unaffected. Some of the changes seem to be due to a superimposition of the nasal-downward eye movement that can be observed in blinks without saccades. In addition, our data, especially the presence of dynamic overshoots, support an effect of blinks on the central programming of the saccades. Finally, studies of the dynamic properties of saccades need to carefully document the occurrence of blinks, which may substantially affect the results.

We are grateful to Dr. Michele A. Basso for critically reading the manuscript. This work was supported by National Eye Institute Grant EY-06717, the Department of Veterans Affairs, the Evenor Armington Fund (to R.J. Leigh), and Deutsche Forschungsgemeinschaft (to K.G. Rottach). Address for reprint requests: R.J. Leigh, Dept. of Neurology, University Hospitals, 11100 Euclid Ave., Cleveland, OH 44106-5000. Received 12 September 1997; accepted in final form 19 February 1998.

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