Action of the Brain Stem Saccade Generator During Horizontal Gaze Shifts. I. Discharge Patterns of Omnidirectional Pause Neurons

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Phillips, James O., Leo Ling, and Albert F. Fuchs. Action of the brain stem saccade generator during horizontal gaze shifts. I. Discharge patterns of omnidirectional pause neurons. J. Neurophysiol. 81: 1284–1295, 1999. Omnidirectional pause neurons (OPNs) pause for the duration of a saccade in all directions because they are part of the neural mechanism that controls saccade duration. In the natural situation, however, large saccades are accompanied by head movements to produce rapid gaze shifts. To determine whether OPNs are part of the mechanism that controls the whole gaze shift rather than the eye saccade alone, we monitored the activity of 44 OPNs that paused for rightward and leftward gaze shifts but otherwise discharged at relatively constant average rates. Pause duration was well correlated with the duration of either eye or gaze movement but poorly correlated with the duration of head movement. The time of pause onset was aligned tightly with the onset of either eye or gaze movement but only loosely aligned with the onset of head movement. These data suggest that the OPN pause does not encode the duration of head movement. Further, the end of the OPN pause was often better aligned with the end of the eye movement than with the end of the gaze movement for individual gaze shifts. For most gaze shifts, the eye component ended with an immediate counterrotation owing to the vestibulococular reflex (VOR), and gaze ended at variable times thereafter. In those gaze shifts where eye counterrotation was delayed, the end of the pause also was delayed. Taken together, these data suggest that the end of the pause influences the onset of eye counterrotation, not the end of the gaze shift. We suggest that OPN neurons act to control only that portion of the gaze movement that is commanded by the eye burst generator. This command is expressed by driving the saccadic eye movement directly and also by suppressing VOR eye counterrotation. Because gaze end is less well correlated with pause end and often occurs well after counterrotation onset, we conclude that elements of the burst generator typically are not active till gaze end, and that gaze end is determined by another mechanism independent of the OPNs.

INTRODUCTION

Over the past three decades, the oculomotor community has made considerable progress toward understanding how the brain stem controls rapid gaze shifts in animals whose heads are restrained from moving. In the head-restrained monkey, rapid gaze shifts are accomplished solely by saccadic eye movements. Horizontal saccades are thought to be generated by pontine and medullary neurons, whose net effect is to provide a burst of excitation to agonist motoneurons and a burst of inhibition to antagonist motoneurons (see Moschova-
components of a gaze shift. In this scenario, all OPNs would be expected to end their discharge with the end of the eye movement per se, and not with the end of the gaze shift. This possibility is diagrammed in Fig. 1C.

A final possibility is that the OPNs are involved in the control of an eye movement command that is typically expressed as an eye saccade, but such a saccade occasionally can be foreshortened by the activity of mechanisms that coordinate eye and head movements. For this to be true, the eye/head coordinating mechanism would be independent of OPN control and would be able to limit eye movement duration (and presumably amplitude) without affecting OPN discharge. This mechanism, therefore, would exist downstream of the OPN-controlled saccade burst generator. In this scheme, shown in Fig. 1D, OPN discharge usually would end with the end of the saccadic eye movement. However, in cases where the downstream coordinating mechanism foreshortens the saccade, the pause would end after the eye saccade. Indeed, the end of the pause should be well correlated with the onset of eye counterrotation due to the vestibuloocular reflex (VOR), which would be expressed only after the eye saccade and its associated OPN pause were over.

In the study reported here, we conclude that the final scheme best fits our observations of OPN discharge during gaze shifts with the head either restrained or unrestrained. Preliminary reports of this work have been published elsewhere (Coble et al. 1994; Ling et al. 1990).

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**METHODS**

Most of the methods used in this paper are detailed elsewhere (Phillips et al. 1995b). Briefly, four juvenile male rhesus macaques were trained to track small jumping visual targets with their heads fully restrained or free to move in the horizontal plane only (unrestrained). Eye position in space (G, gaze) was measured with an electromagnetic search coil, and head position (H) was measured via a single turn precision potentiometer (linearity 0.25%) attached to a low inertia (J = 120 g cm²) restraint post that was coaxial with the spinal column when the animal was seated comfortably in a primate chair. The restraint post allowed for unrestrained movement only in the horizontal plane. Eye position in the head (E) was obtained as the difference between gaze and head position with a resolution of 0.5°.

Extracellular unit activity was recorded with tungsten microelectrodes, which were advanced hydraulically into the brain stem (using a standard Trent Wells microdrive) through a chronically implanted recording chamber. The approximate location of the nRIP was determined in relation to the two abducens nuclei, and its OPNs were identified by their characteristic tonic discharge punctuated by brief pauses for saccadic eye movements. The search condition typically consisted of head-unrestrained gaze movements to visual targets placed at 0° (straight ahead) and 30° to the left and right. Once an OPN was isolated, the animals were presented with horizontal target steps of pseudorandom amplitudes, ranging from ±5° to ±40°. After head-unrestrained data were collected, the animal’s head was secured to the restraint post (Phillips et al. 1995b), and the monkey was presented with target step amplitudes of less than or equal to ±30°. Because head restraint often resulted in loss of the unit, we obtained...
head-restrained data on only 20 of the 44 OPNs recorded in the head-unrestrained condition.

Behavioral and unit data were analyzed on a Macintosh IIfx computer with an interactive program that allowed an investigator to scroll through continuous data and identify gaze shifts for analysis (Fuchs et al. 1994; Phillips et al. 1995b). Velocity traces were obtained by digital differentiation of the digitized eye, head, and gaze position signals. Both the firing patterns associated with gaze shifts and attributes describing the unit activity and the metrics of the gaze, head, and eye movements were saved so that a second program could produce unit histograms and correlations between the various unit and movement attributes.

After the last penetration, the monkeys were killed and perfused transcardially with a saline wash followed by 10% Formalin. Frozen 50-μm sections were mounted and counter-stained with cresyl violet. Representative electrode tracks were reconstructed, guided by marking lesions made at the time of unit recording.

All the surgeries and training procedures were approved by the Animal Care and Use Committee at the University of Washington. The animals were cared for by the veterinary staff of the Regional Primate Research Center. They were housed under conditions that comply with National Institutes of Health standards as stated in the Guide for the Care and Use of Laboratory Animals (DHEW Publication NIH85-23 1985) and with recommendations from the Institution of Laboratory Resources and the American Association for Accreditation of Laboratory Care International.

RESULTS

General observations

We recorded the discharge patterns of 44 OPNs in four animals that were executing horizontal gaze shifts while their heads were free to rotate about a vertical axis. About one-third of the cells were obtained from each of three animals and two cells from the fourth. All OPNs lay rostral to the abducens nuclei on penetrations in which at least one other OPN was isolated or where there was a substantial pass through unresolved but clearly pausing activity.

When the animals’ heads were restrained, their OPNs exhibited discharge patterns like those reported previously (Keller 1974; King 1976; Luschei and Fuchs 1972). When the monkey fixated a stationary target, the OPNs discharged at a steady rate that was independent of eye position (Fig. 2A). This
rate was somewhat lower when the monkey was free to move its head (108 ± 29 spikes/s) than when its head was restrained (118 ± 29 spikes/s), an observation for which we have no explanation. When the animal shifted its direction of gaze in any direction, the neuron ceased firing (i.e., paused). When the head was free to move, eye and head movements both contributed to the overall gaze shift (Fig. 2B). The gaze shift usually began with the onset of the saccadic eye movement and ended either coincident with or after the eye saccade. The head movement generally continued long after both the eye movement and the gaze shift were over. When the head was unrestrained, the OPNs paused for all gaze shifts, whether the head actually moved or not. For example, the OPN in Fig. 2B paused both with the initial large gaze shift and with the later small corrective saccade for which there was no associated head movement.

**Definition of movement components of a gaze shift**

In what follows, we will make arguments about the role of OPNs on the basis of the timing of their pause in activity relative to the beginning and end of the various movement components of a gaze shift. Fundamental to such an analysis is our definition of the onset and end of each of the movement components.
components. The gaze, eye, and head components of a gaze shift often exhibit considerable variation in their time courses, both within the same monkey and from one monkey to another (Phillips et al. 1995b). In general, these differences manifest themselves most at the end of the eye movement, when the eye can either begin to counterrotate immediately (Figs. 2B and 3A) or remain for some time at a constant amplitude, i.e., exhibit a plateau, before counterrotating (Fig. 3B, between the 2 arrows). At the end of an eye movement, the gaze movement also may stop, or it may continue at a much slower velocity in the same direction, i.e., exhibit a “slide” toward its final location (Fig. 3A, between the 2 arrows). To be completely objective about the end of these movement components, as well as the onset of eye counterrotation, we allowed the computer to decide where the movement components started and stopped on the basis of a velocity criterion of 20°/s. The 20°/s criterion was the lowest velocity that we could reliably detect with the noise in our differentiated measure of eye velocity. Furthermore, the choice of 20°/s allowed us to compare our data to that obtained in a cat study that used the same velocity criterion (Paré and Guitton 1998).

Pause duration as a function of component movement duration

Pause duration was nicely related to the duration of either the eye or gaze component of a gaze shift (henceforth called eye and gaze duration) but only poorly, if at all, to the duration of the head component (henceforth called head duration). The relation of pause duration and component duration for a rep-

![Graph showing the relationship between pause duration and movement duration for gaze, eye, and head](image_url)
equally well correlated with eye and gaze duration. However, the slopes of the relations between pause duration and eye duration were equal to or greater than those for pause duration versus gaze duration for all but two of the OPNs (Fig. 5A). The average slope of the pause versus eye duration relation (1.12 ± 0.16) was significantly greater (paired t-test, \( P \leq 0.0001 \)) than that for the pause versus gaze duration relation (0.88 ± 0.13). For most OPNs, the intercept for the pause duration versus gaze duration relation was larger than that for the pause duration versus eye duration relation. The average pause duration intercept for gaze duration was 19 ± 20 ms, whereas that for eye duration was 15 ± 23 ms. Considering both the average intercepts and the slopes, pause duration was larger, on average, for eye durations of >20 ms than for gaze durations of the same size.

On the basis of these data, we conclude that the pause of OPNs does not encode head duration. However, because a line fits the relation between pause duration and either eye or gaze duration equally well (as judged by the \( r^2 \) values), it is impossible to conclude that pause duration is better related to one or the other. Fortunately, some movements, too few to influence substantially the fits of the duration/duration data, exhibited either eye plateaus or gaze slides as illustrated in Fig. 3. The existence of such movements allowed us to examine the relation between pause and eye or gaze duration in a different way by examining the timing of the pause relative to the timing of the eye and gaze components of individual gaze shifts.

**Timing of the pause relative to eye and gaze onset and end pause onset relative to movement onset.** With one exception, the pause of all the OPNs led the onset of the eye movement by slightly more than it led the onset of the gaze movement (Fig. 6A). The average pause leads were 23 ± 11 ms relative to eye movement and 20 ± 11 ms relative to gaze onset. In contrast, pause onset relative to head movement onset varied considerably more from unit to unit (range: -76 to +42 ms with an SD of 24 ms) and led head movement onset by an average of only 8 ms. That the onset of the pause began either before or after the head movement for different OPNs is consistent with our earlier suggestion that OPNs do not control the characteristics of the head movement.

In contrast, for individual OPNs, the substantial mean lead times of the pause relative to both eye and gaze onset (<20 ms) and the small SDs about those means indicate that pause onset could control the onset of either eye or gaze movement. Although SDs of individual neurons varied from -3 to 26 ms, the SDs of average pause lead relative to the eye versus SDs of average pause lead relative to gaze all clustered tightly about the line of slope 1, which indicates equal SDs (Fig. 6B). Therefore this measure does not allow us to sort out whether pause onset preferentially encodes eye or gaze onset. However, the SDs from the mean pause lead times of individual units relative to head movement were almost all larger than those for eye and gaze movement (Fig. 6B), indicating again that pause onset is better timed to initiate eye or gaze movement than head movement.

**Pause end relative to movement end.** The pause of each OPN ended, on average, earlier relative to the end of the gaze shift than to the end of the eye movement (Fig. 7A, all data lie above line of slope 1). This was particularly apparent for

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**Fig. 5.** Comparison of the linear fits of pause duration vs. eye, head, and gaze duration. A: slopes of the linear fits of the relation between eye duration (●) or head duration (○) as a function of the slope of the gaze duration relation. For almost every OPN, the linear fit was steeper for eye than gaze duration. B: square of the linear correlation coefficient \( r^2 \) of the eye and head duration linear fits vs. \( r^2 \) values for the gaze duration fit. Most \( r^2 \) values for gaze and eye duration relations exceeded 0.75, whereas most \( r^2 \) values for the head duration relation were <0.25.
individual trials in which eye plateaus and/or slides in the gaze movement occurred so that gaze velocity fell below 20°/s considerably later than did eye velocity (recall Fig. 3). Furthermore, 41 of the 44 OPNs resumed firing before gaze end (Fig. 7A, pluses). On average, pause end preceded gaze end by 24 ± 15 ms. In contrast, the pause of less than one-half of the OPNs (n = 18) ended before eye velocity fell below 20°/s, and the rest ended after. On average, the pause ended 6 ± 16 ms after the eye had stopped moving. In comparison, the pause of the 20 OPNs recorded with the head restrained ended 11 ± 6 ms before saccade end. With the head free, the pause in these 20 neurons ended 2 ± 12 ms after eye end and 23 ± 15 ms before gaze end. Therefore the timing of the pause end relative to gaze end with the head restrained lay intermediate to the timing of the pause end relative to eye and gaze end with the head unrestrained.

For most of the OPNs, however, the end of the pause was more consistently timed with the end of the eye movement than with the end of the gaze shift. For 37 of 44 units, the SD of the mean time between pause end and eye end was equal to or less than that between pause end and gaze end (Fig. 7B). The few units (n = 7) in which the SD was higher for eye end than for gaze end were recorded in monkey CG, which exhibited occasional eye movement plateaus in which the eye velocity fell below 20°/s well before the onset of eye counterrotation or the end of the gaze movement (as in Fig. 3B). For all the OPNs in that monkey (n = 18), we also calculated the timing of the end of the pause relative to the start of eye counterrotation (7 ± 17 ms). When considered in this way (solid symbols in Fig. 7B), all of the SDs of the mean times between pause end and the start of eye counterrotation were less than or essentially equal to the SDs of pause end relative to gaze end. Because the end of eye movement and the onset of eye counterrotation were identical in animals that exhibited no eye movement plateaus, these data suggest that pause end is more reliably timed to occur with the onset of eye counterrotation for all types of gaze shifts in all monkeys with different gaze shifting strategies. Note that pause end still occurred after eye counterrotation for some OPNs (Fig. 7A).

**FIG. 6.** Timing of the onset of an OPN pause and the beginning of the movement components of a gaze shift. A: onset time of the pause relative to the start of the eye (●) and head movement (○) as a function of the onset time of the pause relative to gaze onset. For most OPNs, average pause onset leads eye onset by slightly more than gaze onset; individual OPNs can begin pausing before or after head movement onset. Negative numbers indicate that pause begins before (leads) the movement. B: SDs of the means of pause onset relative to eye and head onset as a function of the SDs of the means of pause onset relative to gaze onset. SDs for the eye and gaze mean lead times are small and essentially equal, whereas those for the head mean lead times are almost all larger than those for gaze or eye.

**FIG. 7.** Timing of the end of the OPN pause relative to movement components of the gaze shift. A: mean latencies from the end of the pause to the end of eye movement (+) and the onset of eye counterrotation (●) as a function of the latency from the end of the pause relative to gaze end. Negative numbers indicate that pause ends before (leads) the end of the movement. Pause end always leads gaze end but not always eye end. B: SDs of the means of pause end relative to eye end and to eye counterrotation as a function of the SDs of the means of pause end relative to gaze end. For most units, pause end timing is less variable relative to eye end and for all units less (or equally) variable relative to the start of eye counterrotation.
Timing of the end of the pause relative to eye and gaze movement for an OPN in monkey BW. Spike rasters are aligned on the end of the gaze movement (A) or on the end of the eye movement (B). Pause end is more consistently aligned with eye end in this monkey who exhibited no eye movement plateaus. Arrows in A identify trials where the pause ends well before (→) or slightly after (←) the gaze shift. These gaze shifts (n = 85) have head movement components of at least 35°. Rasters have been ordered on increasing pause duration.

To test this statistically, we examined the variability of the time from pause end to either gaze end or eye counterrotation onset in all conditions in all 44 cells. For 28/44 cells, there was a statistically significant difference in the variability of these measures at (P ≤ 0.01). An F-test of the variance of these measures in those 28 cells confirmed that pause end was significantly better related to eye counterrotation onset than to gaze end in 26 cells, and better related to gaze in only 2 cells.

Our suggestion that the start of eye counterrotation appears to be the time in the gaze shift that is most reliably related to the end of the pause also can be supported by examining the timing of individual gaze shifts. In Fig. 8, the end of the pause is aligned with the end of the eye movement, and the end of the gaze movement for a unit in monkey BW. When aligned with the end of the gaze movement (Fig. 8A), the end of the pause is quite variable; it can occur up to 85 ms before gaze lands (raster at leftward arrow) or up to 16 ms after gaze lands (raster at rightward arrow). In contrast, when aligned with the end of the eye movement (Fig. 8B), the timing of the end of the pause is quite consistent. Figure 9 displays several eye and gaze movements aligned on the end of the pause in the same unit. Clearly, pause end (vertical line) is better aligned on eye end than on gaze end; gaze continues to slide forward after the eye begins to counterrotate. Monkey BW did not exhibit any eye movement plateaus, so counterrotation began immediately after its eye had landed.

As noted earlier, monkey CG was inclined to make occasional eye movement plateaus so that its eye counterrotation could begin as much as 250 ms after eye velocity fell to 20°/s. When such movements were frequent, OPNs like the one illustrated in Fig. 10 ended their pause more reliably with gaze end than with eye end; i.e., pause end was better aligned with the end of the gaze shift (Fig. 10A) than with the end of the eye movement (Fig. 10B). However, when the end of the pause was aligned with the start of eye counterrotation, the variability of the timing of the end of the pause was reduced (Fig. 10C) and matched that of pause end relative to gaze end. Figure 11 displays eye and gaze movements aligned on the end of the pause in the same unit. Here, pause end (vertical line) is equally well aligned on gaze end and the onset of eye counterrotation. It should be noted that the gaze shifts illustrated in Figs. 8–11 had head movement components of at least 35°. For gaze shifts accomplished through small head movements, the gaze slides and eye plateaus that allow the dissociation of eye and gaze end were infrequent and, when they occurred, were much smaller.

**Head-restrained OPN activity**

In a further test of our suggestion that pause end encodes the start of eye counterrotation rather than the end of the gaze shift, we examined the timing of some of the same OPNs with the head restrained. In this condition, eye movement and gaze movement are identical. If the OPN pause encodes gaze in all situations, then the timing of the pause relative to gaze end should be equally precise whether the head is restrained or unrestrained.

For the 20 neurons recorded in both head-restrained and head-unrestrained conditions, the end of the pause (as assessed by the SDs of the means of pause end relative to gaze end) was more consistently aligned with the end of gaze shifts when the head was restrained than when it was free to move (Fig. 12A). However, Fig. 12B shows that the end of the pause was, with one exception, as well or better aligned (i.e., had comparable SDs) with the onset of eye counterrotation in head-unrestrained animals as it was with the end of the gaze movement with the head restrained. This was true for gaze shifts both without (○) and with (◇) eye movement plateaus. Taken together, these data support our suggestion that the resumption of OPN activity is involved with encoding eye counterrotation (Fig. 12B) and not the end of the gaze shift (Fig. 12A). However, the consistency of the end of the pause relative to the end of the gaze shift with the head restrained (when gaze is equivalent to eye movement) was usually (for 17/20 neurons) at least as good or better than the consistency of the end of the pause relative to the onset of eye counterrotation with the head unrestrained (SD difference of 6 ± 9 ms, n = 20).
DISCUSSION

The results of this study allow us to draw several conclusions about the role of OPNs during head-unrestrained gaze shifts. First, gaze is not directly under the control of the OPNs. Usually, the end of the pause is better correlated with the end of the saccadic eye movement than with the end of the gaze shift. Also, gaze end is better correlated with pause end when the head is restrained than when it is free to turn (Fig. 12), suggesting that the pause does not encode gaze equally well in all conditions. Therefore the scheme displayed in Fig. 1A is not consistent with our data. Another way of interpreting our data is to suggest that the resumption of firing in primate OPNs is best correlated to the end of the saccadic portion of the gaze shift, which in most cases occurs with the end of the eye saccade. Even if this interpretation is true, one cannot therefore conclude that the pause controls gaze per se because gaze continues for tens of milliseconds after the pause is over. In contrast, the pause of cat OPNs apparently is better related to the end of the gaze shift than to the end of the eye saccade (Paré and Guitton 1989, 1990, 1998).

Second, OPNs have little to do with head movements. The timing of pause onset, end, and duration are poorly correlated with the onset, end, and duration of the head movement. This finding eliminates the control scheme in Fig. 1B as a viable option. Similar data showing a poor relationship between head movement and OPN discharge have been observed in cats during head-unrestrained gaze shifts (Paré and Guitton 1989, 1990, 1998). Third, there are situations in which OPN discharge can be dissociated from the end of the eye saccade, eliminating the scheme shown in Fig. 1C. After some saccades, when the eye remains in a stable orbital eye position even though the gaze shift continues, OPN discharge is best correlated with the onset of eye counterrotation. Taken together, these observations suggest that OPN discharge controls premotor elements of the eye burst generator during gaze shifts and that other elements contribute to the control of gaze through mechanisms that can influence the duration of the eye movements.

FIG. 9. Eye (E_H) and gaze (G) movements aligned on pause end (vertical line) for selected responses of the OPN of Fig. 8.
saccade independent of OPN discharge. We now consider this proposal, which is schematized in Fig. 1D, in more detail.

**Pauses stop when the eyes counterrotate, not when gaze ends**

The saccadic eye components of gaze shifts do not always show a tight temporal correlation with the pause of OPNs (Figs. 10 and 11). This breakdown occurs when the eye movement ends with a long plateau of stable eye position in the orbit before both gaze end and the onset of eye counterrotation. In our experiments, and in those of Freedman and Sparks (1997), such movements did not occur very frequently. In early primate studies (Tomlinson and Bahra 1986b) and some human studies (e.g., Laurutis and Robinson 1986), such movements were observed more frequently, especially when the subjects were making very large gaze shifts to remembered targets. In cats, plateaus of stable eye position predominate (Galiana and Guitton 1992; Guitton 1988; Paré and Guitton 1990, 1998). During eye movement plateaus, the most salient feature of OPN discharge is that it ends well after the eye saccade does. This is clear from our data, and consistent with the data of Paré and Guitton (1998) in the cat. This observation lead those authors to suggest that gaze, not the eye saccade, is controlled by OPNs. However, when there are no plateaus, pause end in our data are better aligned with eye end than with gaze end (Figs. 7B and 8). Even when there are eye plateaus (Fig. 9), pause end is just as well timed with the onset of the now-delayed eye counterrotation as with gaze end.

How might the saccadic system be able to manage this? OPNs pause until the eye begins to counterrotate during gaze shifts with and without eye plateaus, suggesting that the end of activity in the eye burst generator, i.e., pause end, controls the onset of eye counterrotation during gaze shifts. This observation is consistent with the known strong inhibitory connections between saccade burst neurons and both vestibular nucleus neurons and contralateral abducens motor neurons (Hikosaka et al. 1978; Scudder et al. 1988; Strassman et al. 1986; Yoshida et al. 1982). Therefore, when the burst generator is active because OPNs are turned off, eye counterrotation mediated by the VOR is inhibited by two possible mechanisms. The dis-
charge of antagonist motoneurons is suppressed (the pause of motoneurons during off-direction saccades), and/or the VOR pathway through the vestibular nucleus is compromised, although not eliminated, by a pause in the position-vestibular-pause neurons (Scudder and Fuchs 1992). However, release of eye counterrotation will not guarantee that gaze will end. For the gaze shift to end, eye counterrotation must equal head rotation, and this often occurs only well after pause end. Thus a mechanism independent of the burst generator and its OPNs must control the gaze trajectory after the eye saccade is over.

The action of the gaze control mechanism is reflected in the variable slides of gaze toward the target after the end of the saccadic eye movement. These slides, which are present during many gaze shifts (e.g., Fig. 9), increase the variability of the end of the pause relative to the end of the gaze shift for individual OPNs. Similar gaze slides have been reported in humans (Ron et al. 1993) and in nonhuman primates (Phillips et al. 1995a) following double-step target presentations. In such cases they occurred only in the direction of the second step, i.e., in the direction of residual gaze error. Because these slides can be explained by eye counterrotations with gains of <1.0, the gaze control mechanism may act by controlling VOR gain. We favor this explanation, but at least two alternatives have been suggested.

One alternative is that gaze slides are random events that should not be considered to be part of a gaze shift. They are thought to be small and to have little effect on gaze duration. We, however, feel that they are an integral part of a gaze shift because some monkeys employ them in most gaze shifts and in those monkeys they contribute up to 10% of the total 80° gaze shift and add an average of 82 ms to its duration.

A second alternative is that the burst generator can operate in a second mode in which excitatory premotor elements continue their discharge in the face of resumed OPN activity. The suggestion that the burst generator continues to fire after a saccade is over comes largely from work in cats where gaze continues to advance slowly following 1) head-restrained gaze shifts (Missal et al. 1993); 2) head-restrained stimulation of the superior colliculus (Lefèvre et al. 1994; Missal et al. 1996), and 3) unexpected braking of head movement in the course of gaze shifts (Paré and Guitton 1998). In all these cases, gaze must advance by activation of eye motoneurons through the burst generator because no head movement is present to carry the eye. If these examples of slow advancement are similar to gaze slides, then gaze slides also could be explained by an unusually long discharge of premotor burst elements.

But is a low velocity gaze movement in which the eye is counterrotating generated in the same way as a similar velocity eye movement with the head stationary? We think not. In particular, we have never encountered a burst cell whose discharge continued during eye counterrotation, but ceased when gaze velocity dropped below 20°/s (Phillips 1993; Phillips et al. 1996a). Instead, we feel that VOR gain is modulated by gaze error during the slide to allow gaze to reach the target accurately. Indeed, we have preliminary evidence that tonic vestibular pause neurons, interneurons of the VOR in the vestibular nucleus, are modulated during the post-saccadic gaze shift as predicted by our model of gaze control (Phillips et al. 1996b). Consequently, we favor the explanation schematized in Fig. 1D.

In this scheme, the discharge of the OPNs is well correlated with the saccadic eye movement command for both head-restrained saccades and head-unrestrained gaze shifts. However, when the head is free to move, a mechanism that is not under OPN control coordinates eye and head movements to produce accurate gaze shifts. Part of the mechanism limits the duration and amplitude of the expressed eye saccade by subtracting velocity and amplitude from the saccadic eye movement command generated by the OPN-controlled saccade burst generator. This subtraction could be mechanical, because the eye can go only so far in the orbit, or neural, if an inhibitory head movement signal is from the drive provided by the eye burst generator (Fig. 1D). In either case, the commanded eye saccade will be foreshortened. Even though the eye saccade is foreshortened, the burst generator continues to remain active for the duration of the commanded saccade and eye counterrotation due to the VOR would be prevented, resulting in a
plateau of eye position. Only when the burst generator discharges ends can the eye begin to counterrotate.

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