TIME COURSE OF VESTIBULO-OCULAR REFLEX
SUPPRESSION DURING GAZE SHIFTS

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ABSTRACT

Although numerous investigations have probed the status of the VOR during gaze shifts, its exact status remains strangely elusive. The goal of the present study was to precisely evaluate the dynamics of VOR suppression immediately before, throughout, and just following gaze shifts. A torque motor was used to apply rapid (100 deg/s), short duration (20 - 30 ms) horizontal head perturbations in three Rhesus monkeys. The status of the VOR elicited by this transient head perturbation was first compared during 15, 40, and 60 deg gaze shifts. The level of VOR suppression just following gaze shift onset (40 ms) increased with gaze shift amplitude in two monkeys, approaching values of 80% and 35%. In contrast, in the third monkey, the VOR was not significantly attenuated for all gaze shift amplitudes. The time course of VOR attenuation was then studied in greater detail for all three monkeys by imposing the same short duration head perturbations either 40 ms, 100 ms, and 150 ms following the onset of 60 deg gaze shifts. Overall, we found a consistent trend, in which VOR suppression was maximal early in the gaze shift and progressively recovered to reach normal values near gaze shift end. However, the high variability across subjects prevented establishing a unifying description of the absolute level and time course of VOR suppression during gaze shifts. We propose that differences in behavioral strategies may account, at least in part, for these differences between subjects.
INTRODUCTION

The vestibulo-ocular reflex (VOR) operates to stabilize the visual world on our retina by producing compensatory eye movements of equal and opposite amplitudes to the head movements that we make or experience during our daily activities. Without a functional VOR, clear vision would be highly compromised when our head is moving, as for example in a car or when walking. However, in certain behavioral situations, the eye movements generated by the VOR can be counterproductive. For example, primates frequently use a combination of rapid eye and head movements (gaze shifts) to voluntarily redirect their visual axis in space. During such combined eye-head gaze shifts, the eye movement command produced by the VOR would be counterproductive; an intact drive from the VOR pathway would oppose that from the gaze shift pathway and generate an eye movement command in the direction opposite to that of the intended shift in gaze.

Although numerous groups have probed the VOR during gaze shifts, its exact status remains controversial. On the one hand, it had been originally proposed by Bizzi and colleagues that the VOR remains fully functional throughout a gaze shift (Bizzi et al. 1971; Dichgans et al. 1973; Morasso et al. 1973). Indeed, more recent experiments have provided some additional support for this idea by showing that the VOR can be fully operational (Guitton and Volle 1987; Freedman et al. 1998). On the other hand, most more recent studies have shown that the gain of the VOR is attenuated during gaze shifts (Laurutis and Robinson 1986; Pélisson and Prablanc 1986; Tomlinson and Bahra 1986; Guitton and Volle 1987; Pélisson et al. 1988; Tomlinson 1990; Tabak et al. 1996). Furthermore, recordings from Position-Vestibular-Pause (PVP) neurons, which are
believed to constitute most of the intermediate leg of the direct VOR pathway (McCrea et al. 1987; Scudder and Fuchs 1992; Cullen and McCrea 1993), show that the head velocity signal they carry is attenuated during large gaze shifts in a manner that mirrors the behavioral results described above (Roy and Cullen 1998, 2002; McCrea and Gdowski 2003). Thus, these neurophysiological studies are also consistent with the proposal that the VOR is attenuated during gaze shifts.

The conflicting observations described above could result from differences in the methodological approaches that have been utilized. For example, perturbation as diverse as electromagnetic clutches to brake the head (Guitton et al. 1984; Guitton and Volle 1987; Fuller 1983), torque motors (Tomlinson and Bahra 1986; Tabak et al. 1996; Freedman et al. 1998) or hammers (Laurutis and Robinson 1986) to “bump” the head, or whole-body rotations (Pélisson and Prablanc 1986; Pélisson et al. 1988) have been employed. Moreover, the temporal resolution of the applied perturbations has varied dramatically across studies. Neither the duration of the perturbations, their frequency content, nor the time at which they were applied can be easily compared. Such differences in timing could have important implications, given that the status of the VOR most likely has time-varying dynamics during gaze shifts. For instance, it has been proposed that: (a) the VOR is completely disconnected (gain = 0) in an “all or nothing manner” during gaze shifts (Laurutis and Robinson 1986), (b) the magnitude of VOR suppression decays exponentially during gaze shifts (Pélisson et al. 1988), (c) the VOR gain varies linearly with dynamic gaze error during gaze shifts (Lefèvre et al. 1992), and (d) VOR suppression and subsequent recovery displays a high degree of inter-subject and task specific variability (Guitton and Volle 1987).
In order to develop realistic models of gaze control, it is important to evaluate the dynamics of VOR suppression throughout gaze shifts (see recent review by Sparks 1999). Only a single published study has attempted to systematically quantify the time varying dynamics of the VOR during gaze shifts in humans (Tabak et al. 1996). These investigators probed the status of the VOR by applying head oscillations (10 –14 Hz) and torque pulses to a helmet during gaze shifts. It was argued that the magnitude of VOR suppression decays exponentially during large gaze shifts, and that in the wake of gaze shifts, the VOR gain is consistently elevated to a “supra-normal value” – that is, a gain significantly greater than that measured just prior to gaze shift onset. However, because of several technical limitations in this study, it was not possible to precisely determine the timing of VOR suppression. First, as noted by these investigators, the analysis technique applied to oscillations blurred the temporal resolution of VOR gain changes. Second, the head perturbations were of long duration (>200 ms) and were applied beginning more than 100 ms before gaze shift onset. Accordingly, it is likely that feedback pathways involved in gaze shift control, as well as the classic VOR pathways, contributed to the observed responses. Finally, head rotation was measured with a search coil mounted within a bite bar, and any slippage would have resulted in an erroneous characterization of the induced responses.

Here our primary goal was to evaluate the time course and dynamic characteristics of VOR suppression throughout gaze shifts. The time course of VOR attenuation was probed by applying very short duration perturbations to the head (20 – 30 ms) at precise time intervals before, during, and immediately following gaze shifts. Accurate measurement of head motion was ensured by firmly securing a search coil to
the monkey’s skull. In addition, analysis was limited to a very small time window not much longer than the latency of the direct VOR pathways in order to prevent feedback loop effects from biasing our interpretation. Our results demonstrate that the dynamics of the VOR gain attenuation during gaze shifts can vary between animals, but that the VOR gain is consistently restored to normal at gaze shift end.
METHODS

SURGICAL PREPARATION AND DATA ACQUISITION

Three healthy Macaque monkeys (*Macaca mulatta*) were prepared for chronic behavioral experiments. All procedures were approved by the McGill University Animal Care Committee, and were in compliance with the guidelines of the Canadian Council on Animal Care. The methods for surgical preparation of the monkeys, the experimental setup, and the techniques of data acquisition were identical to those recently described (Huterer and Cullen 2002; Sylvestre and Cullen 1999). Briefly, under general anesthesia, a dental acrylic implant was attached to each animal’s skull using stainless steel screws. A stainless steel post, to which the head coil and torque motor were rigidly coupled, was embedded within the implant. An eye coil (18-19 mm diameter, 3 loops of Teflon-coated stainless steel wire) was implanted behind the conjunctiva.

During the experiment, the monkeys were comfortably seated in a primate chair. Gaze and head movements were recorded inside a magnetic field (CNC Engineering), using the magnetic search coil technique (Fuchs and Robinson 1966). The head coil was mounted within a clear plastic mould located within 2 cm of the eye coil. Timing of behavioral paradigms, target motion, torque motor triggering, and data storage were controlled by a QNX-based real-time data acquisition system (REX) (Hayes et al. 1982). Gaze and head position signals were low-pass filtered at 250 Hz (8 pole Bessel filter), sampled at 1000 Hz, and stored on a hard drive for later analysis. Eye position was calculated from the difference between recorded gaze and head position signals.
**BEHAVIORAL PARADIGMS**

The monkeys were allowed complete freedom of head motion (in the pitch, roll, and yaw planes of head movement). Passive horizontal head perturbations were generated using a torque motor (Animatics model 2320), which was securely coupled, through precision universal joints, to a specially designed lightweight aluminum head-holder. A spring system offloaded the weight of the apparatus. Monkeys were trained to track a visual target (HeNe laser, projected onto a cylindrical screen 60 cm from the center of their head) for a juice reward. Horizontal and vertical gaze shifts of variable magnitude were elicited by having the monkeys fixate a stationary target that was then stepped across the horizontal (amplitudes: 15, 40 and 60 deg) or vertical (amplitude: 40 deg) plane. In order to minimize the occurrence of anticipatory gaze shifts, the interval of fixation prior to target stepping was randomly varied between 800 and 1500 ms.

**PASSIVE HORIZONTAL HEAD PERTURBATIONS**

High frequency, passive horizontal head perturbations were applied at intervals before, during and immediately following horizontal gaze shifts. Perturbations were identical to the ‘very short’ perturbation applied by Huterer and Cullen (2002). They had a duration of 20 – 30 ms, a peak head velocity of approximately 100 deg/sec, a peak acceleration of 10,000 - 20,000 deg/sec², and generated total head displacements ~2-4 degs. Figure 1 shows the gaze, eye and head profiles (position and velocity) for representative 15 deg (Fig. 1A), 40 deg (Fig. 1B) and 60 deg (Fig. 1C) gaze shifts; the shaded areas indicate the different intervals over which head perturbations were applied in this study.
For 15 deg and 40 deg horizontal gaze shifts the onset of head perturbation was programmed to occur at one of three different intervals as is illustrated in Figs. 1 A and B: (1) ~30 ms prior to gaze shift onset, (2) 40 ms following gaze shift initiation, and (3) <50 ms after target acquisition, during which time gaze was stable (gaze velocity < 20 deg/sec) but the head was often still moving. For 60 deg horizontal gaze shifts, the onset of head perturbation was timed to occur at one of five different intervals as is illustrated in Fig. 1C. In addition to the three perturbation intervals listed above (-30 ms, 40 ms, +50 ms), the head was also perturbed 100 ms and 150 ms following gaze shift initiation. Note, in order to program the motor to perturb the head prior to gaze shift initiation, we first determined, for each monkey, the mean latency from target stepping to gaze shift onset (Latency\textsubscript{mean}, in ms). By triggering motor perturbation onset after a fixed delay from target stepping (e.g. Latency\textsubscript{mean} – 30 ms), the head could be perturbed prior to gaze shift initiation. In contrast, perturbations applied more than 40 ms after gaze shift onset were triggered after a fixed latency from when gaze velocity exceeded a threshold value (20 deg/sec). The head was perturbed in the direction of the ongoing gaze shift (‘with’ direction) or in the direction opposite to the ongoing gaze shift (‘against’ direction). Passive horizontal head perturbations were also applied during 40º vertical gaze shifts, 40 ms following vertical gaze shift onset. For vertical gaze shifts, only rightward horizontal head perturbations were applied.

*Insert Figure 1*
We refer to trials during which the head was perturbed as *perturbed gaze shifts*. During a given experimental session, monkeys made gaze shifts of each amplitude. However, perturbations were applied for only one condition (e.g. 40 deg gaze shifts, perturbation ‘with’, 40 ms following gaze shift initiation). For horizontal and vertical gaze shifts, head perturbations were randomly applied in 20 – 25% of the trials in which a gaze shift of a given amplitude and direction was elicited. Thus the remaining 75 – 80% of the gaze shifts of this amplitude and direction were unperturbed, and are referred to as *control gaze shifts*. For each perturbation condition, as many as 70, but never fewer than 15, trials were collected. By comparing control gaze shifts with perturbed gaze shifts, we were able to isolate the VOR evoked by the perturbation during the gaze shift.

During each experimental session, passive horizontal head perturbations were also randomly applied while the monkey stabilized gaze by actively fixating an earth stationary target (hence referred to as *control perturbations*). Control perturbations were applied while the monkey’s head was stationary in space in order to evaluate the baseline VOR response on each day. Within each experimental session, as many as 40, but never fewer than 20, trials were collected. By comparing the VOR response to head perturbations applied during gaze shifts with the VOR response to control perturbations, we were able to investigate and characterize the dynamics of vestibulo-ocular reflex suppression.
DATA ANALYSIS

Horizontal and vertical gaze, eye and head position data were imported into the Matlab (The MathWorks) programming environment for analysis. These position signals were digitally filtered using a 51st order Finite-Impulse-Response (FIR) filter with a cutoff frequency of 125 Hz, and differentiated to produce velocity and acceleration traces. A custom algorithm calculated the onset ($T_{onset}$) and end-point ($T_{end}$) of each gaze shift. $T_{onset}$ was determined using a gaze velocity criterion of 20 deg/sec. To evaluate the end-point of a gaze shift, we searched for the first interval greater than 20 ms in duration for which gaze velocity was consistently <20 deg/sec; $T_{end}$ was defined as the first point of that interval. The amplitude (in degrees) and duration (in ms) of each gaze shift was measured. Student’s $t$-tests were then used to compare gaze shift amplitudes, and gaze shift durations, for perturbed versus control gaze shifts. Within each experimental session, average gaze, eye and head profiles (position and velocity) were compiled for each condition.

Analyzing perturbations during gaze stabilization

The gain of the control VOR response was determined as described by Huterer and Cullen (2002). For this analysis we used the VOR evoked by control perturbations (i.e. those that were applied during gaze stabilization, see above). Briefly, for each trial during which the head was perturbed, the gain was calculated as the absolute value of the peak eye velocity divided by the peak head velocity. The analysis was constrained to trials in which peak eye velocity occurred in a window 7 ms following peak head
velocity. Typically, peak eye velocity lagged peak head velocity by approximately 5 - 6 ms, in agreement with our previous estimate of VOR latency (Huterer and Cullen 2002).

*Analyzing perturbed gaze shifts*

Passive horizontal head perturbations applied *during* a horizontal gaze shift occurred while gaze was already rapidly moving, often at velocities greater than 500 deg/sec. Furthermore, for large amplitude gaze shifts, the head was most often already moving (with velocity >100 deg/sec) prior to head perturbation. Thus, in order to determine the components of the gaze, eye and head velocity profiles that resulted from perturbations applied during horizontal gaze shifts, we used a technique similar to the matching method employed by Tabak et al. (1996). For every individual perturbed gaze shift, we searched the set of unperturbed control gaze shifts for the trial for which the gaze velocity profile best matched that of the perturbed trial over an interval which began 10 ms prior to gaze shift onset, and ended 2-3 ms prior to perturbation onset. The ‘best-match’ control gaze shift was obtained using a least squared algorithm, and was visually verified by the experimenter. The control gaze shift was then subtracted from the perturbed gaze shift to provide an estimate of the change in head velocity produced by the perturbation (\( \Delta H \)), as well as the resultant eye and gaze velocities (\( \Delta \dot{E} \) and \( \Delta \dot{G} \), respectively) evoked by the VOR. The VOR gain was then calculated by dividing peak \( \Delta \dot{E} \) by peak \( \Delta \dot{H} \), similar to the method used for control perturbations. In order to verify the robustness of this approach, we also subtracted the ‘second best match’ trial for a subset of trials in each condition, and confirmed that the results were comparable.
Use of the matching method was only required when analyzing the response to head perturbations applied during horizontal gaze shifts. In contrast, transient head perturbations which were applied (a) prior to horizontal gaze shift onset, (b) shortly after horizontal gaze shift target acquisition, and (c) during vertical gaze shifts, occurred while horizontal gaze velocity was essentially stable. Accordingly, the VOR gain could be calculated as was done for control perturbations (see above).

Calculating VOR suppression

The mean control VOR gain was calculated for each day of experimentation (mean ± SE). Student’s t-tests were used to determine whether the VOR gain in response to perturbations applied before, during, and immediately following gaze shifts were significantly different from the mean control VOR gain. A repeated-measures linear regression analysis was used to determine whether the percent attenuation of the VOR during a specific perturbation interval varied as a function of: (a) gaze shift amplitude, and (b) the interval during which the gaze shift was perturbed.
RESULTS

The VOR responses evoked by short duration, passive horizontal head perturbations applied during fixation and applied at intervals before, during, and immediately after gaze shifts of different amplitudes were compared. Figure 2 shows representative individual head velocity profiles in response to rightward and leftward head perturbations that were applied during fixation of an earth stationary target with the head stationary in space. The shaded areas indicate the duration of each perturbation (between 20 – 30 ms, after which time head velocity returned to ~0 deg/sec). As shown in Huterer and Cullen (2002), this method resulted in very stereotyped head velocity profiles. The velocity profile of the head perturbation had frequency content approaching 80 Hz, peak head velocity ~100 deg/sec, and peak accelerations between 10,000 - 20,000 deg/sec² (see Fig. 9 in Huterer and Cullen, 2002).

During large amplitude gaze shifts, all three monkeys utilized coordinated movements of both their eyes and their head. Figure 3 shows example gaze, eye, and head velocity profiles generated during 60 deg horizontal gaze shifts (gray traces, N = 80 individual trials; black traces, averages; panels A, B and C, monkeys B, C and J, respectively). While each monkey utilized a slightly different behavioral strategy, with monkey C typically generating faster eye movements and smaller head movements than monkeys B and J (Table 1), all three subjects generated significant head movements. In general, similar observations were made for smaller amplitude gaze shifts. Note that
monkey C tended to undershoot the target. If anything, this would have biased the results in the opposite direction as we observed. Furthermore, a small catch-up movement was made several milliseconds after the original gaze shift, indicating that the monkey was indeed attentive. Thus, this hypometria was not a concern.

*Insert Figure 3 and Table 1*

Figure 4 illustrates the head velocity trajectories that were evoked by passive horizontal head perturbations (shown in Fig. 2) which were applied 40 ms following the onset of 60 deg horizontal gaze shifts (shown in Fig. 3). Perturbations resulted in very stereotyped responses for all three monkeys. This is illustrated in Fig. 4 where the perturbations were applied in the direction of (‘with’) the head motion. Similarly stereotyped responses were evoked for perturbations in the direction opposite to (‘against’) the head motion. Thus, regardless of the direction, the perturbation was easily discernible relative to the initial voluntary head motion and the head continued to move after the perturbation.

*Insert Figure 4*

**VOR ATTENUATION DURING GAZE SHIFTS**

To characterize the time course of VOR attenuation during horizontal gaze shifts, we isolated the gaze, eye and head signals associated with the response to the imposed
head perturbation. To do so, we used a technique similar to the matching method employed by Tabak and colleagues (see METHODS). Representative pairs of matched perturbed and control gaze shifts are shown in Fig. 5 for all three monkeys. Gaze, eye and head velocity profiles (gray traces, Fig. 5, A, B, and C, respectively) are plotted for 60 deg horizontal gaze shifts, perturbed ‘with’ the direction of gaze, 40 ms after gaze shift onset. Velocity profiles for the control gaze shift that best matched it over the matching interval are superimposed for each example (dashed traces). After the onset of the head perturbation, which began 3 ms after the matching interval ended, the velocity traces for the perturbed and control gaze shift began to diverge. By subtracting the control gaze shift from the perturbed gaze shift, the response to passive head perturbation was isolated. Black traces represent the perturbation-induced changes in head (Fig. 5A), eye (Fig. 5B) and gaze (Fig. 5C) velocity.

\textit{Insert Figure 5}

In Fig. 6, $\Delta G$, $\Delta E$ and $\Delta H$ profiles from Fig. 5 are replotted on the same axis for each monkey; the $\Delta H$ trace has been inverted to facilitate comparison between head velocity and induced eye velocity. Prior to head perturbation, the isolated $\Delta \dot{G}$, $\Delta \dot{E}$ and $-\Delta \dot{H}$ traces approximate 0 deg/sec, which confirms that the control and perturbed trials were comparable over the matching interval. Following the onset of the head perturbation (illustrated by the arrows in Fig. 6A), the eye began to counter-rotate after a delay of approximately 5 - 6 ms, equivalent to our previous estimate of VOR latency.
during fixation (Huterer and Cullen, 2002). For comparison, Fig. 6B shows representative gaze, eye and head velocity profiles in response to a control perturbation applied while the monkey was holding its gaze stable relative to space. The head velocity profiles induced by control perturbations (Fig. 6B) closely resemble the head velocity traces isolated from perturbed gaze shifts (Fig. 6A), and were comparable in duration (20 – 30 ms) and peak velocity (~100 deg/sec). However, for monkeys B and C the peak-to-peak gain of the compensatory eye movement induced by the applied head motion in the control condition was greater than that induced by head perturbation 40 ms into a 60 deg gaze shift. In contrast, for monkey J there was little difference in these two conditions. For the head perturbation applied during these example gaze shifts, the peak gain of the compensatory eye movement was 0.62 for monkey B, 0.57 for monkey C and 0.82 for monkey J. In contrast, control gains in response to these high acceleration perturbations were greater than unity for most animals (see also Huterer and Cullen, 2002).

By comparing the gain of eye movements induced by head perturbations during gaze shifts with the gain of eye movements evoked by the control perturbations, we calculated the percent attenuation of VOR gain using the equation:

\[
\text{\%Atten} = [1 - (\text{Gain}_{\text{perturbed trial}})/(\text{Mean gain}_{\text{control perturbations}})] \times 100 \tag{eq. 1}
\]
For example, for the data shown in Fig. 6A, the %Atten was 46%, 68% and 18% for monkeys B, C and J, respectively. The mean percent attenuation of the VOR was calculated for each gaze shift amplitude, perturbation epoch and perturbation condition across individual trials. Below we consider each perturbation epoch in sequence, beginning with perturbations applied prior to gaze shift onset.

PERTURBATIONS APPLIED ~30 ms PRIOR TO HORIZONTAL GAZE SHIFTS

The dynamics of the VOR were first characterized in response to perturbations applied 30 ms prior to horizontal gaze shifts. In general, the gain of the VOR response to head perturbations in this interval did not differ from the gain of the VOR induced by control perturbations. This is clearly illustrated by the histograms in Fig. 7, A, B and C, which show the percent attenuation of the VOR across all gaze shift magnitudes tested, for monkeys B, C and J, respectively. The response to perturbations applied ‘with’, versus ‘against’ the gaze shift are plotted separately (gray versus black bars, respectively). Regardless of the amplitude of the gaze shift, or direction of head perturbation, the VOR was not significantly suppressed (P>0.05), with two exceptions for 60 deg gaze shifts (P<0.05).

Insert Figure 7

PERTURBATIONS 40 ms AFTER HORIZONTAL GAZE SHIFT ONSET

In contrast to passive head perturbations applied prior to gaze shift onset, perturbations delivered 40 ms after gaze shift initiation occur when gaze and the eyes are
moving rapidly, often in excess of 500 deg/sec. To characterize the VOR evoked during this interval, perturbations were applied during 15 deg, 40 deg and 60 deg gaze shifts. Histograms quantifying the attenuation of the VOR 40 ms following gaze shift onset, for all gaze shift magnitudes and perturbation directions tested, are plotted in Fig 8. In general, attenuation reached significant levels in monkeys B and C, but not in monkey J. For monkey C (Fig. 8B), the gain of the VOR 40 ms into 60 deg gaze shifts was dramatically attenuated, with the maximum percent attenuation approaching 80%. As gaze shift amplitude decreased, VOR attenuation also decreased such that passive head perturbations applied 40 ms into 15 deg gaze shifts resulted in non-significant attenuation. In addition, for this monkey, the magnitude of VOR suppression was greater in response to perturbations of the head ‘against’ the concurrent gaze shift than for perturbations applied in the same direction as (‘with’) the ongoing gaze shift (P<0.01, compare black versus gray shaded bars). Monkey B (Fig. 8A) exhibited attenuation that was intermediate between monkeys C and J; attenuation was generally significant and was greater for 60 deg than 15 deg gaze shifts, but the levels of attenuation were not as striking as those seen in monkey C. Finally, for monkey J, the VOR was only slightly attenuated (between 4 – 16%) across all gaze shift magnitudes tested, but attenuation never reached significance (Fig. 8C). Interestingly, the VOR suppression in monkeys B and J did not consistently differ for perturbations applied ‘with’ versus ‘against’ the ongoing gaze redirection, as was the case for monkey C.

_Insert Figure 8_
PERTURBATIONS 100 and 150 ms AFTER HORIZONTAL GAZE SHIFT ONSET

For horizontal gaze shifts 60 deg in amplitude, the head was perturbed during two additional intra-gaze shift intervals, beginning 100 ms, and 150 ms after gaze shift onset. Note that perturbations 100 ms and 150 ms after gaze shift onset were always applied before gaze shift completion, while gaze velocity remained >20 deg/sec. In general, greater attenuation was observed during both intervals for monkeys B and C, than for monkey J. In monkey B (Fig. 9A), the VOR was significantly attenuated in both ‘with’ (38%) and ‘against’ (41%) directions when the perturbation was applied 100 ms after gaze shift onset. The VOR elicited by perturbations applied 150 ms after gaze shift onset was only attenuated in the against direction (18%). In monkey C, the magnitude of intra-gaze shift VOR suppression was highly dependent on the direction of the head perturbation (Fig. 9B). When perturbations were applied in the ‘against’ direction 100 ms and 150 ms into the gaze shift, the VOR was significantly attenuated by 55% and 44%, respectively. In contrast, when perturbations were applied in the ‘with’ direction, attenuation did not reach significant levels during either interval. Thus, consistent with the results of perturbing 40 ms following gaze shift onset (see Fig. 8B), the magnitude of VOR attenuation was greater in response to perturbations ‘against’ than ‘with’ the gaze shift (P<0.05, compare black with gray shaded bars). In monkey J, VOR responses to head perturbations applied 100 ms after gaze shift initiation were less attenuated for both perturbation directions (on average between 15 to 17%: Fig. 9C) when compared either monkeys B or C. Furthermore, head perturbations timed to occur 150 ms following gaze shift onset elicited a VOR that was not significantly attenuated, regardless of the perturbation direction.
The final epoch over which we characterized the VOR response to head perturbations was immediately following the termination of the gaze shift, where gaze had acquired target but the eye and head often continued to move in opposite directions. When the head was perturbed <50 ms following gaze shift target acquisition, the percent attenuation of VOR gain was near 0%. The histograms in Fig. 10 A, B, and C show the responses of monkeys B, C, and J, respectively. In general, the VOR response was not consistently attenuated in comparison to that elicited by control perturbations. We observed significant (P<0.05) attenuation only in three isolated cases: for one condition in monkey B and two in monkey C, when perturbations were applied ‘with’ the ongoing gaze shifts. Moreover, surprisingly monkey B showed a small but significant enhancement of the VOR when perturbations were applied immediately following larger (i.e. 40 and 60 deg) gaze shifts.

To characterize the time course of VOR suppression, we plotted the percent attenuation of VOR gain versus time from gaze shift onset for 60 deg gaze shifts (Fig.
11); included for comparison is the percent attenuation of VOR gain 30 ms before gaze shift onset, typically ~0%. The results for perturbations ‘with’ and ‘against’ are plotted separately. In each monkey, the attenuation of VOR gain generally decreased with time from gaze shift onset. First looking at monkey C, for whom the trend was most clear, the gain of the VOR was dramatically attenuated (81% and 35% for perturbations ‘against’ and ‘with’, respectively) 40 ms after gaze shift onset. The attenuation of VOR gain decreased with time from gaze shift onset (P<0.05), such that in the terminal interval following gaze shift completion, the VOR was no longer suppressed. In monkey B, attenuation peaked later than in monkey C, at 100 ms following gaze shift onset, and then similarly decreased with time. In monkey J, the attenuation of the VOR generally decreased with time from gaze shift onset; however the attenuation only reached statistical significance in one condition. Note that VOR suppression peaks earliest for monkey C. This may be due to the relatively faster gaze movement dynamics observed in monkey C (see DISCUSSION). Nevertheless, the general trend is similar for all three monkeys.

Influence of Head Perturbation on Gaze Shift Amplitude and Duration

In addition to evaluating the gain and percent attenuation of the VOR at different epochs during horizontal gaze shifts, we determined whether passive head perturbations
affected: (a) gaze shift amplitude (in degrees), and (b) gaze shift duration (in ms). Recall, that the total head displacement resulting from these perturbations was ~ 2-4 degs (see METHODS). Transient head perturbations applied before or during 15 deg, 40 deg and 60 deg gaze shifts in monkeys B and J did not have a consistent effect on gaze shift amplitude. For monkey C, perturbations in the ‘against’ direction for all gaze shift amplitudes, and perturbations in the ‘with’ direction for 60 deg gaze shifts typically influenced amplitude (P<0.05). However, the direction of the effect differed for perturbations that occurred before (decrease) versus during (increase) the gaze shift. Moreover, for all monkeys, regardless of the direction of head perturbation (‘with’ or ‘against’), perturbed gaze shifts were generally of longer duration compared to unperturbed gaze shifts (P<0.001). The increase in duration was less pronounced when perturbations were applied immediately prior to gaze shifts (monkey B: 4 ± 4 ms and 26 ± 4 ms; monkey C: 41 ± 21 ms and 47 ± 22 ms; monkey J: 35 ± 14 ms and 41 ± 19 ms, ‘with’ and ‘against’ directions, respectively), than when perturbations were applied during gaze shifts (monkey B: 7 ± 3 ms and 34 ± 4 ms; monkey C: 69 ± 17 ms and 62 ± 23 ms; monkey J: 41 ± 17 ms and 55 ± 23 ms, ‘with’ and ‘against’ directions, respectively).
**HORIZONTAL HEAD PERTURBATIONS APPLIED DURING VERTICAL GAZE SHIFTS**

In order to determine whether intra-gaze shift VOR suppression was specific to the axis of gaze redirection, passive horizontal head perturbations were also applied 40 ms after the onset of 40 deg vertical gaze shifts. We observed that head perturbations applied in a direction orthogonal to the axis of gaze redirection elicited a robust VOR that was negligibly attenuated in all animals tested. These results are illustrated in Fig. 12, in which histograms show a near zero percent attenuation of the horizontal VOR. Thus our results are in agreement with those of Tomlinson and Bahra (1986), who also found no evidence for intra-gaze shift VOR suppression in rhesus monkeys under similar conditions. Thus, the VOR consistently remained intact for perturbations made in the direction orthogonal to gaze shift.

*Insert Figure 12*

**INFLUENCE OF HEAD PERTURBATION ON SUBSEQUENT HEAD MOVEMENT DYNAMICS**

Passive head perturbations applied during horizontal gaze shifts resulted not only in a transient head deflection (coinciding with the period of time during which the motor was actively engaged), but also altered the subsequent head velocity profile in a manner that persisted throughout the duration of the gaze shift. This is illustrated for monkey C
in Fig. 13. The average head velocity profiles obtained during 60 deg control gaze shifts (gray lines) were compared to the average head velocity profiles obtained during 60 deg gaze shifts that were perturbed ‘with’ and ‘against’: (a) 40 ms into the gaze shift (Fig. 13A), (b) 100 ms into the gaze shift (Fig. 13B), (c) 150 ms into the gaze shift (Fig. 13C), (d) <50 ms after the gaze shift (Fig. 13D). We considered the head velocity profiles for perturbed versus control gaze shifts to significantly differ (gray shaded boxes) when the standard error of the means across trials did not overlap for a period of at least 25 ms (Crane and Demer 2000).

*Insert Figure 13*

When the head perturbation was applied in the ‘with’ direction, 40 ms after gaze shift initiation, we observed that subsequent to torque motor deactivation, the head velocity significantly decreased compared to head velocity during the unperturbed control gaze shift (compare black with gray line in Fig. 13A, left panel). Similarly, when monkey C’s head was perturbed in the ‘against’ direction (Fig. 13A, right panel), there was initially a sudden transient decrease in head velocity, after which the head accelerated such that the instantaneous head velocity for the remainder of the perturbed gaze shift was significantly greater than the head velocity observed during the control gaze shift (gray shaded box). Significant compensatory adjustments in head velocity were also observed after the head was perturbed later during a gaze shift; 100 ms (Fig. 13B) and 150 ms (Fig. 13C) after gaze shift onset. Analogous adjustments in head velocity were observed when the head was perturbed immediately following gaze shift completion – 50
ms after target acquisition (Fig. 13D), thus compensatory head responses were not limited to perturbations applied during the gaze shift. Qualitatively similar observations were made in monkeys B and J (not shown).
DISCUSSION

The primary goal of the present study was to evaluate the time course of intra-gaze shift VOR suppression. The status of the VOR was compared during 15 deg, 40 deg, and 60 deg gaze shifts. The amplitude of VOR suppression measured 40 ms after gaze shift onset increased with gaze shift magnitude in two monkeys, and remained fairly constant and non-significant across all gaze shift magnitudes in a third monkey (Fig. 8). In contrast, passive horizontal head perturbations applied prior to gaze shift onset (e.g. 30 ms before), as well as perturbations applied following gaze shift completion (e.g. <50 ms after), elicited a robust VOR in all monkeys (Figs. 7 and 10, respectively). The time course of VOR gain change was studied in more detail by perturbing the head during two additional intra-gaze shift intervals for 60 deg gaze shifts (beginning 100 and 150 ms after onset). We found that VOR gain was consistently most attenuated shortly after gaze shift onset, and was gradually restored to ~0% attenuation at gaze shift end. However, the high variability across subjects prevented establishing a unifying description of the absolute level and time course of VOR suppression during gaze shifts.

THE STATUS OF THE VOR DURING GAZE SHIFTS

It is generally considered that the VOR is suppressed during large gaze shifts. Our results generally support this conclusion, but show significant subject-to-subject variability in the level of suppression. Indeed, many behavioral perturbation studies, which have been carried out over the past three decades (reviewed in Guitton 1992), have clearly shown that the passive application of head movement during gaze shifts can modify the profile of the gaze movement. Accordingly, it has been argued that the VOR
is not intact during gaze shifts. In the present study, the amplitude of VOR suppression just following gaze shift onset (40 ms) increased with gaze shift magnitude in two monkeys (monkeys B and C), approaching 80% attenuation in one case. In contrast, the results from a third monkey (monkey J) were somewhat unexpected. For this monkey, the VOR was not significantly attenuated for all gaze shift magnitudes. Thus, at first glance, data from monkeys B and C appears to confirm and extend the results of these prior studies, while data from monkey J appears to contradict them.

A more critical analysis of this prior body of behavioral work, however, provides a far more temperate view of VOR modulation during gaze shifts. First, and most importantly, the results of prior behavioral studies are themselves not without controversy. The studies by Bizzi and colleagues (Morasso et al. 1972) originally suggested that VOR gain remained intact during gaze shifts, however these investigators only tested gaze shifts <40 deg in amplitude. Controversy soon followed when larger gaze shifts were probed. Guitton et al. (1984) reported VOR-like eye movements in response to head brakes, but Fuller et al. (1983) reported the absence of a compensatory response. Laurutis and Robinson (1986) and Tomlinson and Bahra (1986) then found that, in primates, the VOR was completely suppressed only when transient perturbations were applied during larger (>40 deg) gaze shifts. However, more recently, other laboratories have reported far more variable levels of VOR attenuation for gaze shifts in this range (Guitton and Volle 1987; Tabak et al. 1996; Freedman et al. 1998).

There are several possible explanations for the large variability in the results obtained across prior perturbation studies, such as important methodological differences in the type of perturbation applied (see INTRODUCTION). A first implication of this
heterogeneity is that, during braking and sudden perturbation studies, the frequency content of the perturbation would be significantly higher than during constant velocity rotations. Since the gain of the VOR was shown to differ from unity during high frequency stimulation (reviewed in Minor et al. 1999 and Huterer and Cullen 2002), the interpretation of any data from perturbation experiments therefore requires a robust estimate of the ‘intact” gain of the VOR in response to the test stimuli. A limitation of most previous studies (the study of Tabak et al. 1996 is the notable exception), but not of the present one, was the inherent assumption that the default gain of the VOR in response to the applied perturbation is unity.

A second major methodological limitation which hinders comparison across prior perturbation studies is that there was no attempt to standardize the contribution of the head motion to the gaze shifts. Furthermore, the experimental apparatus employed in many studies often interfered with the subject’s ability to perform natural head rotations during gaze shifts by imparting significant inertia to the head, and limiting head motion to a single axis of rotation (see for example, Tomlinson and Bahra 1986; Tabak et al. 1996). Thus, it is probable that in some studies head perturbations were primarily applied during gaze shifts for which head movements were relatively small, while in other studies, they were applied during gaze shifts with large head movements. This is a very likely scenario since eye-head coordination can vary greatly as a function of experimental protocol (e.g. Zangemeister and Stark 1982). Differences in head movement strategies could provide an explanation for the differences between subjects, which was seen in the present study, as well as across previous studies. On the one hand, many studies (Lauritus and Robinson 1986; Pelisson and Prablanc 1986; Pelisson et al. 1988 ) have applied head
perturbations during both eye-only saccades and combined eye-head gaze shifts, and have shown that the attenuation of the VOR is comparable in both conditions. This issue was further explored by Lefèvre (1986), who compared the gaze trajectories during gaze shifts with different head movement contributions and concluded that VOR gain is independent of head velocity. On the other hand, Tabak et al. (1996) argued that VOR suppression was well correlated with maximum head velocity, but even in this study head movement was not necessary for VOR suppression. This point is further addressed below with respect to our own data.

When compared to previous investigations, the approach used here was most similar to that employed by Tomlinson and Bahra (1986), Tabak et al. (1996), and Freedman et al. (1998). Specifically, our perturbations were most similar in type, and by extension in frequency content, to the torque motor perturbations utilized in these studies. However, all four studies support very different conclusions regarding the status of the VOR during gaze shifts. Tomlinson and Bahra (1986) used perturbations which were 100 ms in duration and reached maximum displacement within 40-50 ms, and found complete VOR suppression for large gaze shifts. In contrast, Tabak et al. (1996) used longer perturbations which were >200 ms in duration and began 100 ms preceding saccades, and found 30-40% residual VOR function. Finally, Freedman et al. (1998) observed intact VOR responses when more transient perturbations (i.e. 30 ms duration) were used. The perturbations in the present study were of comparable duration (20 - 30 ms), and thus best matched those used in this latter study. Accordingly, when viewed from this perspective, our data from monkey J could be considered to be more consistent with the literature than
are those from monkey B or C. However, it is important to note that to date, Freedman and colleagues have only published a preliminary report of these findings.

**TIME COURSE OF VOR SUPPRESSION**

Our findings regarding the time course of VOR suppression during large gaze shifts (Fig. 11) do not support prior hypotheses that (1) the VOR gain is completely disconnected throughout large gaze shifts (Laurutis and Robinson 1986; Tomlinson 1990), (2) the VOR gain decays exponentially during large gaze shifts (Pélisson et al. 1988; Tabak et al. 1996), or (3) the VOR gain varies linearly as a function of instantaneous gaze motor error (Lefevre et al. 1992). In fact, our results are most consistent with the view presented by Guitton and Volle (1987), who reported considerable inter-subject and task specific variability in the interaction between the VOR and gaze shifts. In addition, we found that the VOR gain returned to control levels immediately following gaze shift completion in 2 monkeys (monkeys C and J). However, in the third animal (monkey B), we found that the VOR gain was actually greater during this interval than for control perturbations. This result is noteworthy, since it is consistent with the findings of Tabak et al. (1996) who reported that human VOR gains are consistently elevated to a supra-normal value in the wake of gaze shifts.

As noted above and in INTRODUCTION, the difference between our results and those of other studies might also result from important technical and analytical limitations in these previous approaches. We addressed this latter consideration by designing a torque motor assembly that did not impede natural head motion, and that allowed us to apply very short duration (20 – 30 ms), high acceleration head perturbations at precisely
timed epochs. Moreover, in order to isolate the VOR response to head perturbations applied during gaze shifts, we modified the matching method technique developed by Tabak et al. (1996). In the approach originally used by these investigators, long matching intervals (beginning 50 ms before and ending 500 ms after gaze shift onset) were used, and as a result matched pairs were rare. Head perturbations were also applied before the gaze shift was underway, and thus the perturbed portion of the gaze shift was utilized in their matching algorithm. In the present study, since we used much shorter duration perturbations, we were able to match trials over a much shorter interval (i.e. beginning 10 ms prior to gaze shift onset, and ending 2 – 3 ms prior to perturbation onset) so as to ensure that our matching interval ended before the onset of the head perturbation. Thus, because the matches were computed using the interval before the head perturbation, the control and perturbed gaze shifts essentially did not differ until the perturbation was initiated.

These methodological differences, and especially the temporal properties of the perturbations / analysis, have other important implications. For example, using model simulations, Laurutis and Robinson (1986) and Galiana and Guitton (1992) have shown that through the use of feedback loops, it is possible to generate VOR-like behaviors (i.e. compensatory eye movement responses) during gaze shifts even in situations where the direct VOR pathways are deliberately disconnected. Such VOR-like responses could have confounded the conclusions of previous studies in which the status of the VOR during gaze shifts was investigated using long duration head perturbations, or analyzed over long time intervals. In our experiments, the peak head velocity induced by head perturbation occurred ~10 ms following the onset of head perturbation, and the
compensatory eye movements induced by the VOR began after a very short latency (5 – 6 ms). Therefore, we were able to limit our analysis of the VOR response to a time interval not much longer than the latency of the direct 3-neuron VOR pathway. Hence, we conclude that the short latency responses to head perturbations that we observed were primarily mediated through classical VOR pathways via interactions with the saccadic burst generator.

**NEURAL SUBSTRATE OF VOR ATTENUATION**

In previous experiments (Roy and Cullen 1998, Roy and Cullen 2002), we have recorded from individual VOR interneurons (position vestibular pause (PVP) neurons) in alert Macaque monkeys during gaze shifts. We observed that the gain of the head velocity signals transmitted by PVP neurons is reduced during gaze shifts in an amplitude dependent manner that is consistent with previous behavioral reports of VOR attenuation in humans and monkeys. Data from one of the monkeys tested in the present experiments (monkey C) comprised most the sample of PVP neurons included in these previous studies. PVP modulation in this animal was dramatically reduced immediately following gaze shift onset, gradually resumed throughout the movement, and was no longer attenuated immediately following the gaze shift. Thus, there is a striking concurrence between PVP neuronal responses and time course of behavioral VOR suppression during gaze shifts (e.g. fig. 11) in this monkey. This observation is consistent with the hypothesis that an attenuation in the activity of the direct VOR pathways during gaze shifts underlies, at least in part, the VOR suppression observed in the present study.
This hypothesis is not a new idea. We and others have previously proposed a mechanism in which the attenuation of PVP neuron discharges during gaze shifts results from inhibitory connections with the brainstem burst generator (reviewed in Roy and Cullen 1998). Here, we propose that this pathway may account for some of the behavioral differences that were observed between monkeys. For example, we have documented in the RESULTS that monkey C generated 60 deg gaze shifts that were much faster (often in excess by 200 deg/s) than those generated by either monkeys B or J. Because saccadic burst neurons during gaze shifts have discharge patterns that are roughly correlated with the gaze velocity (Cullen and Guitton 1997), we can presume that monkey C’s saccadic burst neurons discharged at higher rates than those of the other monkeys. Moreover, since saccadic burst neurons inhibit, albeit indirectly through type II neurons, PVP neuron discharges during gaze shifts (Sasaki and Shimazu 1981; Nakao et al. 1982), it follows that monkey C’s PVP neurons be more inhibited than either monkey B or J’s during large gaze shifts. Thus, if the suppressed responses of PVPs contribute to behavioral suppression, it is not surprising that monkey C’s VOR was the most attenuated during gaze shifts.

**GAZE SHIFTS METRICS**

Prior studies have also shown that perturbed gaze shifts are generally as accurate as unperturbed gaze shifts (Laurutis and Robinson 1986; Guitton and Volle 1987; Tomlinson 1990; Tabak et al. 1996). Our results similarly showed no consistent effect on gaze shift accuracy. Moreover, it has been shown that the effect of head perturbations on gaze shift duration is direction-dependent: head perturbations in the direction of the
ongoing gaze shift shorten gaze shift duration, while head perturbations in the direction opposite to the ongoing gaze shift increase gaze shift duration (Laurutis and Robinson 1986; Tomlinson 1990; Tabak et al. 1996). In contrast to these findings, we observed that transiently perturbed gaze shifts were consistently longer in duration than control gaze shifts, regardless of the direction of head perturbation. This discrepancy could arise due to the more transient nature of the perturbations in this present study compared to previous studies, or to the fact that different criteria have been used to establish the time of gaze shift completion. Although a clear criterion for determining the timing of gaze shift offset was not described in prior studies, investigators generally use a strict velocity threshold (e.g. first point where gaze velocity is less than 20 deg/sec) to mark gaze shift offset. In our study, the use of such a criterion would have been misleading, since a low velocity tail was often observed during the terminal portion of perturbed gaze shifts. Thus gaze shift offset was defined by the first point of a 20 ms interval where gaze velocity was constantly <20 deg/sec (see METHODS).

**PLANE SPECIFIC ATTENUATION**

The VOR consistently remained intact for perturbations made in the direction orthogonal to gaze shift. Overall, our results confirm and extend those of Tomlinson and Bahra (1986) who found no evidence for intra-gaze shift VOR suppression in rhesus monkeys when passive horizontal head perturbations were applied during vertical gaze shifts. In contrast, the human experiments of Tabak et al. (1996) reported the existence of VOR suppression for perturbations that were delivered in the plane orthogonal to saccades. Nevertheless, these latter investigators found that their results were compatible
with some degree of plane specificity, since the attenuation was significantly decreased in the orthogonal plane. As noted above, of these two prior studies our test stimulus was more similar to, albeit still more transient than, that employed by Tomlinson and Bahra (1986) and thus it is encouraging that our results are in agreement with those of this previous investigation. Interestingly, the head perturbations used in the experiments of Tabak et al. (1996) were substantially longer (>200 ms) and started more than 100ms before the saccade. Thus, it is possible that subjects were able to integrate information about this perturbation into their responses in this latter study. Moreover, the lack of VOR attenuation reported in this study and that of Tomlinson and Bahra is probably not due to the fact that the head movement contribution to vertical gaze shifts is generally less than that of horizontal gaze shifts (see Freedman and Sparks 1997). As was noted above, prior studies have shown significant VOR attenuation for saccades made with no head movements (e.g. Laurutis and Robinson 1986).

**GENERAL CONCLUSIONS**

The results of the present study suggest that the level of VOR attenuation during large eye-head gaze shifts varies across subjects. We used a programmable torque motor to apply the most precise temporal resolution to date, and found that VOR gain was highly attenuated in one animal, rather robust in another animal, and reached intermediate levels of attenuation in a third animal. Overall, VOR suppression was maximal early in the gaze shift and progressively recovered to normal control values near gaze shift end. However, we observed considerable variability across subjects, which precluded defining
a common function that could describe VOR suppression during gaze shifts. It is likely that differences in behavioral strategies used during gaze shifts could account, at least in part, for the variations in time courses of VOR attenuation that we observed.
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REFERENCES


FIGURE LEGENDS

**Figure 1:** (A,B,C) Velocity profiles of eye (gray curve), head (black curve), and gaze (dotted curve) movements during representative 15, 40 and 60 deg control gaze shifts. Insets show corresponding position traces. The shaded areas indicate the intervals over which head perturbations were applied in this study. Upward directed traces are in the rightward direction. Dashed horizontal lines indicate velocities of 0 deg/s. Abbreviations: H and \( \dot{H} \): horizontal head position and velocity; E and \( \dot{E} \), horizontal eye position and velocity; G and \( \dot{G} \), horizontal gaze position and velocity.

**Figure 2:** Representative head velocity profiles in response to rightward and leftward control head perturbations applied in monkey C. The shaded interval indicates the short duration of head perturbation (between 20 – 30 ms), after which head velocity returns to \( \sim 0 \) deg/s.

**Figure 3:** Representative velocity profiles during 60 deg gaze shifts for (A) monkey B, (B) monkey C and (C) monkey J. Gray curves are individual trials (N = 80), and thick black curves are averages.

**Figure 4:** Head velocity trajectories when passive horizontal head perturbations were applied 40 ms after the onset of 60 deg gaze shifts. Average head velocities are plotted in black, the individual trials that contribute to the average are plotted in gray. Perturbation applied in the direction of the ongoing gaze shift (i.e. ‘with’) for monkey B (top), monkey
Figure 5: Head (A), eye (B) and gaze (C) velocity profiles are plotted for a 60 deg gaze shift, perturbed in the ‘with’ direction 40 ms after gaze shift onset. Velocity profiles for the control gaze shift that best matched the perturbed gaze shift over the matching interval are superimposed (dashed lines). The differences between control and perturbed velocity profiles (black curves, $\Delta \dot{H}$, $\Delta \dot{E}$ and $\Delta \dot{G}$; panels A, B and C, respectively) provide the isolated response to the head perturbation. The eye response to the perturbation is indicated by the arrow in panel B.

Figure 6: (A) Representative $\Delta \dot{G}$, $\Delta \dot{E}$ and $\Delta \dot{H}$ profiles from Fig. 5 are replotted on the same axis; the $\Delta \dot{H}$ profile has been inverted to facilitate comparison between head velocity and induced eye velocity. The arrow indicates head perturbation onset, after which the eye began to counter-rotate with a latency of ~5 – 6 ms. The gain of the evoked VOR is movement is 0.62 for monkey B, 0.57 for monkey C, and 0.82 for monkey J. (B) Control head perturbations applied during gaze stabilization. Peak eye and head movements are denoted by asterisks. Mean gain $g_{\text{control perturbations}}$ is 1.2 for monkey B, 1.8 for monkey C, and 1.0 for monkey J. The values for the control gains for monkeys C and J were consistent with those reported in Huterer and Cullen, 2002.

Figure 7: (A, B, C) The percent attenuation of the VOR in monkeys B, C and J, respectively. Asterisks denote significant attenuation relative to control response
(P<0.05). The VOR gain was generally not attenuated 30 ms prior to gaze shift onset. The error bars represent standard error.

**Figure 8:** *(A, B, C)* The percent attenuation of the VOR in monkeys B, C and J, respectively. VOR attenuation 40 ms into the gaze shift increased with gaze shift magnitude in monkeys B and C, while for monkey J the VOR was not significantly attenuated for all gaze shift magnitudes. The error bars represent standard error.

**Figure 9:** *(A, B, C)* The percent attenuation of the VOR in monkeys B, C and J, respectively. VOR response to perturbations that were applied 100 ms and 150 ms after 60 deg gaze shift onset. The error bars represent standard error.

**Figure 10:** *(A, B, C)* The percent attenuation of the VOR in monkeys B, C and J, respectively. When the head was perturbed 50ms after target acquisition, the resultant VOR was not consistently attenuated in comparison to control perturbations, for any of the three monkeys. The error bars represent standard error.

**Figure 11:** To characterize the time course of VOR suppression, the percent attenuation of VOR gain versus time from gaze shift onset is plotted for 60 deg gaze shifts, when perturbations were applied ‘with’ *(A)* and ‘against’ *(B)* the ongoing gaze shift. The attenuation of VOR gain generally decreased with time from gaze shift onset, although the magnitude of attenuation varied considerably between monkey B, monkey C and monkey J. The error bars represent standard error.
Figure 12: Horizontal head perturbations were applied 40 ms after onset of 40 deg vertical gaze shifts. Perturbations applied in a direction orthogonal to the axis of gaze redirection elicited a robust VOR that was negligibly attenuated in monkeys B, C and J, respectively. The error bars represent standard error. (inset) Representative traces of vertical gaze velocity (G_v), horizontal eye velocity (E_h) and horizontal head velocity (H_h). The gray shaded trace represents a control vertical gaze shift.

Figure 13: Average head velocity profiles (for monkey C) obtained during 60 deg control gaze shifts (gray lines) were compared to average head velocity profiles obtained during 60 deg gaze shifts that were perturbed in the ‘with’ and ‘against’ directions. Perturbations were applied (A) 40 ms after gaze shift onset, (B) 100 ms after gaze shift onset (C) 150 ms after gaze shift onset, and (D) in the terminal interval of a gaze shift. Head perturbations altered head velocity profile in a manner that persisted throughout the remaining head movement (gray shaded boxes). The thick horizontal bars indicate the interval during which the head perturbation was applied.
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<td></td>
<td>% Cont.</td>
<td>Disp.</td>
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<td>% Cont.</td>
<td>Disp.</td>
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<td>Monkey B</td>
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<td>9.5 ± 4.2</td>
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<td>82 ± 7</td>
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<tr>
<td>Monkey J</td>
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<td>20.4 ± 5.3</td>
<td>144 ± 29</td>
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<td>Average</td>
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<td>66 ± 16</td>
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Legend: % Cont., percent contribution to the gaze shift; Disp., total displacement measured at gaze shift end; Peak, peak velocity; N, number of gaze shifts.
Figure 1
Figure 2
A. Monkey B  

B. Monkey C  

C. Monkey J  

Figure 3
Figure 5

A  Head Velocity

B  Eye Velocity

C  Gaze Velocity

Monkey B

Monkey C

Monkey J

100 deg/s
50 ms

500 deg/s

Matching Interval  Head Perturbation

Perturbed Trial
Control Trial
Difference (ΔH, ΔE, ΔG)
Figure 6
30ms Before Onset

A

Monkey B

Gaze Shift Amplitude

Percent Attenuation (%)

B

Monkey C

Gaze Shift Amplitude

Percent Attenuation (%)

C

Monkey J

Gaze Shift Amplitude

Percent Attenuation (%)

Figure 7
40ms After Onset

A

Monkeys B

B

Monkeys C

C

Monkeys J

Figure 8
Figure 9
50ms Following Gaze Shift

A  
Monkey B

B  
Monkey C

C  
Monkey J

Figures 10
Figure 12
A  Head Perturbed 40 ms Into Gaze Shifts
Perturbed ‘With’  Perturbed ‘Against’

B  Head Perturbed 100 ms Into Gaze Shifts
Perturbed ‘With’  Perturbed ‘Against’

C  Head Perturbed 150 ms Into Gaze Shifts
Perturbed ‘With’  Perturbed ‘Against’

D  Head Perturbed <50 ms After Gaze Shift
Perturbed ‘With’  Perturbed ‘Against’

Figure 13