The Contributions of Vestibular Signals to the Representations of Space in the Posterior Parietal Cortex

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ABSTRACT: **Vestibular signals play an important role in spatial orientation, perception of object location, and control of self-motion. Prior physiological research on vestibular information processing has focused on brainstem mechanisms; relatively little is known about the processing of vestibular information at the level of the cerebral cortex. Recent electrophysiological experiments examining the use of vestibular canal signals in two different perceptual tasks are described: computation of self motion and localization of visual stimuli in a world-centered reference frame. These two perceptual functions are mediated by different parts of the posterior parietal cortex, the former in the dorsal aspect of the medial superior temporal area (MSTd) and the latter in area 7a.**

INTRODUCTION

The vestibular system consists of two sets of organs, the otoliths and the semicircular canals. The otoliths respond to linear accelerations of the head, the canals to rotations of the head. Psychophysical studies have established that these organs play an important role in human spatial orientation.[1,2]

Our research has focused on the canal signals related to head rotation, and examines the cerebral cortical structures and representations that utilize this vestibular cue. More specifically, we are attempting to answer the following two questions: (1) Which structures in the primate cerebral cortex use vestibular canal signals to encode spatial locations of objects and the direction of an animal's self-motion? and (2) How is this information represented and combined with visual signals about self-motion and object location? It is possible that the rules for processing otolith signals at the cortical level will be similar to those we have found for processing canal signals, which are reviewed below.

It has been thought for some time that the posterior parietal cortex (PPC) processes vestibular inputs for spatial awareness. Some support for this notion comes from clinical studies of patients with parietal-lobe damage. These patients exhibit a phenomenon known as "neglect": although their early visual pathways are undamaged, they are unaware of objects and events within the contralesional field. Caloric stimulation of the contralateral

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ear with cold water (or the ipsilateral ear with warm water) can transiently reduce the patents' neglect, suggesting that vestibular signals are important in constructing spatial representations that are compromised with parietal damage.[3]

Prior electrophysiological work has identified specific areas within the PPC that receive vestibular inputs. Grusser and colleagues[4] identified what appears to be the primary vestibular sensory area in the parietal lobe of monkeys, which they named the parieto-insular vestibular cortex (PIVC). About two-thirds of the neurons in this area responded to angular acceleration of the head. They also found a small number of cells in area 7 that had vestibular-related activity.[5] In the medial superior temporal area (MST) neurons have also been found that are responsive to vestibular-canal stimulation.[6–8]

Until recently there has been relatively little work on the nature of the representation of vestibular information in the cerebral cortex. In the studies reviewed here we examine two different types of vestibular/visual interactions in two cortical areas. First we describe research on the use of vestibular-canal angular velocity signals—related to the rate at which the head turns—in conjunction with visual motion signals to estimate the direction of an animal's motion through space. These studies were performed in area MSTd. Then we will examine the use of canal signals related to the position of the head in localizing seen objects in a world-centric reference frame; these studies were performed in area 7a.

THE PROBLEM OF RECOVERING SELF-MOTION DURING GAZE ROTATIONS

Figure 1 shows an example of optical flow patterns generated while driving an automobile. The focus of the expansion (FOE) corresponds to the direction of heading. As diagrammed in FIGURE 2, however, if the eye is rotating, either due to a smooth pursuit eye movements or smooth head movements, then a laminar motion is introduced on the eyes opposite to the direction of gaze rotation. This laminar motion disrupts the focus of expansion. In the special case of approaching a wall (FIG. 2) the focus is displaced in the direction of the eye movement. However, we know from a number of psychophysical studies in humans that the true direction of self-motion can still be perceived during eye movements.[9,10] More recently we have demonstrated that correct heading perception is also recovered during gaze rotations that result from head movements in human observers.[11] In simple terms, the laminar motion field due to gaze rotation appears to be subtracted from the motions due to translation of the observer through the environment. This subtraction is afforded by an extraretinal signal since the same retinal motions that occur in the active gaze-rotation case, but without gaze rotation, lead to no compensation. In the case of pursuit, the source of this extraretinal signal is not known. However, during head movements, we have recently found that the gaze-rotation signal is derived from a combination of vestibular, proprioceptive, and efference copy sources.[11]

NEURAL CORRELATES OF HEADING PERCEPTION DURING PURSUIT EYE MOVEMENTS

The dorsal aspect of area MSTd (FIG. 3) has been found to contain neurons that are selective for motion patterns that are generated during self-motion.[12–27] Different cells are sensitive to expansions, contractions, rotations, spirals, and laminar motions. The largest fraction of cells are selective for expansions and laminar motions.[26] These different pattern selectivities appear to be anatomically organized within cortical columns.[28,29] Cells in MSTd are also active during smooth pursuit eye movements and demonstrate selectivity for pursuit direction.[19,30] Thus area MSTd has the appropriate signals for encoding self motion perception.

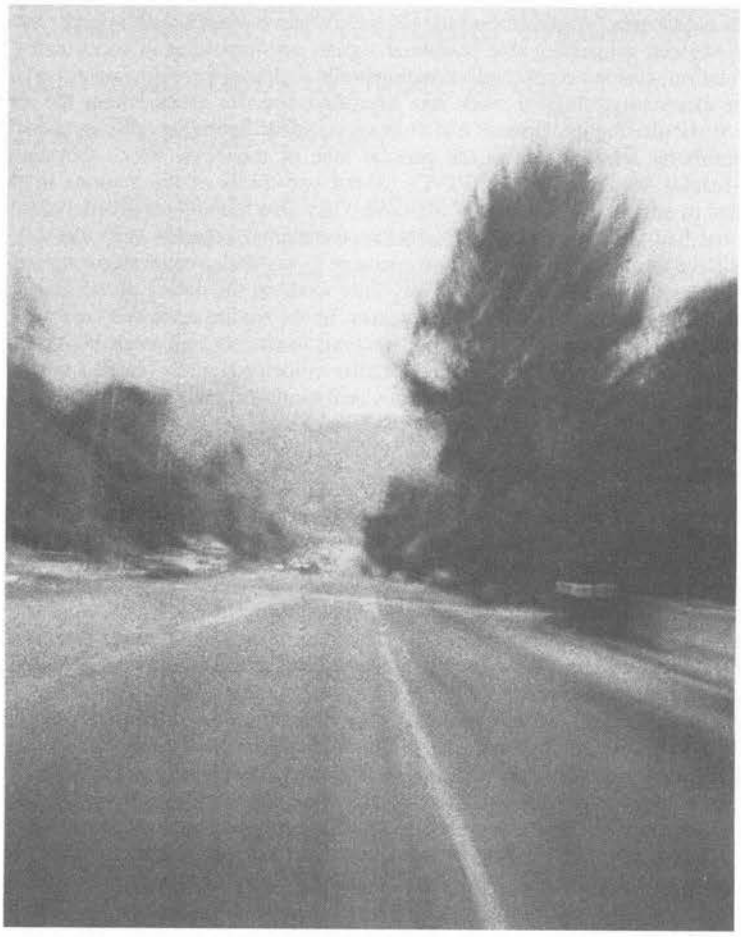

FIGURE 1. Driving down a street generates an optical flow of motion signals. Surrounding objects seem to radiate out from the focus point, expanding toward the edges of the field of vision. Processing of these complex signals occurs in area MSTd. (Photograph by David Bradley.)

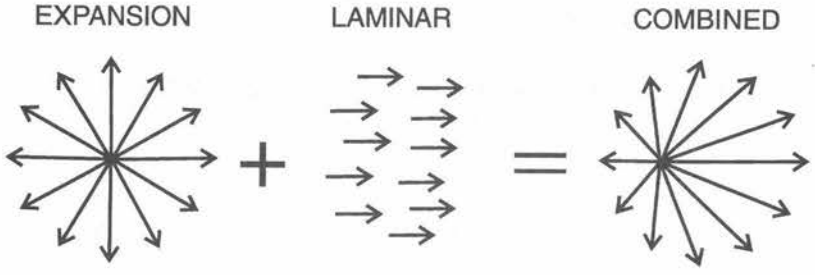

FIGURE 2. When we move forward, the visual world appears to expand. If the eyes are still, the focus position tells us our direction of heading. However, leftward eye movement adds rightward laminar flow motion to the retinal image, which shifts the focus. To recover the heading direction, we must correct for this focus shift. (From Bradley *et al.*[31] Reproduced by permission.)

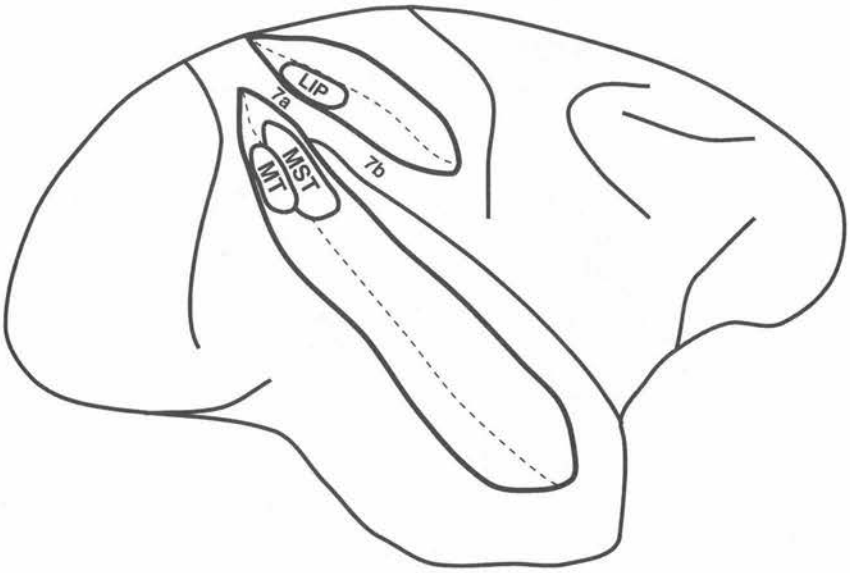

FIGURE 3. Locations of areas discussed in the text drawn on a lateral view of a macaque monkey brain. (From Andersen *et al.*[34] Reproduced by permission.)

Recently we examined the neural mechanism that allows heading direction to be recovered during pursuit eye movements.[31] Duffy and Wurtz[44] have shown that many MSTd neurons are tuned for the location of the focus of expansion. We mapped MSTd focus tuning curves when the monkeys' eyes were stationary, much as Duffy and Wurtz had done, and then again during smooth pursuit eye movements. We found that a large fraction of area MSTd neurons shift their focus tuning curves in order to compensate for the pursuit direction (see FIG. 4, upper panels). This compensation was shown to be due to an extraretinal signal related to the eye pursuit. When the same retinal image was presented on the screen that the animal experienced during pursuit eye movements, but with the eyes stationary (the so-called simulated pursuit condition), then no compensation occurred (FIG. 4, bottom panels). The source of this extraretinal signal is not known, but it could be derived from an efference copy of the eye pursuit command, or proprioceptive signals from the eye muscles and periorbital tissue. These results are very consistent with the human psychophysical results mentioned earlier, and may form the neural basis for correct self-motion perception during pursuit eye movements.

NEURAL CORRELATES OF HEADING PERCEPTION USING VESTIBULAR SIGNALS DURING GAZE ROTATION GENERATED BY HEAD MOVEMENT

Of course we often move our heads as well as our eyes when pursuing objects. This is certainly true during locomotion, where the gaze movements are often quite large in amplitude, requiring head movements. As mentioned before, recent findings from our lab indicate that gaze rotations during head movements are also taken into account to accurately perceive self-motion.[11] However, compensation only occurs if the vestibular signals are present with neck proprioceptive or efference copy head movement signals.

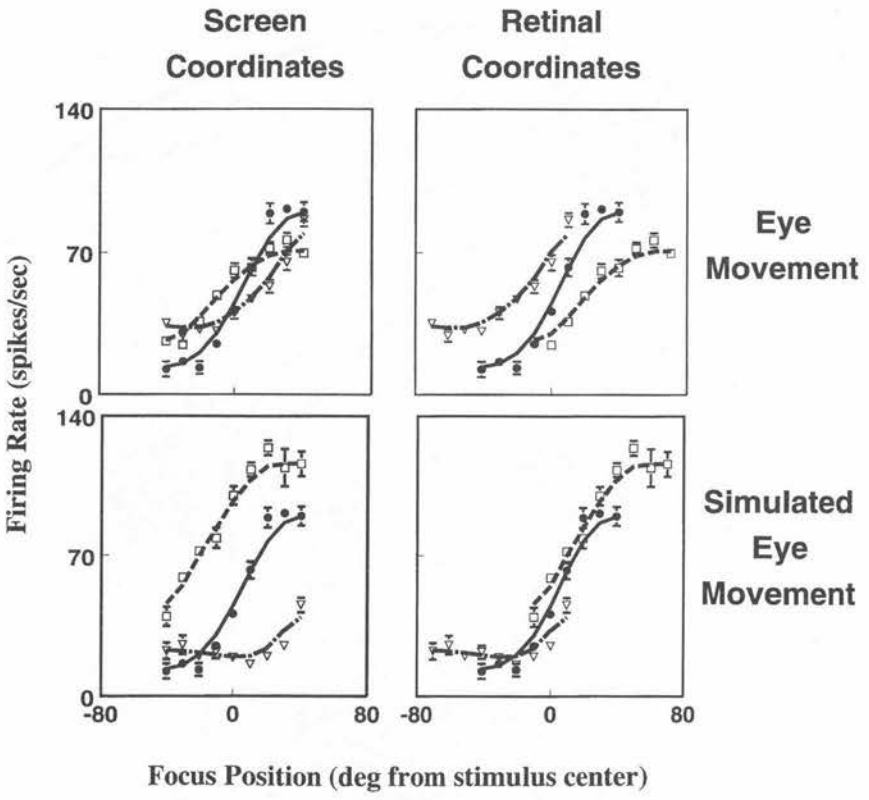

FIGURE 4. An MSTd heading cell. In all panels, the *solid lines* and *solid circles* represent fixed-eye focus tuning (identical in all four graphs), the *dashed lines* and *open squares* are preferred-direction eye movements (real or simulated), and the *dot-and-dashed lines* and *open triangles* are antipreferred-direction eye movements (real or simulated). Data in the left and right columns are identical, except that pursuit curves in the right column were shifted by 30 degrees relative to screen coordinates (thus giving retinal coordinates). The moving-eye focus tuning curves align in screen coordinates (**top left panel**), and thus encode the direction of heading. However, for simulated eye movements, the curves align in retinal coordinates (**bottom right panel**). Smooth curves are five-point moving averages of the data. Data points are shown as the mean ± SEM for four replicates, where each replicate is the mean firing during the middle 500 ms of the stimulus-presentation interval. (From Bradley *et al.*[31] Reproduced by permission.)

We have recently examined whether the focus-tuning curves of MSTd neurons show compensation during smooth head rotations where the vestibular ocular reflex is canceled (VORc). The monkeys sat in a vestibular chair, and the animal's head was fixed to the chair. In the VORc task, the chair was rotated with the fixation point moving in the world as if it was attached to the chair. To successfully pursue the target, the monkeys had to cancel the VOR, either by suppressing it, or by adding a pursuit signal in the opposite direction to cancel the reflex. Using this task, we found that a large number of area MSTd neurons were active for the direction of smooth head rotation

during VORc in the yaw–pitch plane.[32,33] This result corroborates reports of similar activity in MST.[6–8] The novel aspect of our experiment was that we then had the animals produce the gaze rotations during VORc across optic flow fields. A similar paradigm to the eye pursuit experiments was used.[31] We first mapped the focus-tuning curves of individual MSTd neurons with the eyes stationary. Next we had the animal pursue the fixation point across the optic flow displays, either with pursuit eye movements when the chair was stationary, or by canceling the VOR when the chair was moving. We found that there was similar compensation in both the eye movement and VORc conditions.[32] Moreover, cells that compensated for one condition generally compensated for the other condition, and by approximately the same amount.[33] The simulated gaze rotation condition, in which the retinal stimulation was the same as the VORc and pursuit conditions, but the eyes were stationary, produced considerably less compensation.

These results indicate that area MSTd compensates for gaze rotations regardless of whether they are produced by eye or head movements. The compensation during VORc must at some stage utilize vestibular cues. From the current experiments we do not know if compensation in MSTd is due to the direct action of vestibular signals on flow-sensitive neurons. Kawano *et al.*[6,7] and Thier and Ericksen[8] both found that rotating the animal in the dark often produced modulation of activity, but it was usually less than that seen during VORc. This result indicates that there are vestibular-canal-derived signals present in area MST, but we do not yet know if these same signals are the ones responsible for the compensation. An alternative explanation is that a pursuit signal is generated to cancel the VOR, and it is the efference copy of the pursuit command that is used for compensation. If this is the case, then it is possible that compensation during eye movements and VORc result from the same efference copy signal. Finally, it is possible that a combination of both efference copy and vestibular cues account for the VORc result.

REPRESENTING STATIC LOCATIONS IN NONRETINAL COORDINATES

The preceding experiments examined the integration of eye and head movements with visual motion for accurate spatial perception. The next set of experiments to be described examine the interaction of static eye and head position signals with static retinal signals to again produce accurate spatial perceptions of where static stimuli are located in space. An example of such a computation is the accurate reaching to an object, which can be accomplished independent of the exact retinal location of the stimulus, or the direction in which the eyes are looking.

In a series of experiments from our lab over the last decade we have examined how eye and retinal position signals are integrated in areas LIP and 7a of the posterior parietal cortex[34] (see FIG. 3). We routinely found that these cells had receptive fields with fixed retinal locations, but their activity was gain modulated by eye position[35–37] (see FIG. 5). In modeling experiments we designed neural networks that receive eye and retinal position signals and yield locations in head-centered coordinates.[38] The middle layer units that produced the transformation from retinal (at the input) to head-centered (at the output) coordinates were very similar to the PPC neurons; that is, they had retinal-receptive fields gain modulated by eye position. These modeling studies demonstrated that the cells in PPC can represent head-centered locations in a distributed manner. Thus PPC can simultaneously represent both retinal and head centered coordinates in the same population of neurons.

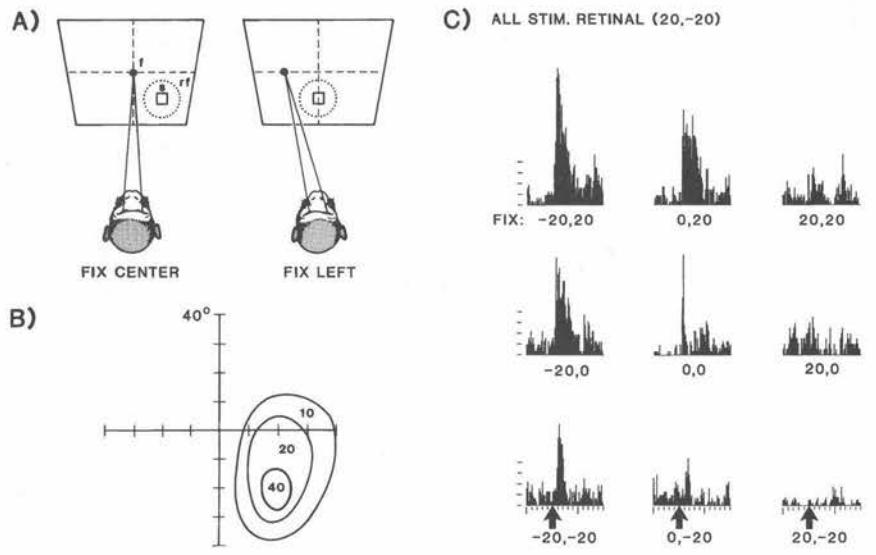

FIGURE 5. (**A**) Method of determining spatial gain fields of area 7a neurons. The animal fixates point *f* at different locations on the screen with his head fixed. The stimulus, *s*, is always presented in the center of the receptive field, r.f. (**B**) Receptive field of a neuron plotted in coordinates of visual angle determined with the animal always fixating straight ahead (screen coordinates 0,0). The *contours* represent the mean increased response rates in spikes per second. (**C**) Spatial gain field of the cell in (A). The poststimulus histograms are positioned to correspond to the locations of the fixations on the screen at which the responses were recorded from retinotopically identical stimuli presented in the center of the receptive field (histogram ordinate, 25 spikes per division, and abscissa, 100 ms per division; *arrows* indicate onset of stimulus flash) modified from Andersen *et al.* [36]

HEAD-POSITION GAIN FIELDS

To go back to our example of accurate reaching, eventually the brain must know where the object is with respect to the hand to make an accurate reaching movement, a computation that requires information about head and limb position as well as eye and retinal position. Thus we next addressed how head position might influence the activity of PPC neurons. To examine this issue we trained monkeys to orient their direction of gaze to different locations with respect to their bodies, by either making eye or head movements. For instance, we would have them look 20 degrees to the left by having them move their heads to the left, or by moving their eyes to the left with the head straight forward. In the former case, the eyes are straight ahead in the orbits, and in the latter the eyes are deviated to the left in the orbits. For many cells in both areas LIP and 7a we found gain fields for head position.[39] The cells demonstrating head-position gain fields also had eye-position gain fields, and the gain modulation functions were the same for head and eye. An example is shown in FIGURE 6. For this neuron, when the monkey looked more to the right, the activity increased for the same retinal location of stimulation (and same saccade) regardless of whether the head (FIG. 6A) or the eye (FIG. 6B) was used to orient the gaze position. The graph of the mean firing rates in the two conditions in FIGURE 6C illustrates that the gain functions for head and eye position for this cell were virtually identical. This similarity between eye and head gain fields was found for the population of cells examined in this study, showing that this category of neurons is modulated by gaze direction, independent of whether that gaze direction is produced by orienting the head or the eyes.

VESTIBULAR CONTRIBUTIONS TO HEAD-POSITION GAIN FIELDS

As with the flow experiments, the head gain fields could be derived from vestibular, neck proprioceptive, or efference copy signals. An interesting distinction can be made between the vestibular source and the other two sources in terms of frame of reference. A vestibularly derived gain would require the integration of a vestibular velocity signal to code head position. This integrated signal would indicate the orientation of the head in the world. On the other hand, the neck proprioceptive signals would likely indicate the orientation of the head on the body. Thus vestibular gain fields would be useful for representing locations of stimuli in world coordinates, whereas neck proprioceptive gain fields would be useful for representing locations in body-centered coordinates.

We have recently begun to address whether vestibular or neck proprioceptive signals contribute to the head gain fields we see in PPC. The vestibular contribution was tested by rotating the entire animal on a vestibular turntable, with the head always straight ahead with respect to the body. Neck proprioceptive contributions were tested by changing the orientation of the body with respect to the head, with the head always in the same orientation with respect to the recording room. The results were extremely interesting. Although one potential outcome of the experiments would have been that both vestibular and neck proprioceptive signals could contribute to the gain fields of single neurons, this was rarely found. Cells generally had gain fields only for one of the two manipulations.[40,41] Even more interesting was the finding that the type of gain field was segregated by cortical area. Area 7a was found to have predominantly vestibularly derived gain fields, whereas area LIP had primarily neck gain fields. This segregation makes sense in terms of the outputs of these two areas. Area 7a projects to the presubiculum and parahippocampal gyrus, and both these structures are closely associated with the hippocampal formation. The finding of "place cells" in this area in rats suggest that at least one important reference frame used by the hippocampus is world-centered.[42] The outputs of LIP are to eye movement centers. Given that shifts in gaze direction are often combined with head and even trunk movements, it is perhaps not surprising to see gain fields consistent with a body-centered reference frame.

CONCLUSIONS

The studies discussed demonstrate that vestibular information is used by the PPC for the perception of self-motion and the spatial location of objects in body and world reference frames. No doubt vestibular cues also contribute to a number of other spatial functions in PPC. Until recently[43] work on vestibular functions in PPC has centered on canal, and not otolith, signals. Otolith signals may be used by parietal areas to perceive orientation with respect to gravity and the perception of linear translation.

Vestibular gain fields may be a common method for integrating the vestibular modality with other senses such as vision. For instance, even in MSTd, many of the cells that did not show compensation did have gain modulation by vestibular inputs.[32] It has been proposed that similar eye pursuit gain-modulations in MSTd may be an intermediate step to the shifting focus-tuning curves that are seen for many cells.[31] Similarly, the vestibular gain-modulated non-shifting fields may be an intermediate step to the cells which show shift compensation under the VORc condition.[32]

Of course, the findings reviewed herein are probably just the tip of the iceberg in terms of the influence that vestibular signals have on cerebral cortical processing. No doubt the questions being asked at the cortical level will be very different from those asked at the brainstem level. Whereas research at lower levels have been concerned with motor control, adaptation, learning, and vestibular motor reflexes, future experiments at the cortical level will probably be most successful in examining perceptual and cognitive processes related to vestibular function. This relatively new field of cortical vestibular research should provide a rich and interesting area of inquiry in the years to come.

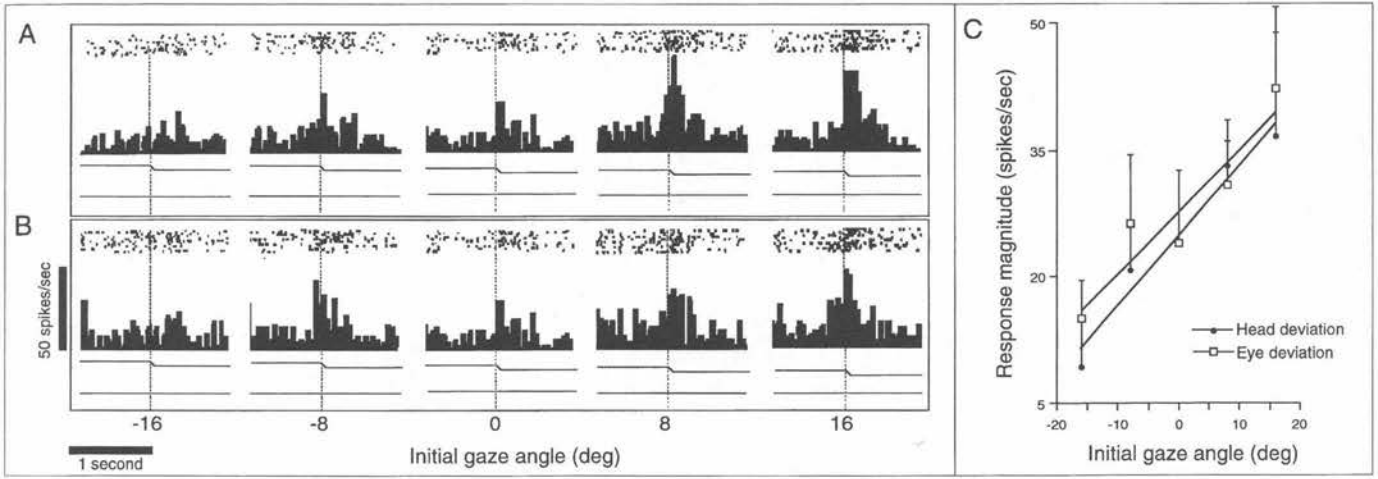

FIGURE 6. Activity of a cell while the monkey is making identical saccades to the left from a fixation point placed at five different gaze positions on the horizontal plane. All trials are aligned with the onset of the saccade, indicated by the *vertical broken lines*. (**A**) The animal has its head oriented toward each of the fixation points, with the eyes centered in their orbits before each saccade. (**B**) The head of the animal is directed toward the center of the screen, with the eyes deviated toward each of the fixation points before each saccade. (**C**) Magnitude of the cell's activity around the time of the saccade (25 ms before to 75 ms after onset of the saccade) as it varies with initial gaze position. *Bars* indicate one standard error. A linear relationship of activity with gaze direction was confirmed by a significant linear regression and by a nonsignificant analysis of variance of the regression residuals. (From Brotchie *et al.*[39] Reproduced by permission.)

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