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A Dynamical Model of Context Dependencies for the Vestibulo-Ocular Reflex

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Abstract

The vestibulo-ocular reflex (VOR) stabilizes images on the retina during rapid head motions. The gain of the VOR, i.e. the ratio of eye to head rotation velocity, measured with the eyes focused at a distance is typically around -1. However, to stabilize images accurately, the vestibulo-ocular reflex response must be modulated by the context in which the response takes place. The context studied in this paper includes eye position, eye vergence and head translation. We first describe a kinematic model of the vestibulo-ocular reflex response given rotational and translational information of the head motion. We then show how the model can be modified to rely solely on sensory information available from the semicircular canals (head rotation), the otoliths (head translation), and neural correlates of eye position and vergence angle. We then suggest a dynamical model and compare it to the eye velocity responses measured in monkeys (Snyder and King, 1992). The VOR response is nearly identical to an ideal theoretical response taking into account sensory input delays. The model captures the dynamical modulation of the VOR for this context. It defines which neural signals should be combined and suggests one possible way to perform the required computations in time. It therefore provides a theoretical explanation for the sensitivity of neurons to multiple inputs (head rotation and translation, eye position, etc.) in the pathways of the VOR.

1 Introduction

The vestibulo-ocular reflex stabilizes images on the retina during rapid head motions: Rotations and translations of the head in three dimensions must be compensated by appropriate rotations of the eye. The compensatory eye movement produced by the reflex is quite complex and depends on different inputs. Because the head's rotation axis is not the same as the eye's rotation axis, the calculations for proper image stabilization of an object must take into account diverse variables such as object distance from each eye, gaze direction, and head translation (Viire et al., 1986; Hine and Thorn, 1987). The stabilization is therefore achieved by integrating information from different sources: head rotations from the semicircular canals of the inner ear, head translations from the otolith organs, eye positions, viewing distance, as well as other context information, such as posture (head tilts) or activity (walking, running) (Snyder and King, 1992; Snyder, Lawrence and King, 1992; Sargent and Paige, 1991; Paige and Tomko, 1991a; Shelhamer, Robinson and Tan, 1992; Tiliket et al., 1993; Baker, Wicland and Peterson, 1987; Grossman et al., 1989). The response of the vestibulo-ocular reflex is therefore "rapidly modulated" by inputs other than head rotation, i.e. by the context of the response. We use this term to contrast it with the slower adaptation of the reflex that requires hours and days within a particular sensory context.

In this paper we concentrate on the immediate context modulation of the vestibulo-ocular reflex which can be described by studying the kinematics of the reflex. The immediate context includes eye position, eye vergence and head translation.

2 The Vestibulo-Ocular Reflex: Kinematic Model

The ideal vestibulo-ocular reflex response is a compensatory eye movement which keeps the image fixed on the retina for any head rotations and translations. We therefore derived an equation for the eye rotation velocity by requiring that a target stays stationary on the retina. The velocity of the resulting compensatory eye rotation can be written as:

$$\vec{\omega} = -\vec{\Omega} + \frac{\hat{g}}{|g|} \times \left[(\vec{e} - \vec{a}) \times \vec{\Omega} - \vec{T} \right] \tag{1}$$

where $\vec{\Omega}$ is the head angular velocity, $\vec{T}$ is a head linear (translation) velocity vector, $\vec{e}$ is a constant eye position vector, $\hat{g}$ and $|g|$ are the unit vector and amplitude of the gaze vector, and × indicates the cross-product between two vectors. This relation holds when $\vec{\Omega}$ and $\vec{T}$ are measured at the axis of rotation. A diagram showing the definition of the vectors is shown in fig. 1. $\vec{e}$ is a constant vector specifying the position of one eye in the head; $\vec{a}$ gives the position of the axis of the head rotation; $\hat{g}$ gives the orientation of the eye relative to the head, and $|g|$ gives the distance from the eye to the object whose image $\vec{\omega}$ stabilizes. Since $\vec{e}$ and $\vec{g}$ are different for the two eyes, $\vec{\omega}$ is also different for the right and left eye; the $\vec{\omega}$ for each eye become equals when the target is at infinity (more than one or two meters in practice).

$\vec{\omega}$ and $\vec{\Omega}$ are rotation vectors which describe the instantaneous angular velocity of the eye and head, respectively. A rotation vector lie along the instantaneous axis of rotation; its magnitude measures the speed of rotation around the axis, and its direction is given by the right-hand screw rule, so that the rotation vector is perpendicular to the plane in which the rotation lies.

Any arbitrary rotation of the head $\vec{\Omega}$ is sensed as the combination of a rotation velocity $\vec{\Omega}_c$ measured by the semicircular canals and a translation velocity $\vec{T}_o$ sensed by the otoliths. It is known in mechanics that any rotation can be accurately described at a point of reference away from its axis of rotation as the combination of a translation and a rotation. This means that an arbitrary rotation with its axis away from one ear always induces a signal in both the otoliths and the semicircular canals, i.e. that these sensors together report both

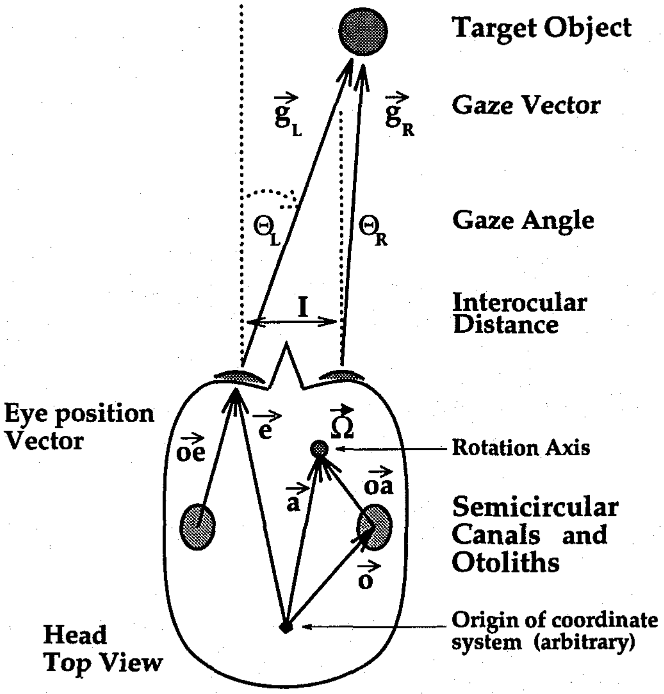

Figure 1: Diagram showing the definition of the vectors used in the equation of the kinematic model of the vestibulo-ocular reflex. Although the equation is valid for arbitrary vectors in three dimensions, all vectors are shown in a plane for simplicity. Note that the choice of origin for the coordinate system is arbitrary. There are three semicircular canals (horizontal, anterior and posterior), and two otolith organs (utricular and saccular maculae) on each side of the head shown here together as shaded areas. The semicircular canal neural afferents encode essentially the head angular velocity in the plane of the canals. The utricular and saccular macula encode respectively linear head movements (translations) in the horizontal and vertical head planes.

a translation and a rotation of the head. The translation velocity vector as measured by the otoliths is in general

$$\begin{aligned} \vec{T}_{o_j} &= \vec{T}_{rotation} + \vec{T} \\ \vec{T}_{o_j} &= (\vec{a} - \vec{o}_j) \times \vec{\Omega} + \vec{T} \\ \vec{T}_{o_j} &= \vec{oa}_j \times \vec{\Omega} + \vec{T} \end{aligned} \tag{2}$$

where $\vec{oa}_j \equiv (\vec{a} - \vec{o}_j)$; $\vec{a}$ is the position vector of the axis of rotation, $\vec{o}_j$ is the position of either the left or right otolith, and $\vec{T}$ is the head translation vector. The compensatory eye velocity using the sensory information of the canals and the otoliths become:

$$\vec{\omega} = -\vec{\Omega}_c + \frac{\hat{g}}{|g|} \times \left[(\vec{e} - \vec{o}_j) \times \vec{\Omega}_c - \vec{T}_{o_j} \right] \tag{3}$$

Defining $\vec{oe}_j \equiv \vec{e} - \vec{o}_j$,

$$\vec{\omega} = -\vec{\Omega}_c + \frac{\hat{g}}{|g|} \times \left[\vec{oe}_j \times \vec{\Omega}_c - \vec{T}_{o_j} \right] \tag{4}$$

Note that $\vec{\omega}$ written this way has the same value whether the left or right otolith (j = left or right) information is used.

Making the reference to each eye (i = left or right) explicit, the equation becomes:

$$\vec{\omega}_i = -\vec{\Omega}_c + \frac{\hat{g}_i}{|g_i|} \times \left[(\vec{e}_i - \vec{o}_j) \times \vec{\Omega}_c - \vec{T}_{o_j}\right] \tag{5}$$

A special case which has been most studied in the literature is the case where the gaze is horizontal and the rotation is vertical. It may be easier to see what happens for this case by writing the equation with dot products. Since $\hat{g}$ and $\vec{\Omega}_c$ (or $\vec{\Omega}$) are then perpendicular, the first term of the following expression in brackets is then zero:

$$\vec{\omega} = -\vec{\Omega}_c + \frac{1}{|g|}\left[\overrightarrow{oe}(\hat{g} \cdot \vec{\Omega}_c) - \vec{\Omega}_c(\hat{g} \cdot \overrightarrow{oe}) - \hat{g} \times \vec{T}_o\right] \tag{6}$$

or

$$\vec{\omega} = -\vec{\Omega} + \frac{1}{|g|}\left[(\vec{e} - \vec{a})(\hat{g} \cdot \vec{\Omega}) - \vec{\Omega}\{\hat{g} \cdot (\vec{e} - \vec{a})\} - \hat{g} \times \vec{T}\right] \tag{7}$$

The semicircular canals decompose and report the rotation of the head $\vec{\Omega}$ by its components along the three canals on each side of the head $\vec{\Omega}_c$: horizontal, anterior and posterior. The canals work in a push-pull manner. An horizontal rotation towards the left (ipsilateral) side increases the left (ipsilateral) horizontal canal afferents activity and decreases the right (contralateral) afferents. (Simpson and Graf, 1985) The two otolith organs on each side report the dynamical inertial forces generated during linear motion (translation) in two perpendicular plane, one vertical and the other horizontal relative to the head. Here we assume that a translation velocity signal ($\vec{T}_o$) derived from or reported by the otolith afferents is available. The otoliths encode as well the head orientation relative to the gravity vector force which we didn't include in this study. (Paige and Tomko, 1991a; Fernandez and Goldberg, 1976; Corey and Hudspeth, 1983; Melvill Jones, 1991)

To complete the correspondence between the equation and a neural correlate, we need to precise a physiological form for $\hat{g}$ and $\frac{1}{|g|}$. $\hat{g}$ is assumed to be given by the output of the velocity-to-position transformation or so-called "neural integrator" which provides eye position information and which is necessary for the activation of the motoneuron to sustain the eye in a fixed position. The integrator for horizontal eye position appears to be located in the nucleus prepositus hypoglossi in the pons, and the vertical integrator in the midbrain interstitial nucleus of Cajal. (Tweed, Misslisch and Fetter, 1994; Crawford, Cadera and Vilis, 1991; Cannon and Robinson, 1987; Cheron and Godaux, 1987; Tweed and Vilis, 1987). The distance from eye to target $\frac{1}{|g|}$ can be written using the gaze angles in the horizontal plane of the head:

$$\text{Right eye:} \quad \frac{1}{|g_R|} = \frac{\sin(\theta_R - \theta_L)}{I\cos(\theta_L)} = \frac{1}{I}\sec(\theta_L)\sin(\theta_R - \theta_L) \tag{8}$$

$$\text{Left eye:} \quad \frac{1}{|g_L|} = \frac{\sin(\theta_R - \theta_L)}{I\cos(\theta_R)} = \frac{1}{I}\sec(\theta_R)\sin(\theta_R - \theta_L) \tag{9}$$

where $(\theta_R - \theta_L)$ is the vergence angle, and I is the interocular distance; the angles are measured from a straight ahead gaze, and take on negative values when the eyes are turned towards the right. Within the oculomotor system, the vergence angle and speed are encoded by the mesencephalic reticular formation neurons (Judge and Cumming, 1986; Mays, 1984; Mays et al., 1986). The nucleus reticularis tegmenti pontis with reciprocal connections to the flocculus, oculomotor vermis, paravermis of the cerebellum also contains neurons which activity varies linearly with vergence angle (Gamlin and Clarke, 1995). It is therefore possible to perform the computations needed to obtain an ideal vestibulo-ocular reflex response with information know to be available physiologically.

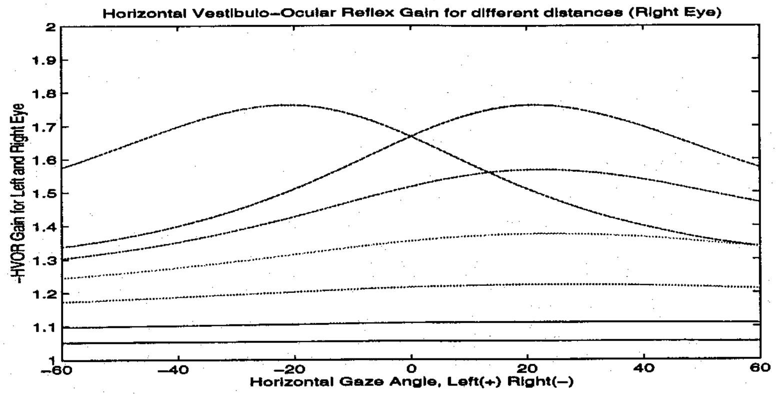

Figure 2: The horizontal vestibulo-ocular reflex gain is shown as a function of horizontal gaze angle for different distances of focus. The left curve shows the gain for the left eye at a distance of 7.5 cm. Starting from the top right of the figure, the set of curves show the gain for the right eye for the following distances: 7.5, 10, 15, 25, 50 and 100 cm. The distance is calculated from the eyes.

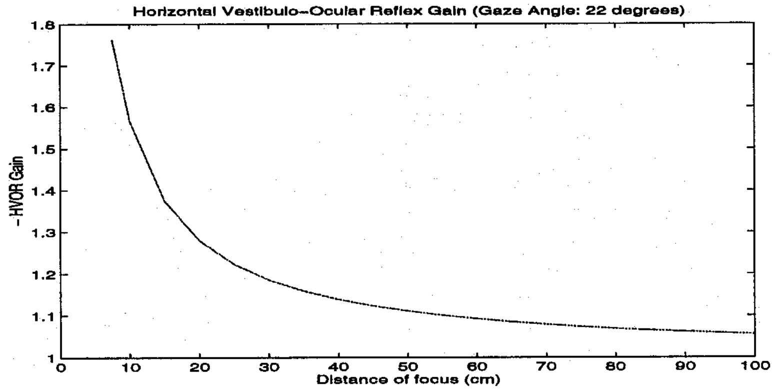

Figure 3: The horizontal vestibulo-ocular reflex gain is shown as a function of distance of focus for a gaze angle of 22 degrees.

The equations that we just described summarize succinctly the modulation of the vestibulo-ocular reflex response which has been observed in humans and monkeys (Snyder and King, 1992; Viire et al., 1986; Paige and Tomko, 1991a; Paige and Tomko, 1991b). It describes different eye velocities with target eccentricity (fig. 2), the inverse distance modulation (fig. 3), the effect of the location of the axis of rotation, and the relation between translation and gaze direction. It therefore does well what it was derived to do: describe the spatial relationship between the different elements of the vestibulo-ocular reflex.

3 Dynamical Model

We add dynamics to the inputs of the model to explain the temporal modulation observed in monkeys when tested with different target distances and positions of the axis of rotation (Snyder and King, 1992).

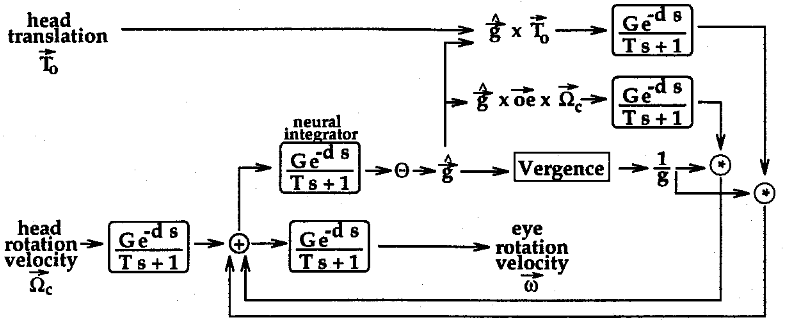

Figure 4: The dynamical model of the vestibulo-ocular reflex used to fit the experimental data shown in fig. 5 and 6 . Only the left side is shown for simplicity. The right side is identical, and connects to the left for the calculation of the vergence angle. Θ represents the angle of rotation in the horizontal plane defined by the horizontal canals. G represents a gain, d a delay, and T a time constant. The matrix transformation from the rotation angle Θ to the gaze direction $\hat{g}$ is not shown for clarity. The rotation matrix is determined by Θ and acts on a unit gaze vector representing the "primary position" (straight ahead gaze). All gains G were 1, except two: head rotation gain was -1, and neural integrator gain $G = T =$ 20s (Robinson, 1981). d and T were variable parameters of the model. Interocular distance I was 3 cm, and an otolith organ was located 5.5 cm directly behind each eye (Snyder and King, 1992).

The dynamical model is presented in fig. 4. For clarity only one eye velocity is shown in the figure even though the other is required to calculate the vergence angle. We modeled the dynamic components of the equation with a time delay and a time constant. Using Laplace transform notation the output response is :

$$e^{-\text{Delay}\, s}\frac{\text{Gain}}{Ts+1} \times \text{Input}(s) \tag{10}$$

where T is a time constant. There is a delay and a time constant for: 1) The semicircular canal response to head rotation velocity. 2) The eye rotation velocity. 3) The neural integrator. 4) The $\hat{g} \times \vec{oe} \times \vec{\Omega}_c$ term in the equation. 5) The otoliths head translation contribution to eye velocity, the term $\hat{g} \times \vec{T}_{o_j}$.

We digitized the data available in Snyder and King, 1992 and fitted the dynamical model to the data. The result is shown in fig. 5 and fig. 6. After multiple unsuccessful trials with different optimization techniques, we found that the closest fit was obtained by setting manually all time constants to 1 ms and the time delays to: 5 ms for the canals, 22 ms for the otoliths, 5 ms for the integrator, 2 ms for the term $\vec{oe}$, and 4 ms for the eye.

4 Discussion

The dynamical model captures the data very well, especially when considering that only the time delays were adjusted. The time constants were set to a minimal value, giving a direct feedthrough of the delayed inputs. This indicates that the VOR response is very close to ideal. It also could indicate that the results of the neural computations are made available quickly with very little build up time.

The oscillations and the faster rise to a peak velocity that can be seen in fig. 6 may indicate 1) that the VOR is slightly closer to an ideal response than the one obtained with the present delayed model, and 2) that a better fit might be obtained with a higher order model. The ideal response has no delays, so that the eye velocity increases earlier, and a higher order model could give the sharper corner observed at the peak velocity in the data. The peak velocity in the data is actually higher than the final one in the model. This might be useful to compensate for the delays and to put back the eyes on target as fast as possible. It would be necessary

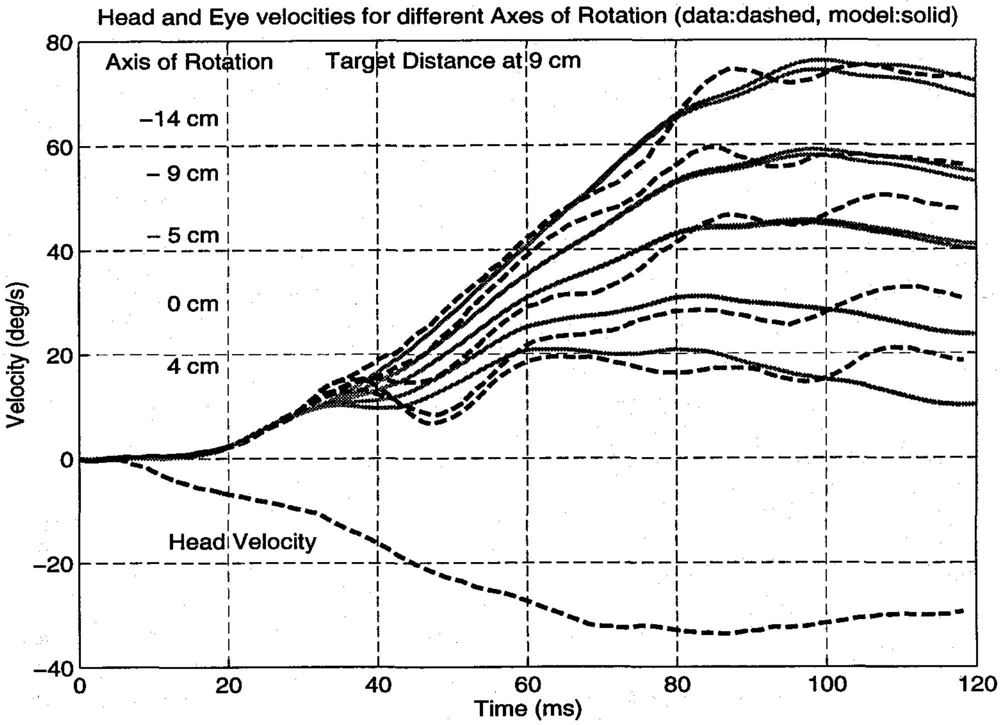

Figure 5: Comparison between the dynamical model and monkey data. Eye velocity responses (positive values) to an abrupt head rotation (negative values) are shown as a function of time for different locations of the axis of rotation. The axis is located along the midsagittal plane behind (negative values) or in front (positive values) of the eyes. The target was located at 9 cm in front of the eyes.

to compare by how much the eyes stray from target due to the response delay to find out if the apparent velocity overshoot is meaningful.

By fitting the dynamical model to the data, we tested the hypothesis that the vestibulo-ocular reflex response is close to ideal once the time constraints imposed by the sensory inputs and the neural networks performing the computations are taken into considerations. We do not suggest that the neural networks implement directly the matrix and vector computations that we used in the model. We merely suggest that since the vestibulo-ocular reflex has a response close to ideal, the neural networks must compute a solution very similar to the one in this model. Mathematically, the matrix and vector representation is only one way to describe the computations involved. Other representations exist such as the quaternion representation which has been studied in the context of the saccadic system (Tweed and Vilis, 1987). Actually any group representation of the three dimensional rotation operator could be used, but the most relevant one would certainly be the group representation of the rotation and translation operators restricted by the symmetry transformations of the canals and otoliths (Hamermesh, 1962). This conjecture still needs to be proven.

The question of how the central nervous system learns the transformations that we described still remains. Our hypothesis is that the cerebellum is one site of learning for these transformations, and that its output modulates the vestibulo-ocular reflex response in real time depending on the context. This view is compatible with the results of Angelaki and Hess, 1995 which indicate that the cerebellum is required to perform

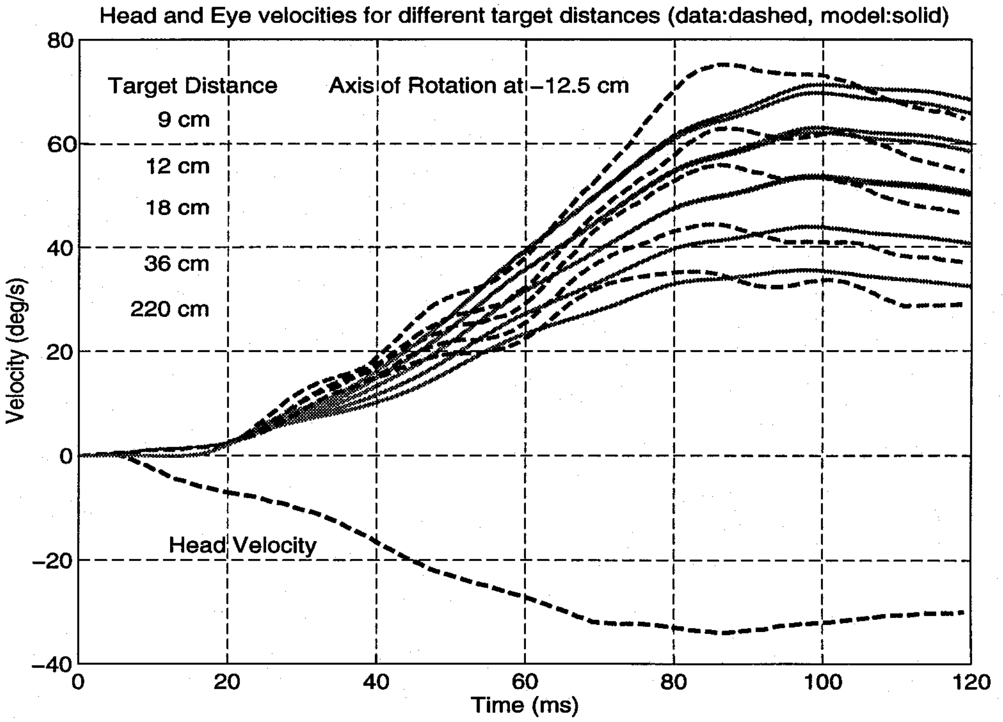

Figure 6: Comparison between the dynamical model and monkey data. Eye velocity responses (positive values) to an abrupt head rotation (negative values) are shown as a function of time for different target distances. The axis of rotation was located 12.5 cm behind the eyes.

correctly an otolith transformation. It would also be consistent with adaptation results in the VOR (e.g. Pastor, de la Cruz and Baker, 1994; Lisberger et al., 1994) To test this hypothesis, we have been working on a model of the cerebellum which learns to anticipate sensory inputs and feedbacks, and use these signals to modulate the vestibulo-ocular reflex response. The learning in the cerebellum and vestibular nuclei is mediated by the climbing fibers which report a reinforcement signal of the error. (Coenen and Sejnowski, in preparation)

5 Conclusion

We have proposed a kinematic model of the vestibulo-ocular reflex which succinctly describes its immediate context modulation, and suggest ways in which different sensory signals may be combined to obtain an optimal response. The dynamical model shows how the oculomotor system may integrate sensory inputs and estimate quantities necessary for the computation as they become available.

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