7.1 Introduction

Each of the four signals recorded from a search coil is the RMS of a precision rectified signal from one of the induction coils (see section 5.2b). The mathematical processes for converting these signals into representations of angular position and velocity in three dimensions, for both the eye and head, are described in this chapter. The axis-angle form, with units of degrees, was chosen to represent angular positions (Schnabolk and Raphan 1994; Raphan 1997, 1998), although the position data from the second study were represented as rotation vectors (Haustein 1989; Haslwanter 1995) in the original descriptive studies (Thurtell 1997; Thurtell et al. 1999). Velocity vectors, with units of degrees per second, were chosen to represent angular velocities (Haslwanter 1995).

Following data acquisition, all files were copied to the hard disk of a DECstation 5000/240 operating under the Ultrix system for off-line analysis. The files, initially in LabVIEW format, were divided into their separate BINARY channels and then converted into ASCII format, using C programs\(^1\). The programs for converting the data into axis-angle form and velocity vectors were custom written in Splus, a statistical analysis and display package (Becker et al. 1988). Further analysis and display of the data was also carried out using custom written Splus programs. The model was implemented using the Microsoft Visual C/C++ programming environment\(^2\). There is a short section describing how the model was developed at the end of the chapter, as relevant to the present study. All components of the model have been previously described in the literature (Schnabolk and Raphan 1994; Raphan 1998; Yakushin et al. 1998; see sections 4.3 and 4.5).

\(^1\)Written by Dr. T. Haslwanter.

\(^2\)Written by Prof. T. Raphan, Dr. C. Schnabolk, and Dr. M. Kunin.
7.2 Scaling the Data

Transformation of an object is taken to include rotation, translation, and stretching of the object. A $4 \times 4$ matrix may be used to simultaneously describe each of these transformations exerted on the object (Paul 1981). As translations of the head and left eye were negligible, and stretching was avoided, rotation was the only transformation of interest in this series of studies. A $3 \times 3$ matrix was therefore sufficient to describe transformations of the head and left eye.

The rotation of an object about the $z$-axis of a coordinate frame by an angle $\theta$ may be described by the rotation matrix

$$R(z, \theta) = \begin{bmatrix} \cos \theta & -\sin \theta & 0 \\ \sin \theta & \cos \theta & 0 \\ 0 & 0 & 1 \end{bmatrix}$$

Likewise, the rotation of an object about the $y$-axis of a coordinate frame by an angle $\phi$ may be described by the matrix

$$R(y, \phi) = \begin{bmatrix} \cos \phi & 0 & \sin \phi \\ 0 & 1 & 0 \\ -\sin \phi & 0 & \cos \phi \end{bmatrix}$$

Finally, the rotation of an object about the $x$-axis of a coordinate frame by an angle $\psi$ may be described by the matrix

$$R(x, \psi) = \begin{bmatrix} 1 & 0 & 0 \\ 0 & \cos \psi & -\sin \psi \\ 0 & \sin \psi & \cos \psi \end{bmatrix}$$

The order of the three base rotations describing a three-dimensional (3-d) rotation cannot be arbitrarily modified, due to the non-commutativity of rotations (see appendix). Consequently, the order of rotations must be fixed according to a sequence. In the current project, the sequence corresponded to the Fick sequence, where there was a rotation about the $z$-axis, then one about the $y$-axis, and lastly a rotation about the $x$-axis. In the notation of transformation mechanics, these sequential rotations may be described by

$$R = R(\psi, \phi, \theta) = R(x, \psi)R(y, \phi)R(z, \theta)$$

where $R$ is a $3 \times 3$ matrix representing the rotation in 3-d space. In the notation of
transformation mechanics, the order of rotations is read and performed from right-to-left. 

$R$ can be calculated by substituting the three rotation matrices representing the rotations about the base axes, so that

$$R = \begin{bmatrix}
\cos \theta \cos \phi & \cos \theta \sin \phi \sin \psi - \sin \theta \cos \psi & \cos \theta \sin \phi \cos \psi + \sin \theta \sin \psi \\
\sin \theta \cos \phi & \sin \theta \sin \phi \sin \psi + \cos \theta \cos \psi & \sin \theta \sin \phi \cos \psi - \cos \theta \sin \psi \\
-\sin \phi & \cos \phi \sin \psi & \cos \phi \cos \psi
\end{bmatrix}$$

(7.1)

where $\theta$ is the horizontal Fick angle, $\phi$ is the vertical Fick angle, and $\psi$ is the torsional Fick angle describing the rotation.

Four elements of $R$ may be obtained directly from the search coil signals

$$R = \begin{bmatrix}
- & - & - \\
H & T_2 & - \\
V & T & -
\end{bmatrix}$$

(7.2)

where $H$ is the horizontal signal, $V$ is the vertical signal, $T$ is the torsional signal, and $T_2$ is the auxiliary torsional signal (see section 5.2f). Since the elements from (7.2) correspond to the elements from (7.1) multiplied by the gains of the search coil, the horizontal, vertical, and torsional Fick angles can be calculated

$$V = G_v \ast -\sin \phi$$

(7.3)

$$H = G_h \ast \sin \theta \cos \phi$$

(7.4)

$$T = G_t \ast \sin \psi \cos \phi$$

(7.5)

where $G_v$, $G_h$, and $G_t$ are the gains of the vertical, horizontal, and torsional channels, respectively. The gain values were calculated from the in vitro calibration data by a program using equations (7.3)-(7.5). Since the gimbal was moved about only one of the three base axes at a time during the calibration (see section 6.4b), $\phi$ was zero (and hence $\cos \phi = 1$) during the horizontal and torsional components of the calibration. Consequently

$$G_v = \frac{-V}{\sin \phi}$$

$$G_h = \frac{H}{\sin \theta}$$

$$G_t = \frac{T}{\sin \psi}$$
For each part of the \textit{in vitro} calibration, the sine of the calibration Fick angle was plotted against the mean signal voltage induced at that angle. A line was fitted to these points using a linear least-squares regression algorithm, and the gradient of the line was considered equal to the gain of the channel in question. The calibration was considered acceptable if the square of the multiple correlation coefficient $R^2$ was greater than 0.999.

7.3 Calculation of Fick Angles and Rotation Matrices

The Fick angles representing the rotations were calculated by rearranging equations (7.3)-(7.5), and substituting the computed gain values and the raw signals from the search coils

\[ \phi = \sin^{-1} \left( \frac{-V}{G_v} \right) \]  
\[ \theta = \sin^{-1} \left( \frac{H}{G_h \cdot \cos \phi} \right) \]  
\[ \psi = \sin^{-1} \left( \frac{T}{G_t \cdot \cos \phi} \right) \]  

7.3a Calculation of the Torsional Fick Angle

Many of the search coils were found to have non-orthogonal direction and torsion induction coils (Bruno and Van den Berg 1997a; Thurtell et al. 1999; see section 5.2c). If the direction and torsion induction coils are not orthogonal, pseudo-torsion is observed during pure vertical movements of the search coil and, therefore, equation (7.8) no longer holds. The angle between the two induction coils $\sigma$ can be calculated if the amount of torsion induced during the vertical and torsional \textit{in vitro} calibrations is known. If the induction coils are not orthogonal ($\sigma \neq 90^\circ$), $\psi$ can be calculated using a modification of (7.8) developed by Bruno and Van den Berg (1997a)

\[ \psi = \sin^{-1} \left( \frac{T - \sin \phi \cdot \sin(\sigma - 90^\circ)}{\cos \phi \cdot \cos(\sigma - 90^\circ)} \right) \]  

where $T$ is the torsional signal from the search coil.
Thurtell et al. (1999) demonstrated that calculations of the torsional Fick angle were more accurate if the non-orthogonality of the induction coils was taken into account during the calculation of $\psi$. Consequently, (7.9) was used to calculate $\psi$ for all data presented in the current project.

7.3b Calculation of Rotation Matrices

As discussed previously, a $3 \times 3$ matrix may be used to describe the rotation of an object in 3-d space (see section 7.2). The matrices representing rotations of the eye and head were therefore computed by simply substituting the corresponding Fick angles into equation (7.1).

7.4 Correction for Search Coil Misalignment

Often the search coils were not ideally positioned on the eye or on the spectacle frame, since a voltage was induced in them during \textit{in vivo} calibrations. Tweed et al. (1990) therefore proposed that the recorded rotations be divided into rotations of the eye or head in the magnetic fields and rotations that misalign the search coil on the eye or spectacle frame. Mathematically

$$ C = R * C_0 $$

(7.10)

where $C$ is the rotation matrix representing recorded rotations of the eye or head in the magnetic fields, $R$ is the rotation matrix representing actual rotations of the eye or the head, $C_0$ is the rotation matrix describing the misalignment of the search coil on the eye or spectacle frame, and $*$ denotes matrix multiplication (Tweed et al. 1990). The actual rotation of the eye or head $R$ may therefore be calculated from (7.10)

$$ R = C * C_0^{-1} = C * C_0^T $$

(7.11)

$C_0^T = C_0^{-1}$, since $C_0$ is an orthogonal matrix. The values of $C$ and $C_0$ are known, as $C$ was calculated from the recorded rotation of the search coil, and $C_0$ may be calculated using the data acquired during the \textit{in vivo} calibration. A program calculated both $C_0$ and $C$, and used these matrices and equation (7.11) to compute $R$.  

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Fick angles describe one rotation in 3-d space using three sequential rotations about each of the base axes of the coordinate system (see section 7.2). Since rotations are non-commutative, Fick angles are not representative of the components of the true rotation that has taken place. The 3-d orientation of the position axis of the rotation and the angle about this axis that the eye or head rotated was therefore calculated (Schnabolk and Raphan 1994; Raphan 1997, 1998) from the matrix $R$, given in its most general form as

$$
R = \begin{bmatrix}
    r_{11} & r_{12} & r_{13} \\
    r_{21} & r_{22} & r_{23} \\
    r_{31} & r_{32} & r_{33}
\end{bmatrix}
$$

The angle $\Phi$ can be calculated directly from the matrix, as follows

$$
\Phi = \cos^{-1} \frac{Tr(R) - 1}{2}
$$

where $Tr(R)$ is the trace of the matrix $R$, defined by

$$
Tr(R) = \sum_{i=1}^{3} r_{ii}
$$

With the angle known, the position axis could then be calculated directly from $R$, as follows

$$
\begin{bmatrix}
    n_1 \\
    n_2 \\
    n_3
\end{bmatrix} = \begin{bmatrix}
    \frac{r_{32} - r_{23}}{2\sin \Phi} \\
    \frac{r_{13} - r_{31}}{2\sin \Phi} \\
    \frac{r_{21} - r_{12}}{2\sin \Phi}
\end{bmatrix}
$$

where $n_1$, $n_2$, and $n_3$ are the torsional, vertical, and horizontal components of the position axis, respectively. The axis-angle components were obtained by simply multiplying the components of the axis by the angle $\Phi$. Thus, $\Phi n_1$ is the torsional component, $\Phi n_2$ is the vertical component, and $\Phi n_3$ is the horizontal component of angular position.

Rotations in 3-d space may also be expressed as rotation vectors (Haustein 1989; Haslwanter 1995). Position data were expressed as rotation vectors in the original descriptive studies for the second study (Thurtell 1997; Thurtell et al. 1999). The rotation
vector corresponding to a given rotation of an object points in the same direction as the axis of the rotation and its length is proportional to \( \tan(\Phi/2) \). The Fick angles may be used to calculate the rotation vector \( RV \) as follows

\[
RV = \frac{1}{1 + \tan(\theta/2)\tan(\phi/2)\tan(\psi/2)} \begin{bmatrix}
\tan\left(\frac{\psi}{2}\right) - \tan\left(\frac{\theta}{2}\right)\tan\left(\frac{\phi}{2}\right) \\
\tan\left(\frac{\phi}{2}\right) + \tan\left(\frac{\theta}{2}\right)\tan\left(\frac{\psi}{2}\right) \\
\tan\left(\frac{\theta}{2}\right) - \tan\left(\frac{\phi}{2}\right)\tan\left(\frac{\psi}{2}\right)
\end{bmatrix} = \begin{bmatrix} RV_x \\ RV_y \\ RV_z \end{bmatrix}
\]

where \( RV_x, RV_y, \) and \( RV_z \) represent the torsional, vertical, and horizontal components of the rotation vector, respectively. In the current study, the rotation vectors were also calculated to aid in the computation of angular velocity (see section 7.7).

### 7.6 Calculation of Eye-in-Head Axis-Angle Data and Rotation Vectors

The “eye” rotations considered in the above calculations have been eye-in-space rotations. As it was essential to know how the eye was rotating within the head, the eye-in-head position was also calculated. The eye-in-space, or gaze, rotation matrix \( R_g \) is equal to the eye-in-head matrix \( R_e \) multiplied by the head matrix \( R_h \)

\[
R_g = R_e \cdot R_h \tag{7.12}
\]

To compute the eye-in-head matrix, equation (7.12) is rearranged

\[
R_e = R_g \cdot (R_h)^{-1} = R_g \cdot R_h^T
\]

where \((R_h)^{-1} = R_h^T\), since \(R_h\) is an orthogonal matrix. The axis-angle and rotation vector representations for eye-in-head position could then be derived from \(R_e\), as described above.

### 7.7 Calculation of Angular Velocity Vectors

The angular velocity of an object rotating in 3-d space is not simply the derivative of angular position. It depends on the rate of change of position with respect to time and on the current position of the object. Angular velocity \( \omega \) was calculated directly from the
rotation vectors $RV$ in the current project, as per Haslwanter (1995) and Aw et al. (1996a)

\[
\omega = \frac{2 \left( \frac{dRV}{dt} + RV \times \frac{dRV}{dt} \right)}{1 + RV^2}
\]

where $\times$ is the cross product of two matrices and $dRV/dt$ is the rate of change of the rotation vector with respect to time. Velocity vectors are such that their direction is parallel with the instantaneous velocity axis in 3-d space and their length is equal to the magnitude of the angular velocity, in degrees per second, at that point in time. As a result of these calculations, the angular position axis and angular velocity axis for a given rotation often will not align in 3-d space (see appendix and section 4.2a).

### 7.8 Calculation of Head Velocity in Head-Fixed Coordinates

When comparing head velocity vectors with eye velocity vectors, it was necessary to ensure that both were expressed relative to the same coordinate frame (Tweed et al. 1994b; Aw et al. 1996a; Thurtell et al. 1999). Since analysis and modelling of the aVOR relies on knowing the head velocity stimulus as sensed by receptors fixed in the head (see chapter 3), a head-fixed coordinate frame was chosen as the reference frame. The head-fixed coordinate frame moves with the head, so head position cannot be expressed in head-fixed coordinates. However, head velocity can be expressed in head-fixed coordinates by simply rotating the velocity vector so that it is expressed relative to the current orientation of the head. As illustrated in figure 7.1, the magnitude of the velocity vector remains unchanged by the rotation into head-fixed coordinates.

Head velocity in head-fixed coordinates was calculated using the method described by Aw et al. (1996a). The magnitude of the rotation vector describing head-in-space position was initially computed

\[
|RV_{hs}| = \sqrt{RV_{hx}^2 + RV_{hy}^2 + RV_{hz}^2}
\]

where $RV_{hs}$ is the rotation vector representing head position in space and $RV_{hx}$, $RV_{hy}$, and $RV_{hz}$ are the three components of this vector. The normalized vector $RV_{hn}$ describing the rotation from head position in space-fixed coordinates to current head position in
head-fixed coordinates was then calculated as follows

$$RV_{hn} = \frac{RV_{hs}}{|RV_{hs}|}$$

The inverse of the angle of the rotation from the reference position to the current head position $\beta$ was also computed

$$\beta = -2 \cdot \tan^{-1}(|RV_{hs}|)$$

Head velocity could then be calculated in head-fixed coordinates, as follows

$$\omega_{hn} = (\omega_{hs} \cdot RV_{hn})^* RV_{hn} + (RV_{hn} \times \omega_{hs})^* \sin \beta - (RV_{hn} \times (RV_{hn} \times \omega_{hs}))^* \cos \beta$$

where $\omega_{hn}$ is head velocity in head-fixed coordinates, $\omega_{hs}$ is head velocity in space-fixed coordinates, $\cdot$ denotes the dot product, and $\times$ denotes the cross product.

**Figure 7.1** Illustration demonstrating the difference between head velocity with reference to a space-fixed coordinate frame and head velocity with reference to a head-fixed coordinate frame. The subject is undergoing a clockwise rotation about the naso-occipital axis of the head, and the head is pitched 30° up in space at the time of the sample. **A.** When the head velocity vector is expressed relative to the space-fixed coordinate frame (dark lines), it is found to be rotated 30° up from the x-axis of the coordinate frame. **B.** When the same vector is expressed relative to the head-fixed coordinate frame (dark lines), it aligns with the x-axis of the coordinate frame. The magnitude of the velocity vector is unchanged – only the orientation of the vector is altered when it is described with respect to a different coordinate system (from Thurtell et al. 1999).
7.9 Calculation of the Orientation of Listing’s Plane

During each test, 90s of eye rotation data were collected while the head was fixed in space, to determine the orientation of Listing’s plane (see section 6.4g). A two-dimensional (2-d) plane was fitted to the data by a C program using a singular value decomposition algorithm to perform a linear least squares fit to the data (Press et al. 1988), so that

\[ RV_x = f + f_y RV_y + f_H RV_z \]

where \( RV_x, RV_y, \) and \( RV_z \) are the torsional, vertical, and horizontal components of the rotation vectors representing eye-in-head position, respectively, and \( f, f_y, \) and \( f_H \) are coefficients. The coefficients were used to rotate the data into Listing’s coordinates (see section 4.2a), using the calculations described in Tweed et al. (1990).

7.10 Saccadic Eye Movement Data Analysis

The saccadic eye movement data were analysed temporally and spatially. The axis-angle and velocity vector components of the data from each subject were initially plotted as time series. Examination of these plots helped to identify data where the head had not remained fixed during the test, and also enabled other common experimental artifacts, such as blinks, to be detected. If the subject blinked or rotated their head during the saccadic paradigms, the data were discarded. Six saccades for each direction in every paradigm were then selected from the remaining data for further analysis.

7.10a Identification of Onset of Saccades

The data were initially divided into epochs, each of which contained the data related to a single change in target position. The time of onset of the initial saccade following each change in target position was determined using a modified version of an algorithm developed by Aw (1996). The algorithm identified the point before peak eye velocity at which the eye velocity was 20°/s. A line was fitted to this and the four data points either side of the point. Another line was fitted to one hundred data points of the
eye velocity trace in the period just prior to the onset of the saccade (where eye velocity was approximately 0°/s). The intersection of these two lines was regarded as the time of onset of the saccade.

7.10b Temporal Analysis of Saccadic Data

The temporal analysis of the saccadic data focussed on examining saccadic metrics and comparing the trends in the eye velocity components from the different paradigms. In the study of saccadic metrics, the position of the eye before the initial saccade was determined by calculating the mean of fifteen eye position data points in the period just prior to the onset of the saccade. The position of the eye after the initial saccade was determined by calculating the mean of fifteen eye position data points following the end of the saccade, once eye velocity was stable at approximately 0°/s. The saccadic amplitude was calculated (in degrees) as the difference between these two positions. Saccades with grossly abnormal amplitudes were not excluded from further analysis. In addition, data from subjects unable to hold steady fixation (for example, due to spontaneous nystagmus) were not excluded from further analysis.

7.10c Spatial Analysis of Saccadic Data

Spatial plots were used to study the spatial orientation of the eye position and velocity data from the saccadic paradigms. Each point on these graphs represents the end of an axis-angle component or velocity vector at an instant in time. Data were plotted in the pitch, yaw, and roll planes to demonstrate their spatial characteristics (see appendix).

The orientation of the eye velocity axis during each paradigm was determined by fitting a line to the spatial data using a linear least squares algorithm in Splus. During horizontal saccades, the eye velocity axis tilted relative to the z-axis in the pitch plane, whereas it tilted relative to the y-axis in the yaw plane during vertical saccades. The angle of axis tilt was therefore calculated as the angle between the fitted axis and the z-axis in the pitch plane for horizontal saccades, and as the angle between the fitted axis and the y-axis in the yaw plane for vertical saccades. The tilt-angle coefficient was then calculated.
by finding the difference in the angle of axis tilt divided by the difference in eye position eccentricity for grouped paradigms, to obtain a measure of how well the half-angle rule was obeyed (Palla et al. 1999).

### 7.11 Angular Vestibulo-Ocular Reflex Data Analysis

Analysis of aVOR data was restricted to a 100ms period beginning 20ms before the onset of head rotation, to exclude the effects of non-aVOR systems such as the cervico-ocular reflex (Bronstein and Hood 1986) and smooth pursuit (Carl and Gellman 1987; Tychsen and Lisberger 1986). These systems have latencies $\geq 80$ms and may therefore have contributed to the responses after 80ms had elapsed.

Saccades did not have to be removed from the aVOR data, as they do not usually occur within 100ms of the onset of a passive head impulse (Aw 1996). Data found to contain evidence of blinks, search coil slippage, or other artifacts were not included in the analysis. In addition, data where the head signals were not within $1^\circ$ of the zero position of the head at the beginning of the impulse were not included in the analysis, as were data where there were anticipatory movements of the head before the onset of the impulse.

#### 7.11a Identification of Onset of Head Impulses

The time of onset of each head impulse was determined using the unmodified algorithm of Aw (1996). The algorithm identified the point before peak head velocity at which the head velocity was $10^\circ$/s; a line was fitted to this and the four data points either side of the point and another line was fitted to the first one hundred data points of the head velocity trace (where head velocity was equal to approximately $0^\circ$/s). The intersection of the two lines was regarded as the time of onset of the head impulse. Following identification of the onset time for each head impulse, the data were cut into 100ms epochs that began 20ms before the onset of the head impulse and ended 80ms after the onset. These epochs were used for the analysis.
7.11b Temporal Analysis of aVOR Data

The temporal analysis of aVOR data involved plotting the position and velocity components of the data as time series. More elaborate aVOR performance analysis indices were not used, as the main aim of the current study was to examine eye velocity axis tilting in the aVOR. Consequently, analysis of the spatial alignment of the eye and head velocity axes was the most useful data analysis approach.

7.11c Spatial Analysis of aVOR Data

Spatial plots were used to display the spatial alignment of the head-in-head and eye-in-head velocity vector data for the impulses. Each point on these graphs represents the end of a velocity vector at an instant in time, whose direction aligns with the axis of rotation and whose magnitude is equal to the instantaneous angular velocity (see figure 7.2). Only data corresponding to the first 80ms of the impulse were displayed (see section 7.11a).

![Figure 7.2](image_url)

**Figure 7.2 A.** The eye and head velocity vectors (arrows) with reference to a head-fixed coordinate frame, illustrated in the roll plane. Each point represents the tip of a velocity vector. The eye velocity vector is inverted, so that the head velocity stimulus can be easily compared with the eye velocity response. **B.** The eye and head velocity vectors, illustrated in the pitch plane (from Thurtell 1997).
To demonstrate any misalignment between the eye and head velocity axes, the velocity vectors were plotted in the pitch, yaw, and roll planes (see figure 7.2). To increase the ease of comparison between the eye and head vectors, the eye response was inverted. Thus, if the aVOR were perfect, the eye and head velocity vectors would lie exactly on top of one another in the spatial plots. Axis tilt would be manifest as a misalignment of the velocity vectors.

### 7.12 Statistical Analysis

Means, medians, and standard deviations were computed for a number of sample populations in both studies, using algorithms in *Splus*. At various stages in the data analysis, a Wilcoxon rank-sum test was performed to establish the existence of significant difference or otherwise between two sample populations, using an inbuilt function in *Splus*. The *P*-value was set at 0.01 and the null hypothesis was that there was no difference in the distributions of the two populations. The Wilcoxon rank-sum test corresponds to the *t*-test, except that the populations are not assumed to have a normal (Gaussian) distribution (Kuzma and Bohnenblust 2001).

### 7.13 Modelling

In both studies, experimental data were compared with simulations of a model of the saccadic system and aVOR. The model was implemented using the Microsoft *Visual C/C++* programming environment. The model contained a number of subdivisions representing the semicircular canals, vestibular afferents (both first- and second-order), saccadic pulse generator, direct pathway, velocity-position integrator (indirect pathway), and ocular motor plant (see figure 7.3).

As the model assumed that the reference eye position corresponded with the primary position, the location of the primary position was determined from the Listing’s plane data (as in Tweed et al. 1990). The position and velocity data were then rotated into
Listing’s coordinates (see sections 4.2a and 7.9), so that Listing’s plane aligned with the roll plane of the head-fixed coordinate frame. The new coordinate frame, which is close to the stereotaxic coordinate frame, will be referred to as the head-fixed coordinate frame in the remaining text of the thesis.

**Figure 7.3** Schematic diagram of the model. The matrix $M$, which transforms motoneuron firing into torque, incorporates the pulley effect by bringing about an eye position-dependent rotation of the torque axis. ($\omega_h$, head velocity; $\omega_v$, vestibular afferent signal; $G$, gain matrix; $g_{11}$, roll component of gain matrix; $g_{22}$, pitch component of gain matrix; $g_{33}$, yaw component of gain matrix; VN, vestibular nucleus; $r_w$, neural signal to activate the direct pathway and the velocity-position integrator; $D_p$, direct pathway; $G_p$ and $C_p$, gain matrices of the velocity-position integrator; $H_p$, system matrix of the velocity-position integrator; $m_n$, neural signal to the extra-ocular muscles; $M$, matrix to transform motoneuron firing into torque; $\Phi$, eye eccentricity from primary position; $\hat{n}$, position axis; $m$, extra-ocular muscle torque; $\omega_e$, eye velocity).

### 7.13a Model of the Semicircular Canals and Vestibular Afferents

The semicircular canal model was identical to that of Yakushin et al. (1998). Since each semicircular canal responds best to angular acceleration about an axis normal to the canal plane, the canal model must incorporate a kinematic transformation of head velocity from head-fixed coordinates into canal coordinates. To achieve this, the head velocity was projected onto each of the canal plane normals. The orientations of the canals, which are approximately orthogonal in humans, were adjusted to agree with those reported in the literature (Blanks et al. 1975).
The canal model incorporated a first-order dynamic system, to produce vestibular afferent firing that is temporally related to the input angular head acceleration. The dominant time constant for each canal was set to 4s, as there is evidence that this is the canal time constant in humans as well as in monkeys (Cohen et al. 1981; Dai et al. 1999). The equations describing the canal dynamics, the transformation of the head velocity signal into canal coordinates, and the transformation of the vestibular afferent signal back into head-fixed coordinates are given in Yakushin et al. (1998).

The vestibular afferent signal ($\omega_v$) activates second-order neurons in the vestibular nuclei (Waespe and Henn 1977, 1978; see figure 7.3). The sensitivities of the second-order neurons were determined by a gain matrix ($G$) relating eye rotation to head rotation along each of the coordinate axes (x, y, and z). The components of the gain matrix ($g_{11}$ for roll, $g_{22}$ for pitch, and $g_{33}$ for yaw) were initially adjusted to give gain values equal to those observed during passive roll, pitch, and yaw head impulses (Aw et al. 1996a). Roll rotations produced an aVOR with a gain of approximately 0.7, while yaw and pitch rotations produced an aVOR with a gain of approximately 1.0. The gain matrix was represented with respect to head-fixed coordinates. The effects of velocity storage (see section 3.8) were neglected in the model, since the head rotations being considered were of short duration (<250ms).

7.13b Model of the Direct Pathway and Velocity-Position Integrator

The signal from the vestibular nuclei ($r_w$) passes through the direct pathway ($D_p$) and to the velocity-position integrator. The integrator was implemented as a commutative vector integrator, characterized by gain matrices, $G_p$ and $C_p$, and a system matrix ($H_p$) that determines the integrator’s dynamics (Schnabolk and Raphan 1994). The parameters of the velocity-position integrator were set as in Raphan (1998). The matrices were represented with respect to head-fixed coordinates. The sum of the outputs from the direct pathway and velocity-position integrator ($m_n$) was used to drive the motoneurons innervating the extra-ocular muscles.
7.13c Model of the Saccadic Pulse Generator

The direct pathway and velocity-position integrator can also receive input from a saccadic pulse generator (Raphan 1998). The saccadic pulse generator in the model represents the combined functions of the superior colliculus and brainstem saccadic pulse generator. The superior colliculus generates a 2-d eye rotation command to position the target image on the fovea. This command is used to drive the saccadic pulse-generating network in the brainstem (Cohen and Komatsuzaki 1972; Keller 1974; Henn and Cohen 1976). The output of the pulse-generating network \( r_w \), a 2-d signal, passes through the direct pathway and to the velocity-position integrator. The direct pathway and the velocity-position integrator cannot be simultaneously driven by the semicircular canals and the saccadic pulse generator; the input to these pathways depends on the position of a switch, as illustrated in figure 7.3.

In the simulations for the first study, the signal from the saccadic pulse generator was adjusted to bring about saccades identical (in direction and amplitude) to those recorded from the subjects. For the second study, the saccadic pulse generator produced a signal to move the eyes into the starting eye position before the onset of the head rotation. The model maintained the initial eye position for 200ms before the onset of the head rotation. As the time constant of the velocity-position integrator was set to 30s (Schnabolk and Raphan 1994), there was negligible decay in the signal from the integrator over the simulation time.

7.13d Model of the Ocular Motor Plant

Activity in the motor neurons \( m_n \) results in the generation of torque \( m \) in the extra-ocular muscles. Due to the effects of the muscle pulleys, the torque axis is rotated in a manner that depends on instantaneous eye position (see figure 2.4). For example, when the eye is elevated by an angle \( \Phi \), the muscle pulley changes the pulling direction of the medial rectus muscle, thereby rotating the torque axis by an angle \( \delta \). In the model, the matrix \( M \) implements the transformation from motoneuron firing to torque. \( M \) is a rotation
matrix that incorporates the action of the pulleys in three dimensions. The transformation is given by:

\[ m = Mm_n \]

The rotation of the eye torque axis by the pulleys occurs about the eye orientation axis, and the angle of rotation is a fraction of the angle \( \Phi \). The angle of torque axis rotation is determined by a pulley coefficient \( k_\phi \), such that

\[ \delta = k_\phi \Phi \]

If \( k_\phi \) is 0.5, the trajectory of a saccadic eye movement driven by a 2-d pulse is constrained so that it perfectly obeys Listing’s law (see section 4.3b). If \( k_\phi \) is 0, for example, there will be a large torsional transient when the eye is driven by a 2-d pulse. As a result, Listing’s law will be violated, since there is no tilt of the torque axis during the saccade.

The ocular motor plant itself was modelled as a second-order dynamic system governed by the inertia of the eyeball, viscous damping by the fluid and tissue surrounding the eye, and the elasticity of surrounding membranes. The plant model is discussed in further detail in Raphan (1998).

7.13e Optimal Model Parameters

In order to determine the optimal pulley coefficient to predict the data in the model simulations for the second study, the minimum mean square error \( (E^2) \) between torsional eye velocities for data \( (\omega_{x\text{(data)}}) \) and model simulation \( (\omega_{x\text{(model)}}) \) was calculated. The pulley coefficient was varied from 0 to 1, in increments of 0.01. The mean square error was computed for each pulley coefficient value as

\[ E^2 = \frac{1}{N} \sum_{i=1}^{N} (\omega_{x\text{(data)}}[t] - \omega_{x\text{(model)}}[t])^2 \]

where \( N \) is the number of samples in the temporal sequence of corresponding model and data sets. Since the data were sampled at 1kHz and the length of the analysis period was 100ms, \( N \) was equal to 100. The optimal pulley coefficient, which gave the minimum mean square error, was determined for each subject and eye velocity trajectory, and over a wide range of roll aVOR gains (see chapter 9).
In the model simulations for the first study, tilting of the eye velocity axis away from Listing’s plane comes about solely due to the pulley effect, as the command signal to the extra-ocular muscles from the saccadic pulse generator is a 2-d horizontal-vertical signal. In the model simulations for the second study, the value of the optimal pulley coefficient reflects the pulley configuration only for a given roll gain. If the signal activating the extra-ocular muscles is a pure horizontal-vertical signal, then any tilting of eye velocity axis away from Listing’s plane occurs due to the effect of the pulleys alone. If there is a torsional component to the signal, as during vestibular-evoked eye movements, eye position-dependent tilting of the eye velocity axis in the pitch plane may occur due to the pulley effect, due to an eye position-dependent alteration in the torsional signal activating the muscles, or due to a combination of both these mechanisms.

7.14 Summary

The data were calibrated and analysed using a number of C and Splus programs. The eye and head position data, initially a series of voltages recorded in space-fixed coordinates, were scaled and converted into axis-angle format. Velocity vectors were then calculated and used to illustrate the spatial characteristics of the eye and head velocity axes, with reference to a head-fixed coordinate frame. The results and discussion for the two studies described in this thesis are presented in the following chapters.