Pergamon

0042-6989(94)00257-6

Vision Res. Vol. 35, No. 12, pp. 1727–1739, 1995

0042-6989/95 $9.50 + 0.00

Mathematics of Three-dimensional Eye Rotations

THOMAS HASLWANTER*

Received 18 July 1994; in revised form 30 September 1994

The recording of three-dimensional eye position has become the accepted standard in oculomotor research. In this paper we review the mathematics underlying the representation of three-dimensional eye movements. Rotation matrices, rotation vectors and quaternions are presented, and their relations described. The connection between search coils and rotation matrices is explained, as well as the connection between eye position and eye velocity. While examples of applications of the formulas to vestibulo-ocular research are given, the methods and mathematical analyses are also useful for studying other motor systems.

Three-dimensional Eye movements Search coils Listing's law Rotations

INTRODUCTION

Research during the last two decades has highlighted the importance of accurate recording of horizontal, vertical *and* torsional components of eye movements for a complete understanding of the oculomotor system and the different afferent inputs contributing to its control. The requirement to accurately measure three-dimensional (3D) eye movements has led to the development of different approaches. The search coil technique has been developed by Robinson (1963), Collewijn, Van der Steen, Ferman and Jansen (1985) and others, and different magnetic field coil systems (e.g. by Skalar Instruments, C-N-C Engineering, Remmel Labs etc.) have become commercially available. More recently, advances in digital image processing technology have led to large improvements in the recording of 3D eye position with camera-based systems (Vieville & Masse, 1987; Ott, Gehle & Eckmiller, 1990; Clarke, Teiwes & Scherer, 1991; Moore, Curthoys & McCoy, 1991).

Together with the development of hardware for eye position measurement, a mathematical basis for a better understanding of 3D rotations has been established (Westheimer, 1957; Nakayama, 1974; Rooney, 1977; Tweed & Vilis, 1987; Hepp, Henn, Vilis & Cohen, 1989; Hepp, 1990; Van Opstal, 1993). More recent research has shown that many of these mathematical principles and control strategies can be applied not only to eye movements, but also to head and arm movements (Straumann, Haslwanter, Hepp-Reymond & Hepp, 1991; Hore, Watts & Vilis, 1992; Miller, Theeuwen & Gielen, 1993).

However, only a relatively small group of people have become comfortable with the complex formalisms, and many researchers without a strong mathematical background have been deterred by the mathematics involved. Although all the pertinent formulas have been published somewhere, it is difficult to find a unified account to allow a coherent understanding of the mathematical and geometrical basis of 3D eye movements. While Van Opstal (1993) has given a concise overview, the present review aims to provide a more comprehensive account.

In the following, the geometrical background is presented in such a way that the reader can develop a basic intuitive understanding of 3D eye movements. Although most relevant formulas are discussed, mathematical proofs which have been published elsewhere have been largely omitted. In the final section examples of applications in vestibulo-ocular research are presented.

ROTATION MATRICES

Conventions and basics

Eye movements in 3D space consist of translations as well as rotations. The discussion here will be restricted to the rotational components of the total eye movement. Translations of the eye, which can be due to a translation of the eye in the orbit (Enright, 1980, 1984), as well as to a head movement, will not be dealt with here, and the terms *eye movement* and *eye position* will refer only to the rotational components. In this paper we will use the following conventions:

*Department of Psychology, University of Sydney, Sydney, NSW 2006, Australia [*Email* thomas@psychvax.psych.su.oz.au].

- scalars are indicated by roman characters (e.g. a);
- vectors are indicated by bold characters (e.g. **r**) or in round brackets

$$\text{(e.g. } \begin{pmatrix} r_1 \\ r_2 \\ r_3 \end{pmatrix}\text{);}$$

- quaternions are indicated by italic characters (e.g. *q*);
- matrices are indicated by outline characters (e.g. $\mathbb{R}$) or in square brackets

$$\text{(e.g. } \begin{bmatrix} R_{11} & R_{12} & R_{13} \\ R_{21} & R_{22} & R_{23} \\ R_{31} & R_{32} & R_{33} \end{bmatrix}\text{);}$$

- vector and matrix elements are indicated by roman characters, with indices denoted by subscripts (e.g. r_1, R_{12});
- multiplications with a scalar are denoted by $*$ [e.g. $\tan(\theta/2) * \mathbf{n}$];
- scalar vector products and matrix multiplications are denoted by $\cdot$ (e.g. $\mathbf{p}\cdot\mathbf{q}$);
- vector cross products are denoted by $\times$ (e.g. $\mathbf{p} \times \mathbf{q}$);
- combinations of rotation vectors or quaternions are denoted by $\circ$ (e.g. $\mathbf{r}_p \circ \mathbf{r}_q$).

The basic formulas for multiplications of matrices and vectors are given in the Appendix. More extensive introductions to vectors, matrices etc. can be found in most textbooks on algebra.

In measuring 3D eye positions, the current eye position is defined by characterizing the 3D rotation from a somewhat arbitrarily chosen reference position to the current eye position. This reference position is usually defined as the position the eye assumes when the subject is looking straight ahead, while the head is kept upright. *Straight ahead* can be defined either as the centre of the oculomotor range, or as looking at a target which is exactly horizontally in front of the eye. In the latter case, eye position in the head is a function of head position in space, when the eye is in the reference position. In the following we will use the latter definition of straight ahead.

To describe the 3D orientation of the eye, Euler's theorem can be applied: it states that for every two orientations of an object, the object can always move from one to the other by a *single rotation* about a fixed axis (Euler, 1775). Until recently, the rotation from the reference position to the current eye position has not been described by the characteristics of this single rotation, but has been decomposed into three consecutive rotations about well defined, hierarchically nested axes (e.g. Goldstein, 1980). The following section will deal with this three-rotation description of 3D eye position, while quaternions and rotation vectors, which characterize the 3D eye position by a single rotation, will be covered in later sections.

One-dimensional movements

In order to define one-dimensional (1D) movements, we first have to establish a head-fixed and an eye-fixed coordinate system to describe the 3D position of the eye in space. Let $\{\mathbf{h}_1, \mathbf{h}_2, \mathbf{h}_3\}$ be a right-handed, head-fixed coordinate system such that $\mathbf{h}_1$ coincides with the line of sight when the eye is in the reference position, $\mathbf{h}_2$ with the interaural axis and $\mathbf{h}_3$ with the earth vertical [Fig. 1(A)]. Let $\{\mathbf{e}_1, \mathbf{e}_2, \mathbf{e}_3\}$ denote an eye-fixed coordinate system (i.e. it moves with the eye) such that $\{\mathbf{e}_1, \mathbf{e}_2, \mathbf{e}_3\}$ coincides with the head-fixed coordinate system $\{\mathbf{h}_1, \mathbf{h}_2, \mathbf{h}_3\}$ when the eye is in the reference position.

Any horizontal rotation of the eye-fixed coordinate system (and thus of the eye) from the reference position to a new position, as indicated in Fig. 1(B), can be described by

$$\mathbf{e}_i = \mathbb{R}\cdot\mathbf{h}_i \qquad i=1, 2, 3. \tag{1}$$

The components of the vectors $\mathbf{e}_i$ are expressed relative to the head-fixed coordinate system $\{\mathbf{h}_1, \mathbf{h}_2, \mathbf{h}_3\}$, and the rotation matrix $\mathbb{R}$ describes a rotation about a space-fixed axis, independent of the orientation of the eye. Since for a purely horizontal eye movement the rotation matrix $\mathbb{R}$ describes a rotation about $\mathbf{h}_3$ by an angle of θ, let us call it $\mathbb{R}_3(\theta)$. It is given by

$$\mathbb{R}_3(\theta) = \begin{bmatrix} \cos(\theta) & -\sin(\theta) & 0 \\ \sin(\theta) & \cos(\theta) & 0 \\ 0 & 0 & 1 \end{bmatrix}. \tag{2}$$

In the same way, purely vertical eye movements—i.e. rotations about $\mathbf{h}_2$—by an angle of ϕ can be described by

$$\mathbb{R}_2(\phi) = \begin{bmatrix} \cos(\phi) & 0 & \sin(\phi) \\ 0 & 1 & 0 \\ -\sin(\phi) & 0 & \cos(\phi) \end{bmatrix}; \tag{3}$$

and purely torsional eye movements—i.e. rotations about $\mathbf{h}_1$—by an angle of ψ can be described by

$$\mathbb{R}_1(\psi) = \begin{bmatrix} 1 & 0 & 0 \\ 0 & \cos(\psi) & -\sin(\psi) \\ 0 & \sin(\psi) & \cos(\psi) \end{bmatrix}. \tag{4}$$

With these definitions, positive θ, ϕ and ψ values correspond to leftward, downward and clockwise (as seen from the subject) eye movements.

For 1D movements no distinction has to be made between rotations about eye-fixed or head-fixed axes. Since the eye-fixed and head-fixed coordinate systems

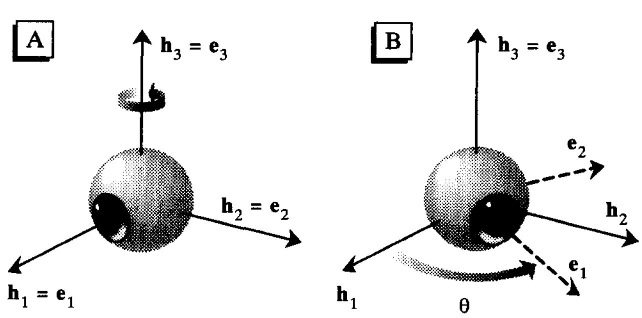

FIGURE 1. Horizontal rotation of the eye about the axis $\mathbf{h}_3$ by an angle θ from (A), the reference position, to (B), a new position.

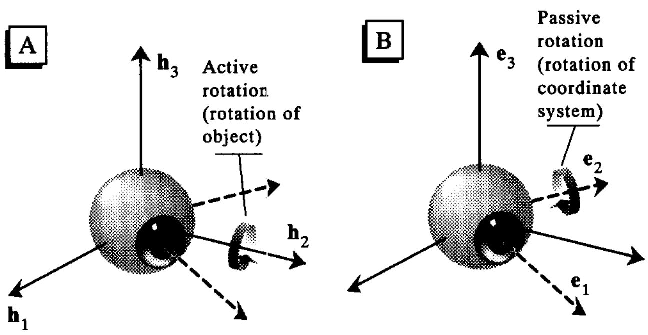

FIGURE 2. In describing a combined horizontal–vertical eye movement, one has to distinguish clearly between (A) rotations about head-fixed axes, which remain fixed, and (B) rotations about eye-fixed axes, which move with the eye.

coincide when the eye is in the reference position, the axis about which the eye rotates is the same in the eye-fixed and head-fixed system.

Three-dimensional movements

To describe the rotation of the eye-fixed coordinate system from the reference position to *any* new position, equation (1) still holds. In other words, the rotation matrix $\mathbb{R}$ still completely describes the current eye position. However, its elements are no longer determined by the relatively simple formulas in equations (2)–(4).

To understand the situation better, let us look at a simple downward eye movement from the position in Fig. 1(B): how should we distinguish between a downward movement of the eye by a rotation about the head-fixed axis $\mathbf{h}_2$ [as shown in Fig. 2(A)], and a downward movement by a rotation about the rotated, eye-fixed axis $\mathbf{e}_2$ [Fig. 2(B)]? The difference between rotations in head-fixed coordinates and eye-fixed coordinates lies in the sequence in which the rotations are executed. This is illustrated in Fig. 3. Figure 3(A) shows a rotation of an object about $\mathbf{h}_3$ by θ, followed by a rotation about the *space-fixed* axis $\mathbf{h}_2$ by ϕ. Mathematically this is described by

$$\mathbf{e}_i = \mathbb{R}_2(\phi)\cdot\mathbb{R}_3(\theta)\cdot\mathbf{h}_i \tag{5}$$

with $\theta = \phi = 90$ deg.

Inverting the sequence of two rotations about space-fixed axes changes the final orientation of the object. This can be seen in Fig. 3(B), where a rotation is first performed about $\mathbf{h}_2$, and then about the *space-fixed* axis $\mathbf{h}_3$. This sequence is mathematically described by

$$\mathbf{e}_i = \mathbb{R}_3(\theta)\cdot\mathbb{R}_2(\phi)\cdot\mathbf{h}_i. \tag{6}$$

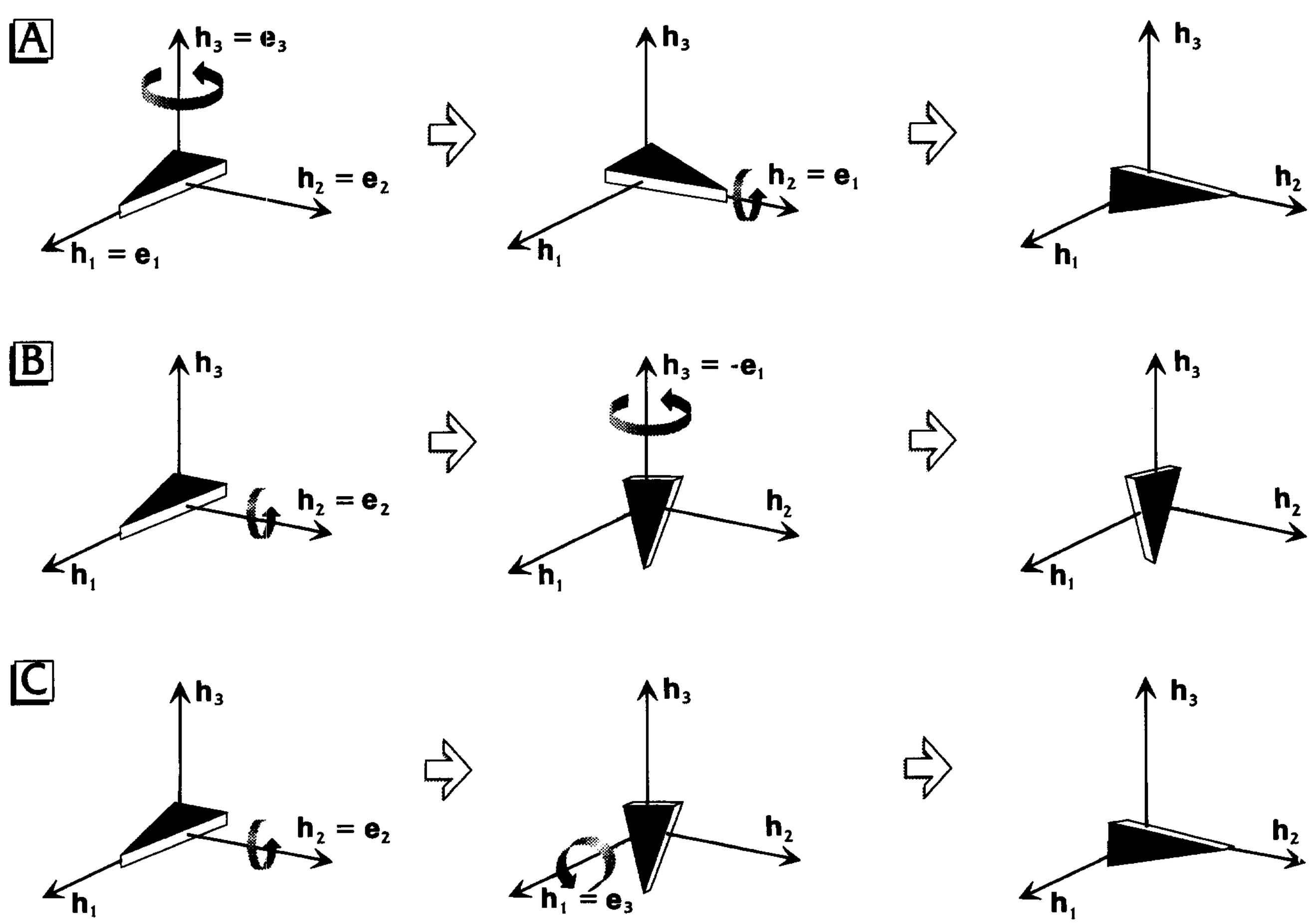

FIGURE 3. (A) A 90 deg rotation about the vertical axis $\mathbf{h}_3$, followed by a 90 deg rotation about the horizontal axis $\mathbf{h}_2$. (B) A 90 deg rotation about the horizontal axis $\mathbf{h}_2$, followed by a 90 deg rotation about the vertical axis $\mathbf{h}_3$. (C) A 90 deg rotation about the eye-fixed axis $\mathbf{e}_2$, followed by a 90 deg rotation about the eye-fixed axis $\mathbf{e}_3$. The final orientation is the same as in (A). Eye-fixed axes and the head-fixed axes are *superposed* because the size of the rotations is in this example exactly 90 deg.

Equations (5) and (6) both describe rotations about space-fixed axes. However, they can also be *re-interpreted* as rotations about eye-fixed axes in the reverse sequence: equation (5) can be re-interpreted as a rotation about the axis $\mathbf{e}_2$ by ϕ, followed by a rotation about the eye-fixed axis $\mathbf{e}_3$ by θ; and equation (6) is equivalent to a rotation about $\mathbf{e}_3$ by θ, followed by a rotation about the eye-fixed axis $\mathbf{e}_2$ by ϕ. Figure 3(A, C) demonstrates that rotations about head-fixed axes and rotations about eye-fixed axes in the reverse sequence lead to the same final orientation. A mathematical analysis of this problem can be found in Altmann (1986).

This also gives the answer to the problem raised by Fig. 2: the combination of two rotations about the head-fixed axes $\mathbf{h}_3$ and $\mathbf{h}_2$, as shown in Fig. 2(A), is mathematically described by equation (5); while the combination of two rotations about the eye-fixed axes $\mathbf{e}_3$ and $\mathbf{e}_2$, as shown in Fig. 2(B), is described by equation (6). Rotations about head-fixed axes are often called *active rotations* or *rotations of the object*, since in successive rotations the axes of the successive rotations are unaffected by the preceding rotations of the object. Rotations about eye-fixed axes are often referred to as *passive rotations* or *rotations of the coordinate system*, since each rotation changes the coordinate axes about which the next rotations will be performed.

A combination of a horizontal and a vertical rotation of the eye in a well-defined sequence uniquely characterizes the direction of the line of sight or *gaze direction*. However, this does not completely determine the 3D eye position, since the rotation about the line of sight, sometime referred to as *cyclotorsion*, is still unspecified. A third rotation is needed to completely determine the orientation of the eye.

Systems that use such a combination of three rotations for the description of eye position generally use *passive* rotations, or rotations of the coordinate system. Such rotations of the coordinate system can easily be demonstrated by considering gimbal systems, in which the hierarchy of passive rotations is automatically implemented.

Figure 4(B) shows a gimbal which corresponds to the *Fick-sequence* of rotations. This sequence of rotations—first a horizontal, then a vertical and then a torsional rotation, has first been used by Fick (1854), and the angles θ, ϕ and ψ for this sequence are often referred to as *Fick-angles*. In the following we will denote Fick-angles by the subscript F (θ_F, ϕ_F, ψ_F). The rotation matrix corresponding to the Fick-sequence of rotations is

$$\mathbb{R}_{Fick} = \mathbb{R}_3(\theta_F)\cdot\mathbb{R}_2(\phi_F)\cdot\mathbb{R}_1(\psi_F). \tag{7}$$

Note the order of the rotation matrices: our discussion of equations (5) and (6) above has shown that with passive rotations, the first rotation matrix on the left describes the first rotation [here this is $\mathbb{R}_3(\theta_F)$], the second matrix from the left the second rotation [$\mathbb{R}_2(\phi_F)$], and the rotation matrix to the right the last rotation [$\mathbb{R}_1(\psi_F)$].

This sequence of rotations—first horizontal, then vertical and then torsional—is arbitrary, and can be

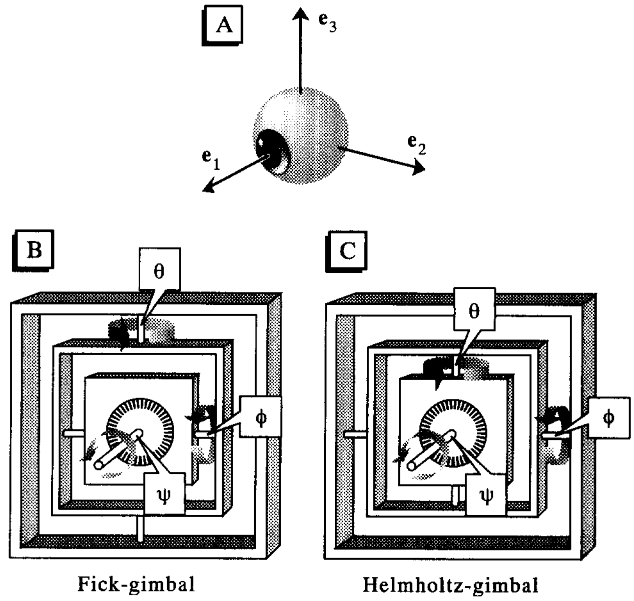

FIGURE 4. In gimbal systems rotations are executed from the outside in. (A) Eye-fixed coordinate system, with the eye in the reference position. (B) In a Fick-gimbal, the eye position is completely characterized by a rotation about the vertical axis e_3 by θ, followed by a rotation about the horizontal axis e_2 by ϕ, and a rotation about the line-of-sight e_1 by ψ. (C) In a Helmholtz gimbal, eye positions are characterized by a rotation first about the horizontal axis e_2 by ϕ, followed by a rotation about the e_3 axis by θ, and then a rotation about the line-of-sight e_1 by ψ.

replaced by a different sequence. von Helmholtz (1866) thought it would be better to start with a rotation about a horizontal axis: while variations in head-pitch make the definition of *horizontal eye movements* difficult, a *vertical eye movement* can easily be defined as an eye movement about the inter-aural axis. Thus Helmholtz characterized eye positions by a vertical rotation, followed by a horizontal and then by a torsional rotation as shown in Fig. 4(C):

$$\mathbb{R}_{Helmholtz} = \mathbb{R}_2(\phi_H)\cdot\mathbb{R}_3(\theta_H)\cdot\mathbb{R}_1(\psi_H). \tag{8}$$

The subscript H indicates that the angles refer to the Helmholtz-sequence of rotations. The explicit forms of $\mathbb{R}_{Fick}$ and $\mathbb{R}_{Helmholtz}$ are given in the Appendix. One should keep in mind that the eye position is characterized by the *values* of the rotation matrix $\mathbb{R}$, and $\mathbb{R}_{Fick}$ and $\mathbb{R}_{Helmholtz}$ only give different parametrizations for the *same* rotation matrix.

Interpretations

An interpretation of the values of the rotation matrix can be found by looking at equation (1): the columns of the rotation matrix $\mathbb{R}$ are equivalent to the vectors of the eye-fixed coordinate system $\{\mathbf{e}_1, \mathbf{e}_2, \mathbf{e}_3\}$ expressed in the head-fixed coordinate system $\{\mathbf{h}_1, \mathbf{h}_2, \mathbf{h}_3\}$. Thus, different values in the rotation matrix $\mathbb{R}$ indicate a different orientation of the eye-fixed coordinate system, i.e. a different orientation of the eye-ball. For example, let us put an artificial eye-ball on a Fick-gimbal [Fig. 4(B)], and turn the gimbal first 15 deg to the left and then (about the rotated axis $\mathbf{e}_2$) 25 deg down, i.e. $(\theta_F, \phi_F, \psi_F) = (15, 25, 0)$.

The orientation of the eye-ball will then be given by the matrix

$$\mathbb{R}_{Fick} = \begin{pmatrix} 0.88 & -0.26 & 0.41 \\ 0.23 & 0.97 & 0.11 \\ -0.42 & 0 & 0.91 \end{pmatrix}. \quad (9)$$

Putting an eye on a Helmholtz-gimbal [Fig. 4(C)], and turning it first 25 deg down, and then 15 deg to the left (about the rotated axis $\mathbf{e}_3$), i.e. $(\theta_H, \phi_H, \psi_H) = (15, 25, 0)$, leads to a different orientation of the eye:

$$\mathbb{R}_{Helmholtz} = \begin{pmatrix} 0.88 & -0.23 & 0.42 \\ 0.26 & 0.97 & 0 \\ -0.41 & 0.11 & 0.91 \end{pmatrix}. \quad (10)$$

The orientation of the eye is in both cases clearly different: e.g. on the Fick-gimbal $\mathbf{e}_3$ is given by (0.41, 0.11, 0.91), whereas on the Helmholtz-gimbal it points in a different direction, (0.42, 0, 0.91).

Experimentally, the 3D orientation of the eye in space can be measured for example with scleral search coils. When a search coil is put into an oscillating magnetic field $\mathbf{B}$, a voltage is induced in the coil (Robinson, 1963). If the coil is characterized by a coil vector $\mathbf{c}$, which is perpendicular to the coil and has a length proportional to the surface surrounded by the coil, the voltage is proportional to the cosine of the angle between $\mathbf{B}$ and $\mathbf{c}$. As pointed out by Tweed, Cadera and Vilis (1990), this leads to a simple correspondence between the values of the rotation matrix and the voltages induced in search coils. This connection can be demonstrated with the experimental setup shown in Fig. 5.

Let

$$\mathbf{B}_i = \mathbf{h}_i * b_i * \sin(\omega_i * t) \qquad i = 1, 2, 3 \quad (11)$$

be three homogeneous orthogonal magnetic fields. They are parallel to the axes of the head-fixed coordinate system $\{\mathbf{h}_1, \mathbf{h}_2, \mathbf{h}_3\}$, have amplitudes b_i, and oscillate at frequencies ω_i. Further, let $\{\mathbf{c}_1, \mathbf{c}_2, \mathbf{c}_3\}$ denote three orthogonal coils which are parallel to the eye-fixed coordinate system $\{\mathbf{e}_1, \mathbf{e}_2, \mathbf{e}_3\}$ and firmly attached to the eye. Then the voltage induced by the magnetic field $\mathbf{B}_i$ in coil $\mathbf{c}_j$, V_{ij}, is given by

$$V_{ij} = R_{ij} * b_i * \omega_i * \cos(\omega_i * t) * c_j \qquad i, j = 1, 2, 3 \quad (12)$$

where $c_j = |\mathbf{c}_j|$ indicates the length of the vector $\mathbf{c}_j$. This gives a direct interpretation of the elements of the rotation matrix $\mathbb{R}$: the voltage induced by the magnetic field $\mathbf{B}_i$ in the coil $\mathbf{c}_j$ is proportional to the element R_{ij} of the rotation matrix $\mathbb{R}$, which describes the rotation from the reference position, where the coils $\{\mathbf{c}_1, \mathbf{c}_2, \mathbf{c}_3\}$ line up with the magnetic fields $\{\mathbf{B}_1, \mathbf{B}_2, \mathbf{B}_3\}$, to the current position. Tweed *et al.* (1990) and Hess, Van Opstal, Straumann, Hepp and Henn (1992) give algorithms for the general case, where the coils $\{\mathbf{c}_1, \mathbf{c}_2, \mathbf{c}_3\}$ do not line up with the magnetic fields $\{\mathbf{B}_1, \mathbf{B}_2, \mathbf{B}_3\}$ when the eye is in the reference position.

In many laboratories the ideal configuration shown in Fig. 5 is replaced by a configuration where only two magnetic fields are available; one is usually vertical (i.e. parallel to $\mathbf{h}_3$), and the other parallel to the inter-aural axis $\mathbf{h}_2$. The coils commonly used for recording 3D eye position are the dual search coils produced by Skalar Instruments (Delft, The Netherlands), which are oriented in such a way that they are approximately parallel to the axes $\mathbf{e}_1$ and $\mathbf{e}_2$ of the eye-fixed coordinate system. With these two eye coils and two magnetic fields, only the following elements of the rotation matrix are available:

$$\mathbb{R} = \begin{pmatrix} - & - & - \\ H & T_2 & - \\ V & T & - \end{pmatrix}. \quad (13)$$

H, V, and T indicate that these signals approximately represent the horizontal, vertical and torsional eye position. However, they are only a rough estimate, and the explicit forms of the Fick- and Helmholtz-matrices (given in the Appendix) have to be used to derive the exact Fick- or Helmholtz-angles from the search coil signals. T_2 is the second signal from the coil aligned with $\mathbf{e}_2$, and is less sensitive to horizontal, vertical and torsional eye position.

Other problems, like the determination of offsets which are frequently superimposed on the induced voltages, are not discussed here, but have been investigated in detail by Hess *et al.* (1992).

Determination of Fick- or Helmholtz-angles from measured search coil voltages quickly leads to the much discussed problem of *false torsion*. Let us, for example, take the case where a person looks left and down, and the measured search coil voltages give the following elements of the rotation matrix $\mathbb{R}$

$$\mathbb{R} = \begin{pmatrix} - & - & - \\ 0.416 & 0.908 & - \\ -0.247 & 0.055 & - \end{pmatrix}. \quad (14)$$

From the elements R_{21}, R_{31} and R_{32} and the explicit form of the Fick-rotation matrix given in the Appendix, the Fick-angles corresponding to this eye position

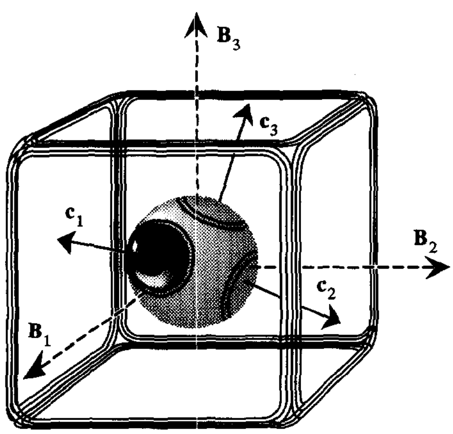

FIGURE 5. An idealized experimental setup with three orthogonal magnetic fields and three orthogonally mounted search coils. The search coils are rigidly attached to the eye, and the coil vectors $\{\mathbf{c}_1, \mathbf{c}_2, \mathbf{c}_3\}$ are parallel to the axes of the eye-fixed coordinate system $\{\mathbf{e}_1, \mathbf{e}_2, \mathbf{e}_3\}$. The magnetic fields $\{\mathbf{B}_1, \mathbf{B}_2, \mathbf{B}_3\}$ are parallel to the head-fixed coordinate system $\{\mathbf{h}_1, \mathbf{h}_2, \mathbf{h}_3\}$.

can be calculated as $\theta_F = 25.4$ deg, $\phi_F = 14.3$ deg and $\psi_F = 3.3$ deg. The same matrix elements and the Helmholtz-rotation matrix yield the corresponding Helmholtz-angles, $\theta_H = 24.6$ deg, $\phi_H = 15.8$ deg and $\psi_H = -3.4$ deg. The values for ψ_F and ψ_H depend on the particular Fick- and Helmholtz-sequence of the rotations. These coordinate system dependent values for ocular torsion are sometime referred to as false torsion. The opposite sign of ψ_F and ψ_H in the given example also shows that one can not simply talk about an "ocular torsion of 3 deg", but has to specify if it is 3 deg in the Fick-system or 3 deg in the Helmholtz-system. This false torsion is only due to the geometric properties of the Fick- and Helmholtz-systems. Near the reference position it can be approximated by

$$\psi_{\text{Fick}} \approx \frac{\theta_{\text{Fick}} * \phi_{\text{Fick}}}{100} \tag{15}$$

$$\psi_{\text{Helmholtz}} \approx -\frac{\theta_{\text{Helmholtz}} * \phi_{\text{Helmholtz}}}{100}$$

where all angles are given in deg. The example further shows that Fick- and Helmholtz-coordinates not only lead to different values for torsion, but also for the horizontal and vertical angles.

Describing 3D eye position as such an arbitrary sequence of multiple rotations has the inherent disadvantage that different sequences lead to different horizontal, vertical and torsional values for the same eye position. However, *Euler's theorem* tells us that any eye position can be reached from the reference position by a *single* rotation about a fixed axis. The next section will deal with *rotation vectors* and *quaternions*, which characterize this single rotation from the reference position to a new eye position.

QUATERNIONS AND ROTATION VECTORS

Quaternions and their relation to rotation matrices

Rotation matrices are not the most efficient way to describe a rotation: they have nine elements, yet only three are actually needed to uniquely characterize a rotation. Another disadvantage of describing 3D rotations with rotation matrices is that the three axes of rotation, as well as the sequence of the rotations about these axes, have to be defined arbitrarily, with different sequences leading to different rotation angles. A more efficient way of characterizing a rotation of the eye is to use a vector, with the direction of the vector given by the axis of the rotation, and its length proportional to the size of the rotation, as shown in Fig. 6. Such a vector has only three parameters, and there is no sequence of multiple rotations involved. The orientation of the vector is given by the *right-hand rule*, i.e. an eye movement left, down or clockwise (as seen from the subject) is described by a vector which points up, left or forward respectively. In this description torsion is *not* defined as a rotation about the line of sight, but as the $\mathbf{h}_1$-component of the vector characterizing the total eye position.

Two kinds of such descriptions of rotations have been proposed in the oculomotor literature: quaternions and rotation vectors. The theory of quaternions was invented and developed by Hamilton in the mid-19th century (Hamilton, 1899). Its original purpose was to define the ratio of two vectors, and hence to be able to rotate one vector into another by multiplication with a third vector. Hamilton found that he could not accomplish this by using three-component vectors, but had to use four-component vectors or *quaternions*.

A detailed treatment of quaternions and their elegant mathematical properties can be found in mathematical texts (Brand, 1948; Altmann, 1986), many papers on eye movements (Westheimer, 1957; Tweed & Vilis, 1987;

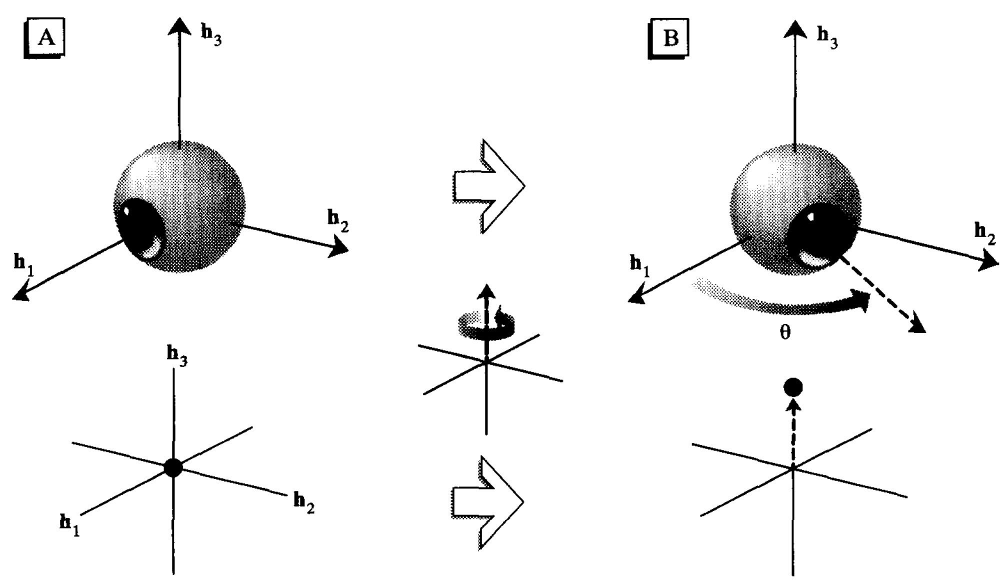

FIGURE 6. Description of 3D eye position by a vector. (A) The eye in the reference position (top) corresponds to the zero-vector (bottom). (B) A different horizontal eye position (top) can be reached by rotating the eye from the reference position about the $\mathbf{h}_3$ axis. This eye position is thus represented by a vector along the $\mathbf{h}_3$-axis, with a length proportional to the angle of the rotation (bottom). Note that usually only the end-point of the vector describing the eye position is shown, *not* the whole vector (bottom).

Hepp *et al.*, 1989; Tweed *et al.*, 1990) and papers in more technical journals (Rooney, 1977; Funda & Paul, 1988). The following description of quaternions will cover only the essential properties of quaternions which describe rotations.

A quaternion q which uniquely characterizes a rotation by an angle θ about an axis $\mathbf{n}$ is given by

$$q = q_0 + (q_1 * i + q_2 * j + q_3 * k) = q_0 + \mathbf{q} \cdot \mathbf{I}, \tag{16}$$

where

$$\mathbf{q} = \begin{pmatrix} q_1 \\ q_2 \\ q_3 \end{pmatrix} \text{ and } \mathbf{I} = \begin{pmatrix} i \\ j \\ k \end{pmatrix},$$

and $\{i, j, k\}$ are defined by

$$\begin{matrix} i \cdot i = -1, & j \cdot j = -1 & k \cdot k = -1 \\ i \cdot j = k, & j \cdot k = i & k \cdot i = j \\ j \cdot i = -k, & k \cdot j = -i & i \cdot k = -j \end{matrix} . \tag{17}$$

The elements $\{q_0, q_1, q_2, q_3\}$ have the following properties:

$$q_0 = \cos(\theta/2) \tag{18}$$

$$|\mathbf{q}| = \sqrt{q_1^2 + q_2^2 + q_3^2} = \sin(\theta/2)$$

$$\mathbf{q} \text{ is parallel to } \mathbf{n}$$

q_0 is often called the *scalar component of the quaternion q*, and $\mathbf{q}$ the *vector component of q*. $\mathbf{q}$ describes the eye position as shown in Fig. 6(B), with the length of the vector given by $\sin(\theta/2)$. It follows from equation (18) that quaternions describing rotations have the length 1, i.e. $\sqrt{q_0^2 + q_1^2 + q_2^2 + q_3^2} = 1$, and are thus called *unit quaternions*. In general, the length of a quaternion does not have to be 1. If it is different, then the quaternion describes a combined rotation and stretching of a vector (Rooney, 1977).

The connection between a quaternion q and a rotation matrix $\mathbb{R}$, both describing the rotation of a vector $\mathbf{x}$ about an axis $\mathbf{n}$ by an angle θ, can be derived from the definition of quaternions in equations (16)–(18)

$$q \circ (\mathbf{x} \cdot \mathbf{I}) \circ q^{-1} = (\mathbb{R} \cdot \mathbf{x}) \cdot \mathbf{I}. \tag{19}$$

Although the left side of equation (19) is a full quaternion, the scalar component evaluates to zero, and does not therefore appear on the right side. The inverse quaternion q^{-1} is for unit quaternions given by

$$q^{-1} = q_0 - \mathbf{q} \cdot \mathbf{I} \tag{20}$$

and the formula for the combination of two quaternions ($\circ$) is given below. For combined rotations, care has to be taken with the sequence of quaternions: if we describe the first rotation about $\mathbf{p}$ with the quaternion p, and the following rotation about the head-fixed axis parallel to $\mathbf{q}$ by the quaternion q, the combined rotation is given by

$$\begin{aligned} q \circ p &= \sum_{i=0}^{3} q_i I_i * \sum_{j=0}^{3} p_j I_j \\ &= (q_0 p_0 - \mathbf{q} \cdot \mathbf{p}) + (q_0 \mathbf{p} + p_0 \mathbf{q} + \mathbf{q} \times \mathbf{p}) \cdot \mathbf{I}. \end{aligned} \tag{21}$$

The right side of equation (21) is obtained by using the definitions of $\{i, j, k\}$ in equation (17). The sequence of the quaternions in equation (21) is important, and the opposite sequence, $p \circ q$, would lead to a different orientation of the eye, as has been shown in the previous chapter. For rotations about head-fixed axes, $\circ$ can be read as "after".

Rotation vectors and their relation to rotation matrices

Since the scalar-component of a unit quaternion does not contain any information that is not already given by the vector part, it can be eliminated by using *rotation vectors* instead of quaternions. The rotation vector $\mathbf{r}$, which corresponds to the quaternion q describing a rotation of θ about the axis $\mathbf{n}$, is given by

$$\mathbf{r} = \frac{\mathbf{q}}{q_0} = \tan(\theta/2) * \frac{\mathbf{q}}{|\mathbf{q}|} = \tan(\theta/2) * \mathbf{n}, \tag{22}$$

with $|\mathbf{q}|$ the length of $\mathbf{q}$ as defined in equation (18).

The development of this parametrization of rotations can probably be attributed to Rodrigues (1840), and the coefficients of the rotation vectors are sometimes referred to as *Euler–Rodrigues parameters* (Altmann, 1986, p. 20). One of the first to rediscover these parameters for the oculomotor field was Haustein (1989), whose paper also provides a good introduction to rotation vectors. The rotation vector corresponding to the rotation matrix $\mathbb{R}$ can be determined easily from the elements of the rotation matrix by

$$\mathbf{r} = \frac{1}{1 + (R_{11} + R_{22} + R_{33})} * \begin{pmatrix} R_{32} & - & R_{23} \\ R_{13} & - & R_{31} \\ R_{21} & - & R_{12} \end{pmatrix}. \tag{23}$$

To establish the relationship between rotation vectors and other descriptions of rotations such as Fick-angles, we have to know how to get the rotation vector for combined rotations. Using equations (21) and (22) we get

$$\mathbf{r}_q \circ \mathbf{r}_p = \frac{\mathbf{r}_q + \mathbf{r}_p + \mathbf{r}_q \times \mathbf{r}_p}{1 - \mathbf{r}_q \cdot \mathbf{r}_p} \tag{24}$$

where $\mathbf{r}_p$ is the first rotation (about an axis parallel to $\mathbf{r}_p$) and $\mathbf{r}_q$ the second rotation (about a head-fixed axis parallel to $\mathbf{r}_q$). For example, with

$$\mathbf{r}_p = \begin{pmatrix} 0 \\ 0.174 \\ 0 \end{pmatrix} \text{ and } \mathbf{r}_q = \begin{pmatrix} 0 \\ 0 \\ 0.087 \end{pmatrix}$$

equation (24) would describe a rotation of 20 deg about the interaural axis $\mathbf{h}_2$, followed by a rotation of 10 deg about the head-fixed yaw axis $\mathbf{h}_3$. According to our discussion above of active and passive rotations, the same formula can also be interpreted as a first rotation of 10 deg about the yaw axis $\mathbf{e}_3$, followed by a second rotation of 20 deg about the rotated, eye-fixed axis $\mathbf{e}_2$—which corresponds to the horizontal and vertical rotation in a Fick-gimbal. The rotation vector corresponding to the full Fick rotation matrix in equation (7) can be obtained by adding a third rotation about the (eye-fixed) line of sight, $\mathbf{e}_1$. Denoting a rotation vector which describes a rotation about an axis $\mathbf{n}$ by an angle θ with $\mathbf{r}(\mathbf{n}, \theta)$, this leads to

$$\mathbf{r} = \mathbf{r}(\mathbf{e}_3,\theta_F)\circ\mathbf{r}(\mathbf{e}_2,\phi_F)\circ\mathbf{r}(\mathbf{e}_1,\psi_F)$$
$$= \frac{1}{1+\tan(\theta_F/2)*\tan(\phi_F/2)*\tan(\psi_F/2)} * \begin{pmatrix} \tan(\psi_F/2) - \tan(\theta_F/2)*\tan(\phi_F/2) \\ \tan(\phi_F/2) + \tan(\theta_F/2)*\tan(\psi_F/2) \\ \tan(\theta_F/2) - \tan(\phi_F/2)*\tan(\psi_F/2) \end{pmatrix} \quad (25)$$

where θ_F, ϕ_F and ψ_F are the Fick-angles.

Close to the reference position, the relations between Fick-angles, Helmholtz-angles, rotation vectors and quaternions can be approximated by the simple formula

$$\begin{pmatrix}\psi\\ \phi\\ \theta\end{pmatrix}_{\text{Fick}} \approx \begin{pmatrix}\psi\\ \phi\\ \theta\end{pmatrix}_{\text{Helmholtz}} \approx 100 * \begin{pmatrix}r_1\\ r_2\\ r_3\end{pmatrix} \approx 100 * \begin{pmatrix}q_1\\ q_2\\ q_3\end{pmatrix} \quad (26)$$

where θ, ϕ and ψ are given in deg.

Donders' law and Listing's law

While looking at a small target, the position of the target determines the gaze direction, but does not specify the amount of ocular torsion about the line of sight. However, as Donders discovered, the torsional eye position is not arbitrary, but uniquely determined by the gaze direction (Donders, 1848). This principle has been called *Donders' law*. It is valid for an erect and stationary head, with the eyes looking at targets at infinity. *Listing's law* goes one step further, by specifying the amount of ocular torsion. Using rotation vectors or quaternions, Listing's law can be formulated very simply: all rotation vectors (or quaternions) characterizing 3D eye position lie closely scattered along a plane. Recordings of eye movements in humans and monkeys show that the standard deviation of rotation vectors describing eye positions from this plane is only about 0.5–1.0 deg. The best fit plane to these data is called *displacement plane* (Tweed *et al*., 1990). Figure 7 shows an example of such a plane. Expressing *the same* eye position data in either Fick- or Helmholtz-angles does *not* lead to data points that lie closely scattered along a plane, but instead to data points which lie on curved surfaces (Suzuki, Straumann, Hess & Henn, 1994).

The orientation of the displacement plane also depends on the reference position used to describe the eye positions. Figure 8 shows that shifting the reference position by 2α deg in any direction shifts the plane of the rotation vectors *describing exactly the same eye positions* by α deg in the same direction. Since we have defined our head-fixed coordinate system such that $\mathbf{h}_1$ is parallel to the line of sight of the eye in the reference position, a shift of the reference position by 2α also leads to a shift of the head-fixed coordinate system by the same amount in the same direction. For example, in Fig. 8(A) the displacement

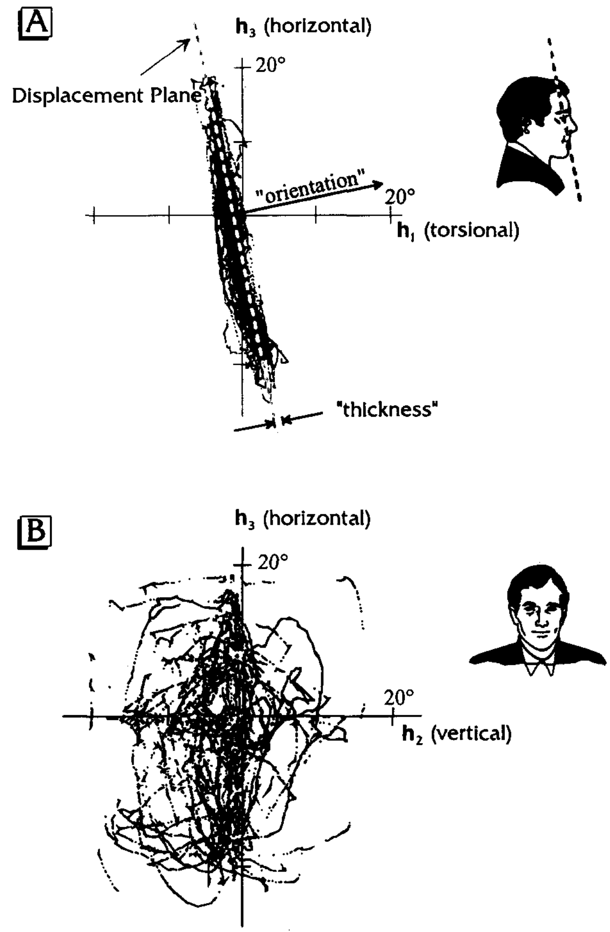

FIGURE 7. (A) Side view and (B) front view of rotation vectors, recorded while the subject was looking around in the light for 90 sec. The $\mathbf{h}_1$-component indicates torsional, the $\mathbf{h}_2$-component vertical, and the $\mathbf{h}_3$-component horizontal eye position. Only the end-points of the rotation vectors characterizing the eye positions are plotted, not the rotation vectors themselves. The reference position was looking straight ahead, and in (A) the best-fit plane (*displacement plane*) to the data is indicated.

plane is perpendicular to the reference position (and thus perpendicular to $\mathbf{h}_1$), and therefore coincides with the $\mathbf{h}_2$–$\mathbf{h}_3$ plane. In Fig. 8(B), the reference position (and thus the head-fixed coordinate system) has shifted 2α deg forward. Since the displacement plane tilts only α deg forward in space, it is now tilted α deg *backward* with respect to the head-fixed coordinate system. The net result is therefore a tilt of the displacement plane in the head-fixed coordinate system in the direction opposite to the shift of the reference position.

For every data-set there is one reference position such that the corresponding displacement plane is exactly perpendicular to the *reference gaze direction*, i.e. the line of sight of the eye in this reference position [Fig. 8(A)]. This position of the eye is termed the *primary position*, and the corresponding displacement plane is termed *Listing's plane*. Some researchers prefer to use the expression *Listing's plane* in a wider sense, and refer to any plane of rotation vectors or quaternions as Listing's plane. In this wider sense, the planes in Fig. 8(A, B, C) would all be Listing's planes. Using equation (24) it can be shown that the vector perpendicular to the displacement plane is

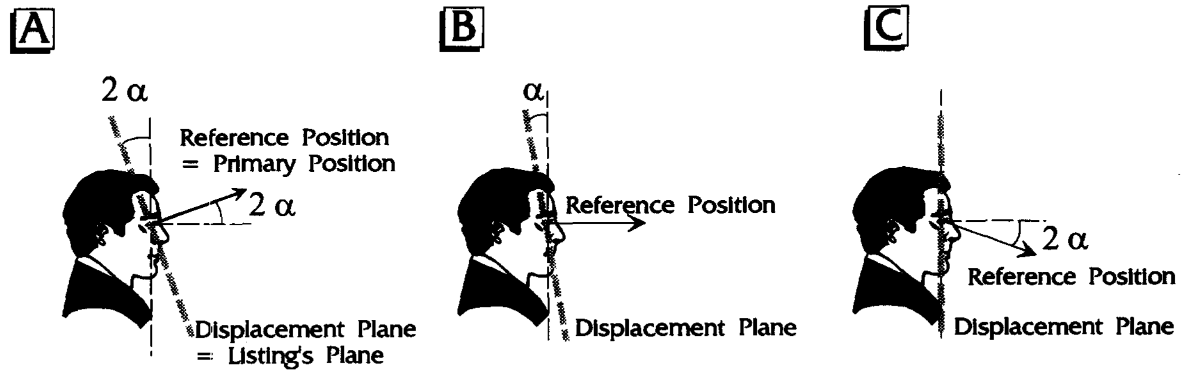

FIGURE 8. Expressing the *same* eye positions with respect to different reference positions leads to planes of rotation vectors with different orientations (displacement planes). (A) When the reference gaze direction is exactly perpendicular to the displacement plane, the reference position is called *primary position*, and the displacement plane *Listing's plane*. In this example, we show a subject whose primary gaze direction is 2α deg up. (B, C) Changing the orientation of the reference position by 2α deg leads to a shift of the displacement plane by α deg. The thin dashed lines indicate the earth horizontal and vertical axes.

exactly halfway between the primary gaze direction (i.e. the direction of the line of sight of the eye in the primary position) and the reference gaze direction (Tweed *et al.*, 1990).

From the description of eye position, we turn in the next section to the description of *eye movements* and *eye velocity*.

MATHEMATICAL DESCRIPTION OF EYE VELOCITY

Eye movements within Listing's plane

To begin with a specific example, consider an eye movement from right to left at an elevation of 20 deg up [Fig. 9(B, C), top row]. Both start and end position of the eye are *Listing's positions*: the rotation vector for the rotation from the reference position [Fig. 9(A)] to either of these positions [Fig. 9(B)] lies in Listing's plane. For simplicity we consider the case where Listing's plane is exactly upright, i.e. that the reference position is the primary position and Listing's plane coincides with the $\mathbf{h}_2$–$\mathbf{h}_3$ plane of our head-fixed coordinate system. About which axis must the eye rotate to get from the start position to the end position? From equation (24) one can derive that the eye must rotate about an axis that tilts 10 deg backward, in order to keep the eye in Listing's plane during the whole movement. Note that all rotation vectors describing the rotations from the fixed reference position to the current eye position lie within Listing's plane [Fig. 9(A)], while the rotation vectors describing rotations from one eye position at 20 deg elevation to another one tilt 10 deg out of Listing's plane [Fig. 9(B)].

From equation (24) we can derive that a purely horizontal eye movement from a start position

$$\mathbf{r}_s = \begin{pmatrix} 0 \\ a \\ b \end{pmatrix}$$

to an end-position

$$\mathbf{r}_e = \begin{pmatrix} 0 \\ a \\ c \end{pmatrix}$$

is described by the rotation vector

$$\mathbf{r}_{se} = \frac{c - b}{1 + a^2 + b{*}c} * \begin{pmatrix} a \\ 0 \\ 1 \end{pmatrix}. \tag{27}$$

This means that for a horizontal eye movement at an elevation α, the axis of eye velocity is tilted $\alpha/2$ deg backward. Note that neither $\mathbf{r}_s$, which describes the rotation from the reference position to the starting position, nor $\mathbf{r}_e$, which describes the rotation from the reference position to the end position, have a torsional component, i.e. a component along $\mathbf{h}_1$. Nevertheless $\mathbf{r}_{se}$, which characterizes the rotation from $\mathbf{r}_s$ to $\mathbf{r}_e$, does have such a component.

There are now two groups of rotation vectors: one which describes each eye position by characterizing the *hypothetical* rotation from a fixed reference position [Fig. 9(A)] to the current position [Fig. 9(B)]; and a second group which describes the *actual* rotation from one eye position to the next [Fig. 9(B, C)]. While all vectors of the former group lie in Listing's plane, rotation vectors of the latter group tilt in general out of Listing's plane. In our example, where the eye is elevated 20 deg, they tilt out of Listing's plane by 10 deg. This is a specific example of the more general rule that when Listing's law holds, the axis of eye velocity always lies in a plane with the following properties: the orientation of this plane depends on the current eye position (i.e. its orientation changes when the eye position changes), and is such that the vector perpendicular to the plane is exactly halfway between the current gaze direction and the primary gaze direction (Tweed *et al.*, 1990).

The axis of the vector describing the eye rotation from one position (e.g. our start position) to the next (e.g. our end position) is also the axis of average eye velocity

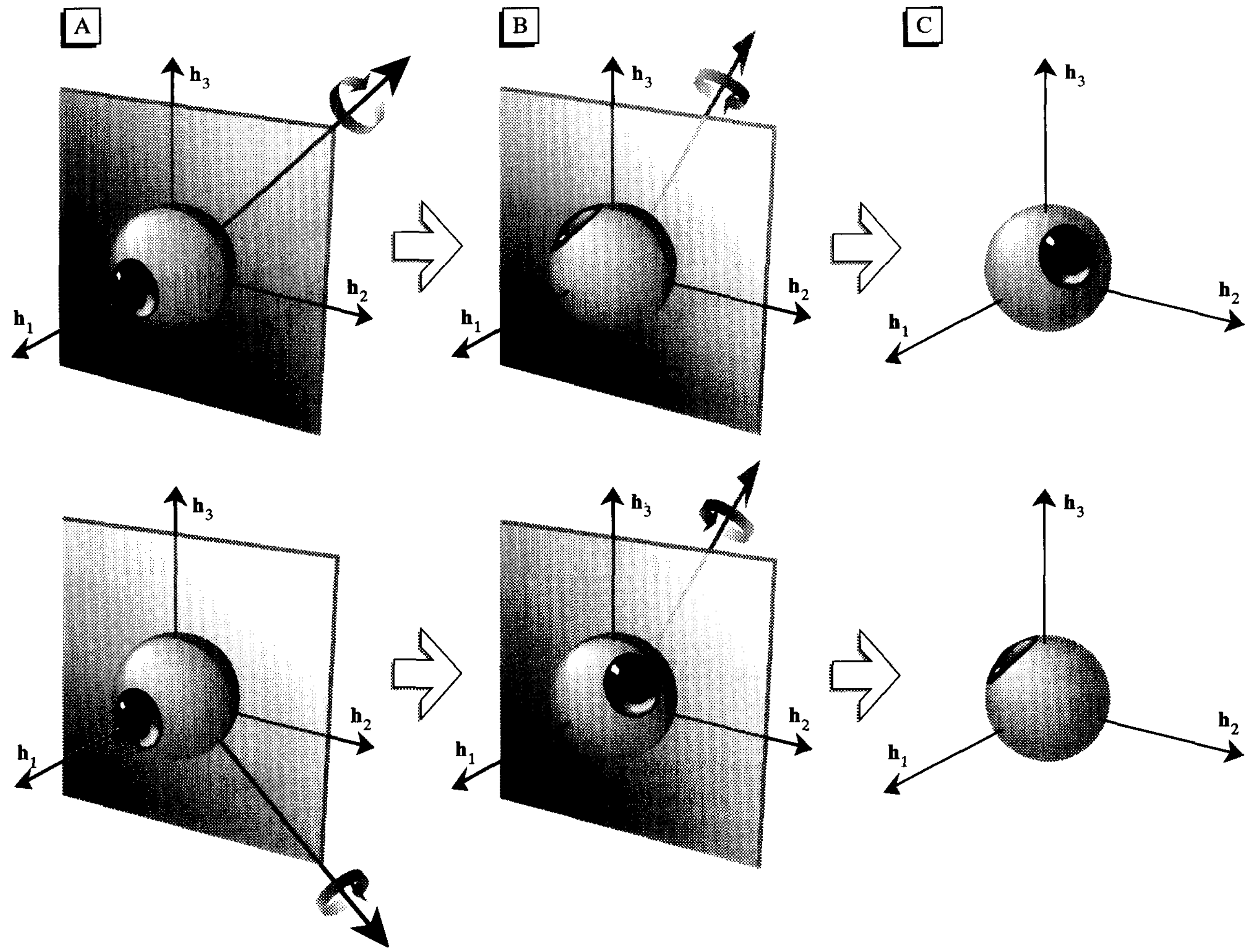

FIGURE 9. (A) Eye in the reference position. (B) Eye positions which have been reached from the reference position by a rotation about the axes indicated with solid arrows in (A). Note that all these axes lie in Listing's plane, indicated by the shaded plane. To get from (B) to a different eye position at the same elevation (C), the eye has to rotate about an axis which does *not* lie in Listing's plane, but tilts out of Listing's plane as indicated by the vectors in (B).

during that movement.† Tweed and Vilis (1990) have shown that during saccades with the head stationary, the eye actually does stay in Listing's plane, and the axis of eye velocity moves out of Listing's plane for saccades from one *tertiary position* (i.e. an eye position with horizontal and vertical components) to another. Minken, Van Opstal and Van Gisbergen (1993) have extended this finding by showing that Listing's law holds even for curved saccades.

In summary, for Listing's law to hold the axis of eye velocity does in general *not* lie in Listing's plane, although all rotation vectors describing eye positions do.

Determination of eye velocity

As pointed out previously, rotation vectors describing eye positions depend on the choice of the reference position. In contrast, the eye velocity does *not* depend on the reference position, since it only describes the movement from the current eye position to the next, which does not involve the reference position.

The simplest formula describing the eye velocity $\boldsymbol{\omega}$ is given in the quaternion notation (Tweed & Vilis, 1987):

$$\omega = 2 * \frac{\mathrm{d}q}{\mathrm{d}t} \circ q^{-1} \tag{28}$$

where $\omega = (0, \boldsymbol{\omega})$ is a quaternion, with $\boldsymbol{\omega}$ the common eye velocity vector. Note that the angular eye velocity depends not only on the time derivative $\mathrm{d}q/\mathrm{d}t$ of the eye position, but also on the current eye position q itself.

Expressed in rotation vectors (Hepp, 1990), equation (28) is equivalent to

$$\boldsymbol{\omega} = 2 * \frac{\frac{\mathrm{d}\mathbf{r}}{\mathrm{d}t} + \mathbf{r} \times \frac{\mathrm{d}\mathbf{r}}{\mathrm{d}t}}{1 + \mathbf{r}^2}. \tag{29}$$

A more complex formula is required if angular velocity is expressed in Fick-angles (Goldstein, 1980):

$$\boldsymbol{\omega} = \begin{bmatrix} \frac{\mathrm{d}\psi_F}{\mathrm{d}t}*\cos(\theta_F)*\cos(\phi_F) & -\frac{\mathrm{d}\phi_F}{\mathrm{d}t}*\sin(\theta_F) \\ \frac{\mathrm{d}\phi_F}{\mathrm{d}t}*\cos(\theta_F) & +\frac{\mathrm{d}\psi_F}{\mathrm{d}t}*\sin(\theta_F)*\cos(\phi_F) \\ \frac{\mathrm{d}\theta_F}{\mathrm{d}t} & -\frac{\mathrm{d}\psi_F}{\mathrm{d}t}*\sin(\phi_F) \end{bmatrix}. \tag{30}$$

†In real saccades the axis of eye velocity is often not constant throughout the saccades (Bains, Crawford, Cadera & Vilis, 1992).

Equations (28)–(30) are equivalent, as they express the same eye velocity in different coordinate systems. The time derivatives of the eye-coordinates—dq/dt for quaternions, for $d\mathbf{r}/dt$ rotation vectors, and $\{d\theta/dt, d\phi/dt, d\psi/dt\}$ for Fick-angles—are often referred to as *coordinate velocity*. This coordinate velocity obviously depends on the parameters chosen to describe the eye position. In contrast, the eye velocity vector $\boldsymbol{\omega}$ describes the actual eye movement, with its axis given by the instantaneous axis of eye rotation and its length by the angular velocity of this rotation, and does not depend on the parametrization of the eye position. The preceding formulas also show that the coordinate velocity is in general not equivalent to the angular velocity $\boldsymbol{\omega}$.

APPLICATIONS

Combined eye–head movements

Using dual search coils, one can directly measure the orientation of the eye in space, often called *gaze*, and the orientation of the head in space. How can the formulas given above be used to derive from these data the position of the eye in the head?

Let $\mathbb{R}_{head}$ be the rotation matrix describing the rotation of the head in a head-fixed reference system, and $\mathbb{R}_{eye}$ describe the rotation of the eye in the head. From a geometric point of view, we first rotate the head, and then the eye in the (now rotated) head. In other words, we use *passive rotations* or *rotations of the coordinate system*. This determines the sequence of the two rotations, and the rotation matrix describing the gaze rotation, $\mathbb{R}_{gaze}$, is—according to the discussion following equations (5) and (6)—given by

$$\mathbb{R}_{gaze} = \mathbb{R}_{head} \cdot \mathbb{R}_{eye}. \tag{31}$$

Using rotation vectors, equation (31) can be expressed as

$$\mathbf{r}_{gaze} = \mathbf{r}_{head} \circ \mathbf{r}_{eye}. \tag{32}$$

This can be rearranged to yield the rotation vector describing the position of the eye in the head, $\mathbf{r}_{eye}$, as

$$\mathbf{r}_{eye} = \mathbf{r}_{head}^{-1} \circ \mathbf{r}_{gaze}. \tag{33}$$

The formula for the combination of two rotation vectors is given by equation (24), and the inverse of a rotation vector can be determined easily by $\mathbf{r}^{-1} = -\mathbf{r}$.

Three-dimensional vestibulo-ocular reflex

Imagine a person sitting upright on a stationary turntable and looking straight ahead. Since Listing's plane is in general not exactly upright, let the person have a displacement plane that is tilted α deg backward from the earth vertical, as shown in Fig. 10. Furthermore, let the eye be in the reference position when the subject is looking straight ahead. As noted in the section on Listing's law, the primary position is in this case tilted 2α deg up with respect to the earth horizontal. What happens when this person is accelerated about the earth vertical axis? In general, the eye won't rotate about exactly the same axis as the head, ω_{head}, but about a different axis, ω_{eye}. It has to choose between two strategies: on the one hand, it would have to rotate exactly about the earth-vertical axis to compensate accurately for the head movement; on the other hand, it would have to rotate about an axis that lies in the displacement plane for Listing's law to hold during horizontal eye movements. Note that for different elevations of the eye, the axis about which the eye has to rotate changes with the elevation of the eye if Listing's law is to be conserved (Crawford & Vilis, 1991). Which strategy does the eye choose? Investigations by Fetter, Tweed, Misslisch, Fischer and König (1992) indicate that a compromise strategy is chosen, and the eye rotates about an axis that is tilted by $\alpha/2$ deg, i.e. an axis which lies halfway between the displacement plane and the earth-vertical axis. In other words, if the axis of head rotation is not exactly perpendicular to the primary position, the eye will not rotate about the same axis as the head, and eye movements will not fully compensate for the head rotation.

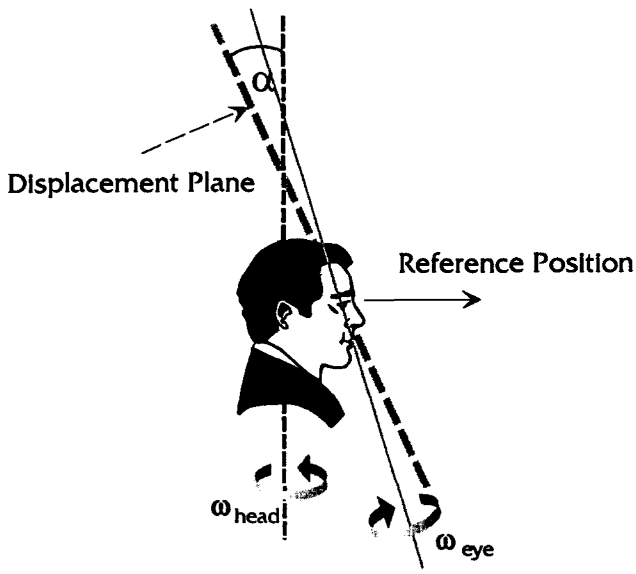

FIGURE 10. Side view of a person whose displacement plane is tilted α deg backward. When the person is rotated about an earth vertical axis, the axis of eye velocity for eye movements elicited by the vestibulo-ocular reflex, ω_{eye}, does not coincide exactly with the axis of head velocity, ω_{head}.

Side-view of Listing's plane

In general, the reference position for eye movements does not coincide with the primary position, and Listing's plane does not line up with the $\mathbf{h}_2$–$\mathbf{h}_3$ plane of the head-fixed coordinate system. To have Listing's plane aligned with the $\mathbf{h}_2$–$\mathbf{h}_3$ plane, one has to rotate the head-fixed coordinate system such that the primary position of the eye corresponds to the zero-rotation vector, and the primary gaze direction coincides with the $\mathbf{h}_1$ axis. Once this is done, a side view of Listing's plane can be obtained by plotting the components of the rotation vector corresponding to horizontal or vertical eye position (r_3 or r_2) vs the component corresponding to the torsional eye position (r_1).

The situation is similar to the "eye in head" problem dealt with above: there, we wanted to separate the rotation from the reference position to the current gaze-position into first a rotation of the head, and then a rotation of the eye within the (rotated) head. Here we want to separate the rotation from the reference position to the current eye position, $\mathbf{r}_{rp\to cp}$, into first a rotation from the reference position to the primary position, $\mathbf{r}_{rp\to pp}$, and then a rotation from the primary position to the current eye position, $\mathbf{r}_{pp\to cp}$. In analogy to equation (33) we can write

$$\mathbf{r}_{pp\to cp} = \mathbf{r}_{rp\to pp}^{-1} \circ \mathbf{r}_{rp\to cp}. \tag{34}$$

If the displacement plane is described by the equation

$$r_1 = \text{offset} + a_y * r_2 + a_z * r_3 \tag{35}$$

where *offset* is the intersection of the displacement plane with the $\mathbf{h}_1$ axis, and

$$\begin{pmatrix} 1 \\ -a_y \\ -a_z \end{pmatrix}$$

is the vector that characterizes the orientation of the plane as shown in Fig. 7, then one can show that $\mathbf{r}_{rp\to pp}$ is given by

$$\mathbf{r}_{rp\to pp} \begin{pmatrix} \text{offset} \\ a_z \\ -a_y \end{pmatrix} \tag{36}$$

CONCLUDING REMARKS

Full understanding of the vestibular system or the oculomotor system requires 3D stimuli, and the measurement and analysis of 3D eye movements. While rotation matrices are an easy way to establish a correspondence between measured values (e.g. search coil voltages) and the rotation of the eye from a reference position to the current position, rotation vectors and quaternions have proven to be more intuitive and efficient. They are non-redundant, using three parameters to describe the three degrees of freedom of rotations; they don't require an arbitrarily chosen sequence of rotations, but describe eye position by a single rotation from the reference position to the current position; they form an intuitive way of parametrizing rotations by expressing them by their axis and size; they allow for an easy combination of rotations; and they permit descriptions and tests of Listing's law in a simple way. But while rotation vectors and quaternions offer many advantages, there are still some situations where the Fick- or Helmholtz-coordinate system may be more appropriate. For example, Fick-angles may be more useful for the description of large gaze shifts (Glenn & Vilis, 1992), and Helmholtz-coordinates may have advantages for the description of conjugate eye movements (Collewijn, 1994). The methods and techniques used for the description of 3D eye movements have also been applied to other motor systems, and have proven useful to find and to describe control strategies for head and arm movements (Straumann *et al.*, 1991; Hore *et al.*, 1992; Miller *et al.*, 1993).

REFERENCES

Altmann, S. L. (1986). *Rotations, quaternions and double groups*. Oxford: Clarendon Press.

Bains, R. A., Crawford, J. D., Cadera, W. & Vilis, T. (1992). The conjugacy of human saccadic eye movements. *Vision Research, 32*, 1667–1684.

Brand, L. (1948). *Vector and tensor analysis* (Chap. 10). New York: Wiley.

Clarke, A. H., Teiwes, W. & Scherer, H. (1991). Videooculography—an alternative method for measurement of three-dimensional eye movements. In Schmidt, R. & Zambarbieri, D. (Eds), *Oculmotor control and cognitive processes* (pp. 431–443). Amsterdam: Elsevier.

Collewijn, H. (1994). Vertical conjugacy: What coordinate system is appropriate? In Fuchs, A. F., Brandt, T., Büttner, U. & Zee, D. (Eds), *Contemporary ocular motor and vestibular research: A tribute to David A. Robinson* (pp. 296–303). Stuttgart: Georg Thieme.

Collewijn, H., Van der Steen, J., Ferman, L. & Jansen, T. C. (1985). Human ocular counterroll: Assessment of static and dynamic properties from electromagnetic scleral coil recordings. *Experimental Brain Research, 59*, 185–196.

Crawford, J. D. & Vilis, T. (1991). Axes of eye rotation and Listing's law during rotations of the head. *Journal of Neurophysiology, 65*, 407–423.

Donders, F. C. (1848). Beitrag zur Lehre von den Bewegungen des menschlichen Auges. *Holländische Beiträge zu den anatomischen und physiologischen Wissenschaften, 1*, 104–145.

Enright, J. T. (1980). Ocular translation and cyclotorsion due to changes in fixation distance. *Vision Research, 20*, 595–601.

Enright, J. T. (1984). Saccadic anomalies: Vergence induces large departures from ball and socket behaviour. *Vision Research, 24*, 301–308.

Euler, L. (1775). Formulae generales pro translatione quacunque corporum rigidorum. *Commentarii Academiae Scientiarum Imperialis Petropolitanae, 20*, 189–207.

Fetter, M., Tweed, D., Misslisch, H., Fischer, D. & König, E. (1992). Multidimensional descriptions of the optokinetic and vestibulo-ocular reflexes. *Annals of the New York Academy of Science, 656*, 841–842.

Fick, A. (1854). Die Bewegungen des menschlichen Augapfels. *Zeitschrift für rationelle Medizin, 4*, 109–128.

Funda, J. & Paul, R. (1988). A comparison of transforms and quaternions in robotics. *IEEE Transactions on Robotics and Automation, 7*, 886–891.

Glenn, B. & Vilis, T. (1992). Violations of Listing's law after large eye and head gaze shifts. *Journal of Neurophysiology, 68*, 309–318.

Goldstein, H. (1980). *Classical mechanics* (2nd edn). Reading, Mass.: Addison-Wesley.

Hamilton, W. R. (1899). *Elements of quaternions*. Cambridge: Cambridge University Press.

Haustein, W. (1989). Considerations on Listing's Law and the primary position by means of a matrix description of eye position control. *Biological Cybernetics, 60*, 411–420.

von Helmholtz, H. (1866). *Handbuch der Physiologischen Optik*. Leipzig: Voss. English translation: *Helmholtz' treatise on physiological optics*. New York: Dover (1962).

Hepp, K. (1990). On Listing's law. *Communications on Mathematical Physics, 132*, 285–292.

Hepp, K., Henn, V., Vilis, T. & Cohen, B. (1989). Brainstem regions related to saccade generation. In *The neurobiology of saccadic eye movements* (pp. 106–112). Amsterdam: Elsevier

Hess, B. J. M., Van Opstal, A. J., Straumann, D., Hepp, K. & Henn, V. (1992). Calibration of three-dimensional eye position using search coil signals in the rhesus monkey. *Vision Research, 32*, 1647–1654.

Hore, J., Watts, S. & Vilis, T. (1992). Constraints on arm position when pointing in three dimensions: Donders' Law and the Fick gimbal strategy. *Journal of Neurophysiology, 68*, 374–383.

Miller, L. E., Theeuwen, M. & Gielen, C. C. A. M. (1993). The control of arm pointing movements in three dimensions. *Experimental Brain Research, 90*, 415–426.

Minken, A. W. H., Van Opstal, A. J. & Van Gisbergen, J. A. M. (1993). Three-dimensional analysis of strongly curved saccades elicited by double-step stimuli. *Experimental Brain Research*, *93*, 521–533.

Moore, S. T., Curthoys, I. S. & McCoy, S. G. (1991). VTM—an image-processing system for measuring ocular torsion. *Computer Methods and Programs in Biomedicine*, *35*, 219–230.

Nakayama, K. (1974). Photographic determination of the rotational state of the eye using matrices. *American Journal of Optometry and Physiological Optics*, *51*, 736–742.

Ott, D., Gehle, F. & Eckmiller, R. (1990). Video-oculographic measurement of 3-dimensional eye rotations. *Journal of Neuroscience Methods*, *35*, 229–234.

Robinson, D. A. (1963). A method of measuring eye movement using a scleral search coil in a magnetic field. *IEEE Transactions on Biomedical Electronics*, *BME-10*, 137–145.

Rodrigues, O. (1840). Des lois géométriques qui régissent les déplacements d'un système solide dans l'espace, et de la variation des coordonnées provenant de ses déplacements considérés indépendamment des causes qui peuvent les produire. *Journal de Mathêmatiques Pures et Appliquées*, *5*, 380–440.

Rooney, J. (1977). A survey of representation of spatial rotation about a fixed point. *Environment and Planning B*, *4*, 185–210.

Straumann, D., Haslwanter, T., Hepp-Reymond, M. C. & Hepp, K. (1991). Listing's law for eye, head and arm movements and their synergistic control. *Experimental Brain Research*, *86*, 209–216.

Suzuki, Y., Straumann, D., Hess, B. J. M. & Henn, V. (1994). Changes of Listing's plane under physiological and pathological conditions. In Delgado-Garcia, J. M., Godaux, E. & Vidal, P. P. (Eds), *Information processing underlying gaze control* (pp. 75–86). Oxford: Pergamon.

Tweed, D. & Vilis, T. (1987). Implications of rotational kinematics for the oculomotor system in three dimensions. *Journal of Neurophysiology*, *58*, 832–849.

Tweed, D. & Vilis, T. (1990). Geometric relation of eye position and velocity vectors during saccades. *Vision Research*, *30*, 111–127.

Tweed, D., Cadera, W. & Vilis, T. (1990). Computing three-dimensional eye position quaternions and eye velocity from search coils signals. *Vision Research*, *30*, 97–110.

Van Opstal, J. (1993). Representation of eye position in three dimensions. In Berthoz, A. (Ed.), *Multisensory control of movement* (pp. 27–41). Oxford: Oxford University Press.

Vieville, T. & Masse, D. (1987). Ocular counter-rolling during active head tilting in humans. *Acta Otolaryngolica*, *103*, 280–290.

Westheimer, G. (1957). Kinematics of the eye. *Journal of the Optical Society of America*, *47*, 967–974.

Acknowledgements—I want to express my sincere gratitude to I. S. Curthoys for his support and valuable comments. This work was supported by NH & MRC of Australia, grant 920205.

APPENDIX

(i) The *scalar product* of two vectors **a** and **b** is defined as

$$\begin{pmatrix} a_1 \\ a_2 \\ a_3 \end{pmatrix} \cdot \begin{pmatrix} b_1 \\ b_2 \\ b_3 \end{pmatrix} = a_1b_1 + a_2b_2 + a_3b_3. \tag{A1}$$

(ii) The *cross product* of two vectors **a** and **b** is defined as

$$\begin{pmatrix} a_1 \\ a_2 \\ a_3 \end{pmatrix} \times \begin{pmatrix} b_1 \\ b_2 \\ b_3 \end{pmatrix} = \begin{pmatrix} a_2b_3 - a_3b_2 \\ a_3b_1 - a_1b_3 \\ a_1b_2 - a_2b_1 \end{pmatrix}. \tag{A2}$$

The resulting vector is perpendicular to a and b, and vanishes if a and b are parallel.

(iii) In general, the *multiplication of two matrices* A and B is defined as

$$\mathrm{A} \cdot \mathrm{B} = \mathrm{C} \tag{A3}$$

with

$$C_{ik} = \sum_j = A_{ij}B_{jk}.$$

This equation can also be used for multiplication of a matrix with a vector, when the vector is viewed as a matrix with three rows and one column.

(iv) Using equation (A3), and inserting equations (2)–(4) into equation (7), $\mathbb{R}_{\mathrm{Fick}}$ can be obtained as

$$\mathbb{R}_{\mathrm{Fick}} = \begin{bmatrix} \cos(\theta_F)\cos(\phi_F) & \cos(\theta_F)\sin(\phi_F)\sin(\psi_F) - \sin(\theta_F)\cos(\psi_F) & \cos(\theta_F)\sin(\phi_F)\cos(\psi_F) + \sin(\theta_F)\sin(\psi_F) \\ \sin(\theta_F)\cos(\phi_F) & \sin(\theta_F)\sin(\phi_F)\sin(\psi_F) + \cos(\theta_F)\cos(\psi_F) & \sin(\theta_F)\sin(\phi_F)\cos(\psi_F) - \cos(\theta_F)\sin(\psi_F) \\ -\sin(\phi_F) & \cos(\phi_F)\sin(\psi_F) & \cos(\phi_F)\cos(\psi_F) \end{bmatrix}. \tag{A4}$$

In the same way, $\mathbb{R}_{\mathrm{Helmholtz}}$ can be obtained from equation (8) by matrix multiplication as

$$\mathbb{R}_{\mathrm{Helmholtz}} = \begin{bmatrix} \cos(\theta_H)\cos(\phi_H) & -\sin(\theta_H)\cos(\phi_H)\cos(\psi_H) + \sin(\phi_H)\sin(\psi_H) & \sin(\theta_H)\cos(\phi_H)\sin(\psi_H) + \sin(\phi_H)\cos(\psi_H) \\ \sin(\theta_H) & \cos(\theta_H)\cos(\psi_H) & -\cos(\theta_H)\sin(\psi_H) \\ -\cos(\theta_H)\sin(\phi_H) & \sin(\theta_H)\sin(\phi_H)\cos(\psi_H) + \cos(\phi_H)\sin(\psi_H) & -\sin(\theta_H)\sin(\phi_H)\sin(\psi_H) + \cos(\phi_H)\cos(\psi_H) \end{bmatrix}. \tag{A5}$$

Care has to be taken, because the exact form of the rotation matrices depends on the definition of $\mathbb{R}$, and definitions different from equation (1) can lead to matrices which are the transpose of the matrices in equations (A4) and (A5).

(v) Expressing the components of a rotation vector in the corresponding Fick-angles leads to equation (25). In an analogous manner, these components can be expressed in Helmholtz-angles, which gives

$$\mathbf{r} = \mathbf{r}(\mathbf{e}_2,\phi_H)\circ\mathbf{r}(\mathbf{e}_3,\theta_H)\circ\mathbf{r}(\mathbf{e}_1,\psi_H) = \frac{1}{1 - \tan(\theta_F/2) * \tan(\phi_F/2) * \tan(\psi_F/2)} * \begin{pmatrix} \tan(\psi_F/2) + \tan(\theta_F/2) * \tan(\phi_F/2) \\ \tan(\phi_F/2) + \tan(\theta_F/2) * \tan(\psi_F/2) \\ \tan(\theta_F/2) - \tan(\phi_F/2) * \tan(\psi_F/2) \end{pmatrix}. \tag{A6}$$