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COMPUTING THREE-DIMENSIONAL EYE POSITION QUATERNIONS AND EYE VELOCITY FROM SEARCH COIL SIGNALS

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Abstract—The four-component rotational operators called quaternions, which represent eye rotations in terms of their axes and angles, have several advantages over other representations of eye position (such as Fick coordinates): they provide easy computations, symmetry, a simple form for Listing's law, and useful three-dimensional plots of eye movements. In this paper we present algorithms for computing eye position quaternions and eye angular velocity (not the derivative of position in three dimensions) from two search coils (not necessarily orthogonal) on one eye in two or three magnetic fields, and for locating primary position using quaternions. We show how differentiation of eye position signals yields poor estimates of all three components of eye velocity.

Eye movements   Search coils   Eye torsion   Listing's law   Quaternions

INTRODUCTION

The eyes rotate with 3 degrees of freedom: horizontal, vertical and torsional (Nagel, 1871; Diamond, Markham, Simpson & Curthoys, 1979; Collewijn, Van der Steen, Ferman & Jansen, 1985). A complete and accurate treatment of many oculomotor questions therefore calls for a three-dimensional approach. However, the mathematics for the convenient measurement and representation of three-dimensional rotations is not commonly used by oculomotor physiologists. The aim of this paper is to present a number of techniques and computer algorithms for recording and analysing eye movements in three dimensions using the search coil method (Robinson, 1963).

The paper describes algorithms for computing eye position and eye velocity (not the derivative of position in three dimensions), for locating primary position and Listing's plane, and for converting data so that eye positions are expressed relative to primary position. The computations use the signals from two search coils on one eye in two or three magnetic field. The coils need not be orthogonal, nor need their locations on the eye be known, so the method can be used with experimental animals, where the coils are sutured separately onto the sclera and placement may be arbitrary. For human subjects, we use the Skalar annulus, a silicone rubber ring which contains two effectively orthogonal search coils and adheres to the sclera by suction. Preliminary results of this work have been reported (Tweed & Vilis, 1987b).

Quaternions and eye position

Our technique for computing eye position differs from the one published by the inventors of the Skalar ring (Ferman, Collewijn, Jansen & Van den Berg, 1987a), because it computes a different representation for angular position. Ferman et al. computed eye position in Fick coordinates, as did Robinson in his original exposition of the search coil technique (1963). But there is no particular mathematical connection between Fick coordinates and the search coil method; we shall show, in fact, that the search coil method lends itself most naturally to treatment using rotation matrices. Nor is the Fick system the most convenient or meaningful representation of eye position; we shall argue that a representation using the four-component rotational operators called quaternions has several advantages. Accordingly, in this paper we use rotation matrices to compute eye position quaternions.

What is the quaternion representation of eye position? A quaternion is a four-component object which can be regarded as the sum of a scalar and a vector: $q = q_0 + \mathbf{q}$. If the eye is displaced from primary position by a rotation of a degrees, and $\mathbf{n}$ is the vector of length 1 lying along the rotation axis, oriented so that the rotation is clockwise when viewed in the direction of $\mathbf{n}$ (or in other words so that when the right thumb points in the direction of $\mathbf{n}$, the fingers curl round in the direction the eye has turned), then we associate with the eye position the quaternion:

$$q = \cos(a/2) + \sin(a/2)\mathbf{n}. \quad (1)$$

This representation may look mysterious at first. The reason is that unlike the Fick or Helmholtz coordinates, quaternions were not invented solely for the purpose of representing angular position: they were invented for their elegant algebra. As a result, while quaternions reflect the algebraic properties of rotations more neatly than the other systems, their expression for a rotation may not seem as natural at first. However, it is easy to get a feel for quaternions because they closely resemble the intuitive representation of rotations in terms of axis and angle: the vector part of the quaternion, $\sin(a/2)\mathbf{n}$, lies along the axis of the rotation and its length, $\sin(a/2)$, is a function of the rotation angle (a near-linear function for angles of less than about 60 deg).

The major advantage of the quaternion representation of eye position is its computational efficiency, especially for questions involving rotation axes and amplitudes—questions which are important to understanding the oculomotor system (Tweed & Vilis, 1987a). For example, questions involving Listing's Law take a very simple form when expressed in terms of quaternions (Westheimer, 1957). (See the Appendix for an introduction to quaternion algebra.) But computation aside, quaternions have at least two further advantages over the widely-used Fick system.

One advantage is symmetry. The Fick system is asymmetric in that it defines the horizontal component of eye position with respect to a head-fixed axis, but the torsional component with respect to an axis fixed in the eye. If experiments show that these two components behave differently, it may not be clear to what extent the asymmetric definitions are responsible. In the quaternion representation all components were defined using a single rotation axis, $\mathbf{n}$, expressed in head coordinates.

The other advantage concerns three-dimensional position plots of movement trajectories. Clearly, the three Fick coordinates could be regarded as a vector, which could be plotted three-dimensionally, but the plotted points would have little geometric meaning. In contrast, we can see from equation (1) that a plot of quaternion vectors would depict the instantaneous rotational displacement of the eye from primary position in terms of axis and amplitude, the plotted vector lying along the axis, and its length a function of the amplitude.

METHODS

Data acquisition

Eye movements were recorded from three adult male human subjects and three *Macaca fascicularis* monkeys. In humans, the position of the left eye was monitored using the Skalar annulus. Each human subject sat with his left eye at the centre of curvature of a black hemispheric dome of radius 1 m, his head stabilized with a bite board. The subject's head was positioned with the sagittal plane vertical, and the angle of pitch was measured to help in later localization of Listing's plane. The subject viewed the fixation target, a small LED on the dome or screen, with both eyes. To elicit a saccade, a computer switched off the LED and switched on another. At the same time, it triggered a data collection program.

The subject's left eye was at the centre of three orthogonal alternating magnetic fields (frequencies: 62.5, 125, 250 kHz). Three voltages from each coil—six channels in all—were sampled 100 or 1000 times/sec. After low-pass filtering (3 dB, 500 Hz), data were digitized and stored on disk. Eye position quaternions and eye velocity were computed off line as described under *Kinematic analysis*.

Data acquisition was identical for the monkey subjects, with the following exceptions. The monkeys had two enameled copper eye coils of 5 mm diameter sutured to the sclera of one eye. Positions of the coils on the eye are not important for the accuracy of the measurements: for ideal data, noise- and distortion-free, our algorithm is indifferent to coil placement, as long as the coils are not parallel. In the presence of electronic noise, however, the sensitivity of the system is greatest when the coils are placed orthogonal to one another. Monkeys in this study had the coils placed on the medial surface of the globe, one pointing up and the other down with relative angles ranging from 84 to 91 deg. Each monkey sat in a primate chair 1 m from a black tangent screen, its head fixed to the chair using an acrylic skull cap. When the monkey made a saccade to the target LED

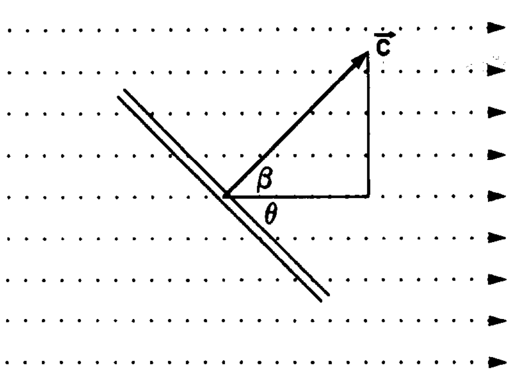

Fig. 1. The voltage recorded from a search coil in a magnetic field is proportional to the component of a unit vector c, orthogonal to the coil plane, in the direction of the field.

within a spatial and temporal window, it was rewarded with a drop of grape drink.

Kinematic analysis

The aim of this section is to compute the angular position quaternion and the angular velocity vector of the eye using two search coils on one eye in three orthogonal magnetic fields. A useful intermediate step in both computations is the calculation of the 3×3 rotation matrix that represents the displacement of the eye, at any moment, from some reference position. Interestingly, the search coil method turns out to lend itself naturally to the determination of rotation matrices, and it is for this reason, even more than for their intrinsic usefulness, that these matrices enter into our analysis.

To see the close connection between rotation matrices and the search coil method we must recall what the signal from a search coil represents. From Robinson's original paper on the method (1963), we know that the signal Y from an eye coil in an alternating horizontal magnetic field is:

$$Y = G_Y \sin\theta; \qquad (2)$$

where G_Y is a constant which depends on the coil and the field, and θ is the angle between the plane of the coil and the direction of the field (Fig. 1). We shall find it convenient to consider a vector **c**, of length 1, perpendicular to the plane of the coil. In Fig. 1, the coil is seen edge-on and our line of sight is perpendicular to the horizontal field direction. It is clear that:

$$Y = G_Y \sin\theta = G_Y \cos\beta; \qquad (3)$$

where β is the angle between **c** and the field. Equivalently, Y is the projection or component of **c** along the direction of the field. Similarly, the vertical signal Z from the coil is the component of **c** along the direction of the vertical field, times some gain factor G_Z. With a third field in the X direction, orthogonal to Y and Z, we can find all three components of **c**:

$$c_1 = X/G_X \quad c_2 = -Y/G_Y \quad c_3 = Z/G_Z; \qquad (4)$$

(see Fig. 2). (In practice, magnetic field strengths were adjusted so that the three gains were equal: $G_X = G_Y = G_Z$.)

If there are only two fields, the third component can often be computed; for example, if we know from the location of the coil that c_1 will always be positive within the oculomotor range, then $c_1 = \sqrt{(1 - c_2c_2 - c_3c_3)}$. With the three-field system, **c** can actually be computed from X, Y and Z knowing only the ratios of the three Gs and not their absolute magnitudes, because if the gains were accidentally scaled wrong, by some common factor k, then **c** would have magnitude k, and normalization would remove the scaling. In contrast, with a two-field system the absolute magnitudes of the two gains must be known. This difference may be of practical importance, because warping of the coils on the eye, which could conceivably occur during an experiment, would be expected to change the absolute values of the gains but not their ratio.

The coordinate system in equation (4) is defined by the magnetic fields. The Y axis is aligned with the horizontal field and the Z axis with the vertical field; the X axis is orthogonal

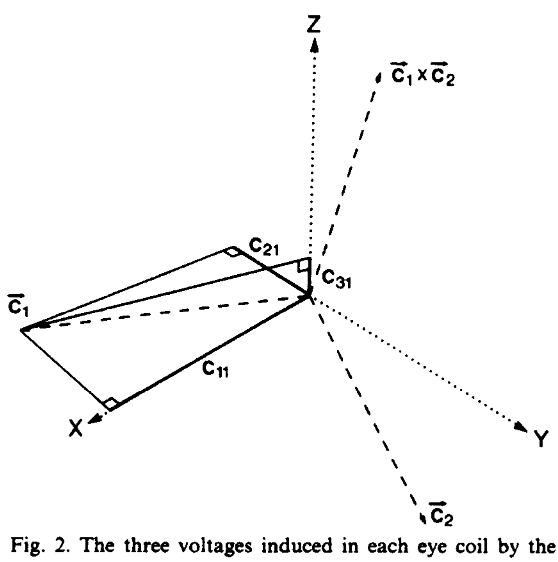

Fig. 2. The three voltages induced in each eye coil by the three magnetic fields are proportional to the components of the associated coil vector **c** in the field directions. From two such vectors and their cross product, one can compute the orientation of the eye.

to both. As might be expected, the positive X direction is forward and the positive Z direction is up. But to get a righthanded coordinate system, we make left the positive Y direction, somewhat contrary to the convention that horizontal signals be positive for deviations to the right. For this reason, the sign of c_2 is opposite that of Y.

If there are two coils on the eye (not necessarily orthogonal), we can compute two unit vectors $\mathbf{c}_1$ and $\mathbf{c}_2$. The vector $\mathbf{c}_3 = \mathbf{c}_1 \times \mathbf{c}_2$, which is not of length 1 unless $\mathbf{c}_1$ and $\mathbf{c}_2$ are orthogonal, can also be computed, giving us the orientations of three vectors fixed on the eye (Fig. 2). From these vectors we construct a 3×3 matrix C with columns $\mathbf{c}_1$, $\mathbf{c}_2$ and $\mathbf{c}_3$. We give the name $\bar{C}$ to the particular C computed when the eye is in whatever we choose to regard as reference position. When the eye is not in reference position, C and $\bar{C}$ will differ, but the two matrices will be related by the equation:

$$C = R\bar{C}; \tag{5}$$

where R is the rotation matrix representing the displacement of the eye from the reference position. The equation:

$$R = C\bar{C}^{-1}; \tag{6}$$

gives us R.

In a moment we shall show how useful this R matrix is for our computations, but first we want to reemphasize that the search coil method, because it yields the projections of vectors along orthogonal coordinate axes, produces rotation matrices virtually automatically. In fact, if we had three orthogonal coils on the eye initially aligned with three orthogonal magnetic fields, and if all gains were ones and minus ones, the nine coil signals would be the nine components of the rotation matrix of the eye. But the above derivation shows that two coils and two fields suffice, if the X components are positive and we know the four gains. With three fields, we need only know the ratios of the three gains for each coil.

A gain value, say the horizontal gain G_Y, for a coil may be determined by turning the coil so that its vector points directly into the horizontal field. Then by equation (2), $Y = G_Y \cos 0 = G_Y$. That is, the gain is the maximum horizontal signal obtainable from the coil; it is also the negative of the minimum obtainable signal.

With the matrix R in hand, the four components of the eye position quaternion q can be obtained by the equations:

$$\begin{aligned} q_0 &= \sqrt{(R_{11} + R_{22} + R_{33} + 1)}/2, \\ q_T &= (R_{32} - R_{23})/4\,q_0; \\ q_V &= (R_{13} - R_{31})/4\,q_0; \\ q_H &= (R_{21} - R_{12})/4\,q_0, \end{aligned} \tag{7}$$

where R_{ij} is the element in the ith row and jth column of R. If the eye is exactly 180 deg from reference position, $q_0 = 0$, and the last three equations must be altered. The component q_0 is called the scalar part of q; q_T, q_V and q_H are the torsional, vertical and horizontal components respectively. But note this important consequence of equation (1): unlike some other measures of ocular torsion, q_T is the component of $\sin(a/2)\mathbf{n}$ along a forward-pointing axis that is fixed in the head; it does not indicate rotation around the line of sight.

To find the angular velocity vector we use the formula for the rate of change of a vector $\mathbf{r}$ that is rotating with angular velocity $\boldsymbol{\omega}$:

$$\dot{\mathbf{r}} = \boldsymbol{\omega} X \mathbf{r}. \tag{8}$$

If we define the matrix Ω as shown:

$$\Omega = \begin{matrix} 0 & -\omega_H & \omega_V \\ \omega_H & 0 & -\omega_T \\ -\omega_V & \omega_T & 0 \end{matrix} \tag{9}$$

Equation (8) gives us the relation

$$\dot{R} = \Omega R, \tag{10}$$

or

$$\Omega = \dot{R}R^{-1}. \tag{11}$$

Because the inverse of a rotation matrix is simply its transpose (obtaining by interchanging rows and columns), R^{-1} is easily found. $\dot{R}$ is computed by numerical differentiation. Again, ω_T is the component of $\boldsymbol{\omega}$ along a forward-pointing axis that is fixed in the head; it is not the component along the line of sight.

Equation (11) shows that $\Omega = \dot{R}$ (i.e. eye velocity equals the derivative of eye position) when the rotation matrix R = identity matrix I (i.e. when the eye is in reference position) or when $\boldsymbol{\omega}$ lies along the axis of the rotation R; so for example $\Omega = \dot{R}$ when the eye is displaced from reference position by a pure horizontal rotation and is currently rotating purely horizontally. When $\boldsymbol{\omega}$ is not aligned with the axis of R, the discrepancy between velocity and derivative increases as R departs further from I (i.e. as the eye rotates farther away from reference position). In the Results section we show some examples of discrepancies between derivatives and velocities when ω is approximately orthogonal to the axis of eye displacement from reference position.

We conclude this section by discussing two technical complications that can arise during kinematic analysis. First, we mentioned above that a coil vector can be computed using only two magnetic fields as a long as the sign of the X component is known. With the Skalar annulus, one coil vector $\mathbf{c}_1$ is parallel with the gaze line and will therefore point forward (i.e. its X component c_{11} will be positive) for all eye positions in the oculomotor range. However, the other coil vector $\mathbf{c}_2$ is orthogonal to the gaze line and will therefore point forward in some eye positions and back in others. For example, if $\mathbf{c}_2$ points directly left when the eye is in primary position, its X component, c_{12}, will be positive for eye positions to the right and negative for positions to the left. It is neverthless possible to find c_{12} with only two fields using the formula:

$$c_{12} = (k - c_{21}c_{22} - c_{31}c_{32})/c_{11}; \tag{12}$$

where k is the dot product $\mathbf{c}_1 \cdot \mathbf{c}_2 = c_{11}c_{12} + c_{21}c_{22} + c_{31}c_{32}$, which is independent of eye orientation, and can therefore be computed in some position where the signs of c_{11} and c_{12} are known; for the Skalar annulus, the two coils are orthogonal, so $k = 0$.

The second complication is that equation (6) alone may not yield the rotation matrix R. Because of crosstalk and nonuniformities in the magnetic fields, C and $\bar{C}$ are often skewed enough that $C\bar{C}^{-1}$ does not have exactly the properties of a rotation matrix; for example its inverse is not exactly equal to its transpose. As a result, equation (7), the formula for computing q from a rotation matrix, can yield errors in the eye position quaternion near reference position. In particular, we found that the quaternions indicated zero displacement from reference position whenever the eye was within 5–10 deg of that position. These errors are elimiated by adjusting the matrix $C\bar{C}^{-1}$ slightly, turning it into a rotation matrix using the Gram–Schmidt process from linear algebra (see e.g. Anton, 1984; Hoffman & Kunze, 1971); that is, writing $\mathbf{r}'_i$ and $\mathbf{r}_i$ for the ith rows of $C\bar{C}^{-1}$ and R, respectively, we let:

$$\mathbf{r}_1 = \mathbf{r}'_1/|\mathbf{r}'_1|;$$

$$\mathbf{r}_2 = [\mathbf{r}'_2 - (\mathbf{r}'_2 \cdot \mathbf{r}_1)\mathbf{r}_1]/|\mathbf{r}'_2 - (\mathbf{r}'_2 \cdot \mathbf{r}_1)\mathbf{r}_1|;$$

$$\mathbf{r}_3 = \mathbf{r}_1 \times \mathbf{r}_2. \tag{13}$$

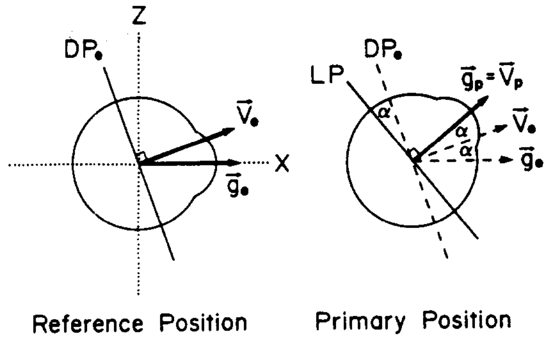

Fig. 3. Geometric relation between gaze directions, displacement planes and primary position. When the gaze direction rotates 2α deg from $\mathbf{g}_e$ to $\mathbf{g}_p$, the associated displacement plane rotates α deg in the same direction.

Primary position

The above computations give us the eye position quaternion with respect to reference position, expressed in the coordinate system defined by the magnetic fields. The angular velocity vector is expressed in the same coordinate system. Not all reference positions and coordinate systems, however, are equally convenient and physiologically meaningful. Listing's law tells us that there is a privileged eye position, the primary position. The law states that given any eye position e, the eye assumes only those orientations that can be reached from e by a single rotation about an axis lying in what we shall call the displacement plane associated with e. Primary position is the unique e in which the gaze line is orthogonal to the displacement plane (Fig. 3). The displacement plane of primary position is called Listing's plane (Helmholtz, 1867). For some purposes it is useful to have reference position correspond to primary position, and to have Listing's plane aligned with some coordinate plane, specifically the $q_T = 0$ plane.

It is difficult to get reference position to correspond to primary position at the time of an experiment because there is no quick method to determine when the eye is in primary position. Moreover, Listing's law holds only inexactly (Ferman, Collewijn & Van den Berg, 1987b), so the theoretical notion of primary position does not correspond precisely to any real eye position. Our approach to this problem is to compute primary position after an experiment and then recalculate the quaternions relative to primary position and put them into a coordinate system where Listing's plane is aligned with the $q_T = 0$ plane.

To do this, we use the fact that, if Listing's law held exactly, then eye position quaternions computed relative to any reference position e (also fitting Listing's law) would all have their vector parts in a single plane, DP_e, the displacement plane of e (Fig. 3), because the vector parts of these quaternions by definition lie along the axes of rotation from e. It can be shown that if $\mathbf{V}_e$ is the forward-pointing vector of length 1 orthogonal to DP_e, then $\mathbf{V}_e$ bisects the angle between $\mathbf{g}_e$ and $\mathbf{g}_p$, the gaze vectors (i.e. the vectors of length 1 pointing along the gaze directions) in position e and primary position p (see proof in the Appendix). It then follows that the quaternion corresponding to primary position, expressed relative to e in magnetic field coordinates, is:

$$p = \mathbf{V}_e \cdot \mathbf{g}_e - \mathbf{V}_e \times \mathbf{g}_e. \tag{14}$$

The first step, therefore, is to find a reference position e fitting Listing's law exactly. Initially, we compute the quaternions of eye position relative to a reference position r, measured when the subject is looking at the centre light in the target array. This centre light is positioned so that the gaze vector $\mathbf{g}_r$ is aligned with the forward-pointing X magnetic field; i.e. so that $\mathbf{g}_r = \mathbf{i} = (1, 0, 0)$ in field coordinates. We compute a plane of best fit to 10,000 eye position quaternion vectors collected over 100 sec while the subject sits with his head still and makes saccades in the light throughout the oculomotor range. This plane is specified by the parameters f, f_V and f_H which are used to express q_T as a function of q_H and q_V:

$$q_T = f + f_V q_V + f_H q_H. \tag{15}$$

If f is not 0, then reference position r does not itself lie exactly in the plane of position vectors; that is, r does not fit Listing's law. But the eye position represented (relative to r) by the quaternion $e = [\sqrt{(1-f^2)}, f, 0, 0]$ *does* lie in the plane and has the same gaze direction as r, i.e. in field coordinates $\mathbf{g}_e = (1,0,0)$. We choose e for the new reference position, reexpressing the eye position quaternions relative to e by right-multiplying them by $e^{-1} = [\sqrt{(1-f^2)}, -f, 0, 0,]$. For example, the quaternion e itself, representing the new reference position relative to the old reference postion r, becomes $ee^{-1} = 1$; this pure scalar quaternion, which by equation (1) represents a 0 deg rotation, is obviously the correct representation for reference position relative to iself.

To find DP_e, one computes a new plane of best fit to the 10,000 eye position vectors reexpressed relative to e. (When the torsional adjustment e^{-1} is small, however, the new plane is almost exactly parallel with the old—within 0.3 deg in our data—and so one could substitute the original plane for DP_e without introducing significant error.) We can compute the normal vector $\mathbf{V}_e$ to DP_e using the f's for that plane:

$$\mathbf{V}_e = (1, -f_V, -f_H)/|(1, -f_V, -f_H)|. \tag{16}$$

Then by (14), the quaternion of primary position relative to e, in field coordinates is

$$p = \mathbf{V}_e \cdot \mathbf{i} - \mathbf{V}_e \times \mathbf{i} = (V_1, 0, -V_3, V_2). \tag{17}$$

The eye position quaternions can now be recomputed relative to primary position by right-multiplying them by $p^{-1} = (V_1, 0, V_3, -V_2)$.

The recomputed quaternions, qp^{-1}, can then be converted to a coordinate system in which $\mathbf{g}_p$ points straight ahead (i.e. in which Listing's plane is aligned with $q_T = 0$) by putting them through the rotation p^{-1}; algebraically, this is done by "conjugating" them with p^{-1} to yield $p^{-1}(qp^{-1})p = p^{-1}q$. Thus both operations—reexpressing the quaternions relative to primary position and changing the coordinate system—are accomplished simply by left-multiplying the quaternions by p^{-1}. Angular velocity vectors and gaze vectors are not expressed relative to any reference position; they are simply rotated by $p^{-1}(\ )p$ to put them into the coordinates where Listing's plane is $q_T = 0$.

In summary, the quaternions are transformed by right multiplying them by e^{-1} and left multiplying them by p^{-1}—q becomes $p^{-1}qe^{-1}$—while angular velocity and gaze vectors are put through the rotation p^{-1}—ω and $\mathbf{g}$ become $p^{-1}\omega p$ and $p^{-1}\mathbf{g}p$.

Calibration

Before the coils are placed in the subject's eye, the magnetic fields are adjusted so that, for each coil, the maximal signals from the three fields are equal: $G_X = G_Y = G_Z$; (these values need not be the same for the two coils). If the magnetic field characteristics are constant day to day, and if the biases of the eye coils of different subjects are approximately equal, then no further calibration is ever necessary: once the fields are set at equal strengths, the algorithms described above compute the orientations of the eye coils for all subjects, regardless of the size and placement of their coils. If there are only two magnetic fields, then we set $G_Y = G_Z$; no further calibration is necessary as long as the biases *and*

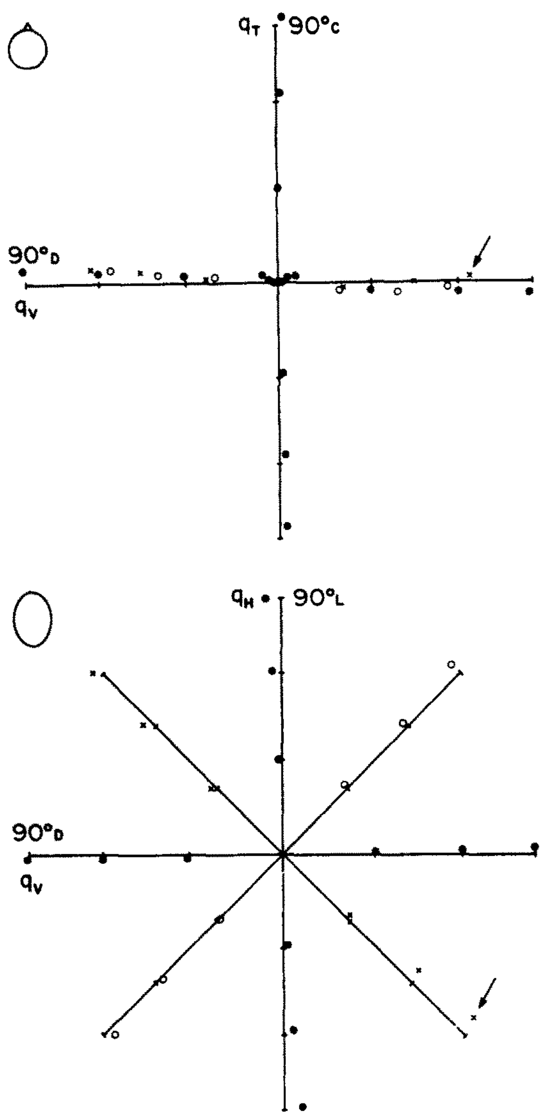

Fig. 4. Measured angular position (quaternion) vectors of a plexiglas eye, viewed from behind (bottom) and above (top), lie close to the actual values (tick marks).

the gains of the coils of different subjects are approximately the same. Since the positioning of the head relative to the centre target light may vary slightly day to day, the matrix $\bar{C}$ defining reference eye position is recalculated at the start of each experiment using the four or six coil voltages recorded when the subject views the centre target light.

RESULTS

Tests of calibration

To test the accuracy of this technique, the Skalar ring that was used in human experiments, or a pair of search coils such as was used with monkeys, was attached to a piece of plexiglas shaped and sized like a human eye. The plexiglas eye was mounted on gimbals and placed in the magnetic fields where the left eye would be during experiments. The *X*, *Y* and *Z* readings of each coil, six readings in all, were entered into a computer program. With the Skalar ring, a reference position was chosen so that the ring was oriented much as it would be in reference position during experiments. The program computed the matrix $\bar{C}^{-1}$ and then displayed the rotation matrix and quaternion representing current eye position relative to reference.

In Fig. 4, dots are the vector part of position quaternions computed from two search coils; tick marks on the coordinate axes are the actual position computed from the gimbal angles. The coordinate axes are determined by the magnetic fields, as described in Methods, but the axes have been renamed, from *X*, *Y*, *Z* to q_T, q_V, q_H, because we are now using them to plot the torsional, vertical and horizontal components of quaternions. Note the switching of horizontal and vertical component directions which occurs because quaternions represent displacements in terms of rotation axes: the coordinate axis for the q_H component—the quaternion component that signifies how far the eye has rotated horizontally—lies vertically along the old *Z* axis, because the rotation axis for a horizontal rotation is oriented vertically; similarly, the q_V axis lies horizontally along the former *Y* axis. Of course, one could switch the positions of the q_V and q_H axes, but then the plotted quaternion vectors would not lie along the displacement axes, and Listing's plane would not be correctly oriented in space.

Heads drawn in the upper left corners of the plots indicate the orientation of the (in this case imaginary) subject's head for different views of the three-dimensional data. Thus the position vectors are viewed from the above in the upper plot and the lower view shows the same vectors from behind.

The best way to interpret quaternion vectors is to use the right hand rule: point the right thumb in the direction of the vector and then the direction the fingers curl round is the direction the eye has rotated away from reference position. For example, consider the position represented by the most eccentric small *x* at lower right in the behind view (indicated by an arrow in Fig. 4); the same position shows up as the rightmost *x* in the above view, lying just slightly forward of the abscissa. For this position, then, the torsional component q_T is approximately zero and the vertical and horizontal components are both negative. By the right hand rule, this position is up and right from reference position: if you point your right thumb down and right, your fingers curl round toward the up and right. The scale on the plot shows that this position is rotated 90 deg away from reference position.

The plot shows that the magnitude of error is never more than 10% for eye positions over a 90 deg range. The system is fairly robust, in that errors of 3–4% in the estimates of relative coil gains, and large shifts in reference position (prior to the calculation of $\vec{C}$), had little effect on accuracy. Similar acuracy and stability were obtained with the Skalar annulus. Deformation of the Skalar ring also had only a small effect on accuracy, presumably because warping only changed the overall sensitivity of the coil and did not change the ratios among G_X, G_Y and G_Z. This finding suggests that differences in shape between the plexiglas and human eyes are unlikely to vitiate the calibration.

There is some independent confirmation that the accuracy of eye position recordings is better than 10% when the coils are on the eye: gaze lines computed from the eye position quaternions are always rotated away from reference position by the same angle as gaze lines determined based on target light locations, with an error of less than 10%.

Source of error

The observed error does not come from the position-computing algorithm, because when fake data representing the signals from a perfect coil system were input to the program, the (roundoff) error in the output was negligible. The error is likely due to magnetic field nonorthogonality or curvature and to biases, crosstalk and other distortions introduced by the electronics.

One way to check for these factors is to display the vectors $\mathbf{c}_1$ and $\mathbf{c}_2$ (defined in *Kinematic analysis*). In a perfect system, these vectors will maintain a constant angle with respect to one another, and they will both lie on a sphere of radius one. A shift of the sphere away from the origin indicates the amount and direction of uncorrected bias in the data collection system. Elongation or flattening of the sphere along a particular axis reveals over- or underestimates of coil gain in that direction. And nonhorizontal movement of a coil vector, say, during horizontal rotation of the gimbals indicates electronic crosstalk or imperfection in the field directions. In some cases it is possible to correct such errors by recentring the sphere or by transforming an ellipsoid shape back into a sphere.

Listing's law

We now examine the positions of a real eye, expressed using quaternion vectors, while a monkey makes saccades with the head stationary. Figure 5 shows the results of the program that computes primary position and shifts the data into Listing's coordinates. Figure 5a shows the vector parts of about 10,000 eye position quaternions, sampled over 100 sec, computed relative to the original reference position and expressed in the coordinate system of the magnetic fields. In the behind view the dots are arranged in a cloud, giving an indication of the oculomotor range in the horizontal and vertical directions. In the right side view, the dots form a band inclined at about an 18 deg angle to the vertical, indicating that the eye position vectors lie in a plane tilted back from the $q_T = 0$ plane. Because of this tilt away from vertical, the above view gives little impression of a planar arrangement. Note that this plane of eye position vectors is not Listing's plane, which contains the vectors of eye positions computed relative to primary position. Rather, it is the displacement plane of reference position, containing the vectors of the same eye positions computed relative to reference position.

To reveal Listing's plane, the eye positions must be reexpressed relative to primary position. Figure 5b shows the reexpressed quaternions in a new coordinate system where Listing's plane is aligned with $q_T = 0$ (ordinate in the right side view; abscissa in the above view). The proximity of all the quaternion vectors to this plane shows that Listing's law is accurate to within about 4 deg in this case over a 100 sec period, even during the saccades. The behind view shows that the former reference position (at the centre of the cloud) was about 36 deg below primary position (the origin), and that primary position is actually near the edge of the oculomotor range for this subject.

To find the orientation of Listing's plane relative to the head, one needs to know both the direction of gaze and the orientation of the head with respect to the magnetic fields when the eye is in reference position.

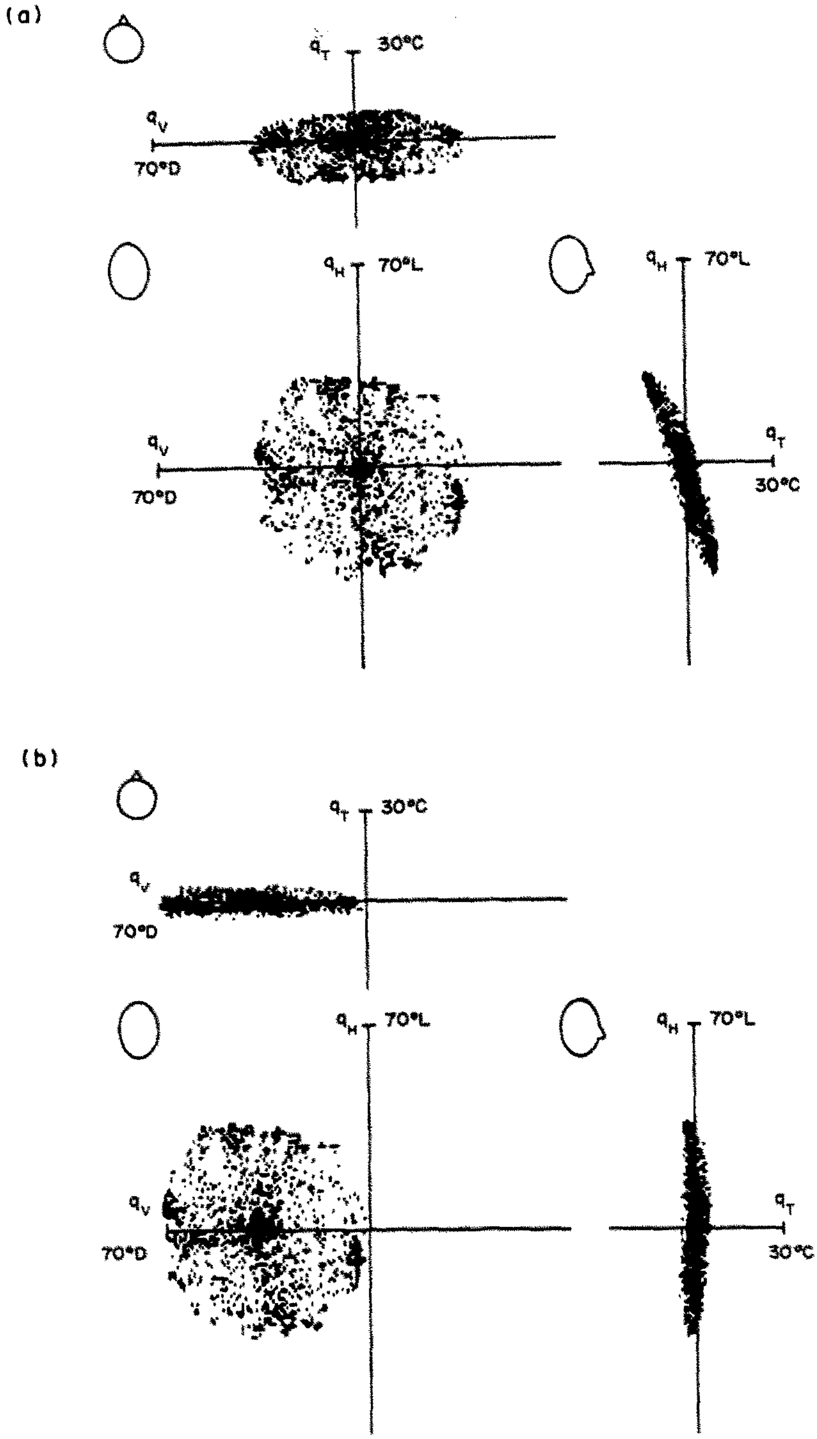

Fig. 5. Picturing Listing's plane. (a) Three views of the eye position vectors of a monkey, computed relative to the straight ahead eye position. The plane visible in the side view is the displacement plane for that eye position. (b) Eye positions recomputed relative to primary position, and rotated so that Listing's plane is aligned with $q_T = 0$.

Velocity traces

Velocity traces of saccades are important for several reasons. One is that velocity plots provide the natural tool for investigating the question of saccade straightness. Straightness is an ambiguous concept for position traces, because different representations (e.g. raw coil signals, Fick or Helmholtz coordinates,

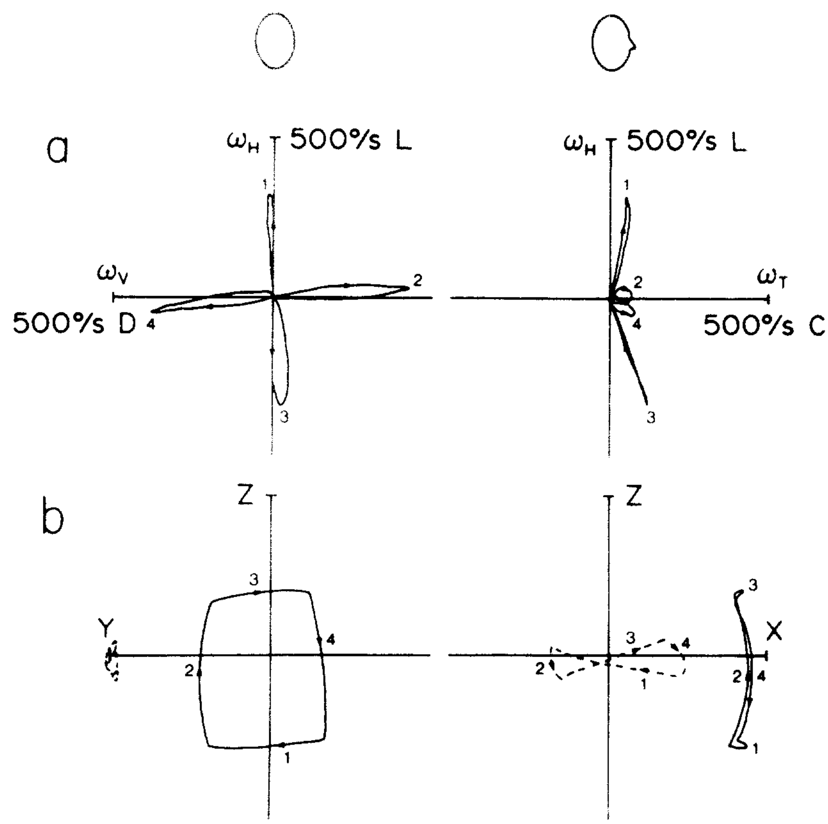

Fig. 6. Four saccades by a human subject. (a) The eye velocity vector points forward, in the positive (clockwise) torsional direction throughout all four saccades. (b) Coil voltage vectors c_1 (solid line) and c_2 (dashed line) during the same saccades.

quaternion vectors) make different trajectories look straight or curved. Mathematically, in fact, the set of all possible eye orientations is a "curved space" (Schutz, 1981), and so the idea of a straight path not does strictly apply but is replaced by the idea of a geodesic. The simplest characterization of the geodesics is that they are the trajectories for which the direction of the angular velocity vector is constant. We therefore say that a saccade is straight if the direction of the velocity vector, the axis about which the eye rotates, is constant throughout the movement.

Another reason for looking at velocity traces is that many current models of oculomotor control propose that motoneurons are driven in part by eye velocity commands (Skavenski & Robinson, 1973; Tweed & Vilis, 1987a). If this idea is correct, then velocity traces will give information about these commands; for example, velocity traces during saccades will indicate the degree of coupling between the various populations of short lead burst neurons which are believed to provide the velocity command during saccades. A third, related, motive for obtaining accurate plots of eye velocity is that velocity trajectories provide tests for different models of the saccadic system (Tweed & Vilis, 1987a).

Figure 6a shows velocity traces for four human saccades which take the gaze point in the clockwise direction around a rectangle centred on primary position. On the left side of the figure we see the traces from a viewpoint behind the subject, and on the right we see the same traces from the subject's right side. For example, the loop labeled "1" is the velocity trajectory for one leftward saccade. The loop begins at zero velocity (the origin); during the acceleration phase the velocity vector grows, mostly up but also (as seen in the side view) slightly forward; after peak velocity is reached, the velocity vector shrinks back to zero along approximately the same straight path. By the right hand rule, this is a leftward saccade with a slight clockwise component. The figure shows that all four saccades have narrow and nearly straight velocity loops, indicating that the axis of rotation is roughly constant during the saccade;

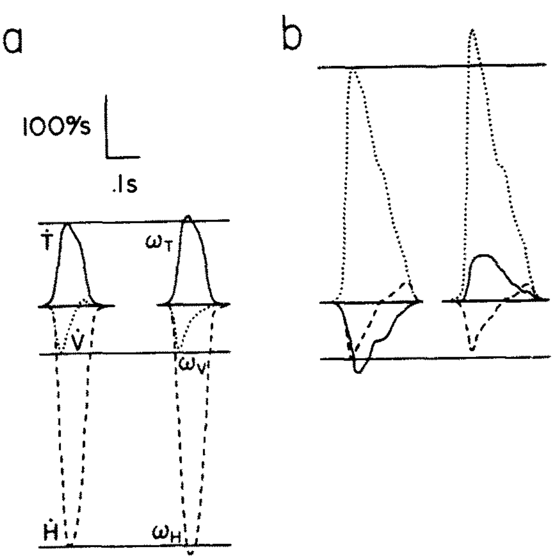

Fig. 7. Derivatives of coil signals (left side of each pair) and velocity components (right side), plotted against time, disagree in all three dimensions.

that is, the saccades are roughly straight. The side view shows that all the loops tilt forward out of Listing's plane (the ordinate in the side view). This finding is in keeping with the geometric fact that fixed-axis rotations that take the gaze point in a clockwise direction around primary position must have forward-pointing axes to keep the position vectors in Listing's plane (Tweed & Vilis, 1987a).

Velocity vs derivatives

We mentioned earlier that angular velocity cannot be computed by differentiating position signals. Figure 6b, plotting the coil voltage $\mathbf{c}_1$ and $\mathbf{c}_2$ during the four saccades of Fig. 6a, gives some indication of what can go wrong when the derivatives of the coil signals are used to estimate velocity. The behind view (left side of figure) shows $\mathbf{c}_1$ (solid line), which points forward roughly in line with the gaze direction, recreating the clockwise circuit of the gaze point around the straight ahead direction, which in this case corresponds to primary position. The vector $\mathbf{c}_2$, which points left in primary position, is not very informative when viewed from behind, but in the side view shows a figure-eight trajectory.

When the derivatives of coil signals are used to estimate eye velocity, the derivative (here called $\dot{H}$) of the Y component of $\mathbf{c}_1$ is taken as a measure of horizontal velocity; the derivative $\dot{V}$ of the Z component of $\mathbf{c}_1$ is the measure of vertical velocity; and, if $\mathbf{c}_2$ points left as in this case, the derivative $\dot{T}$ of the Z component of $\mathbf{c}_2$ is the measure of torsional velocity, with positive $\dot{T}$ indicating clockwise rotation.

Figure 6 shows how this approach seriously misestimates the torsional component of velocity. In all four saccades, the eye is moving circumferentially (orthogonally to the radial, centripetal/centrifugal direction); that is, the eye velocity vector ω is approximately orthogonal to the axis of eye displacement from primary position—a situation that maximizes the discrepancy between derivatives and velocities in any given eye position. The side view in Fig. 6a shows that all four saccades have positive, clockwise torsional velocity components throughout. In the side view in Fig. 6b, the $\mathbf{c}_2$ vector (dashed line) moves upward during saccades 1 and 3, generating positive $\dot{T}$ values to indicate clockwise rotation; but the vector moves downward during saccades 2 and 4, generating negative $\dot{T}$ values to falsely indicate counterclockwise rotation. The problem in saccade 4, for example, is that while the rotation axis is pointing forward, indicating a clockwise component, the $\mathbf{c}_2$ vector is pointing even further forward because the eye is looking right, and so $\mathbf{c}_2$ is in front of the rotation axis. As a result, when the gaze vector $\mathbf{c}_1$ rotates down, the tip of $\mathbf{c}_2$ also moves down.

Figure 7 shows how the time derivatives of the coil signals depart from true angular velocity in all three dimensions. Figure 7a shows the derivatives of the coil signals and velocity plots for saccade 3 from Fig. 6; Fig. 7b shows the same for saccade 4. For each saccade, the derivatives $\dot{H}$, $\dot{V}$ and $\dot{T}$ are plotted against time on the left side; the velocity components ω_H, ω_V and ω_T on the right. In both cases, the solid lines indicate torsional components, dotted lines vertical, and dashed lines horizontal. The plots show that $\dot{T}$ is a reasonable approximation to ω_T during saccade 3, but it points in the wrong direction for a total error of over 200 deg/sec during saccade 4. Less strikingly, but still significantly, $\dot{V}$ and $\dot{H}$ both overestimate and underestimate ω_V and ω_H by up to about 15%—a 50 deg/sec error in the case of $\dot{V}$ in saccade 4. Switching from derivatives to velocities can alter the durations and timing of the torsional, vertical and horizontal components of a saccade, often improving their synchronization and converting biphasic profiles into unidirectional ones, as in the vertical trace for saccade 3.

It is important to realize that the discrepancies between derivatives and velocities in Fig. 7

have been minimized by using a Skalar annulus that is aligned with the magnetic fields in reference position. Nonorthogonal or nonaligned coils would in general lead to larger errors. And finally, differentiation of Fick, Helmholtz, quaternion, or any other eye position coordinates would lead to similar errors, because no change of representation will remove the fact that, for three-dimensional rotations, velocity depends on current position as well the derivative of position (Tweed & Vilis, 1987a).

DISCUSSION

We have described a method for computing three-dimensional eye position and velocity from search coil signals. Eye positions are expressed using four-component objects called quaternions. The last three components of the quaternions—the vector parts, which depict the axis and magnitude of the eye's rotation from some reference position—are used for three-dimensional data plots. The advantages of the quaternion representation over other schemes, such as raw coil signals or Fick coordinates, include easy computations, symmetry, utility for oculomotor models, a simple form for Listing's law and relatively transparent three-dimensional graphics.

The method uses the search coil–magnetic field technology which was first applied to eye movements by Robinson (1963). Compared with the photographic technique developed by Nakayama (1974) for computing the rotation matrix of the eye, the search coil method may be less accurate for static measurements, but it has the advantages that it requires no estimate of the rotational centre of the eye, and it permits a high frequency of eye position measurements (up to 1 per msec in this paper) and therefore allows accurate estimates of eye velocity.

Algorithms for computing position and velocity are described for a system with two search coils (not necessarily orthogonal) on one eye, and three orthogonal magnetic fields. The advantage of using three fields is that the method gives the true orientation of a coil even if the sensitivity of the coil has changed. Thus there is no need to recalibrate for coils of different sensitivities. In special cases (for example, when one eye coil is initially near the frontal plane and the range of eye movements is less than ± 90 deg), it is possible to apply the technique using only two magnetic fields, but the precise sensitivities of each coil must be known. These restrictions on the two-field technique are not due to a flaw in our particular algorithm, but reflect the basic geometry of the problem: it can be shown that in general one needs to know six elements (arranged in two rows or two columns) of a rotation matrix to reconstruct the whole matrix. Equivalently, one needs at least six coil signals in general to compute the orientation of an eye. This requirement holds for any technique that works by finding the locations of two vectors fixed in the eye.

In three dimensions, angular velocity is not the derivative of angular position, and so velocity cannot be computed by digitally differentiating position. A simple, correct formula, equation (11), which incorporates the dependence of angular velocity on current angular position, is used in this paper. We show that computing eye velocity by differentiating position data leads to large errors, particularly in torsional velocity, even in the ideal case of orthogonal eye coils initially aligned with the magnetic fields.

Quaternions and gaze direction

In Fick or Helmholtz coordinates, the vertical and horizontal components of eye position uniquely determine the gaze direction; the torsional component does not affect gaze direction because it merely describes how far the eye is rotated around the line of sight. With quaternions, however, the torsional component q_T does influence gaze direction: since q_T describes how far the eye has rotated around a head-fixed axis orthogonal to Listing's plane, a change in q_T will change the gaze direction unless the gaze direction is also orthogonal with the plane. Thus with quaternions, q_V and q_H do not uniquely determine gaze direction unless q_T is constrained to be a function of q_V and q_H.

The fact that the saccadic system does indeed constrain q_T to be a function of q_V and q_H (Donders' law; Donders, 1847) may indicate that the neural representation of eye position in the oculomotor system is more quaternion-like than Fick-like. Certainly the innervations of extraocular muscles are like quaternion components in that no subset determines the gaze direction. Thus the quaternions may be more physiological than Fick vectors as regards the coding of eye position.

However, this property of quaternions may not be helpful for some types of data interpretation. If there are large deviations from Listing's law, say during torsional head rotation or in the presence of brain lesions, then the behind view of the quaternion vectors will no longer give a good picture of the gaze direction. In these cases, the gaze vector **g**, which has length 1 and points forward along the line of sight, can be computed from q and $\mathbf{g}_e$ (the gaze vector in reference position) by the formula:

$$\mathbf{g} = q\mathbf{g}_e q^{-1}. \tag{18}$$

In summary, quaternions, which represent rotations in terms of their axes and amplitudes, have several advantages over other representations of three-dimensional eye position in current use. The magnetic field—eye coil method, using two eye coils per eye and three magnetic fields, is ideally suited for computing the rotation matrix representing the eye's angular displacement from any reference position. From this matrix and its time derivative, the quaternion of eye position and the angular velocity vector of the eye are easily determined.

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APPENDIX

Quaternions

This section defines some of the basic operations of quaternion algebra (see also Westheimer, 1957; Tweed & Vilis, 1987a; Brand, 1948; Tait, 1890). A quaternion is a four-component object which can be regarded as the sum of a scalar and a vector:

$$q = q_0 + \mathbf{q}; \tag{A1}$$

although the element **q** is technically a bivector (see Riesz, 1958; also *Clifford Algebra* below). Any quaternion q can be written

$$q = |q|[\cos(a/2) + \mathbf{n}\sin(a/2)]; \tag{A2}$$

for some a and some unit vector **n**; $a/2$ is called the angle of the quaternion, **n** its axis, and $|q|$ (the square root of the sum of the squares of the components) its magnitude.

Quaternions can be added and subtracted like four-component vectors. They can also be multiplied and divided. Using indices 0–3 for the four components of a quaternion, the formula for a quaternion product $p = qr$ is:

$$\begin{aligned} p_0 &= q_0r_0 - q_1r_1 - q_2r_2 - q_3r_3; \\ p_1 &= q_0r_1 + q_1r_0 + q_2r_3 - q_3r_2; \\ p_2 &= q_0r_2 + q_2r_0 - q_1r_3 + q_3r_1; \\ p_3 &= q_0r_3 + q_3r_0 + q_1r_2 - q_2r_1. \end{aligned} \tag{A3}$$

To divide by a quaternion q, one multiplies by the multiplicative inverse q^{-1}. If $q = q_0 + \mathbf{q}$, then $q^{-1} = (q_0 - \mathbf{q})/|q|^2$; in particular, if q has magnitude 1 then q^{-1} is simply $q_0 - \mathbf{q}$.

The reason quaternions are regarded as representing rotations is that, for any vector **v** and nonzero quaternion p, the vector:

$$\mathbf{v}' = p\mathbf{v}p^{-1}; \tag{A4}$$

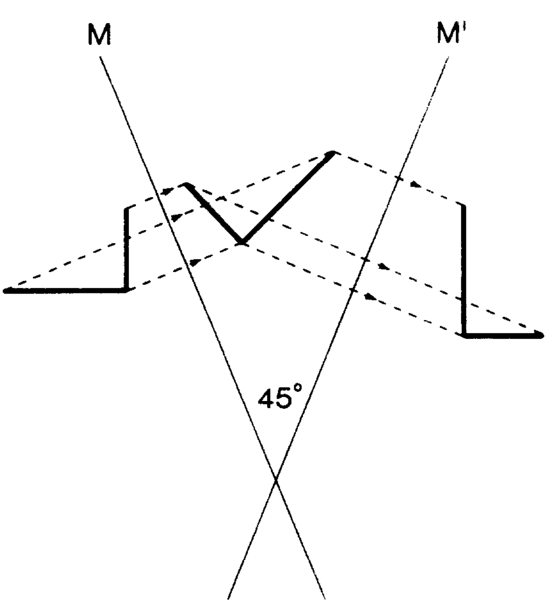

Fig. A1. Two reflections yield a rotation. The L-shaped object is reflected first in mirror M and then in M'. The mirrors are at 45 deg to one another, and intersect along a line orthogonal to the plane of the paper; their effect on the object is a 2×45 deg $= 90$ deg rotation, in the direction from M toward M', about their line of intersection (the object also translates in this example, because for clarity it is drawn displaced from the axis of rotation). Any other mirrors with the same angle and line of intersection will generate the same rotation, as long as the reflections occur in the correct order.

is obtained by rotating $\mathbf{v}$ about the axis of p, through twice the angle of p. The resultant of two rotations can also be computed using quaternion multiplication. That is, rotation p followed by rotation q yields the overall angular rotation qp. Since multiplying any quaternion by 1 leaves the quaternion unchanged, $q = 1$ is the unit quaternion that represents no displacement.

Clifford Algebra

A useful algebraic tool for describing Listing's law is the Clifford product of vectors (Riesz, 1958). The formula for this operation is best expressed using three orthogonal unit vectors $\mathbf{e}_1$, $\mathbf{e}_2$ and $\mathbf{e}_3$:

$$\mathbf{e}_i\mathbf{e}_j = 1 \quad \text{if} \quad i = j, = -\mathbf{e}_j\mathbf{e}_i \quad \text{otherwise.} \tag{A5}$$

To multiply other vectors, express them as linear combinations of the $\mathbf{e}_i$ and multiply term by term. Thus, if $\mathbf{v} = v_1\mathbf{e}_1 + v_2\mathbf{e}_2 + v_3\mathbf{e}_3$ and $\mathbf{w} = w_1\mathbf{e}_1 + w_2\mathbf{e}_2 + w_3\mathbf{e}_3$ then $\mathbf{vw} = v_1w_1\mathbf{e}_1\mathbf{e}_1 + v_1w_2\mathbf{e}_1\mathbf{e}_2 + v_1w_3\mathbf{e}_1\mathbf{e}_3 + v_2w_1\mathbf{e}_2\mathbf{e}_1 + v_2w_2\mathbf{e}_2\mathbf{e}_2 + v_2w_3\mathbf{e}_2\mathbf{e}_3 + v_3w_1\mathbf{e}_3\mathbf{e}_1 + v_3w_2\mathbf{e}_3\mathbf{e}_2 + v_3w_3\mathbf{e}_3\mathbf{e}_3 = (v_1w_1 + v_2w_2 + v_3w_3) + (v_3w_2 - v_2w_3)\mathbf{e}_3\mathbf{e}_2 + (v_1w_3 - v_3w_1)\mathbf{e}_1\mathbf{e}_3 + (v_2w_1 - v_1w_2)\mathbf{e}_2\mathbf{e}_1$. Each product $\mathbf{e}_i\mathbf{e}_j$ $(i \neq j)$ is an object called a bivector, whose geometric interpretation need not concern us. For our present purposes, it is convenient to ignore the distinction between vectors and bivectors by "identifying" $\mathbf{e}_3\mathbf{e}_2$ with $\mathbf{e}_1$, $\mathbf{e}_1\mathbf{e}_3$ with $\mathbf{e}_2$, and $\mathbf{e}_2\mathbf{e}_1$ with $\mathbf{e}_3$; under this correspondence, the computation above shows that the Clifford product can be expressed using the dot and cross products of vector algebra:

$$\mathbf{vw} = \mathbf{v} \cdot \mathbf{w} - \mathbf{v} \times \mathbf{w}. \tag{A6}$$

Reflections and Rotations

It is easy to verify that the Clifford product has the following properties: for parallel vectors, $\mathbf{vw} = \mathbf{wv} = \mathbf{w} \cdot \mathbf{v}$; for orthogonal vectors, $\mathbf{vw} = -\mathbf{wv}$. Because of these properties, Clifford algebra can be used to compute reflections. Thus, let $\mathbf{u}$ be a unit vector and let $\mathbf{v}$ be any vector; $\mathbf{v}$ can be expressed as the sum of two components, one ($\mathbf{v}_p$) parallel with $\mathbf{u}$ and the other ($\mathbf{v}_o$) orthogonal to $\mathbf{u}$. Then $-\mathbf{uvu} = -\mathbf{u}(\mathbf{v}_p + \mathbf{v}_o)\mathbf{u} = -\mathbf{uv}_p\mathbf{u} - \mathbf{uv}_o\mathbf{u} = -\mathbf{uuv}_p + \mathbf{uuv}_o = -\mathbf{v}_p + \mathbf{v}_o$—i.e. $-\mathbf{uvu}$ is $\mathbf{v}$ reflected in the (flat) mirror (through the origin) orthogonal to $\mathbf{u}$.

The connection between Clifford algebra and rotations comes from the fact that any rotation is equivalent to two successive reflections: suppose M and M' are mirrors at an angle of $(a/2)$ deg relative to one another and $\mathbf{n}$ is a unit vector lying along the line of intersection of the planes of M and M'; then reflection in M followed by M' is equivalent to a rotation of a deg about the axis $\mathbf{n}$ in the direction from M toward M' (Fig. A1). If $\mathbf{u}$ and $\mathbf{u}'$ are unit vectors orthogonal to M and M', respectively, we can put any vector $\mathbf{v}$ through this rotation using the reflection formula twice: $\mathbf{v} \to -\mathbf{u}'(-\mathbf{uvu})\mathbf{u}' = (\mathbf{u}'\mathbf{u})\mathbf{v}(\mathbf{uu}')$. Noting that $(\mathbf{u}'\mathbf{u})(\mathbf{uu}') = \mathbf{u}'(\mathbf{uu})\mathbf{u}' = \mathbf{u}'\mathbf{u}' = 1$—i.e. $\mathbf{uu}' = (\mathbf{u}'\mathbf{u})^{-1}$—and writing q for $\mathbf{u}'\mathbf{u}$, we obtain $\mathbf{v} \to q\mathbf{v}q^{-1}$. Application of equation (A6) shows that this q is the quaternion $\cos(a/2) + \mathbf{n}\sin(a/2)$ which we usually use to represent this rotation.

Listing's Law

Suppose the eye assumes only those positions that can be reached from a particular position e by rotating about an axis in a particular plane DP_e, and that $\mathbf{V}_e$ is the forward-pointing unit vector orthogonal to this plane. Then any admissible eye rotation from position e is a Clifford product of the form $\mathbf{VV}_e$ for some forward-pointing unit vector $\mathbf{V}$: since the axis for the rotation $\mathbf{VV}_e$ is parallel with $\mathbf{V} \times \mathbf{V}_e$, and any vector orthogonal to $\mathbf{V}_e$ lies in DP_e, the axis is in DP_e as required.

Suppose q and r are two other admissible eye positions, and that $\mathbf{V}_q$ and $\mathbf{V}_r$ are the vectors such that $q = \mathbf{V}_q\mathbf{V}_e e$ and $r = \mathbf{V}_r\mathbf{V}_e e$. To get from q to r, the eye could go from q to e by the rotation $\mathbf{V}_e\mathbf{V}_q$ (the inverse of $\mathbf{V}_q\mathbf{V}_e$) and then from e to r by $\mathbf{V}_r\mathbf{V}_e$; the rotation from q to r is the composite $(\mathbf{V}_r\mathbf{V}_e)(\mathbf{V}_e\mathbf{V}_q) = \mathbf{V}_r(\mathbf{V}_e\mathbf{V}_e)\mathbf{V}_q = \mathbf{V}_r\mathbf{V}_q$. That is, for any admissible eye position q, there is a vector $\mathbf{V}_q$ such that the rotation to any other admissible position has its axis in the plane orthogonal to $\mathbf{V}_q$. This plane is called the *displacement plane* of q, DP_q.

Let $\mathbf{g}_q$ be the gaze vector in position q—i.e. the unit vector pointing in the gaze direction. We shall now show that the position reached by the rotation $\mathbf{V}_q\mathbf{g}_q$ starting from q does not depend on q; i.e. for any two admissible positions q and r, $\mathbf{V}_r\mathbf{g}_r r = \mathbf{V}_q\mathbf{g}_q q$. Since $\mathbf{g}_r$ is obtained by putting $\mathbf{g}_q$ through the rotation $\mathbf{V}_r\mathbf{V}_q$, we can substitute $(\mathbf{V}_r\mathbf{V}_q)\mathbf{g}_q(\mathbf{V}_q\mathbf{V}_r)$ for $\mathbf{g}_r$ on the left side and simplify to obtain $(\mathbf{V}_q\mathbf{g}_q)(\mathbf{V}_q\mathbf{V}_r)r$, which $= \mathbf{V}_q\mathbf{g}_q q$, confirming the equality. The unique position:

$$p = \mathbf{V}_q\mathbf{g}_q q. \tag{A7}$$

is called *primary position*. The displacement plane of primary position is called *Listing's plane*. Rewriting equation (A7) using (A6), with $q = 1$, yields formula (14) for primary position.

For any admissible position q, the rotation $\mathbf{V}_q\mathbf{g}_q$—about an axis orthogonal to $\mathbf{V}_q$ and $\mathbf{g}_q$, turning in the direction from $\mathbf{g}_q$ toward $\mathbf{V}_q$, through *twice* the angle between $\mathbf{g}_q$ and $\mathbf{V}_q$—aligns $\mathbf{g}_q$ with $\mathbf{g}_p$. That is, $\mathbf{V}_q$ bisects the angle between $\mathbf{g}_q$ and $\mathbf{g}_p$. It follows that in primary position (and only there), $\mathbf{g}_q = \mathbf{V}_q$.