

Available online at www.sciencedirect.com



brought to you by 🚲 COP

Vision Research 46 (2006) 3862-3866

Vision Research

www.elsevier.com/locate/visres

Reflection makes sense of rotation of the eyes

S.J. Judge

Department of Physiology, Anatomy and Genetics, Sherrington Building, University of Oxford, Parks Road, Oxford OX1 3PT, UK

Received 13 March 2006; received in revised form 3 May 2006

Abstract

Our 3-D percept of the world is constructed from the two-dimensional visual images on the retina of each eye, but these images and the relationships between them are affected by the 3-D rotations of each eye. These 3-D eye rotations are constrained to patterns such as Listing's law, or its generalisation 'L2', according to the context. Our understanding of the patterns of such three-dimensional eye rotations, and their effect on the retinal images, has been greatly advanced by the development of algebraic methods (Haustein, 1989; Tweed & Vilis, 1987; Westheimer, 1957) for calculating the effect of eye rotations. But not many would say, with Dirac, that they understand the equations describing the 3-D geometry in the sense that they have "a way of figuring out the characteristic of its solution without actually solving it" (Dirac, according to Feynman, Leighton, & Sands, 1964). I show here how the geometry of 3-D rotations of the eye and their visual effects can be made easier to understand by use of the principle that a rotation through angle α can be achieved by a pair of reflections in planes with an angular separation $\alpha/2$, and a common line that is the rotation axis (Tweed, 1997b; Tweed, Cadera, & Vilis, 1980). Mathematically (see Appendix A), the method is equivalent to decomposing the unit quaternions so successfully used to study three-dimensional eye rotations (Coxeter, 1946).

© 2006 Elsevier Ltd. All rights reserved.

Keywords: 3-D geometry; Eye rotation; Listing's law

1. Introduction

Helmholtz (1910/1962) showed that in viewing a distant scene with the head stationary, the torsional rotation (γ) of the eye is related to the azimuth (α) and elevation (β) of the line of sight, by the formula

$$\tan(\gamma/2) = -\tan(\alpha/2)\tan(\beta/2) \tag{1}$$

He also showed that this is equivalent to the principle that the eye rotates only to those orientations that can be realised by a rotation from a unique 'primary position' (roughly straight ahead) about a single axis in a plane perpendicular to primary position. He termed this Listing's law, and the plane is termed Listing's plane. There is a corollary to Listing's law that has come to be known as the 'half-angle-rule': the axis about which the eye rotates from one non-primary orientation to another is not in Listing's plane but in one tilted away from it by half the angle of eccentricity of the starting orientation. Some have sought to relate the half-angle rule to the recently re-discovered extraocular muscle pulleys (Clark, Miller, & Demer, 2000; Miller, 1989; Sappey et al., 1888; Simonsz, Harting, De Waal, & Verbeeten, 1985) by arguing that the pulley geometry might allow the brain to realise Listing's law more simply (Raphan, 1998), but Tweed, Haslwanter, and Fetter (1998) and Tweed, Haslwanter, Happe, and Fetter (1999) have pointed out that the need for eye rotations to fit different patterns in the vestibulo-ocular reflex undermines this view, and other roles for the pulleys have been proposed (Quaia & Optican, 1998).

My purpose here is to show how thinking in terms of reflections rather than rotations clarifies the relationship of these results, and also to demonstrate the usefulness of the same way of thinking of the geometry underlying the generalisation of Listing's law 'L2' that is needed to account for binocular eye orientation when viewing nearby

E-mail address: sjj@physiol.ox.ac.uk

^{0042-6989/\$ -} see front matter © 2006 Elsevier Ltd. All rights reserved. doi:10.1016/j.visres.2006.05.006

targets. A preliminary account of these results (Judge, 2003) was presented at the ARVO meeting in 2003.

2. Methods

A rotation is equivalent to a pair of reflections in intersecting planes (Tweed, 1997b; Tweed et al., 1990). The rotation axis is the intersection line of the two reflecting planes (RPs), and the angle of rotation is twice the angular separation of the RPs. The angular position of the pair of RPs is immaterial so long as their common axis and angular separation are constant, and this principle that the reflection pairs can be rotated en bloc about the axis of the equivalent rotation to a convenient position is part of why reflection pairs are so useful. Fig. 1 shows an upward rotation of the eye from primary position in one of the coordinate systems commonly used for consideration of eye movements in which the X axis is leftwards, the Y axis upwards and the Z axis forwards. This convention is used throughout. The first (white) RP is chosen to be in the horizontal plane. Reflection in this plane inverts the eye-as indicated by the change from the black half-pupil being lower in Fig. 1A to upper in Fig. 1B. Reflection in the second (green) plane (Fig. 1C) then has two effects: first to undo the up-down inversion caused by reflection in the first (white) plane, and secondly to rotate the eye about the Y (horizontal) axis through twice the angle separating the green and white RPs.

Consider now adding a third (red) reflection plane, again with the same common line/axis. For convenience, rotate the first pair of reflection planes so that the green RP coincides with the red RP (Fig. 1D, with the coincident plane being shown as yellow). Reflections in that yellow plane now cancel one another out, leaving the overall effect of the three RPs (white, green and red) that of reflection in the new position of the white plane (Fig. 1E). So whereas a pair of reflections (about RPs with a common axis) is equivalent to a rotation, three reflections is still a reflection. There is a subsidiary point to emphasise here, which is that in considering the effect of more than two RPs, one must only rotate pairs of reflection planes in a way that preserves the order in which the reflections are considered, because reflections, like rotations, do not commute. To match the convention for rotations, pairs of reflections that correspond to downward, leftward or clockwise rotation from the subject's point of view are reckoned positive.

3. Results

I shall first show why Listing's law and the half-angle-rule are equivalent. Fig. 2A shows a rotation in elevation from primary position (conventionally indicated by the forward, Z, axis) realised by two reflections. The first is in Listing's plane (white); the second in a (green) plane tilted back by half the elevation angle from Listing's plane. Fig. 2B shows a second rotation about a (midline) axis in this tilted plane realised by two reflections, the first in the same tilted (green) plane, and the second in the red plane. Fig. 2C shows both rotations together. Because the middle two (green) reflection planes are identical, their effects cancel out and the overall rotation is that caused by the first (white) and last (red) RPs (Fig. 2D). The first reflection plane is in Listing's plane, and because the rotation axis (blue line) is the one line that lies in both reflecting planes, the rotation axis must lie in Listing's plane. The final position therefore accords with Listing's law.

For the sake of clarity I have set out the argument with the starting position the primary position, and the first rotation a pure elevation, but a very similar argument applies if the first rotation is about any axis in Listing's plane (i.e. when after that rotation the eye is in an arbitrary tertiary position). Call the angle of this rotation α Then a similar geometrical construction to that above, using pairs of reflections, shows that a second rotation from this tertiary position must be about an axis tilted $\alpha/2$ back from the normal to the line of sight in the tertiary position in order for the new eye position to lie in Listing's plane.

The argument above is then general and therefore the half-angle rule is equivalent to Listing's law in its usual formulation.

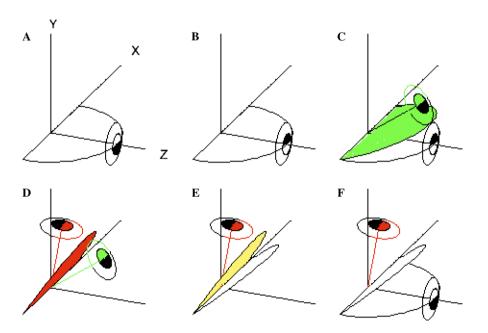


Fig. 1. (A–C) A rotation can be realised by a sequence of two reflections, in planes (white and green) whose common axis is the rotation axis, and whose angular separation is half the rotation angle. (D-F) Adding a third (red) reflection plane converts the rotation back into a reflection, albeit in an intermediate (white) plane. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this paper.)

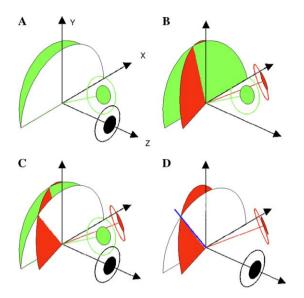


Fig. 2. The half-angle-rule for compound rotations is equivalent to Listing's law. (A) Reflection in the white and green planes (in that order) followed by (B) reflection in the green and red planes, is equivalent to (C and D) reflection in the white and red planes, because the two reflections in the green plane cancel one another out. The rotation (blue axis) formed by the intersection of the white and red planes is necessarily in the white plane, and this is Listing's law. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this paper.)

Note that the position of the two pairs of RPs is constrained by the requirements that the second RP of the first pair, and first RP of the second pair, coincide and that the second rotation obeys the half-angle rule. There is only one way the RPs can be placed.

As a further indication of the value of thinking in terms of reflections and the appropriate diagram, consider formula (1), relating torsion, γ , azimuth, α , and elevation, β , in a Helmholtz coordinate system, where the rotations are specified respectively about the line of sight, about a space vertical axis, and about a space horizontal axis—in that order. Derivation of this result requires some algebraic manipulation even using the quaternion representation of rotations (Tweed, 1997a) and occupies three pages of trigonometry in Helmholtz (1910/1962). Think of formula (1) as expressing the fact that the three rotations specify a right angle triangle in which the sides opposite and adjacent to angle $-\alpha/2$ have length $\tan(\gamma/2)$ and $\tan(\beta/2)$ respectively, so that:

$$\tan(\alpha/2) = -\tan(\gamma/2)/\tan(\beta/2) \tag{2}$$

Where is this triangle? Fig. 3A shows that it is in a horizontal plane unit distance above the centre of rotation of the eye. It is formed by the intersection of the horizontal plane unit distance above the X-Z plane with the red, white and green planes. Fig. 3B shows the positions of the two

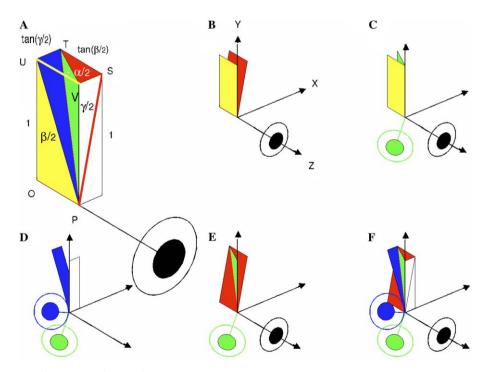


Fig. 3. (A) The equation $\tan(\gamma/2) = -\tan(\alpha/2)\tan(\beta/2)$ relating Helmholtz torsion, γ , azimuth, α , and elevation, β , can be visualised as describing the triangle formed by the intersection of the reflection planes (RPs) for the three rotations with the plane passing through the points S, T, U and V and unit distance above the centre of rotation, O, of the eye. (B) The position of the red and yellow RPs needed to produce torsion γ . The angle (SPV) between the planes is $\gamma/2$. The yellow RP is in the midline. (C) The position of the yellow and green RPs needed to realise azimuthal rotation $-\alpha$. The angle (VTS) between the planes is $-\alpha/2$. (D) The blue and white RPs need to realise the change in elevation, β . The angle (UPV) between the planes is $\beta/2$. The white plane is in Listing's (X-Y) plane. Because the red, green and blue RPs coincide in a single line their combined effect is a single reflection. (We know they meet in a line because we stipulated that in A.) The intersection of that reflection plane (not shown) with the white plane is the rotation axis, which must therefore be in Listing's plane. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this paper.)

RPs (red and yellow in that order) that achieve a torsional rotation, γ . The yellow plane is in the midline (Y–Z) plane. Fig. 3C shows the RPs (yellow and green *in that order*) that achieve azimuthal rotation, $-\alpha$ (negative because the rotation is rightwards), and Fig. 3D shows the RPs (blue and white in that order) that achieve elevation β (positive because the rotation is downwards). As the plane of the triangle is unit distance above the centre of rotation of the eye, the red side of the triangle has length $\tan(\beta/2)$. The white side of the triangle has length $\tan(\gamma/2)$. The angle in the horizontal plane between the red and green planes (in

that order) is $-\alpha/2$. Hence (2) follows.

To see why this configuration is equivalent to Listing's law, note first that because the yellow plane is common to both pairs of reflections, its effects cancel out. Fig. 3E shows that the combination of the torsional and azimuthal rotations is therefore a rotation about the common axis of the red and green RPs. Fig. 3F shows the addition of the RPs (blue and white in that order) achieving an elevation β . Note from Fig. 3A that the red, green and blue planes each have two common points, P and T, and therefore intersect in a single line from P to T. The blue plane therefore passes through the rotation axis of the red and green RPs¹ and the three planes together therefore have the effect of a single reflection, by the principle derived above that three reflections with a common axis are still a reflection. We have now reduced the three pairs of RPs to two-the reflection plane of the reflection that is the compound of the red, green and blue RPs (let us call it the RGB reflection plane), and the white RP, which is in Listing's plane. (Note that to avoid further complicating an already complicated figure the RGB reflection plane is not shown in Fig. 3F.) The rotation the RGB plane and the white plane comprise must therefore be a rotation about an axis in Listing's plane, as required.

Consider now both eyes rather than only one. Listing's law is not valid in convergence, but a generalisation of it known as L2 (Minken & Van Gisbergen, 1994; Mok, Ro, Cadera, Crawford, & Vilis, 1992; Tweed, 1997a; Van Rijn & Van den Berg, 1993) is valid: in convergence by angle v the Listing's planes of each eye rotate temporally by kv, making the angle between them 2kv. There is some debate about the usual value of k (Minken & Van Gisbergen, 1994; Mok et al., 1992; Tweed, 1997a; Van Rijn & Van den Berg, 1993). My purpose here is not to enter into that debate, but only to show that consideration of the eye rotations in terms of reflections makes it easy to see that requiring the epipolar plane (that defined by the lines of sight of the two eyes when viewing a single common real target) to lie on the horizontal retinal meridian of each eye leads to the angle between the Listing planes of the two eyes being v/2—the value one expects from L2 with k = 0.25.

Fig. 4 shows the construction necessary. Consider a convergence position in the horizontal plane achieved by rotat-

ing the left eye angle λ clockwise and the right eye angle ρ anti-clockwise about a vertical axis (as seen from above). For the left eve this is achieved by reflection first in a vertical RP placed $\lambda/2$ anti-clockwise from the fronto-parallel plane, and then by reflection in the fronto-parallel plane. For the right eye the vertical RPs are $\rho/2$ clockwise from the fronto-parallel plane and in the fronto-parallel plane (Fig. 4A). With no elevation (or torsion), the fixation point, the foveae and the horizontal retinal meridia of both eyes are all in the horizontal (X-Z) plane. To maintain them co-planar as (Helmholtz) elevation is altered, elevation must be by a common head-fixed angle. This elevation is accomplished by common (white) RPs in the fronto-parallel plane, followed by reflection in common (red) RPs tilted back out of this plane. In both eyes, the middle two (white) RPs of the convergence and elevation rotations are the same and so cancel one another out, leaving the green and red planes to define the overall rotation axes. The green RP is $\lambda/2$ anti-clockwise from the fronto-parallel plane for the left eye, and $\rho/2$ clockwise for the right. The angle between these two planes is $(\lambda/2) - (\rho/2) = \nu/2$,

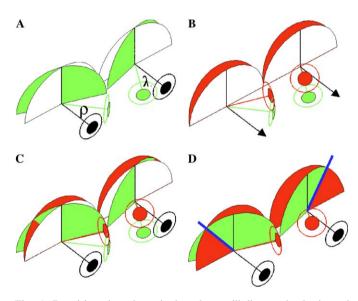


Fig. 4. Requiring that the epipolar plane will lie on the horizontal meridian of each eye, whatever the elevation and azimuth, leads to the same prediction of the divergence of the Listing planes of the two eyes as the generalisation of Listing's law known as L2. (A) The vertical green and white RPs realise convergence that is not necessarily symmetrical. Because in primary position the horizontal retinal meridia of both eyes lie in the epipolar plane, and these rotations are about a common axis normal to that plane, the horizontal meridia continue to lie in the epipolar plane after this convergence. (B) A common rotation in elevation is realised by the white and red RPs. Because the white RPs are coincident, their effects cancel out, and the overall rotation (of each eye) is that realised by the green and red RPs alone. The left eye therefore rotates about an axis in a plane tilted $\lambda/2$ temporally from the fronto-parallel plane and the right eye rotates about an axis tilted temporarily by $\rho/2$. As $\lambda - \rho = \gamma$, where γ is the convergence angle, the Listing planes of the two eyes rotate temporally so that the angle between them is $(\lambda - \rho)/2 = \gamma/2$. This is what is predicted by the generalisation of Listing's law known as L2. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this paper.)

¹ This is a difficult point to appreciate when one first comes to it, and this may be a point to reflect on, if one may pardon the pun.

where $v = \lambda - \rho$, the convergence angle—the result predicted by L2 with k = 0.25.

4. Conclusions

Those familiar with the mathematics of 3-D rotation will suspect that it must be possible to describe reflections using quaternions (Tweed & Vilis, 1987; Westheimer, 1957), or the equivalent rotation vector algebra (Haustein, 1989). The general principles of how this can be done were laid out with great clarity by Coxeter (1946), whose paper appears not be known to the vision or oculomotor communities, and the mathematical relationship between reflections, rotations and quaternions has been discussed more recently by Tweed and co-workers (Tweed, 1997b; Tweed et al., 1990) Coxeter remarked in 1946 that it was curious that neither Cayley nor others who followed him in using quaternions for the discussion of rotations "thought of considering first the simpler operation of reflection and deducing a rotation as the product of two reflections." It is indeed curious that this useful relationship has been so long neglected.

Acknowledgments

I thank the Wellcome Trust for financial support, Dr. Mirek Dostalek and the co-organisers of the Vth Symposium on Paediatric Ophthalmology (Litomysl, 2002) for providing me with the stimulus to think about these issues, and Roger Carpenter, Andrew Glennerster, David Murray, Lance Optican and Andrew Parker, who were kind enough to give me the benefit of their criticism of an earlier draft.

Appendix A. Reflections, quarternions and rotations

A reflection of vector \mathbf{r} is achieved by the operation of left and right multiplication by quaternion q

$$\mathbf{r}' = \mathbf{q} \ \mathbf{r} \ \mathbf{q} \tag{A.1}$$

where q is a unit quaternion with no scalar part, known as a 'pure' quaternion. Pure quaternions have the property that qq = -1. It follows that q^{-1} , the inverse of q, is given by

$$\mathbf{q}^{-1} = -\mathbf{q} \tag{A.2}$$

Also, if p is a second pure quaternion,

$$qp = (pq)^{-1} \tag{A.3}$$

If p and q specify reflection planes related to one another by a rotation through angle $\alpha/2$, then the sequence of reflection q followed by reflection p causes the transformation

$$\mathbf{r}'' = \mathbf{p}\mathbf{q} \ \mathbf{r} \ \mathbf{q}\mathbf{p} \tag{A.4}$$

By the use of (A.3) above

$$\mathbf{r}'' = \mathbf{pq} \ \mathbf{r} \ (\mathbf{pq})^{-1} \tag{A.5}$$

It can be shown that pq is a unit quaternion with scalar part $\cos(\alpha/2)$, where $\alpha/2$ is the angle between the two reflection planes; and vector part magnitude $\sin(\alpha/2)$.

Another way of treating reflections and rotations algebraically is by using Clifford algebra. See http://www.physpharm.fmd.uwo.ca/undergrad/tweedweb/ch6Mirror.htm.

References

- Clark, R. A., Miller, J. M., & Demer, J. L. (2000). Three-dimensional location of human rectus pulleys by path inflections in secondary gaze positions. *Investigative Ophthalmology and Visual Science*, 41, 3787–3797.
- Coxeter, H. S. M. (1946). Quaternions and reflections. American Mathematical Monthly, 53, 136–146.
- Feynman, R. P., Leighton, R. B., & Sands, M. (1964). Lectures on Physics, 2-1. Reading MA: Addison-Wesley.
- 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. (1910/1962). Physiological Optics (Vol. III). New York: Dover (English translation by J.P.C. Southall for the Optical Society of America (1925) from the 3rd German edition of Handbuch der physiologischen Optik (Hamburg: Voss, 1910)).
- Judge, S. J. (2003). Representing rotations as pairs of reflections elucidates the geometry of 3-D eye rotations. *Investigative Ophthalmology & Visual Science*, 44(Suppl. 1), 2129.
- Miller, J. M. (1989). Functional anatomy of normal human rectus muscles. Vision Research, 29, 223–240.
- Minken, A. W., & Van Gisbergen, J. A. (1994). A three-dimensional analysis of vergence movements at various levels of elevation. *Experimental Brain Research*, 101, 331–345.
- Mok, D., Ro, A., Cadera, W., Crawford, J. D., & Vilis, T. (1992). Rotation of Listing's plane during vergence. *Vision Res.*, 32, 2055–2064.
- Quaia, C., & Optican, L. M. (1998). Commutative saccadic generator is sufficient to control a 3-D ocular plant with pulleys. *Journal of Neurophysiology*, 79, 3197–3215.
- Raphan, T. (1998). Modeling control of eye orientation in three dimensions. I. Role of muscle pulleys in determining saccadic trajectory. *Journal of Neurophysiology*, 79, 2653–2667.
- Sappey, P. C. (1888). Traite d'anatomie descriptive avec figures intercalées dans la texte. Tome deuxieme, §5. – Muscles moteurs du globe de l'Oeil (pp. 94–107). Delahaye & Lecrosnier: Paris.
- Simonsz, H. J., Harting, F., De Waal, B. J., & Verbeeten, B. W. J. M. (1985). Sideways displacement and curved path of recti muscles. *Archives of Ophthalmology*, 103, 124–128.
- Tweed, D. (1997a). Visual-motor optimisation in binocular control. Vision Research, 37, 1939–1951.
- Tweed, D. (1997b). Kinematic principles of three-dimensional gaze control. In M. Fetter, T. Haslwanter, H. Misslisch, & D. Tweed (Eds.), *Three-dimensional kinematics of eye, head and limb movements* (pp. 17–31). Amsterdam: Harwood.
- Tweed, D., Cadera, W., & Vilis, T. (1990). Computing three-dimensional eye position quaternions and eye velocity from search coil signals. *Vision Research*, 30, 97–110.
- Tweed, D., Haslwanter, T., & Fetter, M. (1998). Optimizing gaze control in three dimensions. *Science*, 281, 1363–1366.
- Tweed, D. B., Haslwanter, T. P., Happe, V., & Fetter, M. (1999). Noncommutativity in the brain. *Nature*, 399, 261–263.
- Tweed, D., & Vilis, T. (1987). Implications of rotational kinematics for the oculomotor system in three dimensions. *Journal of Neurophysiology*, 58, 832–849.
- Van Rijn, L. J., & Van den Berg, A. V. (1993). Binocular eye orientation during fixation: Listing's law extended to include eye vergence. *Vision Research*, 33, 691–708.
- Westheimer, G. (1957). Kinematics of the eye. Journal of the Optical Society of America, 47, 967–974.