An Alternative Three-dimensional Interpretation of Hering's Equal-innervation Law for Version and Vergence Eye Movements

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In the context of Hering's equal-innervation law, this paper discusses the problem of how the three-dimensional positions of the two eyes, each expressed by a rotation vector, can be separated into contributions of the version and vergence system. As proposed by Van Rijn and Van den Berg [(1993) Vision Research, 33, 691-708], this can be done by taking the sum and difference of the position rotation vectors of each eye. In our alternative procedure the vergence signal is defined as the rotation which transforms the left eye position into the right eye position and the version signal is the common factor in both eye positions that remains after removing the vergence signal. The version and vergence contributions, defined in this way, can be interpreted straightforwardly as rotations. When Van Rijn and Van den Berg applied their definitions to their own data, they obtained the interesting result that the reconstructed version and vergence contributions were effectively limited to two dimensions (2D). The version signal was confined to Listing's plane (no torsion) whereas the vergence signal remained within a horizontal-torsional plane (no vertical vergence). They showed theoretically that a model based on 2D version/2D vergence control will indeed produce the torsional eye positions in near fixations found in their experiments. This model cannot account for a second set of data in the literature [Mok, Ro, Cadera, Crawford & Vilis (1992) Vision Research, 32, 2055-2064]. With our definitions, we found that the simple 2D version/2D vergence control strategy cannot account for the Van Rijn and Van den Berg (1993) data but is nicely compatible with the considerably smaller amount of cyclotorsion in the data collected by Mok et al. (1992). We also show that, in such a system, having 2D vergence control is compatible with minimization of torsional disparity and provides the cyclovergence signals suitable for stabilizing the eyes in the non-Listing positions caused by a vertical saccade in near vision.

INTRODUCTION

The study of three-dimensional (3D) eye movements has become a topic of considerable interest following the introduction of the 3D search coil technique (Ferman, Collewijn, Jansen & Van den Berg, 1987). Another noticeable development is the growing consensus that rotation vectors are well suited for the description of eye rotations. With this tool, an eye position is represented as a rotation about a single axis from a reference position to the actual eye position. The rotation vector is then defined as \( \mathbf{r} = n \cdot \tan(\alpha/2) \), where \( n \) denotes the unit vector pointing in the direction of the rotation axis and where \( \alpha \) represents the size of the rotation angle. The components of the rotation vector, in sequential order, are torsional, vertical and horizontal. This representation (or an equivalent one based on quaternions) is now commonly used in 3D eye movements research laboratories (Hess, Van Opstal, Straumann & Hepp, 1992; Tweed & Vilis, 1987; Haustein, 1989; Van Rijn & Van den Berg, 1993; Minken, Van Opstal & Van Gisbergen, 1993). Tweed and Vilis (1987) and Haustein (1989) argued that such a non-hierarchical way of describing the rotations of the eyes is preferable above systems in which eye positions are specified as rotations about nested axes. This representation is nicely compatible with the way in which eye movements are generated by the six extra-ocular muscles which deal with all rotation axes on an equal basis. In addition, the description of Listing's law in far vision is very simple in this system: all rotation vectors are lying in a head-fixed plane (see e.g. Tweed & Vilis, 1990; Minken et al., 1993). When the rotation vectors are expressed with respect to the
primary position, Listing's law yields rotation vectors, the torsional component of which is zero.

It is generally assumed that the version and vergence eye movements are controlled by distinct neural control systems implementing Hering's law of equal innervation (Carpenter, 1988). When describing 1D eye movements, Hering's notion is mathematically trivial. This is no longer the case in 3D studies considering the binocular coordination of eye movements (Mok, Ro, Cadera, Crawford & Vilis, 1992; Van Rijn & Van den Berg, 1993). One of the main issues to be dealt with in these studies is to what extent the reduction of the number of the degrees of freedom, which has been noticed in the version system (Listing's law), can be generalized to the control of binocular eye positions. In this paper we show that the answer to these questions depends critically on how binocular eye positions expressed in rotation vectors are decomposed into signals attributable to the version and the vergence system. A simple method to derive version- and vergence-related signals from eye position data expressed as rotation vectors was proposed by Van Rijn and Van den Berg (1993). They defined a vergence (g: anti-symmetric) signal as half of the difference of the rotation vectors of the left and right eye. The version signal (s: symmetric part) was defined as the mean (half of the sum) of the rotation vectors of the two eyes. We will briefly refer to this decomposition as the “difference vector scheme”. The difference vector scheme is capable of describing the data collected by Van Rijn and Van den Berg in some simple terms. Basically, both the s and the g signal have only two degrees of freedom. While the s system has negligible torsion, the g system has virtually no vertical component. On the basis of a model, Van Rijn and Van den Berg (1993) showed how these properties may be the consequence of dimensional constraints on the operation of the version and the vergence systems.

The model by Van Rijn and Van den Berg (1993) cannot directly explain the data collected by Mok et al. (1992) who found a considerably smaller torsional vergence than Van Rijn and Van den Berg. The description of the Mok et al. (1992) data in the difference vector scheme yields a 3D vergence signal with a small vertical component and is compatible with a so-called optimal correspondence model (Van Rijn & Van den Berg, 1993). More specifically, the torsional state of the eyes measured by Mok et al. can be understood by assuming that the vergence system tries to achieve minimal binocular torsional disparity. So in summary, the conflicting data sets lead to different model implications: when described in terms of the difference vector scheme, the Mok et al. (1992) data require a more complex (3D) vergence system than the Van Rijn and Van den Berg (1993) data which yield to a parsimonious 2D description. This state of affairs has led us to consider the use of different version and vergence definitions in which the version and vergence contributions can be seen as rotation vectors describing rotations, which is not the case in the difference vector scheme (see footnote on p. 703 of Van Rijn & Van den Berg, 1993). We will use the term “rotation vector system” to distinguish our descriptive system from the “difference vector system”. To clarify the implications of this distinction, we begin with the formal definitions of vergence and version signals in both descriptive systems. We then show that having a 2D version/2D vergence control system leads to quite different binocular fixation behaviour in 3D, depending on whether the system implements movements according to one definition or the other. Finally, we point out that there is an interesting parallel between the data predicted from these two different perspectives and the two actual data sets in the literature (Mok et al. 1992; Van Rijn & Van den Berg, 1993).

**COMPARISON OF THE TWO DESCRIPTIVE SYSTEMS**

**Difference vector system**

When the right (r) and left (l) eye position rotation vectors are expressed with regard to a common reference position, the version signal in this system is defined as a sum vector:

\[ s = (l + r)/2 \]  

while the vergence signal is a difference vector:

\[ g = (l - r)/2 \]

with:
- s, version vector;
- g, vergence vector;
- l, left eye position rotation vector;
- r, right eye position rotation vector.

To what extent do these s and g signals represent the eye movements attributable to the version and vergence system? Van Rijn and Van den Berg (1993) cautiously suggest that s and g are analogues of the classical concept of version and vergence. Why is this caution necessary? Taking the difference in components to characterize vergence is no problem in case one is only interested in horizontal eye movements as was common practice in most earlier studies.

However, as noticed by Tweed and Vilis (1987), for 3D eye movements the difference of rotation vectors is inadequate to characterize the rotation underlying the difference between two eye positions, since 3D rotations do not commute (e.g. 3D motor error is not the difference of actual and desired eye position). Therefore, the version and vergence components computed with the difference vector system, while perfectly able to describe any binocular eye position combination, cannot be interpreted as rotations imposed by the version and vergence control systems. Our alternative approach, which uses the rotation vector product to describe a 3D rotational difference, depicts the version and vergence components as rotational contributions.

**Rotation vector system**

We describe eye positions in three dimensions as rotations from a common reference position. The
positions of the two eyes are fully determined by the pair of rotation vectors which moves each eye from this common reference position to its actual position. Whatever the actual movement made, each eye position in transit can be described with respect to the fixed reference position. Eye positions may be defined in world coordinates or in coordinates rotated to fit Listing’s plane. Our descriptive system transforms these right (r) and left eye (l) rotation vectors into a pair of binocular rotation vectors: the conjugate rotation vector (c) and the disjunctive rotation vector (d). Each binocular eye position is described by first rotating both eyes symmetrically from their common reference position by rotation c and then rotating both eyes anti-symmetrically by d. Thus, the binocular rotation vectors provide a formal description of each binocular eye position as if it was achieved by this sequence of binocular rotations, irrespective of the actual trajectory of the binocular fixation point. Below, we will first explain how to obtain the binocular rotation vectors from the eye rotation vectors. Subsequently, we will modify the inverse procedure: reconstructing eye rotation vectors from a given pair of binocular rotation vectors. The starting point for the computation of binocular rotation vectors is our definition of vergence. We define the vergence signal (v) as the rotation vector characterizing the angular discrepancy between the right and the left eye. Half of this angular discrepancy equals the disjunctive (d) rotation. The vergence rotation vector (v) is computed as follows from the right and left eye position rotation vectors:

\[ v = r \otimes l^{-1} = r \otimes (-l) = n \cdot \tan(\alpha/2) \]  

where:
- v, vergence rotation vector;
- r, right eye-position rotation vector;
- l, left eye-position rotation vector;
- n, unit vector in the direction of the rotation-axis;
- \( \alpha \), angle of rotation about n;
- \( \otimes \), rotation vector product.

The rotation vector product describing the discrepancy between the rotational states of the two eyes r (right eye position) and l (left eye position) is given by (see e.g. Hepp, 1990):

\[ r \otimes l^{-1} = r \otimes (-l) = \frac{r - l - r \times l}{1 + r \cdot l}. \]  

This expression consists of two terms. The first-order (\( r - l \)) term reflects the difference in the components of the rotation vectors representing the position of each eye (cf. Van Rijn & Van den Berg, 1993); the second-order term is the cross-product of the rotation vectors of the two eyes which becomes significant when the rotation vectors r and l are not collinear. For example, when both horizontal vergence and vertical elevation are large, the contribution of the second-order term to the torsional vergence component becomes relevant.

Our definition of the vergence contribution has the attractive property that its outcome does not depend on the chosen reference position. This can be shown by comparing vergence for two different reference positions separated by the rotation characterized by the rotation vector p:

\[ v_1 = r_1 \otimes l_1^{-1} = (r_2 \otimes p) \otimes (l_2 \otimes p)^{-1} = r_2 \otimes p \otimes p^{-1} \otimes l_2^{-1} = r_2 \otimes l_2^{-1} = v_2 \]  

p, rotation from first reference position to second reference position;
\( r_1, l_1 \), rotation from first reference position to the actual eye position;
\( r_2, l_2 \), rotation from second reference position to the actual eye position;
\( r_1 = r_2 \otimes p, r_1 \) can be described as the rotation p followed by \( r_2 \).

To compute the conjunctive (c) contribution to binocular 3D eye position, we need half the v rotation, the so called disjunctive rotation vector d, defined as:

\[ d = n \cdot \tan(\alpha/4) \]  

which is used by taking:

\[ c = d \otimes l = -d \otimes r. \]  

Thus, the c signal is the common deviation from the binocular primary position that remains after removal of the disjunctive (d) contribution from the individual eyes. Notice that \( \alpha \) is divided by 4, so the rotation angle has an amplitude of \( \alpha/2 \), thus equalling half the v rotation. In our approach, every binocular eye position is described as the result of a conjunctive and disjunctive rotation. The right and left eye positions are obtained by computing the following rotation vector products:

\[ r = d \otimes c \]  

\[ l = -d \otimes c. \]  

In the next section we will analyse whether and to what extent the different definitions, used in the difference vector and the rotation vector scheme, have implications for the 3D binocular eye positions that result when the version and vergence control system are constrained to provide only 2D signals.

**IMPLICATIONS**

We will now show that the two definitions lead to different predictions for the torsional state of the eyes when identical constraints on the number of degrees of freedom are imposed.

Van Rijn and Van den Berg (1993), who described their data in terms of the difference vector scheme, noticed that in all cases the vertical part of the vergence signal (\( g_z \)) was almost zero. In an attempt to model the binocular control of eye movements, they then used this as a constraint inherent to the control system. We will characterize this constraint by the statement: "no vertical vergence". As will become clear, this constraint leads to nontrivial differences in the amount of cyclotorsion depending upon the descriptive scheme that is used to define the vergence signal.

Requiring fixation of a target, by itself, does not restrict the torsion in each eye. So, two degrees of
freedom remain after the binocular fixation point has been chosen and the question arises how the brain handles this indeterminacy. Like Van Rijn and Van den Berg (1993), we assume that this problem is solved by imposing two constraints on the version and vergence control systems. The first constraint of this type is that the version system implements Listing's law (no torsional component). The second constraint is that vergence is also dimensionally restricted (no vertical component), so that the rotation vectors for version and vergence are each limited to a plane, which is different for version and vergence. As will become clear below, the consequences of this restriction for torsion depend on whether the difference vector or the rotation vector scheme has been chosen to describe binocular eye positions.

In what follows, it will be necessary to define target position in binocular coordinates. Fixation of a target with both eyes specifies the line of sight of each eye, but the amount of rotation about the line of sight is not restricted. The use of rotation vectors for describing target position would lead to a cumbersome expression in which the rotation about the line of sight is visible in each of the components [see Appendix equation (A1)]. The use of a descriptive system in which the rotation about the line of sight is a parameter (Fick or Helmholtz) is more attractive since then only two parameters are necessary to define the target. For binocular eye movements the Helmholtz coordinate system is most suitable (Carpenter, 1988). The Helmholtz angles are given by elevation $\theta$ (downward corresponds to positive values), azimuth $\alpha$ (leftward corresponds to positive values) and torsion $\psi$ (clockwise corresponds to positive values). In the case of binocular eye movements, a bipolar system is useful. Figure 1 illustrates the bipolar Helmholtz system. In this system target position is specified by the line of sight of the cyclopean eye (elevation $\theta$ and azimuth $\alpha$) and the amount of horizontal vergence ($\Delta \alpha \equiv \nu$). The common torsion ($\psi$) and the difference in vertical ($\Delta \theta$) and torsional ($\Delta \psi$) position complete the six-dimensional parameter set. A condition for binocular fixation is that the lines of sight of the two eyes must intersect ($\Delta \theta = 0$).

To clarify the implications of the two additional constraints mentioned above, we will now express the rotation vectors of the two eyes in bipolar Helmholtz coordinates, first for the difference vector scheme and then for the rotation vector scheme. The transformation of Helmholtz angles for each eye into rotation vectors (Hepp, 1990) and more details about the computation of vergence in the two descriptive schemes, can be found in the Appendix.

**The difference vector scheme: implications of model assumptions**

As explained above, each binocular target position can be defined in terms of a bipolar coordinate system based on Helmholtz angles. Binocular fixation of a target given by $\theta$, $\alpha$, $\nu$ and the further constraint that $\Delta \theta = 0$ (alignment of the two visual axes) requires four degrees of freedom out of the six available (two eyes with three dimensions each). With two additional constraints, provided that these are not contradictory or dependent, all binocular eye positions in three dimensions are completely determined. In the first model considered by Van Rijn and Van den Berg these two additional conditions are imposed on the version and vergence control systems. The first constraint of this type is that the version system implements Listing's law (no torsional component). The second constraint is that vergence is also dimensionally restricted (no vertical component), so that the rotation vectors for version and vergence are each limited to a plane, which is different for version and vergence. As will become clear below, the consequences of this restriction for torsion depend on whether the difference vector or the rotation vector scheme has been chosen to describe binocular eye positions.

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constraints were imposed upon the version and vergence control systems:

1. The version system obeys Listing's law ($s_1 = 0$);
2. Vertical vergence is zero ($g_2 = 0$).

As noted by Van Rijn and Van den Berg, the restriction $g_2 = 0$, by itself, does not prevent the eyes from assuming positions that differ in elevation (Van Rijn & Van den Berg, 1993) and is not equivalent with the requirement that $\Delta \theta = 0$. It restricts vergence to a plane, just as version is restricted to two dimensions. This design reduces the remaining number of degrees of freedom in the control system to four. However, although the components $s_2, s_3, g_1$, and $g_3$ are in general non-zero, the ratio of $g_1$ and $g_3$ depends on $s_2$ [see equation (10)], which effectively reduces the number of degrees of freedom to three. Any binocular fixation position can be reached by the proper choice of the parameters $\theta, \alpha$, and $\nu$. This allows a prediction of the torsion in both eyes as a function of $\theta$ and $\nu$:

$$ r = s - g = \begin{pmatrix} \frac{\theta \cdot \nu}{4} \\ 0 \\ 0 \end{pmatrix} $$

The approximations serve merely to gain a better insight into the functional significance of the version and vergence contributions. As Van Rijn and Van den Berg (1993) noticed, the approximation of $\tan(\rho)$ by $\rho$ introduces errors of the order of 2.5% or less for $\rho$ angles up to 30 deg. Since we focus the analysis on the amount of torsion, the first component of the vergence vector and of the left and right eye position is important. In these equations, convergence corresponds to positive values of $\nu$. This deviation from the convention of Van Rijn and Van den Berg (1993), who gave convergence a negative sign, introduces sign differences when $\nu$ is used, but it is otherwise irrelevant for the purpose of this paper. Downward movements correspond to a positive value of $\nu$ and leftward rotations correspond to positive $\alpha$ values.

Van Rijn and Van den Berg have also done this exercise for a second model which again incorporates the constraint that the version system implements Listing's law while the vergence system now minimizes binocular disparity ($\Delta \psi = 0$) but is not constrained in its vertical component. In this case they found that the predicted amount of torsion in each eye is reduced by a factor of 2, which approximates the amount of torsion Mok et al. (1992) found in near fixations after saccades.

**Implications of the rotation vector scheme**

By using our definition of a conjunctive ($c$) and a disjunctive ($d$) signal (described above) and imposing the same dimensional restrictions on these two signals as above (2D version/2D vergence), the torsional state of the eyes can again be expressed in terms of the bipolar angles shown in Fig. 1. When described in terms of the rotation vector scheme, a binocular eye position can be thought of as the result of two successive rotations. The first rotation is a conjunctive movement made from the common reference position to a peripheral position; in the treatment below we assume that this signal is restricted by Listing's law. In Helmholtz coordinates, Listing's law is expressed by $\tan(\psi/2) = - \tan(\alpha/2) \cdot \tan(\theta/2)$. This can be shown by setting the first component of the rotation vector equal to zero [see
Appendix equation (A1)]. Since the first rotation is conjunctive, the rotation vectors of the left (l) and right eye (r) are equal and can be described by the conjunctive contribution (c):

\[
c = y \times \begin{bmatrix}
0 \\
\tan\left(\frac{\theta}{2}\right) \cdot (1 - \tan^2\left(\frac{\alpha}{2}\right)) \\
\tan\left(\frac{\alpha}{2}\right) \cdot (1 + \tan^2\left(\frac{\theta}{2}\right))
\end{bmatrix}
\]

\[
c \approx \begin{bmatrix}
\frac{\theta}{2} \cdot (1 - \frac{\alpha^2}{4}) \\
\frac{\alpha}{2} \cdot (1 + \frac{\theta^2}{4})
\end{bmatrix} \approx \begin{bmatrix}
0 \\
\frac{\theta}{2}
\end{bmatrix}, \quad (13)
\]

with

\[
y = \frac{1}{1 + \tan^2\left(\frac{\alpha}{2}\right) \cdot \tan^2\left(\frac{\theta}{2}\right)}.
\]

The second rotation necessary to achieve the final binocular eye position is a disjunctive rotation of 9/2 deg. We again impose the restrictions that \( \Delta \theta = 0 \) and that vertical vergence is zero \( (d_2 = 0, \text{ in itself is not enough for binocular fixation}) \). The rotation vector of this movement is described by:

\[
d = \begin{bmatrix}
\sin(\theta) \cdot \tan\left(\frac{\nu}{4}\right) \\
0 \\
\cos(\theta) \cdot \tan\left(\frac{\nu}{4}\right)
\end{bmatrix} \approx \begin{bmatrix}
\frac{\theta \cdot \nu}{4} \\
0 \\
\frac{\theta^2 \cdot \nu}{4}
\end{bmatrix} \approx \begin{bmatrix}
\frac{\theta \cdot \nu}{4} \\
0 \\
\frac{\nu}{4}
\end{bmatrix}, \quad (14)
\]

In the right-hand terms of equations (13) and (14) we neglected second and higher order terms to allow comparison with the formulas in Van Rijn and Van den Berg (1993). The restriction of vertical vergence to zero (second \( d \) component zero) and the requirement that the lines of sight must intersect at all times necessitate two opposite rotations about an axis perpendicular to the plane of regard. This latter property is expressed by the sine and cosine factors in the torsional and horizontal component, respectively [see equation (14)]. The only rotation that implements Listing's law is one about an axis tilted at half eccentricity (Tweed & Vilis, 1987, 1990). Therefore, rotation \( d \) which has full-angle tilt, introduces deviations of Listing's law. The \( d \) rotation can also be derived using the formulas given in the Appendix [equations (A5-A10)].

Also in the rotation vector scheme the restriction of vertical vergence to zero \( (d_2 = 0) \) does not prevent different elevations in the two eyes. This is ensured by requiring that \( \Delta \theta = 0 \), which leads to a rotation axis perpendicular to the plane of regard. To allow a comparison of the different models, \( c \) and \( d \) are combined to left \( (l) \) and right eye \( (r) \) positions. Ignoring second and higher order terms we get for the position of the left eye:

\[
l = d^{-1} \otimes c \approx \begin{bmatrix}
\frac{-\theta \cdot v}{8} \\
\frac{\theta}{2} \\
\frac{\alpha \cdot v}{2} \\
\frac{\nu + \frac{\nu}{4}}{4}
\end{bmatrix}, \quad (15)
\]

and for the position of the right eye:

\[
r = d \otimes c \approx \begin{bmatrix}
\frac{\theta \cdot v}{8} \\
\frac{-\theta}{2} \\
\frac{-\alpha \cdot v}{2} \\
\frac{-\nu + \frac{\nu}{4}}{4}
\end{bmatrix}.
\]

Equations (15) and (16) express the rotation vectors of the two eyes when they fixate a (near) target, provided that the version and vergence signals controlling them are defined according to the rules of the rotation vector scheme and if the dimensional constraints mentioned earlier are imposed on these subsystems. These equations should now be compared with expressions (11) and (12) which give the result of the entirely equivalent exercise for the difference vector scheme. The major point to be noticed is that the same task, under the same constraints, leads to different torsional eye positions: the amount of torsion found in the rotation vector scheme \([(\theta_\nu)/8]\) is half the amount of torsion found in the difference vector scheme \([(\theta_\nu)/4]\). A second point to be noticed is that, in both versions of the 2D version/2D vergence model, this torsional component is fully determined by elevation and horizontal vergence so that, effectively, the number of degrees of freedom is reduced to three.

### DISCUSSION

**Describing version and vergence by rotation vectors**

The present paper illustrates that the outcome of discussions on how the version and the vergence system solve the problem that the two eyes have a redundant number of degrees of freedom for bifoveal fixation (see above), depends on the definition of version and vergence signals. Two quantitative experimental studies are available now (Mok et al., 1992; Van Rijn & Van den Berg, 1993) but, since the reported data show...
considerable differences in the amount of eye torsion in near vision, the problem of how the control systems handle the indeterminacy problem cannot be solved at this moment. One conclusion from the present paper is that just repeating these studies, however essential for knowing the facts, will not be enough by itself. The point is that inferences about the properties of the underlying control mechanisms will depend heavily on one’s concept of version and vergence.

It is clear that any formal definition of these signals requires an appropriate system for describing eye position in three dimensions. Most groups have now adopted a common approach to the description of 3D eye positions by using rotation vectors or an equivalent mathematical tool. This reduces the problem to one of deriving version and vergence signals (in some way) from the rotation vector data of the two eyes. The definition used by Van Rijn and Van den Berg (1993) follows a tradition in earlier 1D work on vergence where one can simply take the difference in horizontal angular positions of the two eyes. Our definition sticks to the description of rotational contributions by rotation vectors. In this system, the pair of version and vergence rotation vectors formally describes how a particular binocular eye position can be achieved by a sequence of a version and a vergence rotation. The version rotation vector describes the first rotation which moves the eyes conjugately from the primary position. Just as in the rotation vectors used for describing eye position (Haustein, 1989), the orientation of the rotation vector denotes the direction of this conjugate gaze shift, while its amplitude specifies the amount of rotation about this axis. The vergence rotation vector subsequently rotates the two eyes equally in opposite directions along axes parallel to its orientation by an amount equal to its amplitude. According to this descriptive system, each binocular eye position can be conceived of as the result of these sequential symmetric and anti-symmetric rotations which bring the eyes from the common reference position to their actual position. Noticing that the difference vector description scheme is nonhierarchical, one may wonder why there should be a need for any rotational sequence in our scheme at all and, if unavoidable, how we arrived at this particular sequential order (first c, then d rotation). Since 3D rotations do not commute, this also applies to the version and vergence rotations computed by following our approach. Consequently, combining these same rotations in the reverse order (first vergence, then version) will yield a different binocular eye position. The need to put the version rotation first follows directly from our definition of vergence as the 3D rotation required to transform the left eye position into the right eye position. Once this rotation is known, the c rotation vector can be computed in the next step of our procedure [see equation (7)] by removing the vergence contribution from the binocular eye position signals. Of course, the descriptive system only makes sense if combining rotations d and c yields again the same binocular eye position from which they were derived. Because of the non-commutative nature of 3D rotations, this is only the case if recombing c and d follows the reverse order as the decomposition used to obtain them. As noticed above, our description of binocular eye positions in terms of the binocular rotation vectors c and d is purely formal and we do not claim a simple relation to the required neural control signals (see also below). Nevertheless, behavioural data (Mok et al., 1992) suggest that the combination of vergence and version eye movements in 3D in the system itself probably has to be nonlinear (see Mok et al., 1992 for a discussion of this point) and our description captures some of this complexity. Of course, in practice, a particular binocular eye position will almost never be achieved by the same sequence of a conjugate and a vergence rotation that is used to characterize it in our formal description. This applies similarly to the broadly accepted use of rotation vectors to describe eye position. For example, when the eye makes an eccentric saccade, each eye position in transit is nevertheless described as a rotation from the primary position to the present position. As has been demonstrated in several studies on version movements, the actual movement can be documented by computing the angular velocity signal (see e.g. Tweed & Vilis, 1990). For saccades in far vision it is known that the angular velocity signal behaves such (half-angle tilting) that Listing’s law is maintained during the movement. Mok et al. (1992) have reported that the angular velocity axis of saccades in near vision is very similar. So far, dynamic studies on 3D vergence movements are not available, so nothing is known on the behaviour of the angular velocity signal in this system. The latter signal can be computed from the vergence rotation vector, using standard procedures.

Model implications of the two descriptive schemes

It should be noticed that the difference vector scheme and the rotation vector scheme both adhere to Hering’s law of equal innervation by decomposing binocular eye positions into combinations of symmetrical and anti-symmetrical signals. Both descriptions are unambiguous: with the expressions given in this paper, it is always possible to go from one descriptive system to the other and to reconstruct the position signals of the two eyes. Since the difference between the two descriptive systems is rather fundamental, using one or the other reflects different 3D interpretations of Hering’s law. By adopting rotations as the basic entity for characterizing the version and vergence contributions to binocular eye positions, the signals reconstructed by our scheme have a different meaning than in the difference vector scheme. Hence, it is not so surprising to find (see above) that imposing 2D constraints on version and vergence signals in each of the two descriptive schemes, leads to different eye positions even when the eyes are required to look at the same target [see equations (11), (12) and (15), (16)]. What is remarkable is that our descriptive scheme, together with these dimensional constraints, predicts eye position signals with cyclovergence components that are close to those reported by Mok et al. (1992). Van Rijn and Van den Berg (1993) could account for these data.
by dropping the no vertical vergence constraint in their model and replacing it by the functional requirement of minimal torsional disparity ($\Delta \psi = 0$). To explain this result with our scheme, it was not necessary to impose any constraint on torsional disparity. As shown in the Appendix, it turns out that, in our description system, requiring zero vertical vergence automatically guarantees minimal torsional disparity. Thus, if indeed the system implements Hering's law in accordance with our definition, it has the intriguing feature that keeping the vergence signal simple (2D) is fully compatible with what might be desirable for the analysis of the binocular visual input (minimal horizontal and torsional disparity). Although this certainly sheds a new light on the existing discrepancy between the data of Mok et al. (1992) and Van Rijn and Van den Berg (1993), it cannot resolve this problem with the present data sets, since the eye position data themselves are different in the two studies. To explain the data from Van Rijn and Van den Berg (1993), who found more cyclo-torsion, the vergence system according to our definition would have to be 3D. In contrast, with their own descriptive scheme, 2D vergence is sufficient for these data. Thus, these analyses lead to the conclusion that each scheme can parsimoniously describe one of the two data sets on the basis of a 2D vergence signal, but requires a 3D vergence signal for the other.

Mathematically, rotation vectors $c$ and $d$ represent the symmetrical and anti-symmetrical rotations which, when applied to the eyes in the reference position, will yield their present position. One cannot simply regard the $d$ signal as a direct indicator for the required signals in the neural centres controlling vergence. For example, executing a vertical conjugate movement while the eyes are held in a converged state, causes cyclo-torsional changes without requiring an active cyclo-vergence control signal. The effect can be understood from the laws of kinematics as follows. Suppose that, in order to fixate a nearby point target at a positive elevation, we begin by first making a disjunctive rotation (far→near) at zero elevation where torsional vergence is zero. Subsequently, in this converged state, a conjunctive saccade (level→up) is made to the target. Such a conjunctive rotation in near vision space introduces a certain amount of torsion, depending on the orientation of the saccadic angular velocity axis (see Mok et al., 1992). Mok et al. found that the angular velocity axes were aligned in the two eyes during such near vision space saccades. This finding is in line with the idea that both eyes are controlled by a common velocity command signal. A common control signal cannot implement Listing's law when the two eyes are converged. Dynamic implementation of Listing's law requires that the angular velocity axis of each eye must be tilted depending upon its eccentricity. Since the eyes are not aligned, it is impossible to tilt the angular velocity axis by the proper amount in each eye simultaneously with a single controller. If, as indicated by the experimental data, the saccadic control system opts for a compromise (i.e. the amount of tilting lies between the requirements of both eyes) this causes opposite torsion in the two eyes. Computation shows that the amount of torsion that is introduced passively during the saccade by this kinematic effect, is quite compatible with the actual amount in the data of Mok et al. (1992).

Mok et al. suggested that keeping the eyes in the new post-saccadic position requires neural holding signals, not only for horizontal and vertical, but also for torsion. To show how the brain may solve this problem, they proposed a nonlinear interaction between version and vergence systems, which would generate appropriate torsional vergence holding signals. Note that what is appropriate in this context is precisely defined by kinematical laws if one can assume that the angular velocity axis of saccades indeed follows the half-angle tilting rule for the cyclopean eye. Clearly, if cyclo-torsion in near vision should match the kinematical cyclo-torsional consequences of saccades, the amount of cyclo-vergence in the preferred model of Van Rijn and Van den Berg (as well as in their data) is too large by a factor of 2. Thus, there is a discrepancy between the cyclo-vergence holding signals offered by the Van Rijn and Van den Berg (1993) model and the requirements that can be deduced from considerations of rotational kinematics. So, to get the proper amount of torsion the vergence system would have to become active during the nearby saccade, thus spoiling the elegance of this model. By contrast, when our descriptive scheme is used in combination with 2D vergence control, this discrepancy does not arise. In the rotation vector scheme the amount of torsion introduced by the 2D conjunctive and the 2D disjunctive signals is equal to the amount of torsion introduced by a nearby saccade. It is remarkable that this same amount of torsion is also derived by the minimization of torsional disparity, which suggests that visual requirements and the need for simple oculomotor control are in nice agreement. In conclusion, the concept proposed in this paper is nicely compatible with the following simultaneous requirements:

(i) simple (2D) vergence and (2D) version control which, since cyclo-vergence is completely coupled to horizontal vergence and elevation, requires only three control signals;
(ii) minimal torsional disparity in the binocular image;
(iii) compatibility with the kinematical consequences of saccades in near vision space.

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APPENDIX

In this Appendix the equations underlying our analysis (see above) will be presented. We start by describing the rotation of the two eyes in terms of bipolar Helmholtz coordinates. Eye position in Helmholtz coordinates is characterized by elevation (θ), azimuth (α) and torsion (v). The conversion of Helmholtz coordinates to rotation vectors is done by equation (A1), and can be verified with some algebra:

\[ r_i = \gamma \times \begin{bmatrix} \tan \left( \frac{\psi_i}{2} \right) + \tan \left( \frac{\alpha_i}{2} \right) - \tan \left( \frac{\theta_i}{2} \right) \\ \tan \left( \frac{\theta_i}{2} \right) + \tan \left( \frac{\alpha_i}{2} \right) - \tan \left( \frac{\psi_i}{2} \right) \\ \frac{\alpha_i}{2} - \tan \left( \frac{\theta_i}{2} \right) - \tan \left( \frac{\psi_i}{2} \right) \end{bmatrix} \]

with

\[ \gamma = \frac{1}{\left( 1 - \tan \left( \frac{\alpha_i}{2} \right) - \tan \left( \frac{\theta_i}{2} \right) - \tan \left( \frac{\psi_i}{2} \right) \right)} \]

In good approximation, this equation can be put in a simpler form, by replacing tan(p) by p and ignoring third and higher order terms:

\[ r_i \approx \begin{bmatrix} \frac{\psi_i + \alpha_i \cdot \theta_i}{2} + \frac{\alpha_i}{4} \\ \frac{\theta_i + \alpha_i \cdot \psi_i}{2} + \frac{\alpha_i}{4} \\ \frac{\alpha_i \cdot \theta_i + \psi_i}{2} - \frac{\alpha_i}{4} \end{bmatrix} \]  

(A2)

In this equation the index i denotes the r and l of the right and left eye position.

We define the bipolar angles α, θ and ψ as the mean of the left and right eye angles and the angles Δθ, Δα and Δψ as the difference of these angles. One can derive the following vectors for version s and vergence g in the difference scheme, as earlier shown by Van Rijn and Van den Berg (1993):

\[ s = \frac{l + r}{2} = \frac{1}{2} \begin{bmatrix} \psi + \theta \cdot \Delta \theta \cdot \gamma \\ \theta + \psi \cdot \Delta \psi \cdot \gamma \\ \psi \cdot \theta \cdot \Delta \theta \cdot \Delta \psi \cdot \gamma \end{bmatrix} \]

(A3)

Note that we denote convergence by a positive sign, which is opposite to the definition of Van Rijn and Van den Berg. The vergence g in the difference scheme is given by:

\[ g = -\frac{l - r}{2} = \frac{1}{2} \begin{bmatrix} \Delta \psi \cdot \theta \cdot \Delta \theta \cdot \gamma \\ \theta \cdot \Delta \theta \cdot \psi \cdot \Delta \psi \cdot \gamma \\ \psi \cdot \theta \cdot \Delta \theta \cdot \Delta \psi \cdot \gamma \end{bmatrix} \]

(A4)

Equations (A3) and (A4) are the general equations of version and vergence in the difference vector scheme when no constraints are imposed. In equation (10), vergence and version were restricted to two planes and binocular fixation was assumed (s_i = 0, g_i = 0 and Δθ = 0).

Next we discuss the computations in the rotation vector scheme. This requires that we express the vergence rotation vector in the rotation vector scheme in terms of bipolar Helmholtz angles. By substituting the approximated rotation vectors of the two eyes [see equation (A2)] into equation (3) we can derive the following equation for vergence in the rotation scheme in terms of bipolar Helmholtz angles (no constraints are imposed and fourth and higher order terms are neglected):

\[ v = r \otimes \gamma^{-1} \]

\[ v = \gamma \times \begin{bmatrix} \frac{\Delta \psi}{2} \left( 1 - \frac{\theta^2 + \alpha^2 - (\Delta \theta)^2}{4} \right) + \frac{\theta \cdot \gamma}{2} \\ \frac{\Delta \theta}{2} \left( 1 + \frac{\theta^2 + \psi^2 - (\Delta \psi)^2}{4} \right) + \frac{\alpha \cdot \Delta \psi}{2} \\ \frac{\psi}{2} \left( 1 + \frac{\theta^2 - \alpha^2 - (\Delta \theta)^2}{4} \right) - \frac{\alpha \cdot \Delta \psi}{2} \end{bmatrix} \]

(A5)

with

\[ \gamma = \frac{1}{\left( 1 + \frac{\theta^2 + \alpha^2}{4} \right)} \]

For binocular fixation the restriction Δθ = 0 must be made, which leads to:

\[ v = \gamma \times \begin{bmatrix} \frac{\Delta \psi}{2} \left( 1 - \frac{\theta^2 + \alpha^2 - (\Delta \theta)^2}{4} \right) + \frac{\theta \cdot \gamma}{2} \\ \frac{\alpha \cdot \Delta \psi}{2} \\ \frac{\psi}{2} \left( 1 + \frac{\theta^2 - \alpha^2 - (\Delta \theta)^2}{4} \right) - \frac{\alpha \cdot \Delta \psi}{2} \end{bmatrix} \]

(A6)

with

\[ \gamma = \frac{1}{\left( 1 + \frac{\theta^2 + \alpha^2}{4} + \frac{\psi^2}{4} \right)} \]

The effect of further restrictions can easily be seen by substitution in equation (A6). For example, it is clear from considering the second component that the restriction v_θ (no vertical vergence), which has to be fulfilled for all azimuth angles (α), has the same effect as the restriction of minimal torsional disparity (Δψ = 0). The restriction imposed on the version system, that it should implement Listing’s law,
leads to a constraint for $\psi$ in both the rotation and the difference vector scheme. In that case the first component of the version signal is zero, which leads to $\psi / 2 = (-a/2)/4$ or $\psi = (-a/2)/2$, by substitution of the bipolar coordinates in equation (A3). In equation (A6) the term $\psi^2$ in the denominator and in the third component may be neglected (fourth order), so that vergence simplifies to:

$$v = \gamma \times \begin{pmatrix}
\frac{\Delta \psi}{2} \left(1 - \frac{1}{4} \left(\theta^2 + \alpha^2 - \frac{\psi^2}{4}\right)\right) + \frac{\theta \cdot v}{2} \\
\frac{\psi}{2} \left(1 + \frac{1}{4} \left(-\theta^2 - \frac{(\Delta \psi)^2}{4}\right)\right) - \frac{\theta \cdot \Delta \psi}{2}
\end{pmatrix}$$

(A7)

with

$$\gamma = \frac{1}{1 + \frac{\theta^2}{4} + \frac{\alpha^2}{4}}$$

The restriction that vertical vergence is zero ($v_2 = 0$, for all $\alpha$) reduces the vergence expression to a quite simple one:

$$v = \gamma \times \begin{pmatrix}
\frac{\theta \cdot v}{2} \\
0 \\
\frac{v}{2} \left(1 - \left(\frac{\theta^2}{2}\right)\right)
\end{pmatrix}$$

with

$$v \approx \begin{pmatrix}
\sin \theta \cdot \frac{v}{2} \\
0 \\
\cos \theta \cdot \frac{v}{2}
\end{pmatrix} \approx \begin{pmatrix}
\sin \theta \cdot \tan \left(\frac{v}{2}\right) \\
0 \\
\cos \theta \cdot \tan \left(\frac{v}{2}\right)
\end{pmatrix} \quad (A8)$$

In this equation, first-order approximations are transformed to expressions that are equivalent to the equations used in this article [see e.g. equation (14)]. The vergence rotation vector $v$ can easily be transformed (by dividing $v$ by 2) into the $d$ contribution which was derived in the section Implications [equation (14)], leading to:

$$d \approx \begin{pmatrix}
\sin \theta \cdot \tan \left(\frac{v}{4}\right) \\
0 \\
\cos \theta \cdot \tan \left(\frac{v}{4}\right)
\end{pmatrix} \approx \begin{pmatrix}
\frac{\theta \cdot v}{4} \\
0 \\
\frac{v}{4}
\end{pmatrix} \quad (A9)$$

This illustrates that the earlier result expressed in equations (14–16) in the section Implications, can also be obtained by a different procedure.