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# Theoretical Explanations of Listing's Law and Their Implication for Binocular Vision

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**We shall discuss three theoretical explanations of Listing's law for conjugate eye movements with the head fixed: the original argument by Helmholtz, which is "sensorimotor" in its attempt to optimize vision by using internal feedback from the oculomotor system, and two comparatively simple recent explanations based on either visual or oculomotor performance. These geometrical demonstrations shed some light on recent generalizations of Listing's law to vergent eye movements.**

Eye movements Listing's law Binocular vision Oculomotor system

## INTRODUCTION

In order to optimize and simplify the difficult task of multidimensional motor control the brain constrains as far as possible redundant degrees of freedom and establishes in its internal representations unique relations between target and motor space (Bernstein, 1967). An important application of this principle to the oculomotor system is Donders' law, which is well established for conjugate eye fixations with the head stationary, and recently also for vergence movements (Mok, Ro, Cadera, Crawford & Vilis, 1992; van Rijn & van den Berg, 1993; Minken & van Gisbergen, 1994). In this case Donders' law states that for each target position in 3-dimensional space the rotation of the two eyes about their direction of sight, which is redundant for fixating a point target, is uniquely determined by neural control, independently of the eye trajectory in the past.

From Donders' law and a principle of "easiest orientation" of the eye, H. von Helmholtz tried to derive Listing's law for conjugate fixation, namely that the rotation axes of the eye are restricted to a head-fixed plane, in the famous Chapter 27 of his "*Handbuch der Physiologischen Optik*". One might ask, whether it is of any physiological relevance to relate by mathematical arguments a strikingly simple parametization of measured "data clouds" to other theoretical concepts, which in biology are only valid up to unavoidable "noise" or "idiosyncrasies of implementation". However, in the case of Listing's law, where in the alert monkey the standard deviation of Listing's plane is often 1/2 deg relative to a torsional oculomotor range of about 30 deg (see e.g. Hepp, van Opstal, Straumann, Hess & Henn, 1993), such an effort is worthwhile in order to understand better the visuo-motor integration in the brain. For this we take Helmholtz as an authority: the 13 pages of highly nontrivial and for a 20th century medical doctor almost incomprehensible mathematical derivations show how much importance he has attributed to the understanding of Listing's law.

In modern language Helmholtz' principle of easiest orientation is a solution of the sensorimotor task of optimal perifoveal vision using an extraretinal signal about eye rotation. In this sense it is well in the mainstream of research on "active perception". It supports the neurophysiological finding of the inseparability of vision and motor control at all but the most peripheral levels and avoids meaningless disputes about the "sensory" or "motor" nature of Listing's law. However, the multidimensional mathematics of a twofold optimizion of visual performance and motor reafference is difficult, and Helmholtz' explanation of Listing's law is still incomplete. In this paper we shall discuss two recent and more elementary derivations of Listing's law, one based on purely visual performance and the other on motor control. Both together are rather amazing in a philosophical sense: Nature can optimize vision by dealing efficiently with noncommutative eye rotations, and the best solution for the saccadic system also optimizes vision!

Recently there have been several attempts to generalize Listing's law to near vision (Mok *et al.*, 1992; van Rijn & van den Berg, 1993; Minken, Gielen & van Gisbergen, 1995), based on partially conflicting data sets. As an application of our methods we shall discuss whether general theoretical principles can resolve this conflict.

## THEORETICAL EXPLANATIONS OF LISTING'S LAW FOR CONJUGATE EYE MOVEMENTS

We shall always assume that the eye is a center-fixed sphere, so that its position is uniquely characterized by the rotation $R$ of an eye-centered relative to a head-fixed coordinate system. For far vision we shall assume the rotations of the left and the right eye, $R_r$ and $R_l$, to be identical in these arbitrary and conveniently fixed coordinate systems.

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*"Visual" explanations of Listing's law*

Here we shall adopt Helmholtz' notations and refer as far as possible to his Chapter 27 (von Helmholtz, 1910) for a number of lengthy calculations, to which the interested reader is referred. As a head-fixed right-handed orthogonal coordinate system for the (cyclopean) eye we take the $x$-axis $\mathbf{e}_x$ in the midsagittal plane close to the center of the oculomotor range, the $y$-axis $\mathbf{e}_y$ through the interocular line and $\mathbf{e}_z = \mathbf{e}_x x \mathbf{e}_y$ ($x$: vector product). The eye-fixed system is characterized by $\mathbf{e}_x'''$ along the direction of sight $\mathbf{s}$ and two orthogonal directions, which are specified by Euler angles $(\theta, \alpha, \omega)$, where $\theta$ is the meridian and $\alpha$ the excenticity of the direction of sight: $\langle \mathbf{e}_x, \mathbf{e}_y, \mathbf{e}_z \rangle$ is first rotated by an angle $-\theta$ about $\mathbf{e}_x$ into $\langle \mathbf{e}_x', \mathbf{e}_y', \mathbf{e}_z' \rangle$, then by an angle $\alpha$ about $\mathbf{e}_z'$ into $\langle \mathbf{e}_x'', \mathbf{e}_y'', \mathbf{e}_z'' \rangle$, and finally by an angle $-\omega$ about the line of sight $\mathbf{e}_x'' = \mathbf{s}$ into the eye fixed system $\langle \mathbf{e}_x''', \mathbf{e}_y''', \mathbf{e}_z''' \rangle$. *Donders' law* states that $\omega$ is uniquely (and differentiably) determined by $\mathbf{s}$, and *Listing's law* (with $\langle \mathbf{e}_x, \mathbf{e}_y, \mathbf{e}_z \rangle$ as primary frame) states that $\langle \mathbf{e}_x''', \mathbf{e}_y''', \mathbf{e}_z''' \rangle$ by a rotation in the $y$–$z$-plane. This is equivalent to $\omega(\theta, \alpha) = -\theta$, because the identity $R(\mathbf{e}_x'', \theta) R(\mathbf{e}_z', \alpha) R(\mathbf{e}_x, -\theta) = R(\mathbf{e}_z', \alpha)$ shows that every fixation position can be obtained by a rotation about an axis $\mathbf{e}_z'$ in the plane orthogonal to the primary direction $\mathbf{e}_x$:

$$\text{Donders' law:} \quad \omega = \omega(\theta, \alpha) = \omega(\mathbf{s}) \tag{1}$$

$$\text{Listing's law:} \quad \omega(\theta, \alpha) = -\theta. \tag{2}$$

By Donder's law all infinitesimal rotations which carry the eye from the Donders position $\omega(\mathbf{s})$ to $\omega(\mathbf{s} + \mathbf{ds})$, where $\mathbf{ds}$ is a infinitesimal change of the direction of sight orthogonal to $\mathbf{s}$, have their axes in a plane $E(\mathbf{s})$. The axis $\mathbf{e}$ and angle of this rotation are uniquely characterized by $\mathbf{ds}$ and the change in $\omega$ is $\mathrm{d}\omega = \cot \lambda' \mathrm{d}s$, if $\lambda'$ is the angle between $\mathbf{e}$ and $\mathbf{s}$ and $\mathrm{d}s = |\mathbf{ds}|$ (see Fig. 11 in Helmholtz, 1910) Let $\mathbf{e}_0$ be the unit vector in $E(\mathbf{s})$ such that the plane $\langle \mathbf{s},\mathbf{e}_0 \rangle$ containing $\mathbf{s}$ and $\mathbf{e}_0$ is orthogonal to $E(\mathbf{s})$, $\lambda$ the angle between $\mathbf{e}_0$ and $\mathbf{s}$ and $\epsilon$ the angle between the planes $\langle \mathbf{s},\mathbf{e} \rangle$ and $\langle \mathbf{s},\mathbf{e}_0 \rangle$. The $\mathrm{d}\omega = \cos \epsilon \cot \lambda \, \mathrm{d}s$.

In this framework we can formulate the principle of *minimal torsional change* by which we would like to determine the Donders surface (1) so that vision is optimized in the following sense: if one looks in the direction $\mathbf{s}$, a distant line element in a perifoveal direction through $\mathbf{s} + \mathbf{ds}$ has a certain orientation which changes by $\mathrm{d}\omega$, if one foveates it by a rotation with axis $\mathbf{e}$ in $E(\mathbf{s})$. Such a torsional change could interfere with our invariant perception of objects at rest between small eye movements, unless it is compensated by the brain. A torsional change is in general unavoidable due to the noncommutativity of eye rotations, which does not allow $\mathbf{e}$ to be always orthogonal to $\mathbf{s}$. For instance, if Listing's law (2) is satisfied, $E(\mathbf{s})$ would be the plane normal to $\mathbf{s}'$, the bisectrix between the line of sight $\mathbf{s}$ and the primary direction $\mathbf{e}_x$ (von Helmholtz, 1910). In the sense of a best quadratic approximation up to order $\mathrm{d}s^2$ we require that the square of the torsional change, averaged over all directions of sight $\mathbf{s}$ in the oculomotor range and all directions $\mathbf{ds}$ orthogonal to $\mathbf{s}$, is minimal for the optimal choice of the Donders surface (1):

*Principle of minimal torsional change:*

$$E_{\mathrm{V}} = \iiint_{\mathrm{D}} (\mathrm{d}\omega_{\mathrm{visual}})^2 \sin \alpha \, \mathrm{d}\alpha \, \mathrm{d}\theta \, \mathrm{d}\epsilon \quad \text{minimal,} \tag{3}$$

where $\mathrm{d}\omega_{\mathrm{visual}} = \mathrm{d}\omega$, and where the integral is over the domain D, the product of the oculomotor range $0 \leqslant \theta < 2\pi$, $0 \leqslant \alpha < \alpha_0(\theta)$ (with the volume element $\sin\alpha \, \mathrm{d}\alpha \mathrm{d}\theta$) and $0 \leqslant \epsilon \leqslant 2\pi$. We shall see that equation (3) has Listing's law (2) as the unique solution, if the oculomotor range is close to *circular*, i.e. if $\alpha_0$ is $\theta$-independent.

Helmholtz tried to derive Listing's law from a far more complicated requirement, where the error is not $(\mathrm{d}\omega_{\mathrm{visual}})^2$ but the square of a *relative torsional change* $\mathrm{d}\omega_{\mathrm{visual}} - \mathrm{d}\omega_{\mathrm{motor}}$. Helmholtz searched for an eye-fixed plane $F$ such that, if the motor system rotates the direction of sight from $\mathbf{s}$ to $\mathbf{s} + \mathbf{ds}$, the torsional change $\mathrm{d}\omega_{\mathrm{motor}}$ of a corresponding infinitesimal rotation with axis $\mathbf{f}$ in $F$, when "fed forward" to the visual system, compensates optimally the apparent eye rotation-induced torsional movement of a perifoveal line segment at rest. Such a compensation can be learnt, because $F$ is eye-fixed, i.e. $\mathbf{s}$-independent, and the brain can use reafferent signals from the oculomotor system, in a similar manner as for keeping the visual world stationary between saccades.

The compensatory torsional change $\mathrm{d}\omega_{\mathrm{motor}}$ can be computed similarly to $\mathrm{d}\omega_{\mathrm{visual}}$: given $\mathbf{ds}$ there is a virtual rotation axis $\mathbf{f}$ and angle which would generate $\mathbf{s} \to \mathbf{s} + \mathbf{ds}$. Then $\mathrm{d}\omega_{\mathrm{motor}} = \cos \mu' \mathrm{d}s = \cos \delta \cot \mu \mathrm{d}s$, where $\mathbf{f}_0$ is such that the plane $\langle \mathbf{s},\mathbf{f}_0 \rangle$ is orthogonal to $F$, $\mu$ the angle between $\mathbf{f}_0$ and $\mathbf{s}$, and $\delta$ is the angle between $\langle \mathbf{s},\mathbf{f} \rangle$ and $\langle \mathbf{s},\mathbf{f}_0 \rangle$. The angle $\kappa = \epsilon - \delta$ is independent of $\mathbf{ds}$, and hence $\mathrm{d}\omega_{\mathrm{motor}} = \cos(\epsilon - \kappa) \cot \mu \mathrm{d}s$. This leads to Helmholtz' requirement for the optimal choice of $\omega(\mathbf{s})$ and $F$:

*Principle of easiest orientation:*

$$E_{\mathrm{VM}} = \iiint_{\mathrm{D}} (\mathrm{d}\omega_{\mathrm{visual}} - \mathrm{d}\omega_{\mathrm{motor}})^2 \sin \alpha \, \mathrm{d}\alpha \, \mathrm{d}\theta \, \mathrm{d}\epsilon = \text{minimal,} \tag{4}$$

where the integration is over the same domain D as in equation (3). The use of a relative torsional change in equation (4) introduces two more parameters, $\mu$ and $\kappa$. The $\epsilon$-integration in equations (3) and (4) can be carried out:

$$\int_0^{2\pi} (\mathrm{d}\omega_{\mathrm{visual}})^2 \, \mathrm{d}\epsilon = \pi \, \mathrm{d}s^2 \cot^2 \lambda \tag{5}$$

$$\int_0^{2\pi} (\mathrm{d}\omega_{\mathrm{visual}} - \mathrm{d}\omega_{\mathrm{motor}})^2 \, \mathrm{d}\epsilon = \pi \, \mathrm{d}s^2 [\cot^2 \lambda + \cot^2 \mu - 2 \cos \kappa \cot \lambda \cot \mu]. \tag{6}$$

Helmholtz succeeded to express $\lambda$ and $\kappa$ in equations (5) and (6) by clever use of infinitesimal rotations parametrized by Euler angles:

$$\cot^2 \lambda = (\partial\omega/\partial\alpha)^2 + [\partial\omega/\partial\theta + \cos\alpha]^2/\sin^2\alpha \quad (7)$$

$$\cos\kappa \cot\lambda = \sin\omega\, \partial\omega/\partial\alpha - \cos\omega[\partial\omega/\partial\theta + \cos\alpha\cos\omega]/\sin\alpha. \quad (8)$$

One sees from equations (6) and (8) that equation (4) as a functional of $\omega(\mathbf{s})$ is independent of $\kappa$. Helmholtz succeeded to prove that $\mu = \pi/2$ is an *extremum* of equation (4) as a function of $\mu$ and as a functional of $\omega(\mathbf{s})$. [Remark that an extremum is not necessarily a minimum, as the example of $f(x) = x^3 - x$ in the interval $[-2,2]$ shows: the absolute minimum of $f$ in $[-2,2]$ is for $x = -2$, while extrema with vanishing derivative $df/dx$ are at $x = -3^{-1/2}$ (local maximum), $x = 0$ (point of inflection), and at $x = 3^{-1/2}$ (local minimum).] Hence, if one requires the extremality of the average relative torsional change, then $F$ has to be chosen orthogonal to the direction of sight. This would be the best choice, if $\omega(\mathbf{s})$ satisfies equation (4), but this does not prove Listing's law. For a circular oculomotor range Helmholtz showed, that $\mu = \pi/2$ is the only extremum and that at the extremum Listing's law is satisfied. There is, however, still a gap in Helmholtz's proof, since an extremum is not necessarily the absolute minimum and not even a relative minimum of the error functional.

On the other hand, the visual error $E_V$ of the principle of minimal torsional change (equation 3) is much easier to handle. First one has to deal with a kinematical problem. The Euler angle parametrization $\omega(\theta, \alpha)$ of $\omega(\mathbf{s})$ should be of the form

$$\omega(\theta,\alpha) = \eta(\theta,\alpha) - \theta, \quad \eta(2\pi,\alpha) = \eta(0,\alpha),$$
$$\partial\eta/\partial\theta \to 0 \quad \text{for } \alpha \downarrow 0, \quad \eta(0,0) = 0, \quad (9)$$

since for $\alpha \downarrow 0$ $\mathbf{s}(\theta,\alpha) \to \mathbf{e}_x$ independently of $\theta$, and since $\omega(\mathbf{s})$ is assumed to be a smooth function of the direction of sight. Under this condition

$$E_V = \pi\, ds^2 \int_0^{2\pi} d\theta \int_0^{\alpha_0(\theta)} d\alpha[\sin\alpha(\partial\eta/\partial\alpha)^2 + (\partial\eta/\partial\theta - 1 + \cos\alpha)^2/\sin\alpha] \quad (10)$$

is well defined, since $[1 - \cos\alpha]/\sin\alpha \to 0$ for $\alpha \to 0$. $E_V = E_{V1} + E_{V2}$ with

$$E_{V1} = \pi\, ds^2 \int_0^{2\pi} d\theta \int_0^{\alpha_0(\theta)} d\alpha\{\sin\alpha(\partial\eta/\partial\alpha)^2 + [(\partial\eta/\partial\theta)^2 + (1-\cos\alpha)^2]/\sin\alpha\} \quad (11)$$

$$E_{V2} = 2\pi\, ds^2 \int_0^{2\pi} d\theta \int_0^{\alpha_0(\theta)} d\alpha(\cos\alpha - 1)(\partial\eta/\partial\theta)/\sin\alpha. \quad (12)$$

If the oculomotor range is circular, then the $\theta$- and $\alpha$-integration can be interchanged and

$$E_{V2} = 2\pi\, ds^2 \int_0^{\alpha_0} d\alpha(\cos\alpha - 1)/\sin\alpha \int_0^{2\pi} d\theta\, \partial\eta/\partial\theta = 0, \quad (13)$$

since by equation (9) the second integral equals $\eta(2\pi,\alpha) - \eta(0,\alpha) = 0$. Since all terms in the integrand of (11) are positive, one sees explicitly that for a circular oculomotor range $E_V = E_{V1}$ attains its *absolute minimum for Listing's law* as given by equation (2):

$$\partial\eta/\partial\theta = \partial\eta/\partial\alpha = 0 \Rightarrow \eta(\theta,\alpha) = \omega(\theta,\alpha) - \theta = \eta(0,0) = 0. \quad (14)$$

If the oculomotor range is not circular, then one can only show that Listing's law is an extremum of $E_V$ as a functional of $\eta$. A necessary and sufficient condition for extremality, $\delta E_V = 0$ for an arbitrary variation $\delta\eta$ of $\eta$ which is periodic in $\theta$, is that $\eta$ is a solution of the Euler–Lagrange equations

$$\partial(\sin\alpha\, \partial\eta/\partial\alpha)/\partial\alpha + (\partial^2\eta/\partial\theta^2)/\sin\alpha = 0. \quad (15)$$

and that at the limit of the oculomotor range the boundary values satisfy

$$\int_0^{2\pi} d\theta \sin\alpha_0(\theta)(\partial\eta/\partial\alpha)(\alpha_0(\theta))\delta\eta(\alpha_0(\theta)) = 0. \quad (16)$$

Both equations are satisfied for Listing's law $\eta = 0$.

### *"Motor" explanation of Listing's law*

Here we shall use the quaternion-based rotation vector formalism (Haustein, 1989). Rotations $R = R(\mathbf{a}, \rho)$ are intrinsically specified by their axis $\mathbf{a}$ and nonnegative rotation angle $\rho \geqslant 0$ (using the right hand rule) or by their rotation vector $\mathbf{r} = \tan(\rho/2)\mathbf{a}$. Then the rotation vector $\mathbf{r}_1 * \mathbf{r}_2$ for the (noncommutative) product $R_1 * R_2$ of two rotations (first action of $R_2$, then of $R_1$) is

$$\mathbf{r}_1 * \mathbf{r}_2 = (\mathbf{r}_1 + \mathbf{r}_2 + \mathbf{r}_1 \times \mathbf{r}_2)/(1 - \mathbf{r}_1 \cdot \mathbf{r}_2), \quad (17)$$

with $\mathbf{r}_1 \cdot \mathbf{r}_2$ the scalar product, and the inverse $R^{-1}$ corresponds to $-\mathbf{r}$. Listing's law states that the rotation vectors for all eye positions during fixation with the head upright and stationary are contained in a plane. Then is always possible to choose a head-fixed coordinate system, in which the primary direction, orthogonal to Listing's plane, is the $x$-axis and coincides with the direction of sight, when the eye is in primary position $\rho = 0$. In these coordinates $\mathbf{r}^x$, $\mathbf{r}^y$, $\mathbf{r}^z$ are called the torsional, vertical and horizontal components of eye position. For Listing positions "true" torsion vanishes, i.e. $r^x = 0$, but this should not be confused with the torsional change $d\omega$ in the "visual" explanations.

To a good approximation, normometric saccades from $\mathbf{r}_1$ to $\mathbf{r}_2$ are fixed-axis rotations (Tweed & Vilis, 1988; Tweed, Misslisch & Fetter, 1994), but with small "blips" which are possibly due to the idiosyncrasies of the eye plane (see, however, Schnabolk & Raphan, 1994). By definition, a fixed-axis rotation from $R_1$ to $R_2$ has the trajectory $R_{21}(t) = R(\mathbf{a}_{21}, \rho(t)) * R_1$ with $\rho(t_1) = 0$ and $\rho(t_2) = \rho_{21}$ at initial and final times $t_1$ and $t_2$. Here $R_1$ and $R_2$ are the rotation matrices corresponding to $\mathbf{r}_1$ and $\mathbf{r}_2$, $R_{21} = R_2 * R_1^{-1}$ (*: matrix product) is the rotation which carries $R_1$ into $R_2$, and $\mathbf{a}_{21}$ and $\rho_{21}$ are the rotation axis and angle of $R_{21}$. It is a mathematical fact that fixed-axis rotations are lines of shortest length (geodesics) on the Lie group SO(3) of rotations (see e.g. Sternberg, 1964). It can be checked by direct calculation (Hepp, 1990) that the rotation vector trajectory $\mathbf{r}_{21}(t)$ of $R_{21}(t)$ is always a straight lines between $\mathbf{r}_1$ and $\mathbf{r}_2$.

These facts imply that, if saccade between two Listing positions $\mathbf{r}_1$, $\mathbf{r}_2$ is a fixed axis rotation, then the entire saccade trajectory $\mathbf{r}_{21}(t)$ lies in Listing's plane. This leads to a simple "motor" explanation of Listing's law: a set of eye positions connected by saccades, which are fixed-axis rotations without violating Donders' law en route, is a plane. If one assumes bilateral symmetry, then the primary direction of this Listing plane lies in the mid-sagittal plane and it is natural to require that the primary direction is close to the center of the oculomotor range, as in the "visual" explanations of Listing's law.

## IMPLICATIONS FOR BINOCULAR EYE MOVEMENTS

There are recent attempts to generalize Listing's law to convergent eye movements. Mok *et al.* (1992) studied isovergence saccades and found a Listing plane for each eye. Relative to the primary direction of far vision the primary directions of both planes were rotated temporally, theoretically by the vergence angle and experimentally by a smaller amount. Van Rijn and van den Berg (1993) studied binocular fixation. They could fit their data by a model, where the rotation vectors **r** and **l** of the right and left eye were represented in terms of a contribution **s** from the version system, which satisfies Listing's law $s^x = 0$, and a contribution **g** from the vergence system with the planar constraint $g^y = 0$:

$$\mathbf{r} = \mathbf{s} - \mathbf{g}, \; \mathbf{l} = \mathbf{s} + \mathbf{g} \quad \text{with} \quad s^x = 0 \quad \text{and} \quad g^y = 0. \tag{18}$$

Both Mok *et al.* and van Rijn and van den Berg find a linear increase of intorsion for upwards and extorsion for downwards cyclopean eye position, but the slope in the second investigation is about twice of that found in the first study.

Another generalization of Listing's law was proposed by Minken *et al.* (1995) by parametizing **r** and **l** in terms of a cyclopean and a vergence contribution, **c** and **v**, using the multiplicative law (equation 17) of rotation vectors

$$\mathbf{r} = \mathbf{v}^*\mathbf{c}, \; \mathbf{l} = (-\mathbf{v})^*\mathbf{c}, \quad \text{with} \quad c^x = v^y = 0. \tag{19}$$

In both (18) and (19), the two planar constraints on **s** and **g** or on **c** and **v** completely fix the two redundant degrees of freedom of the two eyes, as required by Bernstein's principle (1967). With $\mathbf{d} = \mathbf{r}^*(-\mathbf{l}) = \tan(\nu/2)\mathbf{n}$, $\mathbf{n} = \mathbf{d}/|\mathbf{d}|$, $\mathbf{v} = \tan(\nu/4)\mathbf{n}$ and $\mathbf{c} = \mathbf{v}^*\mathbf{l}$ one can solve equation (19) for **c** and **v**. The multiplicative generalization (equation 19) of Listing's law also predicts a linear dependence of torsion with vertical eye position, but with a slope half as large as that in equation (18). A recent experimental study by Minken and van Gisbergen (1994) found torsional vergence components at various levels of elevation, which are intermediate between those predicted by equations (18) and (19). The question arises whether the mathematically rigorous approach to Listing's law for conjugate eye movements can be generalized to vergence movements and give some preference to one or the other of the two conflicting models (equations 18 and 19). A necessary point of departure for the discussion will be the assumption of Donders' law for **r** and **l** during binocular fixation.

The "motor" explanation relies on the fact that saccades are to a good approximation fixed-axis rotations. Due to the different dynamics of the saccadic and vergence system this can only be assumed for isovergence saccades, where it is consistent with the data by Mok *et al.* (1992). If one assumes that isovergence saccades have trajectories which pass through Donders positions, then the rotation vectors of both eyes have to lie on Listing planes, as in the conjugate case. This, however, is not exactly compatible with equations (18) and (19), which lead to exact isovergence planes only when neglecting higher than second order powers in the rotation vectors. A more serious difficulty of the "motor" explanation is to show that the isovergence Listing planes are both temporally rotated by an amount equal to the vergence angle.

The "visual" explanation, based on the principle of minimal torsional change for stereovision, encounters serious geometrical problems and has not yet been carried through in full generality. However, from this point of view the generalization (equation 19) of Listing's law is very attractive, because the expressions for **r** and **l** in terms of **c** and **v** have a clear geometric meaning: Let both eyes fixate a point target with their direction of sight elevated by $\theta$ (the angle of the first rotation of both eyes about $\mathbf{e}_y$) and with their azimuths $\alpha_r$ and $\alpha_l$ (the angles of the second rotation of each eye about $\mathbf{e}'_z$). In terms of $\alpha = (\alpha_r + \alpha_l)/2$ and $\nu = \alpha_r - \alpha_l$ these eye positions have cyclopean and vergence vectors (Minken *et al.*, 1995)

$$\mathbf{c} = (0, \tan(\theta/2)[1 - \tan^2(\alpha/2)],$$

$$\tan(\alpha/2)[1 + \tan^2(\theta/2)])/[1 + \tan^2(\theta/2)\tan^2(\alpha/2)] \tag{20}$$

$$\mathbf{v} = \tan(\nu/4)(\sin\theta, 0, \cos\theta). \tag{21}$$

All other eye positions which fixate the same visual target are of the form

$$\mathbf{r}' = [\tan(\psi_r/2)\mathbf{s}_r]^*\mathbf{v}^*\mathbf{c}, \quad '\mathbf{s} = [\tan(\psi_l/2)\mathbf{s}_l]^*(-\mathbf{v})^*\mathbf{c} \tag{22}$$

with further rotations about the lines of sight $\mathbf{s}_r$ and $\mathbf{s}_l$ of the right and left eye.

For conjugate eye positions with $\mathbf{r} = \mathbf{l} = \mathbf{c}$ satisfying Donders' law, the principle of minimal torsional change and a circular oculomotor range lead to Listing's law for **c**. Assume that for a target with given $\theta$, $\alpha_r$, $\alpha_l$ the convergent eye position (equation 20), equation (21) is obtained from the initial Listing position $\mathbf{r} = \mathbf{l} = \mathbf{c}$ with $\alpha = (\alpha_r + \alpha_l)/2$, $\nu = 0$ by a rotation of **r** by **v** and of **l** by $-\mathbf{v}$ according to equation (21). This rotation is about an axis orthogonal to the directions of sight of both eyes. Hence it does not introduce any torsional deviation. The more general convergent eye movement to equation (22) introduces torsional deviations, unless $\psi_r = \psi_l = 0$.

Hence, if we extend the principle of minimal torsional change by requiring that all convergent Donders eye positions could be reached from the conjugate Donders positions with the same cyclopean **c** without torsional deviation, then equation (19) has been proved for a circular oculomotor range. The same argument is not applicable to the additive generalization (equation 18) of Listing's law, which therefore appears to be less optimal for vision. However, caution is necessary, as one sees when one applies the principle of minimal torsional change to conjugate eye-head fixations (Straumann, Haslwanter, Hepp-Reymond & Hepp, 1991; Glenn & Vilis, 1992). From the point of view of vision one would predict a perfect Listing plane for gaze fixations. However, gaze movements might be more constrained by the biomechanics of the head than by vision, so that the rotation vectors of the eye in the head are expected to be constrained more closely to a plane than those of the eye in space, in particular since Listing's law also optimizes eye saccades.

## CONCLUSION

Listing's law is a very efficient way of implementing Donders' law that minimizes the torsional rotation of the visual field and is the unique implementation where any eye orientation can be reached from any other by a fixed-axis rotation without violating Donders' law en route. The deep insight, that the oculomotor system allows, at least for the "default" case of far vision in a circular oculomotor range, simultaneously an optimal integration of the requirements of vision and motor control, is originally due to Helmholtz. This approach has recently lead to new theoretical ideas about sensorimotor integration and to interesting experiments (see e.g. Hepp *et al.*, 1993). It defies the claim that Nature is just a "tinkerer".

## REFERENCES


Bernstein, N. (1967). *The co-ordination and regulation of movements.* Oxford: Pergamon Press.

Bietenholz, W. (1988). Nicht-abelsche Augendynamik. Diplomarbeit E. T. H., Zürich.

Glenn, B. & Vilis, T. (1992). Violations of Listing's law after large eye and head gaze shifts. *Journal of Neurophysiology, 67,* 309–318.

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

von Helmoltz, H. (1910). *Handbuch der Physiologischen Optik,* (3rd edn). Hamburg and Leipzig: Voss. English translation (1925): *Helmholtz' treatize on physiological optics.* New York: Dover.

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

Hepp, K., van Opstal, A. J., Straumann, D., Hess, B. J. M. & Henn, V. (1993). Monkey superior colliculus represents rapid eye movements in a two-dimensional motor map, *Journal of Neurophysiology, 69,* 965–979.

Minken, A. H. W. & van Gisbergen, J. A. M. (1994). A three-dimensional analysis of vergence movements at various levels of elevation. *Experimental Brain Research, 101,* 331–345.

Minken, A. H. W., Gielen, C. C. A. M. & van Gisbergen, J. A. M. (1995). An alternative 3D interpretation of Hering's equal-innervation law for vergence and version eye movements. *Vision Research, 35,* 93–102.

Mok, D., Ro, A., Cadera, W., Crawford, J. D. & Vilis, T. (1992). Rotation of Listing's plane during vergence. *Vision Research, 32,* 2055–2064.

Schnabolk, C. & Raphan, T. (1994). Modeling three-dimensional velocity-to-position transformation in oculomotor control. *Journal of Neurophysiology, 71,* 623–638.

Spörli, D. (1994) Mathematische Herleitung des Listing'schen Gesetzes aus einem physiologischen Prinzip und Erweiterung auf das Stereosehen. Diplomarbeit E. T. H., Zürich.

Sternberg, S. (1964). *Lectures on differential geometry.* Englewood Cliffs, NJ: Prentice Hall.

Straumann, D., Haslwanter, T., Hepp-Reymond, M-C. & Hepp, K. (1991). Listing's law for eye, head and arm movements and their synergistic control. *Experimental Brain Research, 86,* 209–215.

Tweed, D. & Vilis, T. (1988). Rotation axes of saccades. *Annals of the New York Academy of Science, 545,* 128–139.

Tweed, D., Misslisch, H. & Fetter, M. (1994). Testing models of the oculomotor velocity to position transformation. *Journal of Neurophysiology, 72,* 1425–1429.

Van Rijn, L. J. & van den Berg, A. V. (1993). Binocular eye orientation during fixations: Listing's law extended to include eye vergence. *Vision Research, 33,* 691–708.


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