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Invariant Body Kinematics:

I. Saccadic and Compensatory Eye Movements

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Abstract. A new invariant formulation of 3D eye-head kinematics improves on the computational advantages of quaternions. This includes a new formulation of Listing's Law parameterized by gaze direction leading to an additive rather than a multiplicative saccadic error correction with a gaze vector difference control variable. A completely general formulation of compensatory kinematics characterizes arbitrary rotational and translational motions, vergence computation, and smooth pursuit. The result is an invariant, quantitative formulation of the computational tasks that must be performed by the oculomotor system for accurate 3D gaze control. Some implications for neural network modeling are discussed.

1. INTRODUCTION

Tweed and Vilis (987, 1990a) have put forward a provocative quaternion model of saccadic eye movement. Is it really plausible, though, to contend that biological systems have discovered and implemented the laws of quaternion calculus in oculomotor control? Those laws are, as a matter of fact, inherent in the properties of three-dimensional (3D) rotations, from which Hamilton extracted them a century and a half ago. Although there are many alternative mathematical representations for rotations (employing matrices with various systems of coordinates, for example), Tweed and Vilis have correctly noted that quaternions are computationally the most efficient and, further, are more directly related to the relevant physiological variables. Therefore, environmental pressures toward fast and accurate oculomotor control would favor the evolution of some sort of quaternion implementation in the nervous system.

To this day, even among mathematicians, quaternions are commonly regarded as a mathematical oddity outside the scientific mainstream. However, many workers in fields such as space science have rediscovered for themselves the superiority of quaternions over conventional matrix methods for intensive computations with 3D rotations. Recently, quaternions have been integrated into a more powerful mathematical system called *geometric algebra* (Hestenes, 1986). This system combines all the advantages of quaternions with those of conventional vector calculus and applies to a far larger mathematical domain.

Geometric algebra is best regarded as a mathematical language for expressing geometric concepts. Indeed, it is arguably the optimal encoding of geometric concepts in algebraic form. The grammatical structure of this language is known as Clifford algebra among mathematicians. However, mathematicians have generally overlooked the geometric interpretation of Clifford algebra and so missed most of its implications for science and engineering. It is the interpretation that transforms Clifford algebra from just another curious mathematical structure into a powerful scientific language.

This article presents an *invariant* formulation and analysis of 3D eye-head kinematics in terms of geometric algebra. The term invariant here means coordinate-free, that is, independent of any particular coordinate system. To be sure, the brain employs its own intrinsic systems of coordinates (Ostriker, Llinas & Pellionisz, 1985), but they are only partially known. Indeed, one of the chief problems of neuroscience is to discover the coordinate systems or, if you will, the computational codes employed by the brain. This task can be facilitated by an invariant formulation of body kinematics, providing an unbiased specification of the computational tasks that must be solved by the brain to produce accurate and efficient body movement.

Geometric algebra is an alternative to tensor analysis, which has been employed in sensorimotor theory by Pellionisz and Llinas since 1980. lt is superior to tensor theory in at least two ways. First, tensor theory is *covariant* rather than *invariant*, which means that coordinates play an essential role and transformation laws must be introduced to formulate coordinate-independent relations. Geometric algebra avoids all that. Second, computationally more efficient, in part, because it includes spinors and tensor theory does not. Its computational superiority has been explicitly demonstrated by computer tests on complex calculations in the General Theory of Relativity (Moussiaux & Tombal, 1988).

Besides enabling an invariant formulation of kinematics, geometric algebra facilitates the analysis of alternative control variables, coordinate systems, and kinematic constraints. This is demonstrated below in a detailed analysis of Listing's Law, an empirically based constraint on saccadic eye movement that provides an important clue to the control variables employed by the brain. A second topic treated below is the coupling between eye and head kinematics that must be controlled to produce stable images of the external world as well as to track the images of moving objects.

This paper develops a complete invariant formulation of kinematic computations that are essential for perfect 3D oculomotor control. Such kinematic analysis is an essential prerequisite to understanding how the oculomotor neural system operates, because it describes the computational tasks to be performed. This is evident in the pioneering work of Robinson (1981). He emphasizes that progress in understanding the oculomotor system has been greater than for other motor systems in large part because the functions it performs are so well understood and can be described so precisely. These descriptions are essentially kinematical. Understandably, Robinson's early work and most of the oculomotor research that followed concentrated on one-dimensional kinematics. However, the field is sufficiently mature now for complete 3D kinematics analysis. The geometric algebra employed applies equally well to dynamics (Hestenes, 1986). The whole approach will be set in a broader context in a subsequent paper (Hestenes, 1993). The first to apply quaternions in this field was Westheimer (1957), and the relevance of Clifford algebra has been noted by Tweed, Cadera, and Vilis (1990).

2. GEOMETRIC ALGEBRA

Geometric algebras exist for spaces of any dimension, but we will be concerned here only with the geometric algebra $\mathcal{G}_3$ for the 3D Euclidean space of the physical world. One way to construct $\mathcal{G}_3$ is to define an associative product on an orthonormal set of vectors $\boldsymbol{\sigma}_1$, $\boldsymbol{\sigma}_2$,

$\boldsymbol{\sigma}_3$. For the products of vectors with themselves, we assume

$$\boldsymbol{\sigma}_k^2 = 1 \quad \text{for} \quad k = 1, 2, 3\,, \tag{1}$$

and for the products with each other we assume the anticommutative rule

$$\boldsymbol{\sigma}_i \boldsymbol{\sigma}_j = -\boldsymbol{\sigma}_j \boldsymbol{\sigma}_i \quad \text{for} \quad i \neq j\,. \tag{2}$$

The latter binary products of vectors generate new entities called *bivectors*. There are exactly three such bivectors, and they can be expressed in several alternative forms:

$$\begin{aligned} \boldsymbol{\sigma}_1\boldsymbol{\sigma}_2 &= i\boldsymbol{\sigma}_3 = \mathbf{I}_3 = -\mathbf{k}\,, \\ \boldsymbol{\sigma}_3\boldsymbol{\sigma}_1 &= i\boldsymbol{\sigma}_2 = \mathbf{I}_2 = -\mathbf{j}\,, \\ \boldsymbol{\sigma}_2\boldsymbol{\sigma}_3 &= i\boldsymbol{\sigma}_1 = \mathbf{I}_1 = -\mathbf{i}\,. \end{aligned} \tag{3}$$

The significance of these alternatives needs some explanation. First, note that these three bivectors form a basis for a 3D space of bivectors. Just as any vector $\mathbf{a}$ can be formed from a linear combination of the basis vectors $\boldsymbol{\sigma}_k$ by writing

$$\mathbf{a} = \sum_k a_k \boldsymbol{\sigma}_k = a_1\boldsymbol{\sigma}_1 + a_2\boldsymbol{\sigma}_2 + a_3\boldsymbol{\sigma}_3\,, \tag{4}$$

where the a_k are *scalar* (real number) coefficients; so any bivector $\mathbf{B}$ can be formed by the linear combination

$$\mathbf{B} = \sum_k B_k \mathbf{I}_k\,, \tag{5}$$

with scalar coefficients B_k

Though twofold products of the $\boldsymbol{\sigma}_k$ generate three distinct bivectors, only one new entity is generated by threefold products. That is the *unit, righthanded pseudoscalar*

$$i = \boldsymbol{\sigma}_1\boldsymbol{\sigma}_2\boldsymbol{\sigma}_3 = -\boldsymbol{\sigma}_3\boldsymbol{\sigma}_2\boldsymbol{\sigma}_1\,. \tag{6}$$

This defines the symbol i appearing in eqn (3), and from eqn (3) we see that every bivector can be obtained from a vector by multiplication with i. Therefore, to every bivector $\mathbf{B}$ there corresponds a unique vector $\mathbf{b}$ such that

$$\mathbf{B} = i\mathbf{b} = \mathbf{b}i\,. \tag{7}$$

Multiplication by i is called a *duality transformation* and $\mathbf{B}$ is said to be the *dual* of $\mathbf{b}$. As asserted in eqn (7), multiplication by i is commutative. Furthermore, it is easily proved from eqn (6) that

$$i^2 = -1\,. \tag{8}$$

Therefore, i has the algebraic properties of scalar imaginary unit. However, it is crucial to recognize that i also has a geometric interpretation as a pseudoscalar.

Hamilton's symbols $\mathbf{i}$, $\mathbf{j}$, $\mathbf{k}$ for a quaternion basis were introduced in eqn (3) to show how naturally quaternions fit into geometric algebra. The minus sign appears in eqn (3) because Hamilton adopted a lefthanded basis, whereas we assume that $\{\boldsymbol{\sigma}_k\}$ is a righthanded basis set. Hamilton's rules for quaternion products follow automatically from the more fundamental rules eqns (l) and (2); thus,

$$\mathbf{ij} = (\boldsymbol{\sigma}_2\boldsymbol{\sigma}_3)(\boldsymbol{\sigma}_3\boldsymbol{\sigma}_1) = \boldsymbol{\sigma}_2(\boldsymbol{\sigma}_3)^2\boldsymbol{\sigma}_1 = \boldsymbol{\sigma}_2\boldsymbol{\sigma}_1 = \mathbf{k} = -\mathbf{ji}$$

and

$$\mathbf{i}^2 = (\boldsymbol{\sigma}_2\boldsymbol{\sigma}_3)(\boldsymbol{\sigma}_2\boldsymbol{\sigma}_3) = -(\boldsymbol{\sigma}_3\boldsymbol{\sigma}_2)(\boldsymbol{\sigma}_2\boldsymbol{\sigma}_3) = -1 = \mathbf{j}^2 = \mathbf{k}^2 \,.$$

Note the use of associativity in the derivation. Hamilton originally introduced the term vector for the bivectors $\mathbf{i}$, $\mathbf{j}$, $\mathbf{k}$. Failure to understand the crucial geometrical distinction between vectors and bivectors (see below) has propagated confusion in the literature to this day.

Just as the real and imaginary complex numbers can be added, so scalars and bivectors can be added to form a four-dimensional linear space that can be identified with Hamilton's quaternions. As shown above, products of bivectors generate scalars and other bivectors but never vectors. Thus, the space of quaternions is closed under multiplication, so it is a subalgebra of the geometric algebra $\mathcal{G}_3$.

Independent of any basis, any quaternion Q can be invariantly decomposed into the sum of a scalar part Q_0 and a bivector part $\mathbf{Q} = i\mathbf{q}$; thus,

$$Q = Q_0 + \mathbf{Q} = Q_0 + i\mathbf{q} \,. \tag{9}$$

This is completely analogous to, or better, it generalizes the decomposition of a complex number into real and imaginary parts. Each quaternion Q has a unique conjugate $Q^\dagger$ given by

$$Q^\dagger = Q_0 - \mathbf{Q} = Q_0 - i\mathbf{q} \,. \tag{10}$$

Each Q also has a positive scalar *norm* or *modulus* $|\,Q\,|$ defined by

$$QQ^\dagger = Q_0^2 - \mathbf{Q}^2 = Q_0^2 + \mathbf{q}^2 = |\,Q\,|^2 \,. \tag{11}$$

From this we infer that Q has a unique multiplicative inverse given by

$$Q^{-1} = Q^\dagger |\,Q\,|^{-2} \,. \tag{12}$$

This completes the algebraic fundamentals of quaternion calculus, but there is more to be said about its geometric significance and how it fits into geometric algebra. In particular, it is crucial to recognize that the quantity $\mathbf{Q}$ in eqn (9), which is referred to as a vector in the quaternion literature, must be interpreted as a bivector in geometric algebra to conform to the coherent geometric interpretation to which we now turn.

The standard geometric interpretation of the vectors $\boldsymbol{\sigma}_k$ as representations of (or by) *directed line segments* is illustrated in Figure 1a. Similarly, as illustrated in Figure 1b, the algebraic product of vectors producing bivectors in eqn (3) can be interpreted as a geometric productof directed line segments to produce *directed plane segments*. Note that the order of multiplication determines an orientation for the plane segment, and the two possible orientations can be distinguished algebraically by plus or minus signs, just as for vectors.

Figure 1c illustrates the interpretation of the unit pseudoscalar $i = \boldsymbol{\sigma}_1\boldsymbol{\sigma}_2\boldsymbol{\sigma}_3$ as an oriented *space segment* (or volume element). Lengths, areas, and volumes of line, plane, and space segments are given by the magnitudes of the corresponding vectors, bivectors, or pseudoscalars.

Just as every oriented (straight) line has a direction that can be represented by a unique unit vector, so every oriented plane has a direction uniquely represented by a unit bivector. Bivectors have another important geometrical interpretation. Besides representing the unit directed area element for a unique plane each unit bivector $\mathbf{I}$ is the *generator of rotations* in that plane. Specifically, it satisfies

$$\mathbf{I}^2 = -1\,, \tag{13a}$$

and multiplication by $\mathbf{I}$ of any vector $\mathbf{a}_1$ in the $\mathbf{I}$-plane produces a new vector $\mathbf{a}_2$ orthogonal to $\mathbf{a}_1$ as expressed by

$$\mathbf{a}_2 = \mathbf{a}_1\mathbf{I} = -\mathbf{I}\mathbf{a}_1\,. \tag{13b}$$

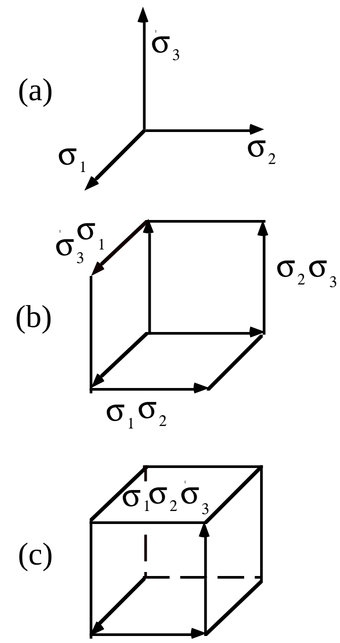

FIGURE 1. A geometric interpretation of orthonormal basis elements in geometric algebra. (a) Unit vectors $\boldsymbol{\sigma}_1$, $\boldsymbol{\sigma}_2$, $\boldsymbol{\sigma}_3$ interpreted as directed line segments. (b) Unit bivectors $\boldsymbol{\sigma}_1\boldsymbol{\sigma}_2$, $\boldsymbol{\sigma}_2\boldsymbol{\sigma}_3$, $\boldsymbol{\sigma}_3\boldsymbol{\sigma}_1$ interpreted as directed plane segments. Note how an orientation (or sense) for each plane segment is determined by the head-to-tail ordering of vectors on the boundary. (c) The unit trivector $i{=}\boldsymbol{\sigma}_1\boldsymbol{\sigma}_2\boldsymbol{\sigma}_3$ interpreted as an oriented volume (pseudoscalar).

Indeed, for $\mathbf{a}_1^2 = 1$, this can be solved for

$$\mathbf{I} = \mathbf{a}_1\mathbf{a}_2 = -\mathbf{a}_2\mathbf{a}_1\,,$$

a generalization of relations in eqn (3) to an arbitrary plane. Furthermore, it can be proved that any given vector, $\mathbf{a}$, lies in the $\mathbf{I}$-plane iff it anticommutes with $\mathbf{I}$ as in eqn (13b).

Generating $\mathcal{G}_3$ from an orthonormal basis has the advantage of leading quickly to the well-known relations for a quaternion basis. But there is a more fundamental, invariant way to generate the geometric algebra. Beginning with a real 3D vector space $\mathcal{V}_3$ of vectors $\mathbf{a}, \mathbf{b}, \mathbf{c}\ldots$, one defines the *geometric product* $\mathbf{ab}$ by adopting the following axioms (or rules):

1. Distributivity:

$$\begin{aligned}\mathbf{a}(\mathbf{b}+\mathbf{c}) &= \mathbf{ab}+\mathbf{ac}\,,\\ (\mathbf{b}+\mathbf{c})\mathbf{a} &= \mathbf{ba}+\mathbf{ca}\,.\end{aligned} \tag{14a}$$

2. Associativity:

$$(\mathbf{ab})\mathbf{c} = \mathbf{a}(\mathbf{bc})\,, \tag{14b}$$

3. Commutativity, for multiplication by any scalar λ:

$$\lambda\mathbf{a} = \mathbf{a}\lambda\,, \tag{14c}$$

4. Contraction:

$$\mathbf{a}^2 = |\,\mathbf{a}\,|^2 \geq 0\,, \tag{14d}$$

where $|\,\mathbf{a}\,|$ is a positive scalar (real number) called the *length*, *magnitude*, or *modulus* of $\mathbf{a}$, and $|\,\mathbf{a}\,|^2 = 0$ iff $\mathbf{a} = 0$.

With these rules, the entire geometric algebra $\mathcal{G}_3$ can be generated from $\mathcal{V}_3$ by multiplication and addition. It is the contraction rule (14d) relating vectors multiplicatively to scalars that sets geometric algebra apart from all other associative algebras. Manipulations as well as notations are the same as in ordinary scalar algebra with the single exception that multiplicative factors cannot be rearranged at will, because multiplication is not generally commutative. One can, for example, divide by nonzero vectors. The *multiplicative inverse* $\mathbf{a}^{-1}$ of a vector $\mathbf{a}$ is defined implicitly by

$$\mathbf{a}\mathbf{a}^{-1} = 1\,. \tag{15a}$$

Multiplying this by $\mathbf{a}$ and using eqn (14d), one gets the explicit expressions

$$\mathbf{a}^{-1} = |\,\mathbf{a}\,|^{-2}\mathbf{a} = \frac{\mathbf{a}}{\mathbf{a}^2} = \frac{\mathbf{a}}{|\,\mathbf{a}\,|^2} = \frac{1}{\mathbf{a}}\,. \tag{15b}$$

We have already used this in solving eqn (13b) for $\mathbf{I}$.

From the geometric product it is convenient to define two other products from the invariant decomposition into symmetric and antisymmetric parts. Thus, the usual *inner product* $\mathbf{a}\cdot\mathbf{b}$ is defined by

$$\mathbf{a}\cdot\mathbf{b} = \tfrac{1}{2}(\mathbf{a}\mathbf{b} + \mathbf{b}\mathbf{a}) = \mathbf{b}\cdot\mathbf{a}\,. \tag{16a}$$

The *outer product* $\mathbf{a}\wedge\mathbf{b}$ is defined by

$$\mathbf{a}\wedge\mathbf{b} = \tfrac{1}{2}(\mathbf{a}\mathbf{b} - \mathbf{b}\mathbf{a}) = -\mathbf{b}\wedge\mathbf{a}\,. \tag{16b}$$

Addition of (16a) and (16b) yields

$$\mathbf{a}\mathbf{b} = \mathbf{a}\cdot\mathbf{b} + \mathbf{a}\wedge\mathbf{b} = \mathbf{b}\cdot\mathbf{a} - \mathbf{b}\wedge\mathbf{a}\,. \tag{16c}$$

It follows from the axioms that the inner product is scalar-valued, and the outer product is bivector-valued. Therefore, eqn (16c) is a decomposition of the product $\mathbf{a}\mathbf{b}$ into scalar and bivector parts. This is the same as the decomposition (9) of a quaternion into scalar and bivector parts, for the product $\mathbf{a}\mathbf{b}$ is quaternion-valued. Conversely, any quaternion $Q = Q_0 + \mathbf{Q}$ can be factored into a product of two vectors, as expressed by writing

$$Q = \mathbf{a}\mathbf{b}\,. \tag{17}$$

This factorization is not unique. However, selecting any nonzero vector $\mathbf{a}$ in the plane of Q (that is, the plane determined by the bivector $\mathbf{Q}$), the vector $\mathbf{b}$ is uniquely determined by

$$\mathbf{b} = \mathbf{a}^{-1}Q = Q^{\dagger}\mathbf{a}^{-1}\,. \tag{18}$$

This generalizes (13b), including the fact that **a** must anticommute with the bivector **Q**.

Comparison of eqn (17) with eqn (10) reveals that

$$Q^\dagger = (\mathbf{ab})^\dagger = \mathbf{ba}\,, \tag{19}$$

so quaternion conjugation can be seen as a consequence of reversing the order of vectors in a geometric product. For that reason, the operation is called *reversion* in geometric algebra. From eqn (6) we can deduce that the unit pseudoscalar, like bivectors, changes sign under reversion, that is,

$$i^\dagger = -i\,. \tag{20}$$

Reversion is analogous to hermitian conjugation in matrix algebra. For any quantities P, Q, it satisfies the relations

$$(PQ)^\dagger = Q^\dagger P^\dagger\,, \tag{21a}$$

$$(P+Q)^\dagger = P^\dagger + Q^\dagger\,. \tag{21b}$$

The dual of the bivector $\mathbf{a}\wedge\mathbf{b}$ is a vector, denoted by $\mathbf{a}\times\mathbf{b}$ so we have

$$\mathbf{a}\wedge\mathbf{b} = i(\mathbf{a}\times\mathbf{b})\,. \tag{22}$$

As the notation suggests, the vector-valued function $\mathbf{a}\times\mathbf{b}$ defined in this way is precisely the cross product of standard vector analysis. Accordingly, eqn (16c) can be written in the form

$$\mathbf{ab} = \mathbf{a}\cdot\mathbf{b} + i(\mathbf{a}\times\mathbf{b})\,. \tag{23}$$

This shows how the two products $\mathbf{a}\wedge\mathbf{b}$ and $\mathbf{a}\times\mathbf{b}$ are contained in geometric algebra and, by virtue of eqn (17), how they are related to quaternions.

The outer product $\mathbf{a}\wedge\mathbf{b}$ is more fundamental than the cross product $\mathbf{a}\times\mathbf{b}$ because it applies in any dimension, including two, whereas the vector cross product is a special feature of three dimensions. However, the relations (22) and (23) make it easy to translate from one to the other, and the cross product will be preferred below, because it is so much more familiar to most readers. The outer product of three vectors $\mathbf{a}\wedge\mathbf{b}\wedge\mathbf{c}$ is a pseudoscalar, and it can be shown to be related to the cross product by

$$\mathbf{a}\wedge\mathbf{b}\wedge\mathbf{c} = i[(\mathbf{a}\times\mathbf{b})\cdot\mathbf{c}]\,. \tag{24}$$

This completes our survey of the fundamentals of geometric algebra. Next we apply it to rotations.

3. THE CALCULUS OF ROTATIONS

Any rigid rotation of a physical body can be described mathematically as a linear transformation of the vector space $\mathcal{V}_3$ that preserves the length of every vector. In geometric algebra, a rotation transforming each vector $\mathbf{r}'$ into a vector $\mathbf{r}$ can be written in the canonical form

$$\mathbf{r} = Q\mathbf{r}'Q^{-1}\,, \tag{25}$$

where Q is a quaternion. Because Q determines the rotation uniquely by this equation, it can be regarded as a mathematical representation of the rotation itself. Accordingly, it will be convenient to use Q itself as *a name for rotation* it represents. Quaternions employed to represent a rotation in this way can be called *spinors* because they are isomorphic to the spinors employed by physicists in a different mathematical guise.

The spinor Q representing a particular rotation is unique up to multiplication by a nonzero scalar λ, for if Q is replaced λQ in eqn (25) the λ cancels to leave the equation unchanged. This arbitrariness can be reduced by normalizing Q to $|Q| = 1$, in which case, according to eqn (12), $Q^{-1} = Q^\dagger$. However, this is unnecessary, and sometimes it is inconvenient.

Equation (25) is the same as the one describing rotations in the quaternion calculus, except that $\mathbf{r}$ and $\mathbf{r}'$ are genuine vectors rather than bivectors as the quaternion calculus inadvertently requires. Moreover, geometric algebra has advantages in parametrizing spinors, as shown below.

Rotations form a mathematical group, which means that the composite of two rotations is equivalent to a third rotation. This is represented with spinors by multiplication. Thus, a rotation Q followed by a rotation P determines a rotation

$$S = PQ\,. \tag{26}$$

In other words, the multiplicative group of spinors is a faithful representation of the rotation group. The 3D rotation group is a three-parameter continuous group, which means that every rotation can be represented by a continuous spinor-valued function of three scalar parameters. There are many such parametrizations, each of value in a different application. We now review several of interest for describing eye and limb movements. It should be remembered, though, that the spinor variable Q in eqn (25) is an *invariant representation* of a rotation in the sense that it is independent of any specific parametrization (or choice of coordinates). Accordingly, it is advisable to avoid making a particular parametrization explicit unless absolutely necessary. Note, for example, that the inverse of eqn (25) is simply

$$\mathbf{r}' = Q^{-1}\mathbf{r}Q\,, \tag{27}$$

and the computation of Q^{-1} from Q is trivial without parametrization.

Rotations can be parametrized by an angle vector $\mathbf{a} = a\hat{\mathbf{a}}$, where $a = |\mathbf{a}|$ is the rotation angle and the unit vector $\hat{\mathbf{a}}$ is the direction of the rotation axis. In this case, the spinor Q is given by the exponential function

$$Q = e^{-i\mathbf{a}/2} = \cos\tfrac{1}{2}a - \hat{\mathbf{a}}\sin\tfrac{1}{2}a\,. \tag{28a}$$

The minus sign is adopted to conform to the standard right-hand rule for the direction of the rotation axis. It does not appear in quaternion formulations employing a left-handed coordinate system. The angle in eqn (28a) is necessarily positive because a change in sign is expressed by reversing the direction of the rotation axis. The one half appears in eqn (28a) because (25) is a bilinear (or quadratic) function of Q, and Q can be expressed as the square root $Q = (e^{-i\mathbf{a}})^{1/2}$. To make eqn (28a) look more like the familiar exponential function in complex variable theory, one can define a unit bivector $\mathbf{I} = i\mathbf{a}$ with $I^2 = -1$ so eqn (28a) takes the form

$$Q = e^{-\mathbf{I}a/2} = \cos\tfrac{1}{2}a - \mathbf{I}\sin\tfrac{1}{2}a\,. \tag{28b}$$

This is actually more fundamental than eqn (28a) because it describes rotation in two dimensions where there is no rotation axis. Also. it is worth noting that a rotation angle should really be regarded as a bivector $\mathbf{I}a$ that specifies the plane of the rotation by its direction $\mathbf{I}$.

The invariant decomposition $Q = q_0 - i\mathbf{q}$ with the normalization $|\,Q\,| = q_0^2 + \mathbf{q}^2 = 1$ specifies a parametrization of Q by the vector $\mathbf{q}$. Computationally, this is the simplest parametrization for evaluating the composite of finite rotations, as is evident in evaluating the product (26). Expressing eqn (26) in the form

$$S = s_0 - i\mathbf{s} = (p_0 - i\mathbf{p})(q_0 - i\mathbf{q})\,,$$

the right side can be expanded, and scalar and bivector parts can be separated to yield the explicit expressions

$$s_0 = p_0 q_0 - \mathbf{p}\cdot\mathbf{q}\,, \tag{29a}$$

$$\mathbf{s} = q_0\mathbf{p} + p_0\mathbf{q}\cdot\mathbf{q} + \mathbf{p}\times\mathbf{q}\,. \tag{29b}$$

This can be expressed as a relation among rotation angles, for comparison with (28a) shows that

$$q_0 = \cos\tfrac{1}{2}a\,, \tag{30a}$$

$$\mathbf{s} = \hat{\mathbf{a}}\sin\tfrac{1}{2}a\,. \tag{30b}$$

However, this trigonometric relation between $\mathbf{a}$ and $\mathbf{q}$ is computationally expensive, an expense that can be avoided if $\mathbf{q}$ rather than $\mathbf{a}$ is used to parametrize rotations. By the way, q_0 and $\mathbf{q}$ are most frequently called *Euler parameters* in the literature (not to be confused with Euler angles).

If Q is not normalized to unity, its relation to the rotation angle is, instead of eqns (30a,b), best expressed by

$$\mathbf{q}/q_0 = \hat{\mathbf{a}}\tan\tfrac{1}{2}a\,, \tag{31a}$$

so

$$Q = q_0(1 - i\hat{\mathbf{a}}\tan\tfrac{1}{2}a)\,, \tag{31b}$$

and

$$|\,Q\,|^2 = q_0^2(1 + \tan^2\tfrac{1}{2}a)\,. \tag{31c}$$

Alternatively, a rotation Q can be parametrized by expressing it as a product

$$Q = ABC \tag{32}$$

of three spinors, each of which is a function of a single parameter alone. An advantage of this approach is that each factor can be chosen to have a fixed rotation axis. Parametrization by Euler angles is of this type, but there are many others, including the coordinates of Fick and Helmholtz that are frequently employed in oculomotor studies.

Applied to an orthonormal frame $\{\boldsymbol{\sigma}_k\}$ as specified in Section 2, eqn (25) determines a new orthonormal frame $\{\mathbf{e}_k\}$ with

$$\mathbf{e}_k = Q\boldsymbol{\sigma}_k Q^{-1}\,. \tag{33}$$

From this, one can calculate the matrix of direction cosines

$$e_{jk} = \boldsymbol{\sigma}_j \cdot \mathbf{e}_k = \langle\, \boldsymbol{\sigma}_j Q \boldsymbol{\sigma}_k Q^{-1} \,\rangle_0 \tag{34}$$

where $\langle\, M \,\rangle_0$ denotes the scalar part of M. The 3×3 matrix $[e_{jk}]$ is the standard matrix representation of a rotation, and eqn (34) expresses it as a function of Q. Conversely, eqn (33) can be solved to express Q as a function of the direction cosines. This inefficient parametrization of rotations is best avoided, and it is mentioned here only to establish the connection to matrix theory.

To complete our survey of parametrizations, we examine the significance of factoring Q into a product of vectors $Q = \mathbf{bc}$. Noting that $Q^{-1} = \mathbf{c}^{-1}\mathbf{b}^{-1}$ and substituting this into eqn (25), it can be seen that eqn (25) can be expressed as the composition of a transformation of the form

$$\mathbf{r} = -\mathbf{c}\mathbf{r}'\mathbf{c}^{-1} \tag{35}$$

followed by a similar transformation with $\mathbf{c}$ replaced by $\mathbf{b}$. To interpret this transformation geometrically, use eqn (16a) in the form $\mathbf{c}\mathbf{r}' = -\mathbf{r}'\mathbf{c} + 2\mathbf{r}' \cdot \mathbf{c}$ to write eqn (35) in the form

$$\mathbf{r} = \mathbf{r}' - 2(\mathbf{r}' \cdot \mathbf{c})\mathbf{c}^{-1} = \mathbf{r}_- - \mathbf{r}_+ \,,$$

where $\mathbf{r}_+ = (\mathbf{r}' \cdot \mathbf{c})\mathbf{c}^{-1}$ is the component of $\mathbf{r}'$ collinear with $\mathbf{c}$, and $\mathbf{r}_-$ is the component orthogonal to $\mathbf{c}$. This proves that eqn (35) is a mirror reflection in the plane with normal $\mathbf{c}$. Therefore, $Q = \mathbf{bc}$ expresses the fact that *any 3D rotation can be expressed as a product of two reflections*. We know, however, from Section 2, that this can be done in infinitely many ways, because every vector in the plane of Q is a factor of Q. This last fact can be exploited to determine a best choice, which we do next.

If $\mathbf{c}$ is a unit vector in the plane of Q that is rotated into a vector $\mathbf{b}$, then, according to eqn (18), we have $Q\mathbf{c} = \mathbf{c}Q^\dagger$ and we can write

$$\mathbf{b} = Q\mathbf{c}Q^\dagger = Q^2\mathbf{c} \tag{36}$$

with $|\,Q\,|^2 = 1$. This can be solved for $Q^2 = \mathbf{bc}$, and the square root can be found by noting that Q^2 is a rotation through twice the angle of Q. Therefore, if $\mathbf{c}$ or $\mathbf{b}$ is selected as a factor of Q, then the other factor must lie half way between $\mathbf{c}$ and $\mathbf{b}$, so we can write down directly

$$Q = (\mathbf{bc})^{1/2} = \frac{(\mathbf{b}+\mathbf{c})\mathbf{c}}{|\,\mathbf{b}+\mathbf{c}\,|} = \frac{\mathbf{b}(\mathbf{b}+\mathbf{c})}{|\,\mathbf{b}+\mathbf{c}\,|}\,.$$

The normalization by $|\,\mathbf{b}+\mathbf{c}\,| = [2(1+\mathbf{b}\cdot\mathbf{c})]^{1/2}$ is actually of no interest, so we can write more simply,

$$Q \doteq (\mathbf{b}+\mathbf{c})\mathbf{c} = \mathbf{b}(\mathbf{c}+\mathbf{b}) = 1 + \mathbf{bc}\,, \tag{38}$$

where the symbol $\doteq$ means projective equality or equality up to a scale factor.

Next, we summarize the fundamentals of rotational kinematics. A time-varying rotation can be expressed as spinor-valued function of time $Q = Q(t)$, where the modulus of Q is constant. It follows by differentiating the fixed constraint $|\,Q\,|^2 = QQ^\dagger$ that Q must satisfy a differential equation of the form

$$\dot{Q} = -\tfrac{1}{2}i\omega Q\,, \tag{39}$$

where the overdot indicates differentiation and the vector $\omega = \omega(t)$ is the *angular velocity* of the rotation. Of course, the angular velocity should really be regarded as a bivector

$$\Omega = i\omega = -2\dot{Q}Q^{-1}\,. \tag{40}$$

Also, the term angular velocity is a misnomer and a more precise term is *rotational velocity*, for ω is not equal to the derivative of the angle $\mathbf{a}$ in eqn (28a) unless the direction of the rotation axis $\mathbf{a}$ is constant. In that case, $\omega = \dot{\mathbf{a}} = \hat{\mathbf{a}}\dot{a}$ can be integrated directly to give

$$\mathbf{a}(t) = \int_0^t \omega(t)\,dt + \mathbf{a}_0 \tag{41}$$

and the solution of eqn (39) is given by eqn (28a). The initial condition $\mathbf{a}_0 = 0$ corresponds to the spinor initial condition $Q(0) = 1$.

For $Q = Q(t)$ and fixed $\mathbf{r}_0$, eqn (25) describes the orbit $\mathbf{r} = \mathbf{r}(t)$ of a point on a sphere of radius $|\,\mathbf{r}\,| = |\,\mathbf{r}_0\,|$. To derive the equation of motion for $\mathbf{r}$ from eqn (39), note that $(i\omega)^\dagger = -i\omega$, so reversion of eqn (38) yields

$$\dot{Q}^\dagger = Q^\dagger(\tfrac{1}{2}i\omega) = \tfrac{1}{2}iQ^\dagger\omega\,, \tag{42}$$

which becomes an equation for Q^{-1} on division by $|\,Q\,|^2$. Now eqns (39) and (42) can be used to evaluate the derivative of eqn (25); thus,

$$\dot{\mathbf{r}} = \dot{Q}\mathbf{r}_0Q^{-1} + Q\mathbf{r}_0\dot{Q}^{-1} = -i\tfrac{1}{2}(\omega\mathbf{r} - \mathbf{r}\omega)\,,$$

so, using the relation (23), we obtain the familiar equation

$$\dot{\mathbf{r}} = \omega \times \mathbf{r}\,. \tag{43}$$

It is of interest to express ω as a function of $\mathbf{r}$. Employing eqns (22) and (16c), we have

$$i\dot{\mathbf{r}}\mathbf{r} = \omega \wedge \mathbf{r} = \omega\mathbf{r} - \omega\cdot\mathbf{r}\,,$$

whence

$$\omega = i\dot{\mathbf{r}}\mathbf{r}^{-1} + (\omega\cdot\mathbf{r})\mathbf{r}^{-1} - \dot{\mathbf{r}}\times\mathbf{r}^{-1} + (\omega\cdot\mathbf{r})\mathbf{r}^{-1}\,. \tag{44}$$

The last term here is the component of ω along $\mathbf{r}$, which, of course, is not determined by $\dot{\mathbf{r}}$ because $\dot{\mathbf{r}}\cdot\mathbf{r} = 0$.

With $Q = Q(t)$, eqn (30) describes a rotating frame $\{\mathbf{e}_k = \mathbf{e}_k(t)\}$ with derivatives

$$\dot{\mathbf{e}}_k = \omega \times \mathbf{e}_k\,. \tag{45}$$

This can be given a variety of interpretations. In particular we may regard $\{\mathbf{e}_k\}$ as a rigid frame, attached to the point $\mathbf{r}$, which rotates as it is *transported* along the path $\mathbf{r}(t)$. We set $\mathbf{e}_1 = \hat{\mathbf{r}}$, so $\mathbf{e}_2$ and $\mathbf{e}_3$ are at every point $\mathbf{r}$ tangent to the sphere on which the frame moves. The velocity $\dot{\mathbf{r}}$ of the path also lies in the tangent plane, and its change of direction is completely described by the first term on the right side of eqn (44). Therefore, the last term in eqn (44) describes the rate at which the angle between $\dot{\mathbf{r}}$ and $\mathbf{e}_2$ or $\mathbf{e}_3$ changes with the motion. Denoting this angle by φ, we can write

$$\omega \cdot \hat{\mathbf{r}} = \omega \cdot \mathbf{e}_1 = \dot{varphi}\,. \tag{46}$$

Adopting a term from physics, let φ be called the *phase* of the motion.

The spinor Q can be factored into the product of a spinor R determining the orbit $\mathbf{r}(t)$ and a spinor determining the phase. Specifically,

$$Q = R\exp\{-\tfrac{1}{2}i\boldsymbol{\sigma}_1\varphi\}\,. \tag{47}$$

with

$$\dot{R} = \tfrac{1}{2}\,\dot{\mathbf{r}}\mathbf{r}^{-1}R = \tfrac{1}{2}\,\dot{\mathbf{e}}_1\mathbf{e}_1 R\,. \tag{48}$$

This result can be proved by substituting eqn (46) into eqn (39); thus,

$$i\omega = -2\dot{R}R^{-1} - 2Q(-\tfrac{1}{2}\boldsymbol{\sigma}_1\dot{\varphi})Q^{-1} = \mathbf{e}_1\dot{\mathbf{e}}_1 + i\mathbf{e}_1\dot{varphi}\,,$$

which agrees with eqn (44).

In differential geometry, the shortest path between two points on a surface is called a *geodesic*, and transport of a frame along a geodesic $\mathbf{r} = \mathbf{r}(t)$ that maintains a fixed angle with the velocity $\dot{\mathbf{r}}$ (so $\dot{varphi} = 0$) is called *parallel transport*. The geodesics on a sphere are, of course, great circles, which are curves with a fixed axis of rotation determined by the endpoints. It follows that the spinor R in eqn (46) for a geodesic from point $\mathbf{a}$ to point $\mathbf{b}$ has an angular velocity of the form

$$\omega_1 = \mathbf{r}^{-1} \times \dot{\mathbf{r}} = \dot{\lambda}\,\mathbf{b} \times \mathbf{a}\,, \tag{49}$$

where $\dot{\lambda} = \dot{\lambda}(t)$ is a scalar-valued function determining the speed of the motion. Therefore, for a specified $\dot{\lambda}(t)$, eqn (48) can be integrated immediately as in eqn (41) to get R in the exponential form (28a). An additional condition is needed to determine $\varphi = \varphi(t)$ in eqn (46) but $\varphi = 0$ is appropriate for parallel transfer.

Integration of eqn (48) along a geodesic yields a spinor describing parallel transport between the endpoints, and the result, for transport from $\mathbf{a}$ to $\mathbf{b}$, can be expressed in the form eqn (38). Parallel transport around a geodesic triangle on a unit sphere with vertices at $\mathbf{a}, \mathbf{b}, \mathbf{c}$ (Figure 2) can be expressed as product of three such spinors $A = 1 + \mathbf{ba}$, $B = 1 + \mathbf{cb}$, $C = 1 + \mathbf{ac}$. The result is a spinor

$$T = CBA = (1 + \mathbf{ac})(1 + \mathbf{cb})(1 + \mathbf{ba})\,. \tag{50a}$$

Expanding and collecting scalar and bivector terms, we have

$$\begin{aligned} T &= 2 + (\mathbf{ab} + \mathbf{ba}) + (\mathbf{ac} + \mathbf{ca}) = \mathbf{cb} + \mathbf{a}(\mathbf{cb})\mathbf{a} \\ &= 2(1 + \mathbf{a}\cdot\mathbf{b} + \mathbf{a}\cdot\mathbf{c} + \mathbf{c}\cdot\mathbf{b}) + \mathbf{c}\wedge\mathbf{b} + \mathbf{a}(\mathbf{c}\wedge\mathbf{b})\mathbf{a} \\ &= 2(1 + \mathbf{a}\cdot\mathbf{b} + \mathbf{a}\cdot\mathbf{c} + \mathbf{c}\cdot\mathbf{b}) + 2\mathbf{a}(\mathbf{c}\wedge\mathbf{b}\wedge\mathbf{a})\,. \end{aligned}$$

Using eqn (24), this can be written

$$\tfrac{1}{2}T = 1 + \mathbf{a}\cdot\mathbf{b} + \mathbf{b}\cdot\mathbf{c} + \mathbf{c}\cdot\mathbf{a} - i\mathbf{a}[\mathbf{a}\cdot(\mathbf{b}\times\mathbf{c})]\,. \tag{50b}$$

As eqn (50b) shows, the net effect of parallel transporting a frame around a geodesic triangle is simply to rotate it around the initial point $\mathbf{a}$. By comparison with eqn (31a), the rotation is through an angle φ given by

$$\tan \tfrac{1}{2}\varphi = \frac{\mathbf{a}\cdot(\mathbf{b}\times\mathbf{c})}{1+\mathbf{a}\cdot\mathbf{b}+\mathbf{b}\cdot\mathbf{c}+\mathbf{c}\cdot\mathbf{a}} \,. \tag{51}$$

If $\mathbf{a}$, $\mathbf{b}$, and $\mathbf{c}$ are mutually orthogonal, the vertex angles of the triangle are all right angles, and eqn (51) reduces to $\tan \frac{1}{2}\varphi = \pm 1$, so we get the classical result $\varphi = \pm\pi$, the sign depending on the orientation of the triangle.

The result (51) belongs to spherical trigonometry, and its derivation shows how the subject can be simplified with geometric algebra. For more of this, see Appendix A of Hestenes (1986).

4. SACCADE KINEMATICS

The skull is a rigid body and so determines a physical reference system called the *head space* in which it is at rest. This section is concerned with saccadic eye movement in the head space. A *saccade* is a rapid shift of gaze in order to fixate a target object in the visual field on the fovea. The direction of the line of sight to the foveated object is called the *gaze direction*, and we represent it by a unit vector g. The fovea subtends an angle of about half a degree in the visual field, so that provides a measure of the accuracy required for gaze control.

For kinematic purposes, the eye can be modeled as a ball in a socket joint, so it has three degrees of freedom. The gaze vector g can then be regarded as rotating with its tail fixed at the center of the eye. Actually, the eye deforms and its center wobbles by as much as 2 ml as the gaze varies over the oculomotor range; nevertheless, the visual axes for different directions intersect at a point (Carpenter, 1988), so the model of a rigidly rotating eye is quite satisfactory for kinematic purposes.

Let $\mathbf{p}$ be a reference gaze direction, fixed in the head space. A saccade from $\mathbf{p}$ to a new direction g can be described by a saccade spinor S satisfying

$$\mathrm{g} = S\mathbf{p}S^{-1} \,. \tag{52}$$

The spinor S not only describes a change of gaze direction but also a rotation of the eye about the gaze direction, which is called *torsion* in the eye movement literature. This differs, however from the concept of torsion in differential geometry, and there is some ambiguity as to how it should be defined. Here I would like to recommend a refinement of terminology in the interest of greater uniformity and precision. In the eye movement literature the term eye position is used ambiguously to mean gaze direction or the orientation of the eye in space. For the latter concept there is already a well-established technical term in

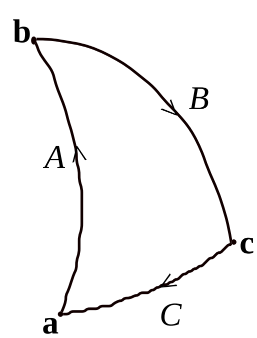

FIGURE 2. Parallel transport about a spherical triangle (i.e., a geodesic triangle) is expressed by a product of spinors describing geodesic motion along each side.

the field of rigid body mechanics, namely, *attitude*. The *attitude* of a rigid body is a specification of how it is positioned or oriented in space, and, as we have seen in the preceding section, this is best described by a spinor. an attitude spinor. The term *attitude control* is well established in aeronautics. Similarly, the term gaze control should be understood as attitude control of the eye or the gaze. Accordingly, a spinor describing the attitude of the eye will be called the *eye attitude*. The saccade spinor in eqn (52) is a particular kind of eye attitude. The term position in mechanics invariably means a particular place or location, as designated by a position vector. The *kinematic state* of a rigid body requires specification of both a *position* (vector) $\mathbf{X}$ and an *attitude* (spinor) R as well as their derivatives: the *translational* velocity $\dot{\mathbf{X}}$ and the *rotational* velocity $\omega = 2i\dot{R}R^{-1}$. These concepts will be needed when combined eye-head kinematics are considered in the next section. Therefore, it seems best to discard eye position in favor of the more precise term eye attitude, or at least restrict it to designating the position of the center of the eye. That much said, we can get back to business.

The structure of the saccade spinor S is completely determined by an empirically derived kinematical constraint called Listing's law (Helmholtz, 1866). There are many equivalent formulations of Listing's law, but here is one more, based on the concepts developed in the preceding section. *Donders' law* (Helmholtz, 1866) asserts that the gaze attitude $S = S(\mathrm{g})$ for any gaze direction g is unique and independent of the path (saccade sequence) by which the eye arrived at g. *Listing's law* asserts further that there is a unique gaze direction $\mathbf{p}$, called the *primary direction*, such that, for any g, $S(\mathrm{g})$ is obtained by parallel transport along a geodesic from $\mathbf{p}$. Accordingly, Listing's law is expressed by the formula

$$S(\mathrm{g}) = 1 + \mathrm{g}\mathbf{p} = 1 + \mathrm{g} \cdot \mathbf{p} + i(\mathrm{g} \times \mathbf{p})\,. \tag{53}$$

The quaternion equivalent of the vector $\mathrm{g} \times \mathbf{p}$ is called the *angular position vector* by Tweed and Vilis (1987), but the term will not be employed here because g is a more direct descriptor. Note that, for all g, the vector $\mathrm{g} \times \mathbf{p}$ specifies the axis of rotation and lies in the plane orthogonal to $\mathbf{p}$ (*Listing's plane*). This is the basis for an alternative formulation of Listing's law already in the literature.

The most significant, new thing about the mathematical formulation of Listing's law by eqn (53) is that the *Saccade attitude* $S(\mathrm{g})$ *is expressed explicitly as an algebraic function of gaze directions* g and $\mathbf{p}$. Also, it will become clear that use of the unnormalized spinor (52) greatly simplifies computations by eliminating the computational costs of normalization.

Actually, for an arbitrarily chosen reference $\mathbf{p}$, *any* gaze attitude $G = G(\mathrm{g})$ can be written in the form

$$G(\mathrm{g}) = (1 + \mathrm{g}\mathbf{p})e^{-i\mathbf{p}\varphi/2} = e^{-i\mathrm{g}\varphi/2}(1 + \mathrm{g}\mathbf{p})\,. \tag{54}$$

Identification of φ as *torsion angle* is one convenient way to define torsion. Based on eqn (54), Donders' law can be formulated precisely as specifying that the torsion angle is a function $\varphi = \varphi(\mathrm{g})$ of g alone, independent of the saccadic path to g. Listing's law then states that there is a choice of $\mathbf{p}$ so that $\varphi = 0$ everywhere. The expression (54) may be most valuable for describing deviations from Listing's law. Indeed, there is empirical evidence for a small path dependent torsion (Ferman, Collewijn, & Van den Berg, 1987a,b; Tweed & Vilis, 1990b). However, the following discussions will be limited to investigating implications of Listing's law.

The spinor (53) describes the change in gaze attitude due to a saccade from primary position. To maintain Listing's law (53), the spinor $S(\mathbf{b}, \mathbf{a})$, describing a saccade between arbitrary gaze directions $\mathbf{a}$ and $\mathbf{b}$, must satisfy

$$S(\mathbf{b}) = S(\mathbf{b},\mathbf{a})S(\mathbf{a})\,. \tag{55}$$

This determines $S(\mathbf{b},\mathbf{a})$ uniquely, for

$$\begin{aligned} S(\mathbf{b},\mathbf{a}) &= S(\mathbf{b})[S(\mathbf{a})]^{-1} \doteq S(\mathbf{b})S^{\dagger}(\mathbf{a}) \\ &= (1+\mathbf{bp})(1+\mathbf{pa}) = (\mathbf{p}+\mathbf{b})(\mathbf{p}+\mathbf{a}) \\ &= 1+\mathbf{pa}+\mathbf{bp}+\mathbf{ba} \\ &= [1+\mathbf{p}\cdot\mathbf{a}+\mathbf{b}\cdot\mathbf{p}+\mathbf{b}\cdot\mathbf{a}] \\ &\qquad - i[(\mathbf{a}-\mathbf{b})\times\mathbf{p}+\mathbf{a}\times\mathbf{b}]\,. \end{aligned} \tag{56}$$

The last term, of course, specifies the rotation axis. The possibility that this axis remains fixed during a saccade has been investigated (Van Opstal *et al.*, 1991). In that case, the angular velocity would be given by

$$\omega(t) = \lambda(t)[(\mathbf{a}-\mathbf{b})\times\mathbf{p}+\mathbf{a}\times\mathbf{b}]\,, \tag{57}$$

and the time development of the saccade spinor is given by eqn (28a) with eqn (41). There are other possibilities to consider, however. Though Listing's law determines the end result (56) of a saccade, it does not determine the path of a saccade between endpoints, so a theoretical analysis of the alternative is advisable.

A huge advantage of the unnormalized form eqn (53) for the saccade spinor is that its derivative is the simple linear function of gaze velocity $\dot{\mathrm{g}}$:

$$\dot{S} = \dot{\mathrm{g}}\mathbf{p}\,. \tag{58}$$

This describes the change in gaze attitude along an arbitrary gaze direction path $\mathrm{g} = \mathrm{g}(t)$, assuming that Listing's law is satisfied at every point on the path. It integrates to a simple additive law for gaze shift:

$$S(\mathbf{b}) - S(\mathbf{a}) = (\mathbf{b}-\mathbf{a})\mathbf{p}\,. \tag{59}$$

It is crucial to note that this result obtains only for unnormalized spinors, so both the scalar part $(\mathbf{b}-\mathbf{a})\cdot\mathbf{p}$ and the vector part $(\mathbf{b}-\mathbf{a})\times\mathbf{p}$ must be computed to get rotation angle by eqn (31a).

To find how the rotational velocity $\omega = \omega(t)$ varies along the path $\mathrm{g}(t)$, use eqn (58) to evaluate

$$2\dot{S}S^{-1} = 2\dot{\mathrm{g}}\frac{(\mathbf{p}+\mathrm{g})}{|\,\mathbf{p}+\mathrm{g}\,|} = \frac{\mathrm{g}(\mathbf{p}+\mathrm{g})}{1+\mathrm{g}\cdot\mathbf{p}}\,.$$

Unlike eqn (40), this has a nonvanishing scalar part, because the norm

$$|\,S\,|^2 = |\,\mathbf{p}+\mathrm{g}\,|^2 = 2(1+\mathrm{g}\cdot\mathbf{p}) \tag{60}$$

is not constant. Just the same, its bivector part yields

$$\omega = \frac{(\mathbf{p}+\mathrm{g})\times\mathrm{g}}{1+\mathrm{g}\cdot\mathbf{p}}\,. \tag{61}$$

Note that this has a torsional component

$$\mathrm{g} \cdot \omega = \frac{\mathbf{p} \cdot (\dot{g} \times \mathrm{g})}{1 + \mathrm{g} \cdot \mathbf{p}} \,. \tag{62}$$

Note also that it implies, for any $\dot{\mathrm{g}}$, that ω lies in a plane with normal $\mathbf{p} + \mathrm{g}$, which is Listing's plane when $\mathrm{g} = \mathbf{p}$. This plane is called the *displacement plane* at g by Tweed and Vilis (1990b), who have amassed direct experimental support for its existence. At this point, we can make some inferences about possible neural implementations of saccadic computations. Employing a normalized spinor $Q = |\, S\,|^{-1} S$, Tweed and Vilis (1987, 1990a) suggest that the time course of Q may be determined by neurally integrating

$$2\dot{Q} = -i\omega Q \,, \tag{62a}$$

with a multiplicative error estimate given by eqn (55) in the form

$$E = Q^* Q^{-1} \,, \tag{62b}$$

where $Q^* = |\, S(\mathbf{b})\,|^{-1} S(\mathbf{b})$ is the target spinor. This has a number of drawbacks. First of all, to compute the right side of eqn (62a) it requires a multiplicative feedback structure that seems unlikely on the basis of current neurophysiological data. Second, it does not take advantage of computational simplifications due to Listing's law or other special features of saccade kinematics. For example, if saccades have a fixed rotation axis, as much data suggests, then ω can be integrated directly, as in eqn (41), and the updated Q can be computed algebraically from eqn (28a) without integration.

The basic problem is to determine what control variable is neurally employed in saccadic computation. Equation (62a) might be appropriate if ω is the control variable. However, since the seminal work of Mays and Sparks (1980, 1981), there has been accumulating evidence consistent with identification of the difference vector $\mathbf{b} - \mathbf{a}$ as the control, neurally represented in the superior colliculus and from there controlling the saccadic generator (Waitzman *et al.*, 1988). Recent evidence (Waitzman *et al.*, 1991) indicates that this control variable is updated as the saccade progresses. Equation (59) agrees perfectly with evidence that the vector difference $\mathbf{b} - \mathbf{a}$ between the desired target gaze direction $\mathbf{b}$ and the present gaze direction $\mathbf{a}$ is the saccadic control variable. Moreover, the additive error correction (59) is much simpler to implement than the multiplicative correction (62b), and it automatically implements Listing's law. It seems likely, then, that the essential multiplication by $\mathbf{p}$ would be implemented in the saccadic generator, if Listing's law applies to saccades generated by the frontal eye fields (Carpenter 1988) without activating the superior colliculus.

If the vector difference $\mathbf{b} - \mathbf{a}$ is indeed the saccade control variable, then the optimal saccadic path from $\mathbf{a}$ to $\mathbf{b}$ is a geodesic with the rotation axis $\mathbf{a} \times \mathbf{b}$. That would not be the rotation axis for the eye as a whole, however. As shown in Section 3, the saccade transition spinor (56) can be factored into the product

$$S(\mathbf{b}, \mathbf{a}) = (1 + \mathbf{b}\mathbf{a}) e^{-i\mathbf{a}\varphi/2} \,, \tag{63}$$

where the first factor is the geodesic spinor and, according to eqn (51), the torsion angle is given by

$$\tan \tfrac{1}{2}\varphi = \frac{\mathbf{p} \cdot (\mathbf{b} \times \mathbf{a})}{1 + \mathbf{a} \cdot \mathbf{b} + \mathbf{b} \cdot \mathbf{p} + \mathbf{p} \cdot \mathbf{a}} \,. \tag{64}$$

The sign in eqn (64) is opposite to the one in eqn (51), because the torsion factor in eqn (63) must cancel the rotation due to saccadic parallel transfer around a closed curve. Without such cancellation, saccades around a closed circuit would rotate the image on the retina. Implementation of Listing's law is a simple way to prevent this. That, in turn, suggests that Listing's law may be a consequence of some adaptive mechanism that enforces Donders' law to prevent retinal torsion from saccadic circuits. A direct experimental test of that possibility would require a means of inducing torsion experimentally.

The key result in all this analysis is the implication of eqn (59) that the simplest way to drive saccades with subtractive feedback based on gaze vectors is with the additive error signal

$$E = (\mathbf{b} - \mathbf{a})\mathbf{p}\,. \tag{65}$$

This involves the geometric product in an essential way, so we cannot help asking if the oculomotor system has learned to compute this product to achieve optimal computational efficiency. Tweed and Vilis (1990a) have already suggested ways that the closely related quaternion product could be implemented neurally. Their analysis has not exhausted the possibilities, however. The ultimate answer must come from experiment, of course, but theory is needed to suggest what to look for and explain what has been found.

As a final minor elaboration of the theory, we can introduce an orthonormal reference basis $\{\boldsymbol{\sigma}_k\}$ fixed in the head frame with $\boldsymbol{\sigma}_3$ designating the upward vertical, $\boldsymbol{\sigma}_2$ the lateral, and $\boldsymbol{\sigma}_1$ the forward direction. Then there is a spinor P determining the primary direction by

$$\mathbf{p} = P\boldsymbol{\sigma}_1 P^{-1} \tag{66}$$

so an arbitrary gaze frame $\{\mathbf{e}_k\}$ is given by

$$\mathbf{e}_k = G\boldsymbol{\sigma}_k G^{-1} \tag{67}$$

with gaze direction $q = \mathbf{e}_1$ and gaze attitude

$$G = SP\,. \tag{68}$$

It seems more likely that the entire attitude P, rather than just the gaze direction $\mathbf{p}$, would be modified by the adaptive mechanism suggested above.

Tweed and Vilis (1990a), like Grossberg and Kuperstein (1989) as well as others, have noted the crucial fact that saccadic error is expressed in terms of a *spatial code* in the superior colliculus that must be converted to a *temporal code* by the saccadic generator before the ocular muscles can be activated. Grossberg and Kuperstein (1989) have recognized that this temporal code must be *adaptively calibrated* to accurately represent eye position (i.e., attitude), and they have proposed muscle linearization networks to accomplish that. This calibration mechanism could do more; for example, it might adjust the temporal code so that eqn (65) is implemented. Only the difference vector $\mathbf{b} - \mathbf{a}$ need be represented in the superior colliculus. The primary vector $\mathbf{p}$ could then be adjusted adaptively to produce accurate saccades.

5. COMPENSATORY KINEMATICS AND PURSUIT

Optimal vision requires fixation of a target object on the fovea. To keep the gaze directed at a target when the head moves, precise compensatory rotations of the eyes are required. This section provides an invariant formulation of eye-head kinematics to specify completely the computations that must be performed by the oculomotor system to achieve perfect compensatory control. The relevant position variables are designated in Figure 3. The first task will be to characterize the compensatory control variables. Head movement is measured by the vestibular system using accelerometers located in the inner ears on each side of the head. Linear acceleration is detected by organs called *otoliths* and rotational acceleration is detected by the *semicircular canals*. The signals are then integrated to produceestimates of the otolith linear velocities $\dot{\mathbf{X}}_1, \dot{\mathbf{X}}_2$, and the rotational velocity of the head ω_H. Kinematically, the simplest choice of a *center* $\mathbf{X}$ for the head is

$$\mathbf{X} = \tfrac{1}{2}(\mathbf{X}_1 + \mathbf{X}_2)\,, \tag{69}$$

so the *translational velocity* of the head is

$$\dot{\mathbf{X}} = \tfrac{1}{2}(\dot{\mathbf{X}}_1 + \dot{\mathbf{X}}_2)\,. \tag{70}$$

The motion of the head is then described as translational motion of the head center along a curve $\mathbf{X} = \mathbf{X}(t)$ while the body rotates about $\mathbf{X}$ with rotational velocity $\omega_H = \omega_H(t)$. Any rigid body motion can be described in this way.

It is a theorem of rigid body kinematics that ω_H is independent of the point chosen as center. Therefore, the semicircular canals in each ear give two independent measurements of the same quantity ω_H. Independent measurements of $\dot{\mathbf{X}}$ and ω_H are also made by the *optokinetic system* from flow patterns of the visual scene across the whole retina. However, we need not consider here how the various measurements are combined into a single best estimate of $\dot{\mathbf{X}}$ and ω_H. Our concern is how compensatory rotations can be computed from these quantities.

As shown below, perfect compensatory control requires an estimate of the target distance from each eye. This can be obtained by triangulation from measurements of gaze direc-

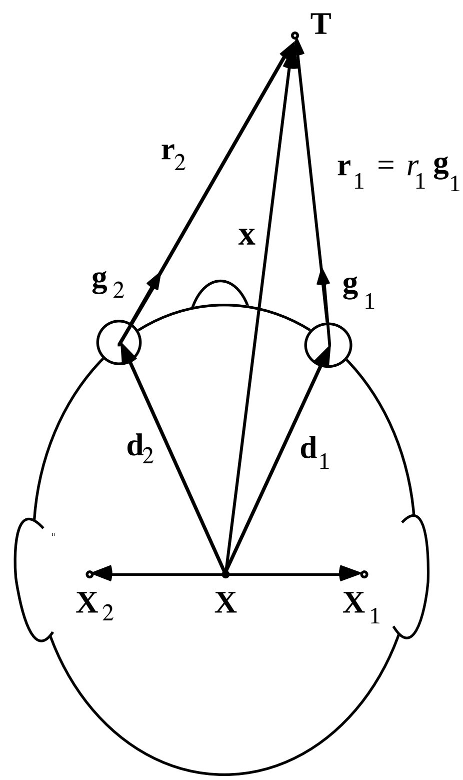

FIGURE 3. Eye, head and target position vectors. The gaze vectors g_1, g_2 of the two eyes point toward a small target position $\mathbf{T}$ at distances $\mathbf{r}_1, \mathbf{r}_2$ from the eye centers. The centers of the left and right eyes are designated by vectors $\mathbf{d}_1, \mathbf{d}_2$ fixed in the head frame; these vectors determine a natural horizontal plane for the head, the head plane. The right and left otoliths are fixed in the head and located at positions $\mathbf{X}_1, \mathbf{X}_2$. The head center is defined as the midpoint $\mathbf{X}=\frac{1}{2}(\mathbf{X}_1+\mathbf{X}_2)$. The position of the target with respect to the head (center) is designated by $\mathbf{x}=\mathbf{T}-\mathbf{X}$. No restrictions are placed on the target position; in particular, the target need not lie in the head plane.

tions. The relevant variables are depicted in Figure 4, and elaborated detail from Figure 3. The baseline for the triangulation is described by the vector $\mathbf{d} = \mathbf{d}_2 - \mathbf{d}_1$, the directed distance from the right to left eye. The equation for the triangle with vertices at the two eyes and the target is

$$r_1 \mathrm{g}_1 - r_2 \mathrm{g}_2 = \mathbf{d}\,. \tag{71}$$

The problem is to solve this equation for the distances r_1 and r_2. The variable r_2 can be eliminated by employing the outer product. because $\mathrm{g}_2 \wedge \mathrm{g}_2 = 0$, so

$$r_1 \mathrm{g}_1 \wedge \mathrm{g}_2 = \mathbf{d} \wedge \mathrm{g}_2\,.$$

Solving this by division and introducing alternative parametrizations defined below, we obtain

$$r_1 = \frac{\mathbf{d} \wedge \mathrm{g}_2}{\mathrm{g}_1 \wedge \mathrm{g}_2} = \frac{d \sin\theta_2}{\sin(\theta_1 + \theta_2)} = \frac{\beta_2 d}{\alpha_1\beta_2 + \alpha_2\beta_1}\,. \tag{72a}$$

Similarly.

$$r_2 = \frac{\mathbf{d} \wedge \mathrm{g}_1}{\mathrm{g}_1 \wedge \mathrm{g}_2} = \frac{d \sin\theta_1}{\sin(\theta_1 + \theta_2)} = \frac{\beta_1 d}{\alpha_1\beta_2 + \alpha_2\beta_1}\,. \tag{72b}$$

It is worth noting that these solutions of the triangle in Figure 3 amount to applications of the law of sines from trigonometry or Cramer's rule from linear algebra, both of which are automatically included among the computational capabilities of geometric algebra (Hestenes, 1986).

Geometrically, an angle describes a relation between two directions. Accordingly, the angles in Figure 4 are defined algebraically by the geometric products

$$\mathrm{g}_1 \hat{\mathbf{d}} = e^{\mathbf{I}\theta_1} = \alpha_1 + \mathbf{I}\beta_1\,, \tag{73a}$$

$$(-\hat{\mathbf{d}})\mathrm{g}_1 = e^{\mathbf{I}\theta_2} = \alpha_2 + \mathbf{I}\beta_2\,, \tag{73b}$$

where $\hat{\mathbf{d}} = \mathbf{d}/d$ with $d = |\,\mathbf{d}\,|$, $\mathbf{I}$ is the unit oriented bivector for the plane of the triangle, and $\alpha_k = \cos\theta_k$, $\beta_k = \sin\theta_k$. Multiplying eqn (73a) by eqn (73b), we obtain

$$\begin{aligned} \mathrm{g}_1\mathrm{g}_2 &= e^{\mathbf{I}(\theta_1+\theta_2)} \\ &= \beta_1\beta_2 - \alpha_1\alpha_2 - \mathbf{I}(\alpha_1\beta_2 + \alpha_2\beta_1) \end{aligned} \tag{74}$$

Finally, the expressions in eqns (72a,b) are obtained by taking the ratio of the bivector parts of eqn (73a,b) to those of eqn (74).

This completes the derivation of the eqns (72a,b) for computing target distance. As noted before, the angles such as θ_1 and θ_2 are not likely to be employed by the brain, because computation of trigonometric functions and inverse trigonometric functions is unnecessarily expensive. The parameters α_k, β_k, or, better, the Euler parameters of the gaze attitude

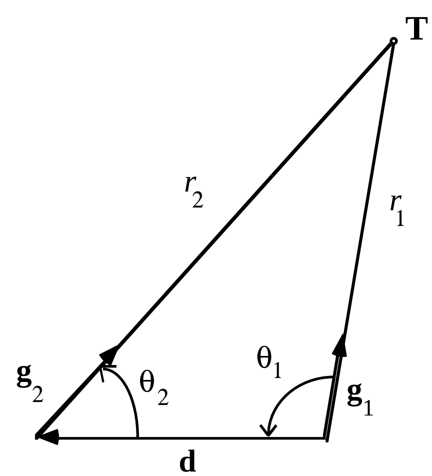

FIGURE 4. Target distance by triangulation. The result can be computed from the vectors g_1, g_2, $\mathbf{d}$.

spinors are more likely. Evidently, computations would be simplest if the primary gaze directions $\mathbf{p}_k$ for each eye are coplanar with $\mathbf{d}$. This should be checked experimentally.

Our next task is to determine the rotational velocity of the gaze directions g_k required to keep the target foveated during arbitrary target and head motions. According to Figure 3, the gaze directions are determined by the triangle constraint

$$\mathbf{x} = \mathbf{T} - \mathbf{X} = \mathbf{d}_k + r_k \mathrm{g}_k \tag{75}$$

for $k = 1, 2$. As this constraint holds for each eye separately, it will be convenient to suppress the subscripts in the following analysis, writing

$$\mathbf{x} = \mathbf{d} + r\mathrm{g}\,. \tag{76}$$

As in (3.20), the rotational velocity of the gaze is related to the gaze velocity $\dot{\mathrm{g}}$ by

$$\omega_g = \mathrm{g} \times \dot{\mathrm{g}} + (\mathrm{g} \cdot \omega_g)\mathrm{g}\,. \tag{77}$$

The torsion rate $\mathrm{g} \cdot \omega_g$ is not affected by the constraint (76), so we set it to zero to keep images from rotating on the retina.

To evaluate eqn (77), differentiate eqn (76) and use

$$\dot{\mathbf{d}} = \omega_g \times \mathbf{d} \tag{78}$$

to get

$$\dot{\mathbf{x}} = r\dot{\mathrm{g}} + \dot{r}\mathrm{g} + \omega_g \times \mathbf{d}\,. \tag{79}$$

Inserting this into eqn (77), we get

$$r\omega_g = \mathrm{g} \times \dot{\mathbf{x}} - \mathrm{g} \times (\omega_g \times \mathbf{d})\,. \tag{80}$$

This is related to the *compensatory rotational velocity* of the eye ω_E by

$$\omega_g = \omega_H + \omega_E\,. \tag{81}$$

Therefore,

$$r\omega_E = -\omega_H + \frac{1}{r}\,\mathrm{g} \times \dot{\mathbf{x}} + \frac{1}{r}\,\mathrm{g} \times (\mathbf{d} \times \omega_H)\,. \tag{82}$$

This can be expressed in an alternative form by employing the vector identity

$$\mathrm{g} \times (\mathbf{d} \times \omega_H) = (\mathrm{g} \cdot \omega_H)\mathbf{d} - (\mathrm{g} \cdot \mathbf{d})\omega_H \tag{83}$$

and noting from eqn (76) that $\mathrm{g} \cdot \mathbf{d} + r = \mathrm{g} \cdot \mathbf{x}$. Whence, with $\mathbf{r}^{-1} = \mathrm{g}/r$,

$$\omega_E = -(\mathbf{r}^{-1} \cdot \mathbf{x})\omega_H + \mathbf{r}^{-1} \times \dot{\mathbf{x}} + (\mathbf{r}^{-1} \cdot \omega_H)\mathbf{d}\,. \tag{84}$$

This equation was derived by Viirre *et al.* (1986) in a study of the gain of the vestibulo-ocular reflex (VOR). Consistent with earlier experimental results, they found a dependence of the gain on the target distance r as required by the equation. Equation (82), however, appears to be more directly relevant to neural computation.

Equation (82) expresses ω_E as a sum of terms dependent on three different sources of information, so the terms can be computed in parallel and combined additively (presumably in the vestibular nuclei) to produce a resultant eye movement command. The dominant term in eqn (82) is, of course, the first term $-\omega_H$, which has been extensively studied in VOR research and is often the only term considered in theoretical analysis. This term has the same value for both eyes.

The last term on the right side of eqn (82) is a *vergence correction* that is significant only for near targets. Because the variables r, g, and $\mathbf{d}$ are different for each eye, the correction is different for each eye. The double cross product need not be directly computed neurally because the identity eqn (83) can be employed. Evidently, the only way to compute the vector $\mathbf{d}$ internally is by error correction from visual feedback, so the cerebellum must be involved in the computation. Recent improvements in the precision of gaze direction measurements make it possible to evaluate experimentally the accuracy with which this VOR vergence correction is made.

In the cyclops approximation where $\mathbf{d}$ is neglected, so the eye is regarded as centered in the head, eqn (82) reduces to

$$\omega_E = -\omega_H + \frac{1}{r}\,\mathrm{g}\times\dot{\mathbf{x}}\,. \tag{85}$$

According to eqn (75),

$$\dot{\mathbf{x}} = \dot{\mathbf{T}} - \dot{\mathbf{X}}\,, \tag{86}$$

so for a fixed target we have $\dot{\mathbf{x}} = -\dot{\mathbf{X}}$, and the last term in eqns (82) or (85) describes the compensatory rotation for translational self-motion. On the other hand, for a moving target and fixed head, we have $\dot{\mathbf{x}} = \dot{\mathbf{T}}$, and the same term describes the eye rotation required to follow an object in *smooth pursuit*. This strongly suggests that the (phylogenetically recent) smooth pursuit system co-opts the neural output mechanisms of the (phylogenetically old) vestibular system. There is some experimental support for this conclusion (Eckmiller, l981; Collewijn, 1985).

With $\omega_H = 0$, substitution of eqn (78) into eqns (82) or (84) leads right back to eqn (77), which can be written

$$i\omega_E = \frac{1}{r}\,\mathrm{g}\wedge\dot{\mathbf{x}} = \mathrm{g}\wedge\dot{\mathrm{g}} = \mathrm{g}\dot{\mathrm{g}}\,. \tag{87}$$

This is just a way of describing the retinal slip of the moving target image if the eye remains stationary. This means that the cross product $\mathrm{g}\times\dot{\mathbf{x}}$ need not be computed neurally. lt is just a formal way of selecting the tangential (retinal slip) component of $\dot{\mathbf{x}}r^{-1}$, which is independent of r in the cyclops approximation. The radial component of r along g is, of course, eliminated by the cross product, so it need not be computed neurally.

The above description of compensatory kinematics is expressed with respect to an external reference system called the *workspace* in robotics. However, the head space is more natural for neural computations. Vectors in the two reference systems are related by

$$\mathbf{d} = H\mathbf{d}'H^{-1}\,, \tag{88a}$$

$$\mathrm{g} = H\mathrm{g}'H^{-1}\,, \tag{88b}$$

where the primes denote vectors in head space, and $H = H(t)$ is the *head attitude* spinor. The vector $\mathbf{d}'$ is constant, but

$$\mathrm{g}' = E\mathbf{p}'E^{-1}\,, \tag{89}$$

where $\mathbf{p}'$ is the primary direction and $E = E(t)$ is the eye attitude spinor in head space. Insertion of eqn (88b) into eqn (87) gives

$$\mathrm{g} = G\mathbf{p}'G^{-1}\,, \tag{90}$$

where

$$G = HE \tag{91}$$

is the eye attitude in the workspace. Transformed to head space, eqn (76) becomes

$$\mathbf{d}' + r\mathrm{g}' = H^{-1}\mathbf{x}H = \mathbf{x}'\,. \tag{92}$$

Similarly, with

$$\omega_g = H\omega_g' H^{-1}, \quad \omega_H = H\omega_H' H^{-1}, \quad \omega_E = H\omega_E' H^{-1}, \tag{93}$$

eqn (76) becomes

$$\omega_g' = \omega_H' + \omega_E'\,. \tag{94}$$

in head space.

For given angular velocities the equations of motion for the attitude spinors are, by definition,

$$\dot{H} = -\tfrac{1}{2}i\omega_H H = H(-\tfrac{1}{2}i\omega_H')\,, \tag{95a}$$

$$\dot{E} = -\tfrac{1}{2}i\omega_E' H\,, \tag{95b}$$

$$\dot{G} = -\tfrac{1}{2}i\omega_g G = -\tfrac{1}{2}i(\omega_H + \omega_E)G\,. \tag{95c}$$

But $\dot{G} = \dot{H}E + H\dot{E}$, so eqn (94) can be put in the form

$$\omega_g' = 2i(H^{-1}\dot{H} + \dot{E}E^{-1})\,. \tag{96}$$

It is noteworthy that this equation in head space completely separates head and eye contributions to gaze shift, in contrast to

$$\omega_g = 2i\dot{G}G^{-1} = 2i(\dot{H}H^{-1} + HE^{-1}\dot{E}H^{-1})\,, \tag{97}$$

the corresponding equation in workspace.

Finally, because inner products like $\mathrm{g} \cdot \mathbf{d} = \mathrm{g}' \cdot \mathbf{d}'$ are invariant under a change of reference system, transformation of eqn (82) to head space yields

$$\omega_E' = \omega_H' + \frac{1}{r}\,\mathrm{g}' \times (H^{-1}\dot{\mathbf{x}}H) + \frac{1}{r}\,\mathrm{g}' \times (\mathbf{d}' \times \omega_H')\,. \tag{98}$$

Differentiation of eqn (92) with the help of eqn (95a) yields

$$H^{-1}\dot{\mathbf{x}}H = \dot{\mathbf{x}}' + \omega_H' \times \mathbf{x}'\,. \tag{99}$$

Inserting this into eqn (96), we obtain

$$\begin{aligned}\omega'_E &= -\frac{1}{r}\,\mathrm{g}' \times \dot{\mathbf{x}} - (\mathrm{g}' \cdot \omega'_H)\mathrm{g}' \\ &= \mathrm{g}' \times \dot{\mathrm{g}}' - (\mathrm{g}' \cdot \omega'_H)\mathrm{g}' \,. \end{aligned} \tag{100}$$

As remarked about eqn (86), this is nothing more than an equation for directly cancelling the observed retinal slip. It suggests that the optokinetic system might work by translating slip into gaze vector kinematics, as expressed by eqn (100). Of course, evaluation of $\dot{\mathrm{g}}'$ in terms of vestibular inputs takes eqn (100) back to eqn (98).

The eye attitude E represents the command that must be sent to the eye muscles to hold the gaze after smooth pursuit or compensatory rotation. It can be computed from inputs ω'_H and $H^{-1}\dot{\mathbf{x}}H$ by integrating eqn (95) with ω'_E given by eqn (98). However, as noted in the discussion of saccades, it is doubtful that the multiplicative structure required by the right side of eqn (95) exists in oculomotor neural networks. Rather, it is more likely that E is parametrized neurally by the gaze direction g', with compensatory torsion determined by integrating the last term on the right side of eqn (100). This is not the place to try resolving the issue. It is enough that the computational requirements for perfect compensatory eye motion and target pursuit have been set down in invariant form. Geometric algebra has the flexibility needed to analyze all computational possibilities systematically to discover which ones have been neurally implemented *in vivo*.

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