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On Listing's Law

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Dedicated to Res Jost and Arthur Wightman

Abstract. Listing's law states that visual directions of sight are related to rotations of the eye so that all rotation axes lie in a plane. The geometry of $SO(3)$ indicates several plausible algorithms how the human brain could relate vision to eye movements satisfying Listing's law, and suggests crucial experiments which we have carried out.

1. Introduction

Mathematical objects, like the quantum mechanical rotation group $SU(2)$, are intrinsically beautiful and "unreasonably efficient" in theories of our physical world. Both R. Jost and A.S. Wightman have made wonderful use of $SU(2)$ in their scientific work and teaching. Mathematicians often haven the Platonic attitude that objects like $SU(2)$ are ideas which exist independently of our material world. Neurobiologists see them more materialistically related to cortical activity patterns in the brains of ensembles of mathematicians and laid down in their published common knowledge. While the philosophical issue [1] is undecidable, a natural scientist can ask the more modest question, whether the $SU(2)$ is represented in our brain and, if so, whether in a given hardware implementation of the nervous system, as coarsely described by neuro-anatomy, geometry allows us to make experimentally refutable predictions about the operations of the human neural network.

The $SO(3)$ is intrinsically linked to our sensori-motor periphery. In the labyrinth of the inner ear, for instance, rotatory movements of the head induce flow patterns in 3 almost orthogonal semicircular canals, which at intermediate frequencies are transduced as head angular velocity. The $SO(3)$ also appears in the configuration space of our limbs and, in its purest form, in the kinematics of the eye.

The purpose of this note is to explain some simple geometrical ideas around Listing's law for eye movements and their relation to foveal vision and central visuo-oculomotor transformations in man. The geometry of $SU(2)$ suggests novel ways for interpreting neural activity in the brain in terms of parameters of the external world, which we are investigating in our laboratory. As an introduction to the neurophysiology of vision and eye movements we recommend recent reviews [2, 3, 4].

2. Kinematics of the Eye

In a good approximation the eye is a center-fixed sphere. We shall only consider conjugate eye movements with parallel lines of sight of both eyes, so that the $SO(3)$ is the configuration space of a "double eye." We choose a head-fixed right-handed orthonormal system with $\mathbf{e}_1$ in the frontal, $\mathbf{e}_2$ in the lateral and $\mathbf{e}_3$ in the upwards direction and an eye-fixed system $\mathbf{e}'_1, \mathbf{e}'_2, \mathbf{e}'_3$ with $\mathbf{e}'_1$ along the direction of sight. Every eye position is given by the rotation $R=(R_{ij})$ with $\mathbf{e}'_i=\Sigma\mathbf{e}_k R_{ki}$. Let $\mathbf{e}$ with $\|\mathbf{e}\|=1$ and $0 \leqq \varrho < \pi/2$ be the axis and angle of $R(\mathbf{e}, \varrho)$ by the right-hand rule, where we restrict ourselves to *foreward eye positions* as a simple neighborhood of the natural oculomotor range. In this range eye positions R are uniquely characterized by *rotation vectors* [5]

$$\mathbf{r}=\tan(\varrho/2)\mathbf{e} \ , \tag{1}$$

and also the product $R_1 R_2$ has this representation with

$$\mathbf{r}_1 \circ \mathbf{r}_2 = \frac{\mathbf{r}_1+\mathbf{r}_2+\mathbf{r}_1 \wedge \mathbf{r}_2}{1-\mathbf{r}_1 \cdot \mathbf{r}_2} \ . \tag{2}$$

Equation (2) follows from the local isomorphism between $SO(3)$ and $SU(2)$, given by $R(\mathbf{e}, \varrho) \leftrightarrow \cos(\varrho/2) - i\sin(\varrho/2)\Sigma e^i \sigma_i$, using the multiplication rules for the Pauli matrices σ_i. We shall always rely on this correspondence between $R(\mathbf{r})$ and $\mathbf{r}$.

Saccades are stereotyped rapid eye movements, which move the eye from R_1 to R_2 along a geodesic in $SO(3)$, i.e. with a fixed-axis rotation [6]

$$R(t)=R(\mathbf{e}, \varrho(t))R_1 \ , \tag{3}$$

where $\mathbf{e}$ is the axis and ϱ the angle of $R_2 R_1^{-1}$. The angular trajectory $\varrho(t)$ increases strictly from $\varrho(t_1)=0$ at the start t_1 to $\varrho(t_2)=\varrho$ at the end t_2 with bell-shaped velocity $\dot{\varrho}>0$ and an almost linear increase of duration t_2-t_1 with amplitude ϱ. The rotation vectors of saccades between forward eye positions are straight lines:

Lemma 1. *Let* $\|\mathbf{r}_1\|<1$ *and* $\|\mathbf{r}_2\|<1$. *Then the geodesic (3) between* R_1 *and* R_2 *has the form*

$$\mathbf{r}(t)=\mathbf{r}_1+\sigma(t)(\mathbf{r}_2-\mathbf{r}_1) \ , \tag{4}$$

where $\sigma(t_1)=0, \sigma(t_2)=1$ *and* $\dot{\sigma}(t)>0$ *otherwise.*

Proof. $R(\mathbf{e}, \varrho)$ has the rotation vector $\mathbf{r}_2 \circ (-\mathbf{r}_1)$, which multiplied by $\tau(t)=\varrho(t)/\varrho$ gives the rotation vector of $R(\mathbf{e}, \varrho(t))$. For t close to t_1 the latter can be composed with $\mathbf{r}_1$. Here the terms with $\mathbf{r}_1 \wedge \mathbf{r}_2$ cancel, and one obtains (4) with

$$\sigma(t)=\frac{\tau(t)(1+\|\mathbf{r}_1\|^2)}{1+\tau(t)\|\mathbf{r}_1\|^2+(1-\tau(t))\mathbf{r}_1 \cdot \mathbf{r}_2} \ . \tag{5}$$

Since for forward eye positions (5) is analytic in $0 \leqq \tau \leqq 1$, (4) follows by continuation in τ.

For an "axiomatic" derivation of Listing's law, which is a geometrization of data on visual after-images by Listing and Helmholtz [7], we take the experimental facts that during fixation the direction of sight determines uniquely the eye position (Donders law) and that the set of Donders points is invariant under saccades connecting them (*saccade invariance* [8, 9]). For concreteness we take the subset $V = \{\mathbf{s} : \|\mathbf{s}\| = 1, \mathbf{s} \cdot \mathbf{e}_1 > 1/\sqrt{2}\}$ as the head-fixed *visual saccade range*, which can be viewed by directing the eye towards it, such that $\mathbf{s}$ becomes the line of sight through the center of the pupil to the *fovea*, the highest acuity spot on the retina.

Lemma 2 (Listing). *Let* $\mathbf{s} \to \mathbf{e}_2'$ *be a map of the visual saccade range* V *onto forward eye positions* $\mathbf{e}_1' = \mathbf{s}, \mathbf{e}_2', \mathbf{e}_3' = \mathbf{e}_1' \wedge \mathbf{e}_2'$, *whose graph contains with any two positions the geodesic (3) between them. Then the corresponding rotation vectors lie in a plane through the origin, which satisfy in an adapted head-fixed frame*

$$\mathbf{r}(\mathbf{s}) \cdot \mathbf{e}_1 = 0 \ , \quad \mathbf{r}(\mathbf{e}_1) = \mathbf{0} \ . \tag{6}$$

– Helmholtz [7] has tried to prove Listing's law from Donders law without assuming saccade invariance and from a "principle of easiest orientation." Our elementary proof uses the fact that saccades as geodesics on $SO(3)$ (hence also characterized by an extremal principle) are straight lines in the Euler-Rodrigues coordinates (1).

– We shall call the saccade invariant set of Donders positions *Listing's positions*, the set of its rotation vectors (6) *Listing's plane* and the line of sight normal to it *primary direction*. In the monkey, the primary direction lies in good approximation in the symmetry plane of the head and in the plane of the horizontal semicircular canals [10]. This and a well-adapted geometrical arrangement of eye muscles [11] allows a very efficient generation of compensatory eye movements in response to head rotations, where the eye can move out of Listing's plane and make saccades with any axis of rotation.

– Also for visually evoked saccades in Listing's plane the brain matches sensory and motor coordinates in a very efficient way: When seeing a target at the direction $\mathbf{s}_2$ with the eye in Listing position $\mathbf{r}_1$, the components $s_{21}^k = \mathbf{s}_2 \cdot R(\mathbf{r}_1)\mathbf{e}_k$ are the coordinates of the target relative to the fovea, which are almost identical to the saccade vectors in (4):

Lemma 3. *Let* $\mathbf{s}_2$ *be a direction in space in the visual range* V *and* $\mathbf{s}_{21} = R(-\mathbf{r}_1)\mathbf{s}_2$. *Then the solution* $\mathbf{r}_2$ *of* $\mathbf{e}_1 \cdot \mathbf{r}_2 = 0$ *and* $R(\mathbf{r}_2)\mathbf{e}_1 = \mathbf{s}_2$ *is*

$$\mathbf{r}_2 = \mathbf{e}_1 \wedge \mathbf{s}_2/(1 + \mathbf{e}_1 \cdot \mathbf{s}_2) \ , \tag{7}$$

$$\mathbf{r}_2 - \mathbf{r}_1 = \mathbf{e}_1 \wedge \mathbf{s}_{21}/2 + O(\varrho^3) \tag{8}$$

up to cubic corrections in $\mathbf{r}_1$ *and* $\mathbf{r}_2$, *which introduce relative errors of less than.* 08 *in a visual and oculomotor range of* 25 deg.

Proof. We choose the head-fixed frame by taking $\mathbf{e}_2$ according to Donders law when $\mathbf{e}_1$ is the line of sight. For any 3 directions of sight $\mathbf{s}_1, \ldots \mathbf{s}_3$ the triangle with the corners $\mathbf{r}(\mathbf{s}_1),\ldots\mathbf{r}(\mathbf{s}_3)$ consists of Donders positions because of saccade invariance. Hence by a triangulation of V one shows that all Donders positions satisfy $\mathbf{r}\cdot\mathbf{n}=0$ for some unit vector $\mathbf{n}$. $\mathbf{e}_1$ is the primary position, if $\mathbf{e}_1=\mathbf{n}$, which can always be achieved by rotating the head-fixed system around $\mathbf{e}_1\wedge\mathbf{n}$ with twice the angle between $\mathbf{e}_1$ and $\mathbf{n}$ [5].

Obviously (7) is a Listing position. Using (1) and

$$R(\mathbf{e},\varrho)\mathbf{x}=(\mathbf{x}\cdot\mathbf{e})\mathbf{e}+\sin(\varrho)\mathbf{e}\wedge\mathbf{x}-\cos(\varrho)\mathbf{e}\wedge(\mathbf{e}\wedge\mathbf{x})\ , \tag{9}$$

one shows that $R(\mathbf{r}_2)\mathbf{e}_1=\mathbf{s}_2$. By expanding (9) up to $O(\varrho^3)$ one obtains for $k=1,2$,

$$\begin{aligned} s^k_{21}&=(R(\mathbf{r}_2)\mathbf{e}_1\cdot R(\mathbf{r}_1)\mathbf{e}_k)\\ &=2(\mathbf{r}_2-\mathbf{r}_1)\cdot(\mathbf{e}_k\wedge\mathbf{e}_1)+O(\varrho^3)\ , \end{aligned} \tag{10}$$

since $\mathbf{r}_1\cdot\mathbf{e}_1=\mathbf{r}_2\cdot\mathbf{e}_1=\mathbf{e}_1\cdot\mathbf{e}_k=0$. The *torsional* 1-component of $\mathbf{r}_2-\mathbf{r}_1$ is zero by Listing's law, while the vertical and horizontal components satisfy

$$r^2_2-r^2_1\approx -s^3_{21}\ ,\quad r^3_2-r^3_1\approx s^2_{21}\ . \tag{11}$$

In the visual and saccadic system the errors increase with the distance from the fovea and the saccadic amplitude. As a measure of the relative error ε in (8) we therefore take the quotient of the Euclidean distance of $\mathbf{r}_2-\mathbf{r}_1$ from $\mathbf{r}_{21}=\mathbf{e}_1\wedge\mathbf{s}_{21}/2$ (expressed in radians using $\varrho=2\arctan(\|\mathbf{r}\|)$) and the angle $\phi=\arccos(s^1_{21})$ between target direction and the direction of sight. In the periprimary range the linear approximation is very good: If ϕ and the angles of $\mathbf{r}_1$ and $\mathbf{r}_2$ are less than 15, 25, 30 deg, then $\varepsilon<0.025, 0.08, 0.12$, respectively.

3. On the Implementation of Listing's Law in the Brain

In the last section we have solved the computational problem how to generate a saccade from a Listing position $\mathbf{r}_1$ to a visual target in the direction $\mathbf{s}_2$ using the retinal error $\mathbf{s}_{21}$. The implementation of this algorithm in the brain depends on the "hard-ware" architecture of the central nervous system. In order to work out eyperimentally testable alternatives we shall briefly summarize some important findings (see [4]).

Lesion studies and the analysis of firing patterns of identified neuronal populations in the behaving monkey delineate the following main pathway for visually evoked saccades:

$$\mathrm{VIS}\rightarrow\mathrm{SC}\rightarrow\mathrm{RF}\rightarrow\mathrm{MN}\ . \tag{12}$$

VIS are visual and visuo-motor areas which transform images of "pixels" on the retina and select a target vector $\mathbf{s}_{21}$. The understanding of visuo-spatial operations in this distributed network is still incomplete, but rapidly progressing, and provides an interesting window through many high-level cortical and subcortical areas.

SC, the superior colliculus, carries a neuronal motor map which, when only the direction $\mathbf{e}'_1$ of the eye is recorded, seems to be topologically related to to retina: Microstimulation at a point P on the SC motor map elicits a saccade, by which the eye is driven from $\mathbf{r}_1$ to $\mathbf{r}_2=\mathbf{r}_1+\mathbf{d}$, where the saccade vector $\mathbf{d}$ appears to depend on P

but not on the initial eye position. In the same $2d$ analysis single neurons in SC in the neighborhood of P show an intense burst of activity preceding all visual saccades to $\mathbf{d}(P)$. Somehow idealized SC appears to have a $2d$ map of central pattern generators, where a network of neurons at P generates a saccade with vector $\mathbf{d}(P)$, either when stimulated by a retinal target at $\mathbf{d}(P)$ or after a small local current injection. These neurons carry an abstract motor command, in the sense that their firing generates a preprogrammed motor pattern, but the trajectory of the saccade (3) is not temporally encoded by the neural firing rate [12].

RF consists of several areas in the reticular formation, one for the generation of the horizontal and one for the vertical-torsional components of all visually- and head motion evoked $3d$ saccades. Here the present $3d$ analysis [13] has been made only in the linear approximation and therefore without quantifying the non-commutative aspects of $SO(3)$. Lesions in one of the specific subareas of RF permanently abolish the generation of the corresponding saccade components. By their firing pattern the local neurons are identified as *directed burst neurons*: they are silent except shortly before and during saccades, where the firing rate $f(t)$ is in a fair approximation a linear combination of the component of eye velocity $\dot{x}(t)$ and acceleration $\ddot{x}(t)$ in a direction $\mathbf{e}$ (which as the sensitivities λ and μ depends on the neuron):

$$f(t)=\lambda\dot{x}(t)+\mu\ddot{x}(t) \ . \tag{13}$$

Hence in the linear approximation the number of spikes in the burst

$$n=\int_{1}^{2} f(t)dt=\lambda(x(t_2)-x(t_1))\approx 2\lambda(\mathbf{r}_2-\mathbf{r}_1)\cdot\mathbf{e} \tag{14}$$

is proportional to the component of eye position change, since $\dot{x}(t_1)=\dot{x}(t_2)=0$.

MN are the motoneurons for the 12 eye muscles, which receive the saccadic eye velocity and acceleration input from RF. In addition, RF feeds into a reverberatory network INT, called the *position integrator*, which transforms as in (14) the eye velocity-acceleration input pattern into an eye position signal, which is needed by MN for holding the eye between saccades.

If one extends the mathematical analysis of Listing's law up to the first non-trivial non-abelian corrections (the best one can hope to measure with the present techniques in this highly nonlinear distributed system), (12) allows several alternative implementations:

- The motor map in SC can be either *retinal*, i.e. parametrized by

$$\mathbf{d}_{21}=\mathbf{r}_2-\mathbf{r}_1\approx\mathbf{e}_1\wedge\mathbf{s}_{21}/2 \ , \tag{15}$$

or *rotatory*, i.e. parametrized by

$$\mathbf{q}_{21}=\mathbf{r}_2\circ(-\mathbf{r}_1)\approx\mathbf{d}_{21}+\mathbf{r}_1\wedge\mathbf{r}_2 \ . \tag{16}$$

A retinal organization of the SC means that the visual saccades encoded by the command neurons form a $2d$ map without a torsional component. Stimulation at a point representing $\mathbf{d}$ on the retinal map with the eye at initial position $\mathbf{r}$ leads to $\mathbf{r}'=\mathbf{d}+\mathbf{r}$, and the eye displacement within the oculomotor range is always independent of the initial eye position. A second stimulation at $\mathbf{d}'$ drives the eye to $\mathbf{d}+\mathbf{d}'+\mathbf{r}$. Hence the stimulation induced eye rotation commands act commutatively and leave Listing's plane invariant.

A rotatory SC map has to be 3-dimensional, since for $\mathbf{r}_1$ and $\mathbf{r}_2$ in Listing's plane and not collinear $\mathbf{r}_1 \wedge \mathbf{r}_2$ is torsional. Therefore one should find command neurons in the SC, which fire with the highest rate when not only $\mathbf{r}_2-\mathbf{r}_1$ is close to a specific value but also $\mathbf{r}_1 \wedge \mathbf{r}_2$. Two consecutive SC stimulations at $\mathbf{q}$ and then at $\mathbf{q}'$ should drive the eye to $\mathbf{q}\circ\mathbf{r}$ and then to $\mathbf{q}\circ\mathbf{q}'\circ\mathbf{r}$. Since $\mathbf{q}\circ\mathbf{q}'-\mathbf{q}'\circ\mathbf{q}\approx 2\mathbf{q}\wedge\mathbf{q}'$, this action of $SO(3)$ is not commutative and does not preserve Listing's plane.

– Similary the velocity coding (13) of the directed burst neurons in RF can either be in terms of *coordinate velocity* $\dot{\mathbf{r}}$

$$f(t)=2(\lambda\dot{\mathbf{r}}(t)+\mu\ddot{\mathbf{r}}(t))\cdot\mathbf{e}\ , \tag{17}$$

or in terms of *angular velocity* $\boldsymbol{\Omega}$

$$f(t)=(\lambda\boldsymbol{\Omega}(t)+\mu\dot{\boldsymbol{\Omega}}(t))\cdot\mathbf{e}\ . \tag{18}$$

In the first alternative (14) holds, while otherwise the non-abelian relation

$$\boldsymbol{\Omega}=2(\dot{\mathbf{r}}+\mathbf{r}\wedge\dot{\mathbf{r}})/(1+\|\mathbf{r}\|^2) \tag{19}$$

implies for a fixed-axis rotation (3) $n\approx 2\lambda(\mathbf{r}_2-\mathbf{r}_1+\mathbf{r}_1\wedge\mathbf{r}_2)\cdot\mathbf{e}$. In this case a crucial experiment is to investigate (for neurons in the vertical-torsional area of RF with a not purely vertical on-direction) whether a linear fit of n relative to $\mathbf{d}\cdot\mathbf{e}$ or to $\mathbf{q}\cdot\mathbf{e}$ is better for $3d$ saccades in the neighborhood of Listing's plane with a fixed vertical and a variable torsional component.

The answer to these questions is important for understanding the neural operations along (12). A *quaternion model* has been proposed [14], in which Listing's law is implemented upstream between VIS and SC, in which the representation of visually-evoked saccades in SC is rotatory and where the firing rate of the directed burst neurons in RF is in terms of angular velocity. This introduces a number of nonlinear multiplicative feedbacks involving quaternion operations on the level of SC, RF and INT and necessitates neurons, whose firing patterns have never been observed. There is a much simpler *vector model*, which is an extension of [15]:

– With the eye in the Listing position $\mathbf{r}_1$ and the target in $\mathbf{s}_2$ VIS determines $\mathbf{s}_{21}$, which is linearly transformed by (15) into the SC address $\mathbf{d}_{21}$. For large saccades the $O(\varrho^3)$ error will be compensated by a small corrective saccade.

– The SC pattern generator at $\mathbf{d}_{21}$ generates the velocity pattern $\sigma(t)$ for the saccade (4), which is distributed linearly to burst neurons in RF with on-directions $\mathbf{e}$ via synaptic strengths proportional to $\mathbf{d}_{21}\cdot\mathbf{e}$.

– The velocity output of RF is linearly transformed by INT as in (14) into the new eye position $\mathbf{r}$ to be used by MN.

– If MN needs an eye velocity signal proportional to $\boldsymbol{\Omega}(t)$ (e.g. if the firing rate of the motoneurons is linearly related to the muscle contraction velocity and if the moment directions of the muscles are approximately constant [16]), then this signal is generated downstream of RF by a feedback circuit, which also adapts the central eye position signal **r** to the static requirements of each muscle.

The vector model can be extended to incorporate the pathway generating head-motion induced saccades and compensatory eye movements and feedback protecting visual saccades against perturbations. A second, direct pathway from VIS to RF via the frontal eye fields is of secondary importance in the normal monkey [17].

4. Conclusion

The purpose of this note was to show how geometrical ideas together with information from functional anatomy can lead to predictive models in neurophysiology. Our ideas about possibly observable second order effects related to a neural implementation of $SO(3)$ were the content of a paper submitted Spring 1989 to a neuroscience journal. Because of its mathematical "user unfriendliness" the article could not pass the referee, like a short Jost-to-Wightman note [18] in the good old days, where the Physical Review Letters were unresponsive to mathematical physics and neural networks.

In the meantime we have completed the crucial experiments with microstimulation of SC and the $3d$ analysis of neuronal firing patterns in SC and RF and have found in both structures strong evidence against the quaternion model and consistence with the vector model [17, 19]. In addition, we have studied Listing's law in humans for the rotatory degrees of the eye, head and arm in different reaching and grasping paradigms. In all three systems unconstrained movements in the configuration space $SO(3)$ are by neural control restricted to $2d$ planes in rotation vector coordinates, and the trajectories in these planes are often closely correlated [20], reducing the dimensionality of configuration space from 9 to 2 in the spirit of Bernstein's theory of synergistic control [21]. We expect that Listing's law and the geometry of $SO(3)$ will become an important tool to understand the neurodynamics of multidimensional sensori-motor systems [22].

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