

TENSOR NETWORK MODEL OF THE "THREE-NEURON VESTIBULO-OCULAR REFLEX-ARC" IN CAT

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Abstract

The "three-neuron vestibulo-ocular reflex-arc" represents a classic example of a basic sensorimotor transformation in the central nervous system. Nevertheless, hitherto no quantitative model has been forwarded to explain how the existing three-neuron network may accomplish this transformation. The present study, using tensor network theory, attempts to provide such a model by interpreting, in terms of neuronal networks, sensory analysis by projection-type (covariant) vectors, motor synthesis by parallelogram-type (contravariant) vectors, and representing sensorimotor integration by a covariant embedding of the sensory space into motor space and a transformation of the covariant intention to a contravariant execution by a metric-type network. The anatomical measurements of the sensory and motor reference frames of the vestibulo-ocular reflex provide the data necessary for a structurofunctional interpretation. This is accomplished here by a calculation of the neuronal network transformations in between these frames. All networks, when lumped together, were previously described by a single matrix. In contrast, by using the Moore-Penrose generalized inverse, tensor network theory can establish numerically exact predictions of neuronal connections even in case of an over-complete transformation from three vestibular canals to six extraocular muscles. This improvement aims to permit an interpretation of the morphologically known interim expression, in the vestibular nuclei, of the vestibulo-oculomotor signal. The networks here show other additional features: (a) a contracted vestibular tensor which combines a metric and a vestibulo-ocular covariant sensorimotor embedding transformation in order to approximate better the structural properties of this reflex-arc, and (b) a covariant motor metric tensor, which arises as the Moore-Penrose generalized inverse of the covariant motor metric tensor. Comparison of the calculated networks with experimental data appears to confirm the interpretation of sensorimotor transformations of intrinsic CNS coordinate systems by tensor network theory.

1. Introduction

1.1 Background of tensorial modeling of the vestibulo-ocular reflex

The neuronal network underlying the vestibulo-ocular reflex (VOR), which stabilizes the retinal image by compensating for head movements with an equal but opposite eye movement, has long been known to include a "three-neuron reflex-arc" (Lorente de Nò, 1933; Szentágothai, 1943). The classic three-neuron arc is involved in the actual chain of transformations from vestibular to extraocular muscle frames that are intrinsic to the CNS. Although an approach has been promulgated to interpret "the vestibulo-ocular reflex as a tensorial response" (Pellionisz and Llinás, 1980) a multidimensional quantitative model of the three-neuron vestibulo-ocular reflex has not been hitherto offered.

From the point of view of *external description*, this transformation was featured previously by a single "brain-stem matrix", lumping separate neuronal networks into one step (Robinson, 1982; Ezure and Graf, 1984b). The tensorial approach, as shown in Pellionisz (1985b), attempts to explain the overall function in terms of the *internal neuronal network-transformations of intrinsic CNS coordinates*. Two important differences inherent in this approach are (a) answering the question how the CNS may transform from sensory coordinate systems into motor coordinate systems that are *overcomplete* because they have a more than necessary number of coordinate-axes, (b) providing a quantitative structure-function explanation for separate morphological formations existing within the VOR, such as the vestibular and oculomotor nuclei. The presented tensorial approach proposes a solution for both problems; by explaining the sequence of sensorimotor transformations by contravariant sensory metric, covariant embedding, and a contravariant metric-type transformation invoking the Moore-Penrose generalized inverse (Pellionisz, 1984). The scheme has been quantitatively elaborated for the known sensory and motor frames of the vestibulo-ocular mechanism in man (Pellionisz, 1985b).

The present study was motivated by the aim of closing the gap between theoretical proposals and experimental findings. The system analysis approach to the VOR that flourished through the past decade concentrated on the characterization of the reflex in the *temporal domain*, but did not produce a multidimensional quantitative account of the morphological structure for spatial coordination. Thus, at the present stage of development the tensorial approach is focused, in a complementary manner, on morphology. We provide a quantitative account of how the multidimensional transformations may be implemented by existing neuronal networks. A theoretical foundation has already been established (Pellionisz and Llinás, 1982a) by which later analysis can lead to quantitative elaboration of space-time aspects of CNS sub-systems as soon as their structural features are confirmed.

In this paper, two major developments are described that extend beyond the earlier tensorial model of the human VOR (Pellionisz, 1985b). First of all, it is inevitable that a quantitative elaboration of the VOR is offered for species in which experimentation can test the model's predictions. Thus, we expand here the modeling from the human to the cat. Second, in the earlier study the Moore-Penrose generalized inverse was

proposed as a theoretical solution for the problem of overcompleteness encountered in VOR modeling. This solution is further elaborated in the present paper to the extent that the model's predictions closely correlate with existing structural features of the VOR and this match is discussed at length. The solution itself was necessary, since the motor system exhibits a higher number of dimensions (6) than the sensory (3), so the transformation is only *approximated* by a "brain-stem matrix" (i.e. requires inverting a singular matrix). The Moore-Penrose generalized inverse scheme yields a 3-step network. Since the anatomical reality suggests that the minimum number of neurons required in the chain of transformations is only three, we also emphasize the possibility that the sensory metric and the sensorimotor covariant embedding transformations are performed by the CNS in a single contracted step. Since this contraction may be implemented in the CNS in different ways, theoretical studies raise questions for ongoing experimentation as to how this transformation is performed (Graf *et al.*, 1986).

1.2 Background of multidimensional modeling of the vestibulo-ocular reflex

Although specific in nature, the present study is a continuation of a more general multidimensional approach that reaches back a century and a half. The basic underlying notion is that the CNS is a distributed, parallel system. Indeed, in the structure of the VOR there are separate sets of transformations from the set of the vestibular semicircular canals to the neurons in the vestibular nuclei and further, to those in the oculomotor nuclei. This fact well supports the fundamental view that this sensorimotor system is organized in a parallel, distributed manner. For the VOR, it has been known since the classical studies of Flourens (1828) that each of the extraocular muscles can be activated by each of the vestibular semicircular canals (see Helmholtz, 1896; Weiland, 1898; Lorente de Nò, 1932; Szentágothai, 1943, 1950; Cohen *et al.*, 1964). The parallel character of the neuronal network underlying the VOR, plus such specific features as the existence of a sequence of separate transformations and the overcompleteness have therefore confronted investigators with two basic questions: (1) how to deal quantitatively with such distributed overcomplete network transformations, (2) how to interpret functionally the two interim stations, the vestibular and oculomotor nuclei inserted between the sensory input from the labyrinth and the motor output in the extraocular apparatus.

In order to arrive at an answer suitable for a quantitative representation of a multi-variable sensorimotor apparatus such as the VOR, an appropriate conceptual and formal approach had to be developed. Multidimensional approaches have long been pioneered, conceptually by Lorente de Nò (1932, 1933), experimentally by Szentágothai (1943, 1950), and formally by Krewson (1950) and Westheimer (1957). More recently, a tensor approach has been elaborated for interpreting the structure and the function of the CNS in general (Pellionisz and Llinás, 1978, 1979a,b) and of the VOR in particular (Pellionisz and Llinás, 1980). Briefly, the concept that the CNS is organized in a parallel fashion is formalized by assuming its neuronal networks perform geometrical transformations on multidimensional activity-vectors expressed in coordinate systems that are intrinsic to the structure (e.g. in frames

composed of vestibular and extraocular muscle rotational axes). This formal analysis is based on the primary notion that the CNS expresses vectorial representations of external physical invariants (such as body movements) in these various general systems of coordinates with tensor-transformations between the frames via neuronal networks. The primary experimental goal in this multidimensional approach is, therefore, to reveal quantitatively the intrinsic frames of references. Secondly, one can then explore physiologically the activities expressed in these frames at different levels; e.g. neurons, muscle fibers, muscles, or joint structures. Morphological research, in turn, complements the effort by revealing the neuronal networks that specifically implement the underlying general vector transformations. As for modeling and theory, the task is to provide a quantitative conceptual interpretation of all the procured data.

Since the tensorial approach was introduced (Pellionisz and Llinàs, 1980), a number of papers have been published in oculomotor research that utilize one or several of the above conceptual, experimental and formal aspects (Schultheis and Robinson, 1981; Graf and Simpson, 1981; Simpson and Graf, 1981; Goldberg *et al.*, 1982; Robinson, 1982; Simpson, 1983; Ezure and Graf, 1984a,b; Peterson *et al.*, 1984; Graf *et al.*, 1983). The tensorial approach provides for a formal treatment of non-orthogonal intrinsic coordinates (e.g. distinguishes covariant and contravariant expressions), and thus emphasizes not an external description but attempts to explain how function emerges from actual neuronal networks. As such, tensor notation can be employed to model structural properties (e.g. the overcompleteness) of the VOR, and provide an exact quantitative solution to the problem of coordination in case of such overcomplete sensorimotor mechanisms.

The present paper is aimed specifically at interpreting the vestibulo-ocular apparatus as a "three-neuron reflex-arc" in a morphologically realistic manner with regard to spatial coordination of compensatory eye movements. The analysis is based on the distinction of covariant sensory and contravariant motor expressions (Pellionisz and Llinàs, 1980). Methodologically, it utilizes the three-stage general scheme of sensorimotor coordination, employing the Moore-Penrose generalized inverse of the covariant metric tensor (Pellionisz, 1983a,b). Mathematically, the problem of motor coordination (i.e. transformation in the *overcomplete* sensorimotor systems, such as the VOR) is treated tensorially as a covariant-contravariant eigen-vector-problem, through the generalized inverse of the covariant metric tensor (Pellionisz, 1984, 1985b). As for the structure of the neuronal network, the precursor to the present study is the tensor model of the three-neuron arc of the vestibulo-collic (neck-motor) reflex (Pellionisz, 1985a, Pellionisz and Peterson, 1985). Quantitatively, the present paper is based on the experimental establishment of the intrinsic frames of reference inherent in the sensory and motor mechanisms (Blanks *et al.*, 1972; Ezure and Graf, 1984a, respectively). Brief preliminary reports on this study have been presented in Graf and Pellionisz (1985) and Pellionisz (1985c).

2. Tensor network model of the "Three-neuron vestibulo-ocular reflex-arc" in cat

2.1 Extrinsic and intrinsic systems of coordinates in the VOR

When relating CNS function to physical entities external to the living organism, the complex multivariable relationships of sensory and motor components can conveniently and concisely be given in *systems of coordinates*. Such frames can either be selected by Nature or by her investigators (Simpson and Graf, 1985).

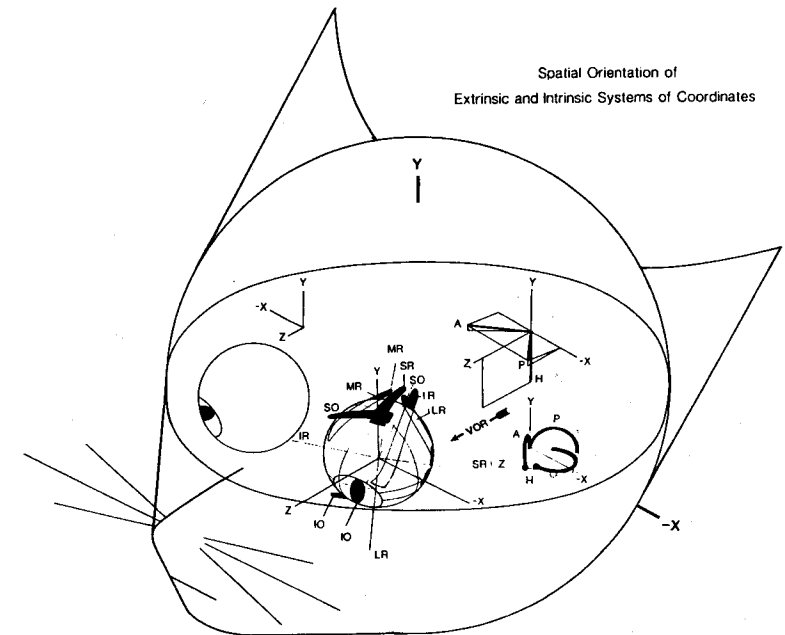


Fig. 1. Spatial orientation of the vestibular and oculomotor intrinsic coordinates in the cat. Two kinds of coordinate systems are shown: one is used for external description, the other one is intrinsic to the VOR. The extrinsic system is selected here as a body-symmetrical Cartesian three-dimensional orthogonal frame with medial (X), dorsal (Y) and anterior axes (Z). The intrinsic systems of coordinates are expressed in this XYZ extrinsic frame for both the sensory and motor apparatus by means of the rotational axes belonging to the horizontal (H), anterior (A) and posterior (P) semicircular canals and to the lateral rectus (LR), medial rectus (MR), superior rectus (SR), inferior rectus (IR), superior oblique (SO) and interior oblique (IO) extraocular muscles. The set of paired vestibular canals is shown displaying the semicircular canals and their rotational axes. The diagram of the eye muscle orientation is drawn utilizing a computer model (Ostriker *et al.*, 1985).

Investigators customarily use coordinate systems for the oculomotor apparatus and the vestibular sensory mechanism like the XYZ Cartesian orthogonal systems of coordinates shown in Fig. 1. This choice of a particular extrinsic frame is based simply on familiarity with this most commonly used reference frame. In this paper, extrinsic representation employs two orthogonal XYZ frames for each side of the body, with right-hand and left-hand rules for the respective sides. An advantage of this convention is that all XYZ data are identical for both sides, positive XYZ denoting medial, dorsal and anterior directions, respectively. The head is positioned in a manner that the XZ plane is aligned with the paired horizontal vestibular canals (cf. Fig. 2 and the original data-sources by Blanks *et al.* (1972) for the vestibular canals and for the extraocular muscles by Ezure and Graf (1984a). In this model, data are used for the *paired* set of vestibular canals, similarly as in Robinson (1982).

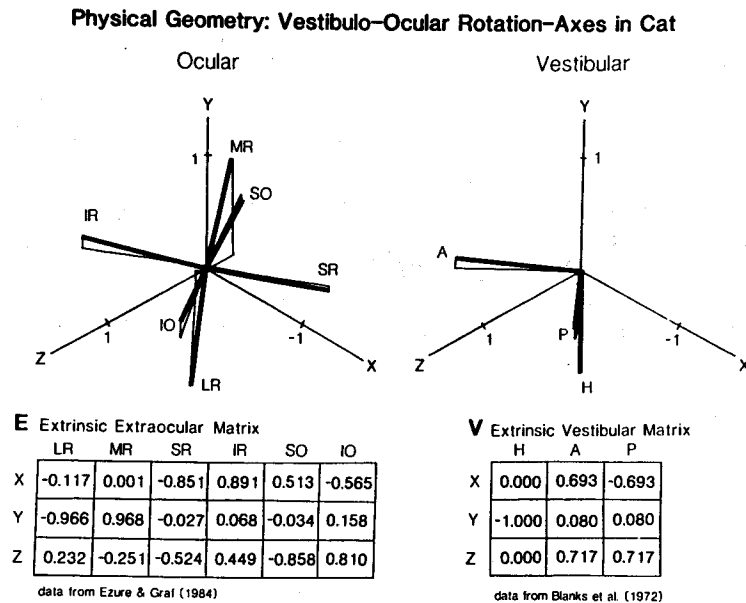


Fig. 2. Data source for the physical geometry of the sensory and motor systems of coordinates intrinsic in the VOR. The rotational axes around which the individual extraocular muscles turn the eye are displayed in the form of an eye-matrix (E), data by Ezure and Graf (1984a). The rotational axes around which the vestibular semicircular canals measure head-movement are denoted by A (belonging to the *paired* coplanar ipsilateral anterior — contralateral posterior canals), by P (belonging to the ipsilateral posterior — contralateral anterior canals), and by H (belonging to the bilateral horizontal canals). Data by Blanks *et al.* (1972) are shown as a vestibular matrix V. The orientation of the head was chosen in the original anatomical studies to align the XZ plane with the plane of paired horizontal canals.

The spatial orientation of the eye muscles is shown schematically in Fig. 1 by means of a computer model display (Ostriker *et al.*, 1985). The sensory and motor axes are also presented in Fig. 2, where normalized Cartesian vector components of each rotational axis are tabulated, and the intrinsic three dimensional sensory and six dimensional motor frames of reference are visualized.

As can be observed in Figs. 1–2, the intrinsic sensorimotor axes in cat are not too far from an orthogonal arrangement. However, for an understanding of sensorimotor mechanisms in general, solutions need to be considered first that are independent of the orthogonality or non-orthogonality of the coordinate axes. Then, the advantages that arise from approaching throughout evolution these special arrangements such as orthogonality or minimum-completeness could be revealed.

2.2 Tensorial scheme of the VOR

The fundamental task is to reveal how sequential parallel networks of the “three-neuron reflex-arc” transform a head rotation, given by a sensory reception vector, expressed in the intrinsic sensory frame (Fig. 2V), into a motor execution vector expressed in the intrinsic motor frame (Fig. 2E). In this transfer, the frame changes from sensory to motor. It is equally important, however, that the type of vector used in these different expressions also changes. The sensory vector is covariant (each canal independently measures a cosine component of the head-movement), while the motor vector is contravariant (eye movement produced by the interdependent action of muscles is the physical resultant of the components). Transformations changing both the frame and the type of vectorial expression can be implemented according to a basic tensorial scheme (Pellionisz, 1985c). This interpretation is based on the fact that a “reference-frame-free” physical invariant that is extrinsic to the CNS can be represented by neuronal activity-vectors in both co- and contravariant forms in both the sensory and motor frames. Thus, four different basic vectorial expressions are possible, and between them three tensor transformations may exist, expressed by network-matrices. These are the (a) vestibular metric tensor, transforming covariant sensory reception into contravariant sensory perception, (b) sensorimotor covariant embedding, yielding an intention-type (covariant) expression in the motor frame and (c) motor metric-type transformations, yielding the contravariant (executable) counterpart of the motor intention vector. These transformations have been shown in general abstract tensor notation, in quantitative matrix expression, and in neuronal network implementation for the VOR in man (Pellionisz, 1985b). The present study follows that treatment in its principles and procedures, with two main differences here; (a) this model is worked out for an experimentally accessible species, the *cat*, and (b) a multidimensional interpretation is provided for the *three-neuron reflex-arc*.

The first expression of the external physical invariant (a movement) in natural intrinsic coordinates occurs in the primary vestibular neurons connected to the semicircular canals. This is a physically obvious *covariant* vectorial representation, given in the vestibular frame of horizontal, anterior and posterior canal axes (H,A,P, respectively). At the effector part of the VOR system, the compensatory eye movement emerges as the physical resultant of six extraocular eye muscle contractions.

Thus, the motor output is a *contravariant* vectorial expression. The question is how the CNS produces the contravariant six-component vector from the covariant three-component vector. This is a *general biological problem* of coordination. This paper focuses on the *morphological problem* of how existing "reflex-arcs" in the CNS actually perform a sequence of network-transformations. From a theoretical viewpoint, the transformation can also be viewed as a *mathematical problem* of how tensorial expressions can be obtained in an overcomplete space (i.e. in more than the three dimensions for physical movements).

The earlier general elaboration (Pellionisz, 1985b,c) utilized two interim vectors; the contravariant expression of the invariant in the sensory frame (sensory perception), and the covariant expression in the motor frame (motor intention). The first of three necessary transformations to obtain these expressions is a contravariant sensory metric g^p . This step transforms a covariant expression of sensory *reception* into contravariant sensory *perception*, both expressed in the same sensory frame. The last step is a motor metric-type transformation g^{ie} which provides a similar conversion of motor *intention* to motor *execution* in motor space. The sensorimotor transformation in between these two metric-type conversions is a covariant embedding c_{ip} , that transforms a contravariant sensory perception into a covariant motor intention. In this paper, the possibility is explored that the CNS may employ a *contracted vestibular tensor* (the matrix-product of the contravariant vestibular metric and vestibulo-ocular embedding) in a one-step operation. Such scheme, together with a separate oculomotor metric transformation yields a two-step operation, observed in the morphological representation of the VOR as the "three-neuron" reflex arc.

2.2.1 Vestibular tensor: transformation from covariant sensory to covariant motor expression

The vestibular metric g_{rp} can be directly calculated following the definition of a covariant sensory metric tensor:

$$g_{rp} = \cos(\alpha_{rp})$$

The *contravariant vestibular metric* g^{rp} can be calculated by inverting the covariant vestibular metric:

$$g^{rp} = (g_{rp})^{-1}$$

The numerical components of this contravariant metric, as calculated from the covariant vestibular metric shown in Fig. 3A, are presented in Fig. 3B.

The *sensorimotor covariant embedding* transformation c_{ip} is a necessary step, since in any sensorimotor system a neuronal network converts the expression of the external physical invariant in a *sensory* frame into another expression given in a *motor* frame. For an understanding of the nature of sensorimotor integration, an exact explanation must be provided of how such a transformation may occur in the CNS. An advantage of the proposed sensory- to motor transformation is that it may be

Contracted Vestibular Tensor in Cat

A Covariant Vestibular Metric

$$g_{rp} = \cos(\alpha_{rp}) = \begin{bmatrix} 1.000 & -0.080 & -0.080 \\ -0.080 & 1.000 & 0.040 \\ -0.080 & 0.040 & 1.000 \end{bmatrix}$$

B Contravariant Vestibular Metric

$$g^{rp} = (g_{rp})^{-1} = \begin{bmatrix} 1.011 & 0.077 & 0.079 \\ 0.077 & 1.007 & -0.034 \\ 0.079 & -0.034 & 1.009 \end{bmatrix}$$

C Vestibulo-Ocular Embedding

$$c_{ip} = \cos(\alpha(m_{is}^p)) = \begin{bmatrix} 0.966 & 0.080 & 0.170 \\ -0.968 & -0.102 & -0.103 \\ 0.027 & -0.968 & 0.212 \\ -0.068 & 0.945 & -0.290 \\ 0.034 & -0.262 & -0.973 \\ -0.158 & 0.202 & 0.985 \end{bmatrix}$$

D Contracted Vestibular Tensor

$$v_i^r = g^{rp} \cdot c_{ip} = \begin{array}{c} \begin{matrix} & H & A & P \\ LR_v & 0.991 & 0.080 & 0.248 \\ MR_v & -0.995 & -0.174 & -0.177 \\ SR_v & -0.030 & -0.980 & 0.249 \\ IR_v & -0.019 & 0.956 & -0.330 \\ SO_v & -0.063 & -0.228 & -0.970 \\ IO_v & -0.066 & 0.158 & 0.975 \end{matrix} \end{array}$$

Fig. 3. Vestibular tensors, yielding a contracted vestibular tensor in cat. A: Covariant metric tensor, expressing the cosine components of the rotational axes of the semicircular canals. B: Contravariant sensory metric, calculated as the inverse of the covariant metric. C: Sensorimotor transformation tensor, its matrix calculated by the covariant embedding procedure, which yields the cosine components of the respective axes of the sensory- and motor frame of reference. D: Single vestibular tensor, contracted as the matrix product of the contravariant vestibular metric (B) and the vestibulo-ocular embedding (C). Note, that the contracted vestibular tensor yields its output to the second order vestibular neurons in the vestibular nuclei. This is reflected by using muscle designators in D marked with a subscript v: (LR_v . . . IO_v), to denote covariant output of the vestibular tensor. Calculations presented in this Figure (and throughout the paper) were performed by the computer for 7 digits. Results, however, are shown rounded for three; thus verification of the matrix-products based on rounded data would be imprecise.

performed from any i to any j dimensional frame of reference (including j greater than i). The operation can be implemented by a neuronal network where the input-output connections correspond to the cosines of the angles between the axes of the *sensory* frame (in which *perception* is expressed) and the axes of *motor* frame (in which the *intention* is expressed):

$$c_{ip} = \cos(\alpha(m_{is}^p))$$

The matrix of vestibulo-ocular covariant embedding tensor is presented in Fig. 3C and the contracted vestibular metric- and sensorimotor embedding (yielding a single vestibular tensor) is tabulated in Fig. 3D.

Several prominent features of the contracted vestibular tensor are noteworthy. First, it provides with a quantitative prediction of a set of connectivities between vestibular canals and secondary vestibular neurons. This may open the way to directly relating experimental data on single cells to theoretical models. Second, as seen in Fig. 3, the vestibular tensor can be calculated even in case of overcompleteness (with a higher number of secondary than primary vestibular neurons). Third, one wishes to emphasize that if one contracted *all* transformations into a single brainstem matrix (Robinson, 1982), then it would not conform to morphological observations, since the transformation does not appear to occur in one step (cf. Baker *et al.*, 1981). By contrast, the contraction employed here yields the morphologically long-established network of the three-neuron reflex-arc (Lorente de Nò, 1933; Szentágothai, 1943, 1952). Fourth, this representation is capable of interpreting morphological and physiological findings reporting on a certain degree of convergence on single neurons in the vestibular nuclei from several different canals. The issue of the degree of convergence is presently far from being completely settled and it also appears uncertain if the found convergences are established by mono- or polysynaptic connections (cf. Markham and Curthoys, 1972; Baker *et al.*, 1983; Kasahara and Uchino, 1974; Precht, 1979a,b; Graf *et al.*, 1986). Nevertheless, a clarification of these problems would remain difficult without such theoretical and modeling approaches that are capable of handling such convergences and can also result in specific predictions of both their site and extent (Figs 3, 5). Fifth, the contracted vestibular tensor is a prominent example of the fact that while tensor network theory is based on the distinction of covariant and contravariant expressions assigned to invariants, some entities as the vestibular tensor are neither covariant nor contravariant but mixed. Finally, it is mentioned here (and will be elaborated in the Discussion) that the contraction of two of the three operations in the tensorial scheme of sensorimotor transformation can be obtained in an alternative manner, by contracting not the first and second but the second and third steps (cf. Graf *et al.*, 1983; Graf and Ezure, 1986).

The vestibular tensor employed the covariant embedding procedure, which yields a vectorial expression of the invariant in the required motor space. However, it is given in a *covariant* form, which would result, if physically executed, an *improperly* synthesized invariant with erroneous amplitude and direction. Therefore, the covariant sensorimotor embedding procedure necessitates a final contravariant motor metric tensor-type transformation (Pellionisz and Llinás, 1980, 1982a).

2.2.2 Oculomotor tensor: covariant- to contravariant motor transformation

Given a motor frame of reference, embodied in the six rotational axes corresponding to the contraction of individual eye muscles, the *existence* of both co- and contravariant-type expressions of an invariant can be verified in the following manner. Given a six-component vector of the firing of six pools of motoneurons, the *physical sum* of the ensuing eye-muscle contractions will result in an eye movement. Such a motoneuron vector is, therefore, contravariant. In turn, the set of orthogonal projections, which are drawn from the physical object of the emerging eye-movement to the axes of the motor frame, will uniquely determine six covariant vector com-

ponents. Since both a covariant and a contravariant expression exist for an invariant even if the frame of reference is overcomplete, the remaining question is *how to establish their relationship*.

The principles of covariant- to contravariant transformation. Interpretation of the covariant motor intention to contravariant oculomotor execution transformation is based on the following argument. The process of rendering a covariant to each contravariant in a unique manner determines pairs of vectors (the eigenvectors), where the two expressions are identical, except for scaling by constants (the eigenvalues). The unique Moore-Penrose generalized inverse matrix that performs the required covariant- to contravariant transformation can be established from the eigenvectors and eigenvalues (for general principles see Albert, 1972; Ben-Israel and Greville, 1980; for elaboration see Pellionisz, 1984, 1985b).

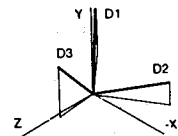
Oculomotor Tensor in Cat Moore-Penrose Generalized Inverse of the Covariant Metric

A Covariant Oculomotor Metric $g_{ie} = \cos(\alpha_{ie})$ B Eigenvectors of the Oculomotor Tensor(s)

$$g_{ie} = \begin{bmatrix} 1.000 & -0.933 & 0.004 & -0.066 & -0.226 & 0.101 \\ -0.993 & 1.000 & 0.105 & -0.046 & 0.183 & -0.051 \\ 0.004 & 0.105 & 1.000 & -0.995 & 0.014 & 0.052 \\ -0.066 & -0.046 & -0.995 & 1.000 & 0.070 & -0.129 \\ -0.226 & 0.183 & 0.014 & 0.070 & 1.000 & -0.990 \\ 0.101 & -0.051 & 0.052 & -0.129 & -0.990 & 1.000 \end{bmatrix}$$

	E1	E2	E3
LR	-0.490	-0.230	-0.452
MR	0.456	0.304	0.447
SR	-0.107	0.653	-0.250
IR	0.168	-0.644	0.236
SO	0.528	-0.037	-0.463
IO	-0.482	0.111	0.514
L	2.292	2.035	1.674

C Contravariant Oculomotor Tensor $g^{ie} = (g_{ie})^+ = \sum_m (1/L_m) \cdot (E_m > E_m)$

$$g^{ie} = \begin{bmatrix} 0.253 & -0.253 & 0.017 & -0.027 & 0.016 & -0.048 \\ -0.253 & 0.256 & 0.009 & 0.000 & -0.024 & 0.058 \\ 0.017 & 0.009 & 0.252 & -0.250 & 0.032 & -0.018 \\ -0.027 & 0.000 & -0.250 & 0.249 & -0.015 & 0.002 \\ 0.016 & -0.024 & 0.032 & -0.015 & 0.250 & -0.255 \\ -0.048 & 0.058 & -0.018 & 0.002 & -0.255 & 0.265 \end{bmatrix}$$


	D1	D2	D3
X	0.842	-1.184	-0.052
Y	0.835	0.474	0.989
Z	-0.941	-0.639	0.832

Fig. 4. Oculomotor tensor in cat arising as the Moore-Penrose generalized inverse of the covariant motor metric. A: Covariant motor metric tensor, composed of the cosines of the angles among the rotational axes belonging to individual eye muscles. B: Eigenvectors (E) and corresponding eigenvalues (L) of the covariant oculomotor metric as shown in A. The physical directions, belonging to these eigenvectors ("oculomotor eigendirections: D") are shown in the bottom part of B. C: Contravariant oculomotor metric-type transformation matrix, which converts the covariant motor intention vectors into contravariant motor execution vectors. The matrix of g^{ie} is composed of the dyads of eigenvectors of g_{ie} , with coefficients that are the inverses of each corresponding eigenvalue.

The covariant oculomotor metric tensor g_{ie} can be expressed in a unique manner since its elements are the cosines of the angles among the axes:

$$g_{ie} = \cos(\alpha_{ie})$$

This matrix, as shown in Fig. 4A, is both real-valued and symmetric. A difficulty arises, however, if one attempts to calculate the contravariant metric by inverting the covariant metric g_{ie} . This could be done if the manifold was Riemannian, and thus tensor analysis were applicable in the form used in the mathematics of general relativity. However, in the multidimensional spaces that govern overcomplete systems of coordinates in the CNS, the covariant metric is singular. Therefore, although mathematical means exist that describe particular solutions among the infinite possible transformations from a covariant set into a set of contravariant components, a unique solution cannot be identified by simply inverting this singular covariant metric. The problem does not lie with assigning the covariant components to an invariant, since this is a unique procedure in the sensory frame. The difficulty arises in the motor apparatus, because the invariant can physically be assembled in an infinite number of different combinations of contravariant components, as was recognized for eye movements as early as 1898 by Weiland. In tensor network theory a solution to this uniqueness problem was suggested by hypothesizing that in overcomplete multidimensional hyperspaces of the CNS the covariant-contravariant transformation is implemented by the Moore-Penrose generalized inverse of the covariant metric tensor (Pellionisz, 1983a,b, 1984). The proposal of employing this constraint in order to arrive at a unique covariant-contravariant transformation is supported by a set of four considerations, predicated upon the fact that mathematical explanations of CNS function must include a demonstration that the suggested operations can, indeed, be done by the existing neuronal apparatus in the CNS.

First, the constraint provided by this generalized inverse yields not only a unique, but also an advantageous vectorial expression in which the sum of the squares of the components is minimal (it is a so-called least-squares solution, cf. Albert, 1972). Such expression of the movement, requiring minimum-energy, is a potentially advantageous feature for the CNS. Second, the Moore-Penrose generalized inverse is not only both a feasible and an advantageous solution of the overcompleteness-problem in the CNS, but also recent quantitative experimental evidence demonstrates that it appears, in fact, to be utilized in motor processes such as in the coordination of human forelimb-muscles (Gielen and Zuylen, 1986) or of the neck-muscles in cat (Peterson *et al.*, 1985). Thirdly, as elaborated elsewhere (Pellionisz and Llinás, 1985), tensor network theory demonstrates that the components necessary for constructing the Moore-Penrose generalized inverse (i.e. the eigenvectors of the motor system) can be made available in the CNS by the physical means of oscillatory reverberations. And fourthly, the proposed process of Metaorganization also explains how the CNS may use these eigenvectors to develop and modify a neuronal network that implements the Moore-Penrose inverse transformation (Pellionisz and Llinás, 1985).

The quantitative establishment of covariant- to contravariant transformation. Since the proposed approach is based on the preservation of eigenvectors of the overcom-

plete covariant-contravariant system, these eigenvectors and eigenvalues of the motor frame must be established first. Any of the standard available means for calculating the eigenvectors produces the results tabulated in Fig. 4B. These eigenvectors are expressed by their intrinsic (oculomotor) components (E_1, E_2, E_3), and they are also given in the XYZ Cartesian components (D_1, D_2, D_3).

Given that the contravariant-to-covariant relation is established by the covariant metric tensor (transforming an eigenvector into an eigenvector *magnified* by an eigenvalue), the contravariant metric-type transformation is expected to change the same covariant eigenvector into a contravariant one *reduced* by the same eigenvalue. This solution leads to the Moore-Penrose generalized inverse (denoted by symbol $^+$) of the covariant metric, which yields the required matrix:

$$g^{ie} = (g_{ie})^+ = \sum_m (1/L_m) \cdot (E_m > < E_m)$$

where L_m and E_m are the m -th eigenvalue and eigenvector, $1/L_m$ is taken as 0 if $L_m = 0$, and symbol $> <$ denotes the dyadic (outer) product of the latter (in detail in Pellionisz and Llinás, 1985). The resulting contravariant oculomotor tensor is presented in Fig. 4C.

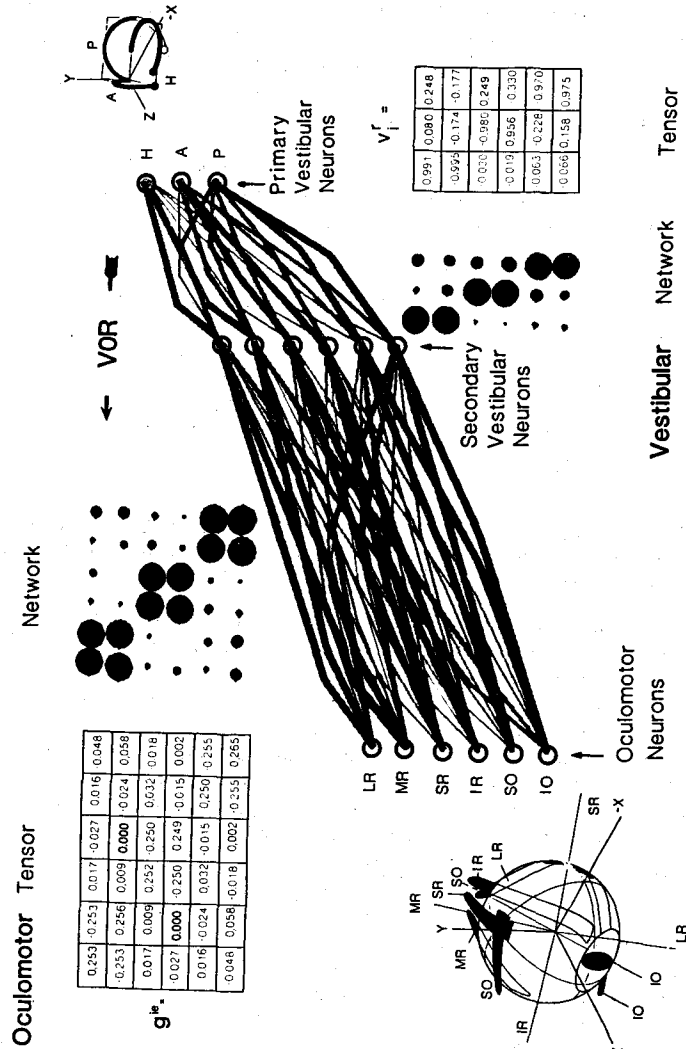
2.3 A tensorial blueprint of the transformation-networks accomplishing an overcomplete VOR function via an interim station at the vestibular nuclei; yielding a model of the "three-neuron reflex-arc"

The chain of VOR transformations is complete, after having determined the oculomotor tensor g^{ie} implementing the covariant- to contravariant motor transformation together with the contracted vestibular tensor v_i^j , as shown in Fig. 5.

The presented network model of the sensorimotor transformation accomplishes the goals set in the Introduction. The model utilizes non-orthogonal intrinsic frames of reference and converts a three-dimensional sensory input vector into an overcomplete six-dimensional motor output vector. The required interim expression corresponds to the morphological facts that the VOR pathways do not constitute a single "brain-stem matrix", but form distinct parts with specific structural and functional properties (cf. Lorente de Nò, 1933).

The tensor network model presented in Fig. 5 comprises several levels of abstraction, describing the three-neuron vestibulo-ocular reflex-arc (a) verbally, as a contracted vestibular tensor-transformation followed by an oculomotor transformation, (b) by abstract tensor notation, defining v_i^j and g^{ie} , (c) numerically, by matrices calculated for the specific rotational axes in cat, established by experimental data from the sensory and motor periphery (Ezure and Graf, 1984a; Blanks *et al.*, 1972), (d) graphically, by patch-diagrams of the matrices, in order to facilitate visualization (the area of each patch is proportional to the corresponding matrix element), (e) by a network-representation of the tensor-transformation, where positive and negative matrix components may be realized by excitatory (red) and inhibitory (blue)

Tensor Network Model of the "Three-Neuron Vestibulo-Ocular Reflex-Arc" in Cat



pathways. Note that in this model the vestibular semicircular canals were paired (cf. Robinson, 1982). As a result, if for one paired connection between a primary and secondary vestibular neuron the balance of monosynaptic excitatory (ipsilateral) and polysynaptic inhibitory (contralateral) signals is negative, that particular path appears in the present concise model as a monosynaptic inhibitory connection.

3. Discussion

In complementing experimental analysis with theoretical synthesis the most important question is whether there is *any* model that can account for the set of available data. Once there is a quantitative three-neuron reflex-arc model, a further question is how well its predictions agree with existing experimental data. The following discussion compares experimentally established vestibulo-ocular reflex connections, including the three-neuron-arc, to our theoretical predictions of the vestibulo-oculomotor projections. VOR calculations are based on the assumption that eye movements are fully compensatory along all three degrees of freedom of an eye movement.

3.1 Comparison of data and predictions at the level of distributed networks

Relating the model shown in Fig. 5 to data is convenient at several different levels. The tensorial method of calculating the sensorimotor transformation matrices enables a quantitative prediction of both the first neuronal network (from the labyrinth to the vestibular nuclei monosynaptically; vestibular tensor v_{ij}^j , Fig. 3D) and the second set of connectivities (from the vestibular nuclei to the motoneurons in the oculomotor nuclei; the oculomotor tensor g^{ie} , Fig. 4C). Therefore, the most thorough comparison would be to relate directly the quantitative electrophysiological and morphological data of these two (vestibular and oculomotor) subsystems to the model's predictions. There are, however, several problems that preclude complete verification at this junction, partly the incompleteness of the available data-set, partly its theoretical consequence that the possibility cannot be excluded that the CNS employs a tensor-contraction that is different from the one favoured and elaborated

Fig. 5. Tensor network model of the "three-neuron vestibulo-ocular reflex-arc" in cat. The H,A,P vestibular semicircular canals are connected to the LR,MR,SR,IR,SO,IO extraocular muscles by a neuronal network through the vestibular nuclei. The first part of this "three-neuron-arc" is the connection from primary vestibular neurons to secondary vestibular neurons. The necessary transformations are given by the vestibular and oculomotor tensors, explained (a) verbally, (b) in abstract tensor formalism as v_{ij}^j and g^{ie} , (c) by their numerical components in the form of two matrices, (d) pictorially, in the form of a "patch diagram" (positive and negative numbers in red and blue), (e) by a schematic, yet quantitatively exact network representation, where the connections between input and output neurons appear as path-bundles. Color and cross section of each line correspond to the respective matrix components: The diameter of each connecting line is proportional to the cross-section of neuronal bundles shown in the patch-diagram. For an enhanced visual perception, patch diagrams are enlarged four times compared to the diameters in the network, and the vestibular system is shown with four times heavier lines than the oculomotor network.

n this paper. In the present model, contraction of two of the three theoretically required VOR transformations (cf. Pellionisz, 1985b) is implemented by combining the first two matrices as shown in Fig. 5: $B^{cr} = g^{ie} \cdot (c_{ip} \cdot g^{pp})$. However, another expression yields the same overall result if the last two transformations are contracted: $B^{cr} = (g^{ie} \cdot c_{ip}) \cdot g^{pp}$. Given the fact that all three matrices of the right side of this equation are presented in Figs. 3–4, the alternative transformation-tensors can be asily expressed. The alternative vestibular tensor (instead of V_i') would be g^{pp} itself, exactly as shown in Fig. 3B, thus the numerical values of the components of this matrix are not repeated here. The alternative oculomotor tensor (instead of g^{ie}) would be the contraction of vestibulo-oculomotor embedding (c_{ip} , shown in Fig. 3C) and contravariant oculomotor tensor (g^{ie} , shown in Fig. 4C). The resulting product is

$$g^{ie} \cdot c_{ip} = \begin{pmatrix} 0.500 & -0.207 & 0.017 \\ -0.502 & -0.020 & 0.014 \\ 0.034 & -0.491 & 0.079 \\ -0.050 & 0.479 & -0.115 \\ 0.090 & -0.158 & -0.479 \\ -0.154 & 0.132 & 0.492 \end{pmatrix}$$

In this alternative case the vestibular metric appears as a matrix closer to a ronecker-delta (diagonal) matrix (cf. g^{pp} in Fig. 3B), indicating that the required coordinate-transformation would predominantly be implemented in between the vestibular nuclei and the oculomotor neurons. This possibility would be somewhat different from the other case shown in this paper, where $(c_{ip} \cdot g^{pp})$ yields a rather heavy lot of off-diagonal cross-connections between the primary and secondary vestibular neurons (see v_i' , Fig. 3D). Resolving which tensor contraction is employed in the CNS depends on further experimental investigation to settle the presently open issue of the magnitude of such cross-connections (see e.g. Graf *et al.*, 1986). Teleological reasoning postulates no convergence from primary vestibular neurons of various semicircular canals onto single secondary vestibular neurons (Robinson, 1982), and in some species such convergences have not been found (Kasahara and Uchino, 1974; Reisine and Henn, 1984). On the other hand, labyrinthine convergence, although not necessarily monosynaptically, on vestibular neurons in the cat has been demonstrated both natural and electrical stimulation (Curthoys and Markham, 1971; Markham and Curthoys, 1972; Baker *et al.*, 1983; Graf *et al.*, 1986). These latter observations, depending on the extent of convergence, appear to require representations such as the predicted vestibular metric, or contracted vestibular tensor (B and D in Fig. 3), though in this first attempt at modeling the three-neuron reflex-arc we have used predicted vestibular canals (cf. Robinson, 1982) and polysynaptic (e.g. contralateral inhibitory) connections are not explicitly represented, these are important aspects of further elaborations of the tensor approach.

Identification of the axonal arborization patterns of second order vestibulo-oculomotor neurons supports the possibility that sensorimotor coordinate system transformation also occurs between the vestibular nuclei and the oculomotor neurons (Graf *et al.*, 1983; Graf and Ezure, 1984). These neuroanatomical data corroborate

electrophysiological findings of diffuse vestibulo-oculomotor projections (Uchino *et al.*, 1980).

Therefore, the spatial coordination performed by the vestibulo-ocular reflex was intentionally modeled here in a form that would facilitate its comparison with the matrix-analysis approach (Robinson, 1982; Ezure and Graf, 1984b). This paper emphasizes only two of the most important differences; namely that the tensor model of the VOR is represented in a structurally distributed manner and that the system is overcomplete. The tensor model of the three-neuron reflex-arc resolves both problems by predicting the interim vectorial expression of the gaze signal at the vestibular nuclear level and does it for the *overcomplete* VOR. In other respects, this model is presented similarly to others by, for example, combining the six vestibular canals (of the two sides) into a single set of three paired canals. This simplification complicates direct comparison of model-predictions with existing morphology, and is not necessarily required by the tensor approach. This will permit an elaboration of a VOR model which explicitly and quantitatively represents all six canals and the otoliths as well as all twelve (or any number of) muscles rotating the two eyes.

Another worthy consideration in connection with the fundamental question of the emergence of network-transformations is that the VOR is not a closed-loop sensorimotor system (cf. Pellionisz, 1985b). Therefore, it may be inappropriate at the present early stage of tensor network models of gaze to aim at a full elaboration and verification of a model of the VOR that is abstracted from the context of the full hierarchy of reflexes involved in gaze. Accordingly, we feel that it is more appropriate to provide here a first, simple and approximate model of the three-neuron reflex arc so that the morphological comparisons may be introduced while we are considering the VOR as part of a hierarchical gaze and retino-extraocular primary reflexes. In a hierarchical model system not only three-neuron-arc pathways between vestibular and oculomotor nuclei have to be represented, but also the indirect paths that involve the cerebellum and reticular formation (Pellionisz and Peterson, 1985; Pellionisz, 1986, 1987).

3.2 Comparison of the VOR model and experimental data at the overall level of a contracted "brain-stem matrix"

All the above considerations point to the fact that expecting a full numerical verification of the present model may be at this time premature, in light of an incomplete experimental quantification of the connections. Therefore, rather than pretending that this first and therefore, by definition, approximate model of the three-neuron arc is the ultimate representation, we focus attention on the issue of how this model *improves* our understanding compared to previous lumped models of the VOR. Thus, in the remainder of the paper we evaluate how closely the quantitative predictions of the distributed network approximate the available anatomical and physiological data, in comparison with models that did not elaborate a three-neuron reflex-arc. Since the matrix analysis approach utilizes a lumped brain-stem matrix, for comparison purposes only we also express this matrix B as:

$$B^{er} = g^{ie} v_i^r = \begin{vmatrix} & \text{H} & \text{A} & \text{P} \\ \text{H} & 0.504 & 0.010 & 0.058 \\ \text{A} & -0.508 & -0.058 & -0.026 \\ \text{P} & 0.004 & -0.496 & 0.099 \\ \text{LR} & -0.023 & 0.485 & -0.135 \\ \text{MR} & 0.040 & -0.138 & -0.470 \\ \text{SR} & -0.106 & 0.106 & 0.478 \end{vmatrix}$$

Note that this "brain-stem matrix", used only for comparison with earlier models, is contracted from the three-neuron-arc model applied to an overcomplete three-to-six dimensional system, and thus yields a non-square array. It could not have been provided by inverting the one-step transformation matrix (Robinson, 1982) and could only be estimated by extending that approach (Ezure and Graf, 1984b). The above matrix, instead of yielding unitary signals for paired eye muscles, provides separate excitatory and inhibitory signals for the agonist-antagonist pair, which results in maximal values of about 0.5 for each muscle.

Another more fundamental observation points out that the contracted brain-stem matrix is invariant to the circumstance which components are contracted because of the associativity of matrix-products: $B^{er} = (g^{ie} \cdot c_{ip}) \cdot g^{rp} = g^{ie} \cdot (c_{ip} \cdot g^{rp})$. Thus, the vestibular metric can either be contracted with the vestibulo-ocular embedding, leaving the oculomotor metric separate (as shown in Fig. 5) or, according to the aforementioned alternative possibility, to contract the last two matrices, leaving the vestibular metric separate. The alternative models yield slightly different connectivities for the three-neuron reflex-arc. However, *from the point of view of the present general comparison of the model with the data, these alternatives are identical, since the overall brain-stem matrix applies to both cases.*

In order to further facilitate such brain-stem-matrix comparison of the tensor model with experimental data, the connections from the paired vestibular canals are given below for each eye, although our body-symmetrical notation implicitly expresses the transformations to either side:

	left eye			right eye		
	H	A	P	H	A	P
LR	-0.504	-0.010	-0.058	+0.504	+0.058	+0.010
MR	+0.508	+0.058	+0.026	-0.508	-0.026	-0.058
SR	-0.004	+0.496	-0.099	+0.004	+0.099	-0.496
IR	+0.023	-0.485	+0.135	-0.023	-0.135	+0.485
SO	-0.040	+0.138	+0.470	+0.040	-0.470	-0.138
IO	+0.106	-0.106	-0.478	-0.106	+0.478	+0.106

These matrices quantify the excitatory and inhibitory signals originating from the left side horizontal (H) and vertical (A,P) semicircular canals, which activate the six extraocular muscles of each eye. Comparison of these results with the earlier models demonstrates their advantage over previous approaches which did not provide a description for *overcomplete* (three-to-six dimensional) systems (Robinson, 1982),

and yielded representations of such systems only by *approximated* numerical values (Ezure and Graf, 1984b).

In the following, the predictions of the model with the available experimental data are presented separately for the horizontal and vertical (anterior and posterior) canal systems. Following the classical three-neuron-arc terms of Szentágothai (1943), the connections are called according to their strength as principal and accessory paths, the latter divided into the subclasses of stronger characteristic- and the weaker tertiary connections. Typically, characteristic connections are about half as strong, and the tertiary paths are less than a tenth of the strength of the principal connections (cf. also Cohen *et al.*, 1964; Uchino, 1980). The data are represented as connections from the left labyrinth to both eyes.

Horizontal canal system. The horizontal part of the calculated overall system of connectivities (columns 1 and 4 in the six-column matrix representing connections from the labyrinth to both eyes) exhibits the well-known principal excitatory connections from the (left) labyrinth to the contralateral (right) lateral rectus (.504) and ipsilateral (left) medial rectus muscles (.508). The antagonists of the above muscles, the contralateral (right) medial rectus (-.508) and the ipsilateral (left) lateral rectus muscles (-.504) receive the principal inhibitory input. The other connections, corresponding to the minor matrix-components (columns 1 and 4) are quantitatively predicted to be about 5 to 100 times weaker than the principal connections [cf. p. 43-45 in Szentágothai, 1952]. Experimental evidence substantiating the existence of such secondary characteristic connection is unsettled. While Cohen *et al.* (1964) and Furuya and Markham (1981) have reported some input to vertical eye movers from the horizontal vestibular system based on electromyography and intracellular horseradish peroxidase (HRP) studies, Uchino *et al.* (1979) did not find any significant three-neuron-arc connections to vertical extraocular motoneurons via intracellular recordings from oculomotor neurons following horizontal canal stimulation. Since both the calculated and experimental components of horizontal canal to vertical eye muscle connections are one or two orders of magnitude weaker than the principal connections, the quantitative predictions do not conflict with available experimental evidence, especially since finding an absence of such connections in one study does not mean that they do not exist.

Vertical semicircular canal system. The inputs to the left (ipsilateral) eye from the left semicircular canals (columns 2,3) are described first. The anterior canal (column 2) sends principal excitatory connections to the ipsilateral superior rectus (.496) and the principal connection to the ipsilateral inferior rectus (-.485). These principal connectivities have been in the literature since Szentágothai's (1943) classical description of the three-neuron reflex arc (Ito *et al.*, 1973a,b, 1976a,b). The contraction of the ipsilateral superior oblique from anterior canal stimulation has been proposed [cf. center of Fig. 11 in Szentágothai, 1952] and also verified utilizing electromyography by Cohen *et al.* (1964). A possible neuroanatomical substrate of this connectivity was provided by intracellular horseradish peroxidase (HRP) studies (Graf and Ezure, 1986). A demonstration of a direct inhibition of the antagonist to the above muscle, the inferior oblique, is not available, although the existence of such connection was proposed by Ezure and Graf, 1984b. In general, such inhibitory

influence could be established indirectly, via inhibition of excitatory connections from the coplanar (posterior) canal on the contralateral side (see Cohen *et al.*, 1964). The weak inhibition of the ipsilateral lateral rectus muscle (-0.010) is in accordance with the reported occasional inhibitory postsynaptic potentials (IPSPs) in lateral rectus motoneurons following ipsilateral anterior canal stimulation (Uchino *et al.*, 1980). An ipsilateral medial rectus contraction (.058), following stimulation of the same canal, has been reported by Cohen *et al.* (1964). However, effects upon the lateral eye movers could also be explained by an effect of stimulus-spread from the anterior canal ampulla to the adjacent horizontal canal ampulla.

The posterior canal (column 3) sends its principal excitatory inputs to the ipsilateral superior oblique (.470) and its principal inhibitory inputs to the ipsilateral inferior oblique muscle ($-.478$). These connections were already established by the classical studies [cf. Table in page 40 in Szentágothai, 1952]. The excitatory input upon the ipsilateral inferior rectus, a characteristic influence of about one third in strength (.135) has been reported in early studies [cf. Figs. 13–14 in Szentágothai, 1952]. These synaptic effects were shown more recently by the electromyographic recordings of Cohen *et al.* (1964), intracellular recordings by Uchino *et al.* (1980), and by intracellular HRP injection by Graf *et al.* (1983). The existence of direct inhibition of the antagonist to the above muscle, the ipsilateral superior rectus ($-.099$), has long been proposed [cf. Table on page 40 in Szentágothai, 1952] and is evident from intracellular recordings by Uchino *et al.* (1980). In the present model, the accessory (characteristic and tertiary) connections are predicted to be 3 to 50 times weaker than the principal connections (columns 2,3 and 5,6). Experimental evidence is not available to verify directly the projections from the posterior canal to the horizontal eye movers; the excitation of the ipsilateral medial rectus (.026) and inhibition of the ipsilateral rectus ($-.058$). Since, however, these tertiary projection-coefficients are weak (a full order of magnitude weaker than the principal connections), the uncertainty in the literature concerning these connections (Cohen *et al.*, 1964; Ezure and Graf, 1984b) does not necessarily conflict with the quantitative predictions of the tensor model.

Projections from the left vertical semicircular canals to the right (contralateral) eye (columns 5,6) indicate the long-established principal excitatory connection from the anterior canal (column 5) to the inferior oblique (.478) and the principal inhibitory connection to the superior oblique ($-.470$). A characteristic excitatory connection appears to the superior rectus (.099). The existence of such a pathway is supported, based on electromyography (Cohen *et al.*, 1964), intracellular recordings (Uchino *et al.*, 1980) and neuroanatomical methods via intracellular HRP injection (Graf and Ezure, 1986). A direct characteristic inhibitory connection to the antagonist of this muscle, the contralateral inferior rectus ($-.135$), has also been established by intracellular recordings of IPSPs in inferior rectus motoneurons following contralateral anterior canal stimulation (Uchino *et al.*, 1980), and also by intracellular HRP injections of Graf and Ezure (1986). Excitatory influence upon the contralateral lateral rectus, in congruence with the calculated result (.058), has been reported (Cohen *et al.*, 1964; Uchino *et al.*, 1980), although possible effects of a stimulus-spread may also account for these experimental results.

The posterior canal projections to the contralateral inferior rectus in an excitatory fashion (.485) [cf. Table on page 40 in Szentágothai, 1952] and to the contralateral superior rectus as inhibition ($-.496$). Characteristic connections appear as excitation of the contralateral inferior oblique (.106) and as inhibition of the contralateral superior oblique ($-.138$). The calculated excitation of the contralateral inferior oblique is supported by electromyographical results of Cohen *et al.* (1964). On the other hand, results by Uchino *et al.* (1980) and Graf and Ezure (1986) indicate inhibitory input upon inferior oblique motoneurons, following contralateral posterior canal stimulation. The calculated inhibition of the superior oblique could be effected indirectly via inhibition of known excitatory pathways from the coplanar anterior canal on the contralateral side. The input to the contralateral horizontal eye movers, namely the inhibition of the medial rectus ($-.058$) and excitation of the lateral rectus (.010) is not demonstrated in the literature (Cohen *et al.*, 1964; Ezure and Graf, 1984b). However, the coefficients of these calculations are 10 to 20 times smaller than the principal connections, so that a lack of their direct demonstration is not entirely surprising.

The calculated results in cat show a remarkable separation of the vertical and the horizontal eye movement systems with only weak cross-coupling between vertical canals and horizontal eye movers, and horizontal canals upon vertical eye movers. Although cross-coupling between the vertical and the horizontal canal systems have been demonstrated at the level of the vestibular nuclei (Baker *et al.*, 1983) the innervation of the horizontal and vertical eye movements is reasonably well separated. This may arise from the fact that the vestibulo-ocular sensors and effectors in the cat constitute one of the best approximations of an orthogonal arrangement among the species and even for sensorimotor systems in general. The non-orthogonality, and thus the inseparability of the subsystems is significantly more conspicuous in other species (e.g. rabbit, cf. Simpson, 1983; Simpson and Pellionisz, 1984; Ezure and Graf, 1984a; Mazza and Winterson, 1984).

The present approach, which preserves the individuality of all six extraocular muscles, and enables an exact calculation of overcomplete networks, is within reasonable agreement both with the results arising from the matrix analysis approach where the agonists and antagonists were paired to keep the degrees of freedom in the sensory and motor system equal, providing an approximate quantification of the overcomplete system (Ezure and Graf, 1984b). The present solution is in keeping with the notion that the extraocular muscles in the cat work, to a great degree, in agonist-antagonist pairs. This can be seen e.g. from the close match of the innervation-coefficients between extraocular muscles which are agonist-antagonist pairs. This organization is reasonable in light of the close collinearity in cat of the rotational axes of the pair of agonist-antagonist muscles (Fig. 2). Furthermore, the results of both studies are in agreement with electromyographic recordings during natural vestibular stimulation (Peterson *et al.*, 1984). That study also demonstrated the low degree of cross-coupling between horizontal and vertical eye movers, and the inherent reduction of the degrees of freedom of the eye movement system by organizing it close to agonist-antagonist muscle pairs.

3.3 General implications of the quantitative predictions of tensor network models of CNS "reflexes" for morphological research

Tensor network theory aims at developing a complex yet natural approach to view the CNS as it evolved through the phylogenetic process, not how it could have been designed in engineering approaches (for example, for easy service, aiming at specificity and separability of modules). According to our view, the vestibulo-ocular reflex should be treated in its multidimensional entirety, as it coordinates, via 6 eye muscles, compensatory eye movements in 3 dimensional physical space. This is in contrast to viewing it as an assembly of three separable subsystems, where each was designed to control horizontal, vertical and torsional movements, respectively.

The comprehensive view conforms with classical approaches, taken e.g. by Sherrington (1906), who emphasized that envisioning CNS function in terms of simple reflexes might be a "purely abstract conception, because all parts of the nervous system are connected together". It appears that the "reflexology" that ensued after Sherrington's epoch-making studies gradually overemphasized the significance of obvious connections that can be found in complex neuronal networks at the expense of subtle, yet demonstrably existing secondary (and tertiary) pathways. Because of such trend towards simplification, the brain appeared more and more as being constructed of separable simple reflexes; e.g. the VOR was considered as composed of separable, orthogonal horizontal, vertical and torsional gain-control reflexes.

Aiming at understanding Nature's general solution for sensorimotor transformations, tensor network theory re-emphasizes the need for interpreting entire networks, not only the prominent connections inherent in them. Perhaps even more importantly, at the same time it also provides not only the conceptual, but also the formal means of how to accomplish such interpretation. As for experimentation, the task of arriving at a synthesis calls for substantial further developments of morphological and physiological methods that are suitable for quantitatively revealing relative strengths of connections within entire neuronal networks.

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References

- Albert, A. (1972). *Regression and the Moore-Penrose Pseudoinverse*. Academic Press, New York.
- Baker, R., Evinger, C. and McCrea, R. A. (1981). Some thoughts about the three neurons in the vestibulo-ocular reflex. In: *Ann. N.Y. Acad. Sci.* 374, pp. 171-188.
- Baker, J., Goldberg, J., Herrmann, G. and Peterson, B. (1983). Convergence of canal inputs to secondary neurons in cat vestibular nuclei. *Soc. Neurosci. Abst.* 9, 315.
- Ben-Israel, A. and Greville, T. N. E. (1980). *Generalized Inverses: Theory and Applications*. Robert E. Krieger Publ, New York.
- Blanks, R. H. I., Curthoys, I. S. and Markham, C. H. (1972). Planar relationships of the semicircular canals in the cat. *Am. J. Physiol.* 223, 55-62.
- Cohen, B., Suzuki, J. I. and Bender, M. (1964). Eye movements from semicircular canal nerve stimulation in the cat. *Ann. Otol. Rhino. Lar.* 73, 153-165.
- Curthoys, I. S. and Markham, C. H. (1971). Convergence of labyrinthine influences on units in the vestibular nuclei of the cat. I. Natural stimulation. *Brain Res.* 35, 469-490.
- Ezure, K. and Graf, W. (1984a). A quantitative analysis of the spatial organization of the vestibulo-ocular reflexes in lateral and front-eyed animals. I. Orientation of semicircular canals and extraocular muscles. *Neuroscience* 12, 85-93.
- Ezure, K. and Graf, W. (1984b). A quantitative analysis of the spatial organization of the vestibulo-ocular reflexes in lateral and front-eyed animals. II. Neuronal network underlying vestibulo-oculomotor coordination. *Neuroscience* 12, 95-109.
- Flourens, P. (1826). Experiences sur les canaux semi-circulaires de l'oreille, dans les mammifères. *Mem. Acad. Roy. Sciences de l'Institut de France* 9, 467-477.
- Furuya, N. and Markham, C. H. (1981). Arborization of axons in oculomotor nucleus identified by vestibular stimulation and intra-axonal injection of horseradish peroxidase. *Exp. Brain Res.* 43, 289-303.
- Gielen, C. C. A. M., Zuylein, E. J. (1986). Coordination of arm muscles during flexion and supination: Application of the tensor analysis approach. *Neuroscience* 17, 527-539.
- Graf, W. and Ezure, K. (1986). Morphology of vertical canal related second order vestibular neurons in the cat. *Exp. Brain Res.* 63, 35-48.
- Graf, W., Baker, J., Peterson, B. W. and Wickland, C. R. (1986). Differential canal-canal convergence in second-order vestibulo-oculomotor neurons in the cat. *Soc. Neurosci. Abst.* 12, part 2: 214.11.
- Graf, W., McCrea, R. A. and Baker, R. (1983). Morphology of posterior canal related secondary vestibular neurons in rabbit and cat. *Exp. Brain Res.* 52, 125-138.
- Graf, W. and Pellionisz, A. (1985). Morphology and a tensor network model of the three-neuron vestibulo-ocular reflex arc in cat. *Soc. Neurosci. Abst.* 11, 1041.
- Graf, W. and Simpson, J. I. (1981). The relations between the semicircular canals, the optic axis and the extraocular muscles in lateral-eyed and frontal eyed animals. In: *Progress in Oculomotor Research. Developments in Neuroscience*. Vol. 12. Eds: A. Fuchs and W. Becker. Elsevier/North-Holland Biomedical Press. New York, Amsterdam, Oxford. pp. 409-417.
- Goldberg, J., Baker, J., Schor, R. and Peterson, B. (1982). Vertical canal contribution to horizontal eye movements. *Soc. Neurosci. Abst.* 8, 419.
- Helmholtz, H. (1896). *Handbuch der Physiologischen Optik*. Zweite Auflage. Voss: Leipzig.
- Ito, M., Nisimaru, N. and Yamamoto, M. (1973a). The neural pathways mediating reflex contraction of extraocular muscles during semicircular canal stimulation in rabbits. *Brain Res.* 55, 183-188.
- Ito, M., Nisimaru, N. and Yamamoto, M. (1973b). The neural pathways relaying reflex inhibition from semicircular canals to extraocular muscles of rabbits. *Brain Res.* 55, 188-193.
- Ito, M., Nisimaru, N. and Yamamoto, M. (1976a). Pathways for the vestibulo-ocular reflex excitation arising from semicircular canals of rabbits. *Exp. Brain Res.* 24, 257-271.

- Ito, M., Nisimaru, N. and Yamamoto, M. (1976b). Postsynaptic inhibition of oculomotor neurons involved in vestibulo-ocular reflexes arising from semicircular canals of rabbits. *Exp. Brain Res.* **24**, 273–283.
- Kasahara, M. and Uchino, Y. (1974). Bilateral semicircular canal inputs to neurons in cat vestibular nuclei. *Exp. Brain Res.* **20**, 285–296.
- Krewson, W. E. (1950). The action of the extraocular muscles. A method of vector-analysis with computation. *Trans. Am. Ophthalmol. Soc.* **48**, 443–486.
- Lorente de Nò, R. (1932). The regulations of eye positions and movements induced by the labyrinth. *The Laryngoscope.* **42**, 233–332.
- Lorente de Nò, R. (1933). Vestibulo-ocular reflex arc. *Arch. Neurol. Psychiatry* **30**, 245–291.
- Markham, C. H. and Curthoys, I. S. (1972). Convergence of labyrinthine influences on units in the vestibular nuclei of the cat. II. Electrical stimulation. *Brain Res.* **43**, 383–396.
- Mazza, D. and Winterson, B. J. (1984). Semicircular canal orientation in the adult resting rabbit. *Acta Otolaryngol.* (Stockholm) **98**, 472–480.
- Ostriker, G., Pellionisz, A. and Llinás, R. (1985). Tensorial computer model of gaze — I. Oculomotor activity is expressed in non-orthogonal natural coordinates. *Neuroscience* **2**, 483–500.
- Pellionisz, A. (1983a). Sensorimotor transformation of natural coordinates via neuronal networks: conceptual and formal unification of cerebellar and tectal models. In: R. Lara and M. Arbib (Eds) *COINS Technical Report 83–19*, U. Mass. Amherst, MA on II. Workshop on visumotor coordination in frog and toad — models and experiments.
- Pellionisz, A. (1983b). Brain theory: connecting neurobiology to robotics. Tensor analysis: utilizing natural coordinates to describe, understand and engineer functional geometrics of intelligent organisms. *J. Theoret. Neurobiol.* **2**, 185–211.
- Pellionisz, A. (1984). Coordination: a vector-matrix description of transformations of overcomplete CNS coordinates and a tensorial solution using the Moore-Penrose generalized inverse. *J. Theor. Biol.* **110**, 353–375.
- Pellionisz, A. (1985a). Tensorial brain theory in cerebellar modeling. In: *Cerebellar Functions*, (Eds Dichgans, J., Precht, W.) Springer, Heidelberg, pp. 201–229.
- Pellionisz, A. (1985b). Tensorial aspects of the multidimensional approach to the vestibulo-ocular reflex and gaze. In: *Adaptive mechanisms in gaze control. Facts and theories*. Eds Berthoz, A. and Melvill-Jones, J. Elsevier.
- Pellionisz, A. (1985c). Tensor network theory of the central nervous system and sensorimotor modeling. In: *Brain Theory* (Eds Palm, G. and Aertsen, A.), Springer Verlag, Berlin-Heidelberg-New York, 121–145.
- Pellionisz, A. (1986). Tensor Network Theory and its Application in Computer Modeling of the Metaorganization of Sensorimotor Hierarchies of Gaze. In: Proc. "Neuronal Networks for Computing". AIP 151, New York: American Institute of Physics, pp. 339–344.
- Pellionisz, A. (1987). Vistas from Tensor Network Theory: A Horizon from Reductionistic Neurophilosophy to the Geometry of Multi-Unit Recordings. In: *Computer Simulation in Brain Science* (ed. by R. Cotterill), Cambridge University Press (in Press).
- Pellionisz, A. and Llinás, R. (1978). A formal theory for cerebellar function: The predictive distributed property of the cortico-nuclear cerebellar system as described by tensor network theory and computer simulation. *Soc. Neurosci. Abst.* **4**, 68.
- Pellionisz, A. and Llinás, R. (1979a). Cerebellar coordination: Covariant analysis and contravariant synthesis via metric tensor. A tensorial approach to the geometry of brain function. *Soc. Neurosci. Abst.* **5**, 105.
- Pellionisz, A. and Llinás, R. (1979b). Brain modeling by tensor network theory and computer simulation. The cerebellum: distributed processor for predictive coordination. *Neuroscience* **4**, 323–348.
- Pellionisz, A. and Llinás, R. (1980). Tensorial approach to the geometry of brain function. Cerebellar coordination via metric tensor. *Neuroscience* **5**, 1761–1770.
- Pellionisz, A. and Llinás, R. (1982a). Space-time representation in the brain. The cerebellum as a predictive space-time metric tensor. *Neuroscience* **7**, 2949–2970.

- Pellionisz, A. and Llinás, R. (1982b). Tensor theory of brain function. The cerebellum as a space-time metric. Chapter 23. In: S. Amari and M. A. Arbib (Eds) *Competition and Cooperation in Neural Nets*. Proc. of the U.S.-Japan Joint Seminar, Kyoto, Japan. Lecture notes in Biomathematics #45 (managing S. Levin, Ed.), Springer Verlag: Berlin-Heidelberg-New York, pp. 394–417.
- Pellionisz, A. and Llinás, R. (1985). Tensor network theory of the Metaorganization of functional geometrics in the CNS. *Neuroscience* **16**, 245–273.
- Pellionisz, A. and Peterson, B. W. (1985). Tensor models of primary sensorimotor systems, such as the vestibulo-colic reflex (VCR) and of the metaorganization of hierarchically connected networks. *Soc. Neurosci. Abst.* **11**, 83.
- Peterson, B., Baker, J., Wickland, C. and Pellionisz, A. (1985). Relation between pulling directions of neck muscles and their activation by the vestibulocollic reflex: tests of a tensorial model. *Soc. Neurosci. Abst.* **11**, 83.
- Peterson, B., Baker, J., Goldberg, J. and Wickland, C. (1984). Kinematic organization of cat vestibulo-ocular reflex (VOR) *Soc. Neurosci. Abst.* **10**, 49.9.
- Precht, W. (1979a). Labyrinthine influences on the vestibular nuclei. In: *Reflex Control of Posture and Movement*. Progress in Brain Research, Eds Granit, R. and Pompeiano, O. Elsevier, **50**, 369–381.
- Precht, W. (1979b). Vestibular mechanisms. *Ann. Rev. Neurosci.* **2**, 265–289.
- Reisine, H. and Henn, V. (1984). Transformation in three dimensions between primary and secondary vestibular neuronal signals in the Rhesus monkey. *Soc. Neurosci. Abst.* **10**, 49.7.
- Robinson, D. A. (1982). The use of matrices in analyzing the three-dimensional behaviour of the vestibulo-ocular reflex. *Biol. Cybern.* **46**, 53–66.
- Schultheis, L. W. and Robinson, D. A. (1981). Directional plasticity of the vestibulo-ocular reflex in the cat. In: B. Cohen (Ed.) *Vestibular and Oculomotor Physiology: International Meeting of the Barany Society*, New York Academy of Sci., New York, pp. 504–512.
- Sherrington, C. (1906). *The Integrative Action of the Nervous System*. Scribner, New York.
- Simpson, J. I. (1983). Transformation of coordinates intrinsic to the vestibulo-ocular reflex. *Soc. Neurosci. Abst.* **9**, 315.
- Simpson, J. I. and Graf, W. (1981). Eye muscle geometry and compensatory eye movements in lateral-eyed and frontal-eyed animals. *Ann. N.Y. Acad. Sci.* **374**, 20–30.
- Simpson, J. I. and Graf, W. (1985). Selection of frames of reference by nature and its investigator. In: *Adaptive Mechanisms in Gaze Control. Facts and Theories*. Eds Berthoz, A. and Melvill-Jones, J. Elsevier.
- Simpson, J. I. and Pellionisz, A. (1984). The vestibulo-ocular reflex in rabbit as interpreted using the Moore-Penrose generalized inverse transformation of intrinsic coordinates. *Soc. Neurosci. Abst.* **10**, 909.
- Szentágothai, J. (1943). Die zentrale Innervation des Augenbewegungen. *Arch. Psychiat. Nervkrankh.* **116**, 721–760.
- Szentágothai, J. (1950). The elementary vestibulo-ocular reflex arc. *J. Neurophysiol.* **13**, 395–407.
- Szentágothai, J. (1952). *Die Rolle der Einzelnen Labyrinthrezeptoren bei der Orientation von Augen und Kopf im Raume*. Akadémiai Kiadó, Budapest.
- Uchino, Y., Suzuki, S., Miyazawa, T. and Watanabe, S. (1979). Horizontal canal input to cat extraocular motoneurons. *Brain Res.* **177**, 231–240.
- Uchino, Y., Suzuki, S. and Watanabe, S. (1980). Vertical semicircular canal inputs to cat extraocular motoneurons. *Exp. Brain Res.* **41**, 45–53.
- Westheimer, G. (1957). Kinematics of the eye. *J. Opt. Soc. Am.* **67**, 967–974.
- Weiland, C. (1898). Are our present ideas about the mechanism of the eye-movements correct? *Arch. Ophthalm.* **27**, 46–64.