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BRAIN FUNCTION: CEREBELLAR COORDINATION VIA  
A METRIC TENSOR**

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# TENSORIAL APPROACH TO THE GEOMETRY OF BRAIN FUNCTION: CEREBELLAR COORDINATION VIA A METRIC TENSOR

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**Abstract**—Based on our previous assumption that the brain must be considered a tensorial entity (PELLIONISZ & LLINÁS, 1979a), a concise model for cerebellar function is proposed: *The cerebellum acts as a metric tensor establishing a geometry for the CNS motor hyperspace.*

This view assumes that the brain is a 'geometrical object', that is to say, (1) activity in the neuronal network is vectorial, and (2) the networks are organized tensorially: i.e. activity vectors remain invariant to changes in reference-frames. Understanding brain functions becomes, then, the establishment of the inherent geometrical properties of the activity vectors and, more fundamentally, the determination of the properties of the multi-dimensional internal space (a frequency hyperspace) in which the vectorial transformations occur. A basic question is the form in which vectors are expressed. Are the components orthogonal projections to an oblique set of coordinate-axes or are they the parallelogram vectorial components? Beyond this, the question arises as to whether the CNS hyperspace is endowed with a geometry determined by a *metric tensor*.

Thus the problem of motor coordination is approached geometrically: in these terms intended movements, i.e. intended movement vectors, are generated in the CNS in reference to the three-dimensional space. These movements are executed, however, by the multiparameter system representing the musculo-skeletal apparatus. Given this increase in dimensionality the question of uniqueness needs to be answered: how are the particular components of a motor vector established if they only represent one choice out of the infinite set of possible vectorial solutions?

The tensorial treatment of motor coordination suggests that the problem is solved by the embedding of the external three-space into the multidimensional CNS space and that this hyperspace is endowed with a metric tensor represented, for movements, by the cerebellar neuronal network. Thus, a unique implementation of the three-dimensional intended movement is possible by a proposed two-step scheme: First, an intended movement vector is specified by an overcomplete number of CNS covariant vector-components. Second, since covariant components cannot be used directly to execute a movement vector (they yield 'dysmetric' movements), they are transformed into contravariant, physical, components of the final motor output. This transformation is the proposed role of the cerebellar metric tensor, resulting in a coordinated unique implementation of movements.

While in this paper the vectorial components transformed by the metric are treated as space coordinates, it has not escaped our attention that the movement space-time is actually four dimensional. This point will be elaborated in a forthcoming paper in which the above concept of metric tensor is expanded to include space-time coordinates. Thus, the predictive feature of cerebellar action together with the metric concept provide a unified approach to the dynamic properties of motor control.

Beyond providing a geometrical model of motor coordination by the cerebellum, the tensorial approach suggests that the 'covariant analysis' and 'contravariant synthesis', via metric tensor, may be a general principle of the organization of the CNS.

IN A RECENT paper we have expressed the general hypothesis that the brain should be regarded as a 'geometrical object' (PELLIONISZ & LLINÁS, 1979a). That is, (1) a system where activity patterns in neuronal networks are to be regarded as vectors, and also (2) where the role of such networks is to generate an internal CNS space in which the vectorial relations are established tensorially. This approach implies that while the neuronal networks of a particular brain are individual, there exists an invariant geometrical property (for the class of all similar input and output relations) that is common for all networks. This is a

formal equivalent of the approach implicit in brain research which aims at understanding *the* brain from studies of individual particular brains.

Thus, given a *particular* neuronal network, its activity is determined by the connectivity between input and output neurons. This network matrix establishes a relation between the patterns of activity (e.g. spiking frequencies) of the input and output neurons. As an example, if a bundle of  $n$  nerves could carry light, as in fiber optics, and if action potentials could generate flashes, the input and output patterns (pictures) would be described as vectors in an  $n$ -dimensional space. In abstract terms, then the activity pattern of a population of  $n$  neurons is defined as an  $n$ -dimensional vector, where the  $n$  coordinate components are the  $n$

Abbreviations: CNS, central nervous system. VOT vestibulo-oculomotor tensor.

frequencies, and thus the connectivity matrix establishes a transformation of the input vector 'pattern' into an output vector. Obviously it is the physical arrangement of 'wires' in the particular connectivity matrix that determines the input-output transformation. Our fiber optics example also tells us that given diameter irregularities of the fibers one may distort a picture (enlarge or reduce a portion, etc). However, the same distorted picture-picture relation may be obtained by reflecting the input onto a curved mirror, or an appropriate lens. Thus, rather than describing the properties of the different sets of transformations by vectors and matrices (i.e. how points of the picture are carried through the network), the reference-frame invariant tensorial approach can express, in a universal manner, the optical transformation without connectivity matrices.

Indeed, when considering brain function, the realization that activity vectors are expressed via reference-frame invariant *tensorial* entities makes it possible to approach the concept of function beyond the idiosyncratic vector and matrix features of any individual brain circuitry. As a consequence, attention may be shifted from the vector components (expressed in specific coordinates) to the study of vectors themselves, and even more importantly, to the properties of the space of the vectors. In short, in order to describe the global properties of CNS function it is an absolute necessity that the intrinsic geometrical properties of the CNS hyperspace be understood. For example, questions such as whether the brain hyperspace is endowed with a metric tensor immediately arise.

In this paper we point out that motor coordination is intimately related to the geometry of the CNS hyperspace. This approach provides both the necessary concepts as well as the tools to deal with the reference-frame invariant properties of CNS vectors. We hold that useful insights may be obtained not merely by amalgamating the components of the distributed neuronal activities into a single vector, but also by removing these vectors from specific coordinate

systems via their tensorial interpretation. This work has been presented in a preliminary form (PELLIONISZ & LLINÁS, 1979b).

## COORDINATED MOVEMENTS AS TENSORIAL ENTITIES

Movements of the body are physical vectors and as such invariant to reference-frames. This feature, as is also the case with the reference-frame invariant character of physical laws (e.g. that of concerning forces and accelerations), is the basis of the tensorial approach to motor coordination which is implemented in the CNS by the cerebellum.

Consider, for example, a simple limb movement, such as raising an arm. Suppose that a limb is composed of only an upper and lower arm, each of length  $r$ , and that it can move only in two dimensions (Fig. 1). Let the hand move with an 'up' displacement vector,  $\bar{U}$ . Strictly speaking, in this movement we are actually changing the angles  $\alpha$  and  $\beta$  at the shoulder and at the elbow. Transforming these two quantities in a particular manner (depending, for example, on the initial limb position) results in the upward displacement vector,  $\bar{U}$ . Whereas  $\bar{U}$  is a physically existing objective entity, the *same* vector is expressed in two fundamentally different kinds of frame of reference. One type can be applied to the external physical space in which the movement is executed while another type of coordinate system refers to the internal multidimensional space in which the movement vector is generated.

Formally, these two different spaces can be incurred by an infinite number of particular reference-frames. For example, considering arm movements restricted to a two-dimensional plane, the limb-displacement is a two-dimensional vector, given by an ordered set of two quantities ( $x$  and  $y$ , using Cartesian orthogonal rectilinear reference-frame, or  $R$  and  $\Psi$ , using polar orthogonal curvilinear coordinate-system, and so on). Similarly, the same physical vector can be

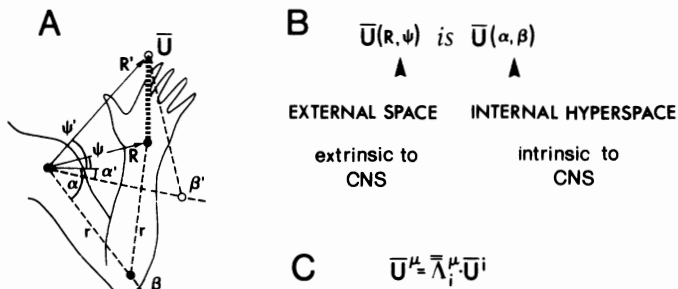


FIG. 1. Limb movement as a tensorial entity. (A) An upward displacement vector  $\bar{U}$  is a physical entity which can be expressed in different reference-frames: E.g. by the  $R, \Psi$  polar coordinate system, or by the  $\alpha, \beta$  ordered set of two quantities. (B) The two shown reference-frames are of fundamentally different kinds:  $R, \Psi$  applies to the CNS-independent external space, the  $\alpha, \beta$  is to the space inherently connected to CNS. The limb-displacement vector occurs in both spaces. (C) Different expressions of the one  $\bar{U}$  vector are related by the limb-displacement tensor,  $\bar{\Lambda}_i^\mu$ .

expressed relative to a variety of internal reference-frames; some of them only indirectly related to the CNS. In terms inherent to the 'body', the ordered set of quantities may be the two angles at the shoulder and at the elbow, or the contraction produced by the flexor and extensor muscles, or, in terms of the CNS, the sums of firing frequencies of the motoneurons innervating them. It must be emphasized that the difference between the two kinds of reference-frames is that one set is external (extrinsic) to the CNS, in the sense that it exists independently of the CNS, while the other kinds of reference-frames are dependent on, and reflect the properties and constraints of, the CNS.

Given the above and given that a tensor is a reference-frame invariant vector-relationship (cf. HOFFMANN, 1966), the limb movement is, by definition, a tensorial entity. Thus, as shown in Fig. 1, the limb displacement can be characterized by the movement expressed as a vector (tensor of rank one) in both the external space and the internal hyperspace, and the different vectorial expressions can be transformed from one to the other by the transformation matrix of  $\bar{A}_i^\mu$ . As KRON (1939) pointed out in his epoch-making tensor-theory of electrical networks, the entirety of the transformation-matrices establishing relations among expressions in different reference-frames of a physical vector is one 'geometrical object', where the particular matrices are different expressions of one tensor.\*

Thus, in tensorial terms the implementation of a straight upward limb-displacement is seen as follows. The intended movement vector  $\bar{U}$  is characterized as a sum of a  $y$  and an  $x$ -component, relative to the external frame of reference. However, in order to execute the displacement, the vector must of necessity be present internally. An ordered set of two quantities of  $\alpha$  and  $\beta$  has to be established, via the transformation by  $\bar{A}$ . The reference-frame invariance of movement-vectors can be used to introduce a formal geometrical definition of coordination: *Motor coordination is a geometrical transformation of an intended movement-vector into an executable expression of the same vector.* Although both vectors are expressed in the CNS the intended vector specifies the external goal vector measured in bodily terms, whereas the execution vector generates the movement.

While in the above case the needed  $\alpha, \beta$  internal components can be directly transformed from the external  $x, y$  components through the limb-movement tensor,  $\bar{A}$ , one has to point out a fundamental problem in the general case. If the internal spaces employed by the body and CNS have more dimension than the external, the execution of, e.g., a two-

dimensional movement) by an arm with *three* degrees of freedom) is theoretically not unique. In fact, the number of possibilities of decomposing a two-dimensional vector into *three* components is infinite. Still, in practice particular individual solutions do occur every time the body moves. This paper provides a hypothetical scheme by which this uniqueness problem of the coordination could be solved by virtue of a cerebellar metric tensor.

*Quantitative expressions of a limb-movement tensor*

Let us provide a simple quantitative example of limb movements as tensors. In general, the limb-movement tensor determines the relationship between different expressions of the limb-displacement vector  $\bar{U}$ . The general expression of an infinitesimal  $\bar{U}$  by  $\mu$  infinitesimal components may be

$$\bar{U}^\mu, \text{ e.g. } \bar{U} = \bar{U}(\alpha, \beta).$$

While  $\bar{U}$  can be expressed in both the intrinsic and extrinsic frames of reference:

$$\bar{U} = \bar{U}(x, y) \text{ or } \bar{U} = \bar{U}(R, \Psi) \text{ or } \bar{U} = \bar{U}(\alpha, \beta)$$

there is a relationship among all of these, expressing the same geometrical object. In tensorial terms, and using the Einstein summation convention

$$\bar{U}^\mu = \bar{A}_i^\mu \cdot \bar{U}^i.$$

For example, selecting a polar system of coordinates as external reference frame, and  $\alpha, \beta$  as a body-reference-frame, the expression becomes:

$$\bar{U}^\mu(\alpha, \beta) = \bar{A}_i^\mu \cdot \bar{U}^i(R, \Psi).$$

In this expression the  $\bar{A}_i^\mu$  limb-movement tensor has the following four particular components:

$$\bar{A}_i^\mu = \frac{\partial \bar{U}^\mu}{\partial \bar{U}^i} = \begin{pmatrix} \frac{\partial \alpha}{\partial R} & \frac{\partial \alpha}{\partial \Psi} \\ \frac{\partial \beta}{\partial R} & \frac{\partial \beta}{\partial \Psi} \end{pmatrix}.$$

These particular values can be established, if

$$\alpha = \Psi - \arccos \frac{R}{2r} \quad \text{(see Fig. 1)}$$

$$\beta = \pi - 2 \arcsin \frac{R}{2r}$$

Therefore, after the above partial differentiation the limb-movement tensor is

$$\bar{A}_i^\mu = \frac{\partial \bar{U}^\mu}{\partial \bar{U}^i} = \begin{pmatrix} \frac{\partial \alpha}{\partial R} & \frac{\partial \alpha}{\partial \Psi} \\ \frac{\partial \beta}{\partial R} & \frac{\partial \beta}{\partial \Psi} \end{pmatrix} = \begin{pmatrix} \frac{1}{2r} \cdot \frac{1}{\sqrt{1 - \frac{R^2}{4r^2}}} & 1 \\ -\frac{1}{r} \cdot \frac{1}{\sqrt{1 - \frac{R^2}{4r^2}}} & 0 \end{pmatrix}$$

\* It seems necessary to point out that a tensor need not be a square matrix; differential geometry routinely utilizes rectangular projection tensors: e.g. two-by-three matrices for embedding a two-dimensional surface into a three-dimensional space (cf. COBURN, 1955, p. 216).

For the sake of a quantitative example, let us assume that the length of the arm is  $r = 10$  units, and suppose that the intended displacement vector specifies that the hand should move 1 unit farther and 0.2 radian lower ( $\Delta R = 1, \Delta \Psi = 0.2$ ). In this case, the desired components of the movement vector, relative to the intrinsic  $\alpha, \beta$  reference-frame can be established from the components. For convenience, assume that  $R \ll r$ . (This means that the hand stays close to the shoulder. As can be seen above, it greatly simplifies the given expression of the limb-movement tensor). Thus:

$$\begin{aligned} \bar{U}(\alpha, \beta) &\approx \begin{pmatrix} \frac{1}{2r} & 1 \\ -\frac{1}{r} & 0 \end{pmatrix} \cdot \bar{U}(R, \Psi) \\ &= \begin{pmatrix} 0.05 & 1 \\ -0.1 & 0 \end{pmatrix} \cdot \begin{pmatrix} 1 \\ 0.2 \end{pmatrix} = \begin{pmatrix} 0.25 \\ -0.1 \end{pmatrix}. \end{aligned}$$

Therefore, increasing  $\alpha$  by 0.25 radian and changing  $\beta$  by  $-0.1$  radian the hand is displaced by the desired vector,  $\bar{U}$ . Since the intended movement vector  $\bar{U}$  was expressed in the extrinsic frame of reference and now the bodily components of the same vector are established, a *coordinated movement is made*.

When handling such problems mathematically one tends to employ, for reasons of convenience, orthogonal, rectilinear Cartesian frames of reference. However, even the  $\alpha, \beta$  intrinsic reference-frame shows none of the above convenient features. E.g., by changing  $\alpha$  or  $\beta$  one finds that the respective hand-displacements are almost never perpendicular to each other, indicating that the reference-frames are not orthogonal, but oblique. The displacements by  $\alpha$  or  $\beta$  are not even straight lines: the system of coordinates is not rectilinear, but curvilinear. Accordingly, the expression of the limb-movement tensor in this non-Cartesian, oblique, curvilinear intrinsic reference-frame is position-dependent; the actual values of the components are different at different points of the hyperspace. Thus, the quantitative expression of the tensor-components is a set of non-constant quantities.\* Therefore, in a coordinated action the transformation must always be available in an 'updated' form, corresponding to the actual position of the arm (cf. LLINÁS, 1974). While this requirement is serious, the overcompleteness of the intrinsic hyperspace relative to the external space poses the even more fundamental uniqueness problem which is analyzed below.

#### TENSORIAL OPERATIONS IN THE OVERCOMPLETE INTRINSIC CNS-HYPERSPACE

Consider a limb restricted to movements within a

\* In special cases, as above, when limiting the movement to the shoulder vicinity, a careful selection of a polar coordinate system for the external space yields a tensor that can be simplified to a set of constants.

two-dimensional external space; however, let the limb be composed of *three* joints. With the corresponding angles of  $\alpha, \beta$  and  $\gamma$  between them, any given movement vector can be produced by any one of an *infinite* number of combinations of  $\alpha, \beta$  and  $\gamma$  alterations (cf. Fig. 2). However, every time a hand movement occurs there is just *one* actual implementation. It is also known that the cerebellum plays a key role in the process of arriving at this unique choice. The question therefore is: By what scheme can the cerebellum implement this coordination? As an example of the above, let us take the classical demonstration by HOLMES (1939) of the cerebellar dysmetria in a patient with a (left side) hemicerebellar lesion (see Fig. 2B). Here the intended displacements of the grossly simplified three-parameter system of the hand are given by two-dimensional vectors, expressed relative to the physical space (pointing to four corners of a square). As illustrated, a coordinated movement (a unique expression of the intended vectors in the higher than two-dimensional CNS hyperspace) can be implemented by the right normal side. In contrast, a coordinated movement cannot be executed with the left hand in accordance with the cerebellar disturbance produced by the unilateral lesion. The left hand displays what is known as a dysmetric motor action.

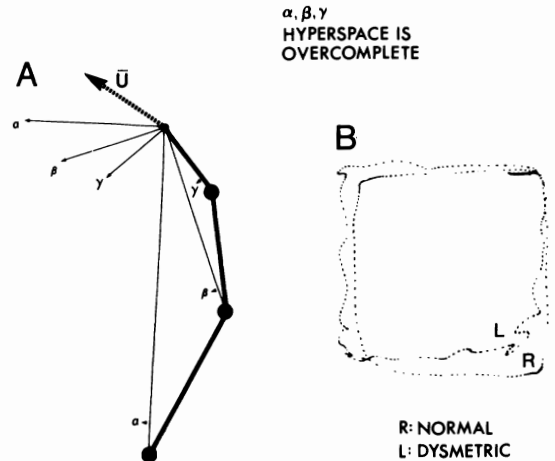
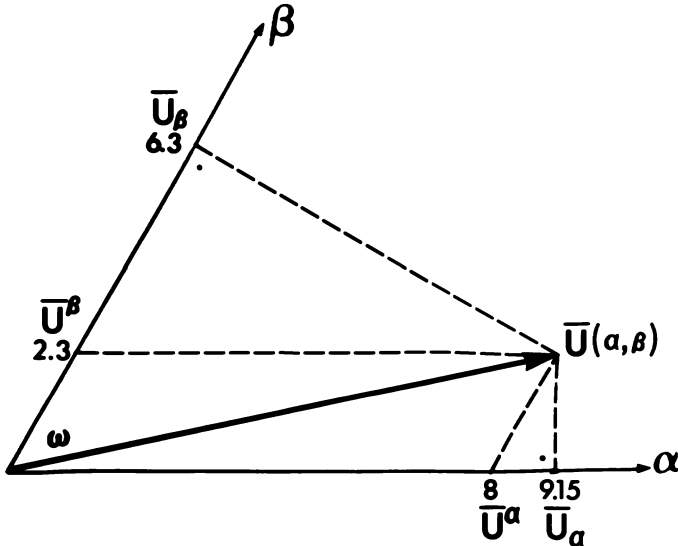
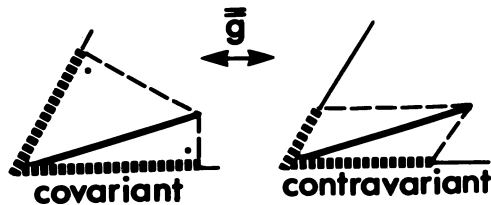


FIG. 2. The uniqueness problem of implementing an intended movement vector by a higher dimensional executor system. (A) A three-segment limb is to execute a two-dimensional intended vector  $\bar{U}$ , by virtue of changing the three coordinates of  $\alpha, \beta$  and  $\gamma$ . The arrows at the joints indicate the infinitesimal changes of  $\alpha, \beta, \gamma$  joint-angles. The  $\alpha, \beta, \gamma$  system of coordinates at  $\bar{U}$  shows the displacement corresponding to infinitesimal changes of the angles. (B) While the internal  $\alpha, \beta, \gamma$  space is overcomplete, in reality the intended movement vectors are decomposed to an overcomplete number of components. Moreover, the used procedure is affected by cerebellar lesion: recorded hand movements, pointing to four corners of a square, shows satisfactory execution with the corresponding cerebellar hemisphere intact (R), while because of cerebellar damage, the movement of the left hand (L) shows haphazard movements known as dysmetria (B is after HOLMES, 1939).

# COVARIANT AND CONTRAVARIANT VECTOR COMPONENTS



GEOMETRY OF THE SPACE GIVES THEIR RELATION BY THE METRIC TENSOR



# COVARIANT METRIC TENSOR

$$\bar{g}_{ij} = \sum_a \frac{\partial x^a}{\partial y^i} \frac{\partial x^a}{\partial y^j}$$

# CONJUGATE TENSOR (CONTRAVARIANT METRIC)

$$\bar{g}^{ij} = \frac{\text{cofactor } \bar{g}_{ij}}{\text{determinant } g}$$

$$\begin{aligned} \bar{U}^i &= \bar{g}^{ij} \cdot \bar{U}_j \\ \bar{U}_i &= \bar{g}_{ij} \cdot \bar{U}^j \end{aligned}$$

$$\begin{pmatrix} 2.3 \\ 8 \end{pmatrix} = \begin{pmatrix} 1.3 & -0.6 \\ -0.6 & 1.3 \end{pmatrix} \cdot \begin{pmatrix} 6.3 \\ 9.15 \end{pmatrix}$$

$$\begin{pmatrix} 6.3 \\ 9.15 \end{pmatrix} = \begin{pmatrix} 1 & 0.5 \\ 0.5 & 1 \end{pmatrix} \cdot \begin{pmatrix} 2.3 \\ 8 \end{pmatrix}$$

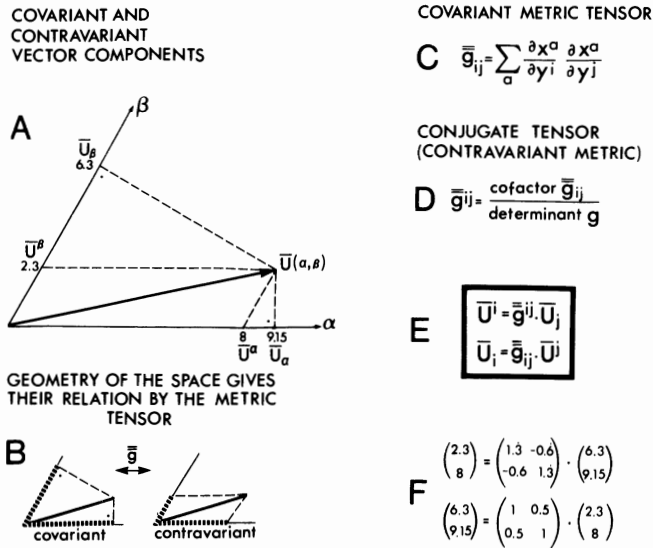


FIG. 3. Covariant and contravariant components of a vector, and their relation established by the geometry of the space of the vector. (A) The covariant components (lower index) can be established independently from one another, but they do not physically compose the vector. (These components, also called resolved parts are established by perpendicular projections.) Contravariant components (upper index) physically add up to the resultant,  $\bar{U}$ ; however, they cannot be established independently from one another. (B) The numerical relation of the two sets of components is determined by the metric tensor which describes the geometry of the space. (C) Expression of the metric tensor in covariant form. (D) Expression of the contravariant metric tensor. (E) Relation of covariant and contravariant components, as determined by the metric tensor. (F) Numerical example of the relation of covariant and contravariant components shown in A and E.

In order to understand the manner in which the cerebellum implements this coordination, note that the displacement can be vectorially expressed both in the two-dimensional external space and in the three-dimensional intrinsic CNS hyperspace, i.e. the two-space can be regarded as a surface embedded into a three-space. Thus, the displacement, as an invariant line-element lies both in the embedded and in the embedding spaces. In order to analyze the vectorial expressions in these spaces the first question to be asked is whether these vectors are expressed by covariant or contravariant components.

*Covariant and contravariant vector-components and the metric tensor*

Some of the relevant features of covariant and contravariant vector-components and their transformation through the metric tensor, are summarized in Fig. 3. Given an arbitrary, oblique, two-dimensional frame of reference and a metric tensor, a single  $\bar{U}(\alpha, \beta)$  vector may be expressed both by its covariant components  $\bar{U}_i$  and by its contravariant parts  $\bar{U}^i$ ,  $\bar{U}^i$  are termed the 'physical components' since they, when added according to the parallelogram rule, *actually provide the resultant vector*,  $\bar{U}$ . In contrast as it is shown in Fig. 3, the covariant components do not have this feature, their physical sum not being equivalent to  $\bar{U}$ . On the other hand, covariant vectorial components have the important property that *a given vector component along one direction can be uniquely*

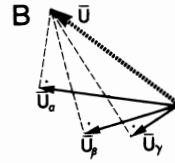
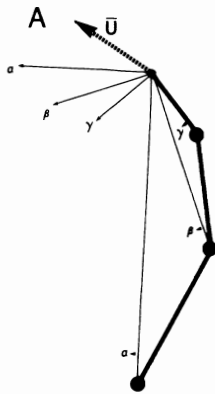
*determined, independently of the total number of coordinate axes or of the direction of other axes.* Indeed, a covariant component is determined by taking the inner product with the unit vector in one coordinate direction, i.e. by establishing a perpendicular to the given axis. We call this *the principle of independence of covariant vector components.* Such a feature does not apply to the contravariant components, for which the establishing of any one component requires that all the other directions of the coordinates be known: that is to say, *the physical components, which are actually capable of generating the executing vector, and interdependent.*

The geometry of the hyperspace determines through the metric tensor, the relation of covariant and contravariant sets of components. This geometry can be expressed as shown in Fig. 3, in both covariant and contravariant forms. The  $\bar{g}_{ij}$  matrix is the covariant metric tensor, its conjugate,  $\bar{g}^{ij}$  is the contravariant metric tensor. Thus, the two sets of components are related through the following expressions:

$$\begin{aligned} \bar{U}^i &= \bar{g}^{ij} \bar{U}_j \\ \bar{U}_i &= \bar{g}_{ij} \bar{U}^j. \end{aligned}$$

A numerical example given in Fig. 3 shows the actual calculations from one set of vectorial components to the other in the depicted case.

Our central tenet regarding the geometrical concept of coordination is that *the CNS must transform covari-*

COVARIANT FEATURE ANALYSIS  
OF THE IMAGE VECTOR

$$C \quad \bar{U}^i = \bar{g}^{ij} \cdot \bar{U}_j$$

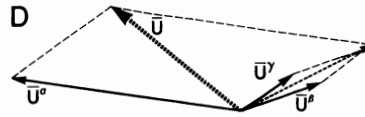
CONTRAVARIANT SYNTHESIS  
BY THE METRIC TENSOR

FIG. 4. Covariant analysis and contravariant synthesis via a metric tensor. (A) Given a two-dimensional intended vector  $\bar{U}$  and three  $\alpha, \beta, \gamma$  axes of an overcomplete reference-frame, the decomposition could be performed by a two-step operation. (B) Firstly, covariant components of  $\bar{U}$  can be established, using the geometry of the two-space, to any number of directions independently. (The perpendicular projections, i.e. inner products, provide the 'features' of the desired  $\bar{U}$  vector in any coordinate direction.) (C) Secondly, provided that the  $\alpha, \beta, \gamma$  space is geometrical and its metric tensor is available (in contravariant expression), the corresponding set of contravariant components can be established. (D) Contravariant components, which physically generate the displacement vector  $\bar{U}$ . (As shown in B, the added up covariant components do not even point into the direction of  $\bar{U}$ .)

## A INTENDED MOVEMENT VECTORS



## B COVARIANT CONTROL-DYSMETRIA

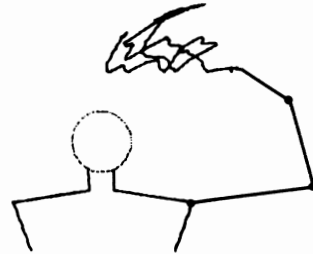
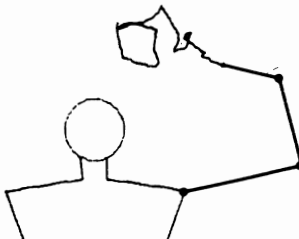
C CONTRAVARIANTS BY  
CONSTANT METRIC TENSORD CONTRAVARIANTS BY  
POSITION DEPENDENT METRIC

FIG. 5. Computer model of the execution of two-dimensional intended movement vectors by a three-segment limb, using the covariant analysis and contravariant synthesis, via a metric tensor. (A) Letters OK, representing two-dimensional intended movement vectors by each segment of the letters. (B) Dysmetric writing: the intended vectors are decomposed into covariant components (as in Fig. 4B), and the three-segment arm is moved directly according to the *covariant* components. Note the ataxic, 'dysmetric' movement which, characteristically, is better in some directions, while much worse in others. (C) Introducing a matrix of  $3 \times 3$  constants as a metric tensor of the  $\alpha, \beta, \gamma$  space, the covariant components are transformed into contravariant (physical) components, which are capable of executing the intended vectors. The characteristic distortion of the writing is the result of the position-independence of the metric. (D) Execution of the intended vectors by using a position-dependent metric, where the embedding of the three-space into the internal hyperspace is homomorphic at each point of the writing; i.e. the CNS hyperspace is curved.

ant components of a vector into their contravariant counterparts. If an intended movement vector is termed a 'movement image', the covariant features of this 'image' may be established independently along any given coordinate-axis. It also should be noted that there is no limit to the number of such covariant 'features', since the inner products, the perpendiculars, can be determined for any number of coordinate-axes. Note that establishing the inner products, i.e. 'taking the perpendicular' implies the use of the geometry of the embedded space. For example in the case of a two-dimensional external space and a three-dimensional CNS hyperspace the covariant components are established on the tangent plane of a surface that is embedded into the three-space. However, for the actual generation of the physical vector, the contravariant components are required. Thus, it is fundamental that the covariant set of components be transformable into the set of contravariants. This implies that, as proposed in this paper, CNS motor vectors reside in a hyperspace which is endowed with a metric tensor.

#### *Covariant analysis and contravariant synthesis through a metric tensor*

The above consideration permits the elaboration of a conceptual scheme which allows the decomposition of a vector, given in a lower dimensional space, into components expressed in an overcomplete hyperspace. The scheme is demonstrated in Fig. 4.

Given a three-segment limb, it was shown above that at any of its positions, the  $\alpha$ ,  $\beta$  and  $\gamma$  axes of coordinates establish a reference-frame that is overcomplete compared to a two-dimensional intended movement vector  $\bar{U}$ . Given the non-trivial assumption that the *intrinsic CNS hyperspace is endowed with a metric tensor*, the contravariant  $\bar{U}^i$  set of components can be established by applying the metric tensor  $\bar{g}^{ij}$  to the vector  $\bar{U}_j$ . As shown in Fig. 4, such a set of contravariant components will actually create the required vector  $\bar{U}$ .

We consider this two-step operation to be a general principle applied by the CNS tensorial networks: (1) determining separately and independently from each other the covariant components ('features') of a move-

ment image vector using the geometry of the embedded space, (2) transforming the covariant components into contravariant physical components through the metric tensor which establishes the geometry of the internal hyperspace. The first step, then, is a mechanism for analysis, since the characteristic features along different directions are 'measured' by establishing covariant components. However, these cannot create the vector. The second step is the mechanism for synthesis. Knowing the features of the intended result and the geometry of the space in the form of contravariant metric tensor, the actual resultant vector is provided by their product.

#### CEREBELLAR COORDINATION VIA A METRIC TENSOR WHICH ESTABLISHES THE GEOMETRY OF THE INTERNAL HYPERSPACE

In the above terms, a coordinated movement is seen as follows. An intended movement-vector is formulated in the CNS in reference to the embedded extrinsic physical three-space. This 'movement image' vector is resolved into covariant components along the coordinate-axes determined by the  $\alpha$ ,  $\beta$  and  $\gamma$  changes. The result of this analytic process is the set of features which the desired vector must possess. However, since the covariant components cannot be used to generate the desired vector, the covariant set of components must *undergo a transformation via the contravariant metric tensor of the hyperspace*. Since the cerebellum was represented by a tensor  $\bar{\theta}$  (PELLIONISZ & LLINÁS, 1979a), it is our proposal that *the cerebellar tensor acts as a contravariant metric which determines a geometry in the intrinsic hyperspace*. Therefore, the cerebellum would function by transforming the covariant components of the intended movements into contravariant components.

A computer-illustration of this principle is given in Fig. 5 using a limb composed of three segments moving within a two-dimensional plane. For a set of two-dimensional intended-movement vectors let us assume that the hand writes the letters 'OK'. In this case, the covariant components of the intended vectors can be established at every point of the writing movement. At each position of the limb one can determine perpendicular projections (inner products) to the momentary axes of  $\alpha$ ,  $\beta$ ,  $\gamma$  reference-frame. If, however, these covariant components are being used to generate the displacement (changing  $\alpha$ ,  $\beta$  and  $\gamma$  according to the values of covariant parts), the resulting limb-movement is a haphazard set of displacements (Fig. 5B).\*

In the next step (Fig. 5C) a symmetric matrix of  $3 \times 3$  constants was set up to act as a contravariant metric tensor, establishing a position-independent intrinsic geometry of the  $\alpha$ ,  $\beta$ ,  $\gamma$  internal hyperspace. Then the set of covariant components are transformed via this tensor to the contravariant components. Thus the two-dimensional intended vectors

\* Note that such 'writing' resembles that ataxic, so-called dysmetric, movement of patients with cerebellar disease (cf. Fig. 2). In both Figs 2 and 5 the error in the direction and magnitude of the movement is *not* uniform: some intended vectors are less distorted—cf. last two segments of K—while some other vectors are grossly inadequate; see the connecting segment from O to K: This is because the sum of covariant components points into a direction that is sometimes similar to, and sometimes quite different from, the direction of intended vector: it depends on their relative directions. (It is only for the *eigenvectors* of the cerebellar tensor, for which the covariant-contravariant transformation does not make a change of the direction. Such eigendirections of the movement are not affected by cerebellar lesion.)

are executed by the three-parameter limb in a particular style. As seen, the generated displacements are fair, but not correct, implementations of the intended vectors.

The 'writing' in the above case shows distortions which are characteristic for the individual choice of the intrinsic geometry, which in the above example is a position-independent geometry. (In other words, the  $\alpha, \beta, \gamma$  hyperspace is flat, has no curvature.) However, embedding of the external space (in this case a two-dimensional one) into an internal, overcomplete three-dimensional hyperspace is geometrically faithful to a flat hyperspace only at first approximation. But when the metric tensor is position-dependent (Fig. 5D), the two-space can be locally more conformable with the three-space in which it is embedded and the execution of intended movement-vectors more accurate.

#### THE VESTIBULO-OCULAR 'REFLEX' AS A TENSORIAL RESPONSE

The tensorial nature of coordination can also be illustrated in systems considerably more complex than elementary limb-movements. One such motor system is the so-called vestibulo-ocular 'reflex', which has been well characterized functionally (see e.g. ROBINSON, 1975; CARPENTER, 1977). Unfortunately, since a formal definition of 'reflex' is not available, one may assume that, for instance, the activation of the lateral rectus muscle of the eye, following horizontal head rotation, is a 'reflex'.

However, in the case of vestibulo-ocular reflex it seems evident that this motor response is a tensorial entity. Consider, for example, a head rotated around its center point in three dimensions. The head-displacement may be represented by a three-dimensional vector in Euclidean space 'spelled out' in any one of the infinite number of possible reference-frames. Let, for example, the head-displacement vector be  $\bar{H}^v = \bar{H}(p, y, r)$  where  $p, y$  and  $r$  are the angles of the pitch, yaw and roll of the head. Note, however, that the head-displacement itself is a physical entity that is an *invariant* of the reference-frame applied: all the different expressions represent *the same vector*. As is well known, the vestibulo-ocular reflex moves the eye in order to compensate for the head movement. Thus, the eye moves with a pitch, yaw and roll:  $\bar{E}^i = \bar{E}(P, Y, R)$ . This eye displacement is also a vector, a reference-frame invariant physical entity. Thus, by definition, the reference-frame invariant vector-vector relationship of  $\bar{E}$  and  $\bar{H}$  is tensorial:

$$\bar{E}^i = \bar{\Omega}_v^i \cdot \bar{H}^v$$

where  $\bar{\Omega}_v^i$  is the vestibulo-oculomotor tensor (VOT).

From the above expression the conceptual difference between vestibulo-ocular reflex and VOT may not seem as significant as it actually is. However, by tensorial treatment, some possible misconceptions may be pointed out regarding vestibulo-ocular re-

sponses. One such tempting oversimplification is that both  $H$  and  $E$  vectors may be expressed in the same external Euclidean space using identical  $p, y$  and  $r$  reference-frame axes ( $p = P, y = Y, r = R$ ). (However, even this is only true at first approximation at best, since the head and eye are not co-centered.)

Nevertheless, by so doing, one could 'slice' the  $\bar{E} = \bar{\Omega} \cdot \bar{H}$  vector-vector function into three 'separate components' as

$$\bar{E}^P = f^1(\bar{H}^p)$$

$$\bar{E}^Y = f^2(\bar{H}^y)$$

$$\bar{E}^R = f^3(\bar{H}^r)$$

where the  $f^2$  scalar-scalar function would be the 'horizontal vestibulo-ocular reflex'.

Since it is much easier to establish one or even all of the three  $f$  functions than it is to establish the properties of the system as a whole, the above simplification is tempting. However, it is a deceptive oversimplification that must be explicitly stated, since

$$\bar{E}(P, Y, R) = \begin{pmatrix} \bar{\Omega}_1^1 & \bar{\Omega}_1^2 & \bar{\Omega}_1^3 \\ \bar{\Omega}_2^1 & \bar{\Omega}_2^2 & \bar{\Omega}_2^3 \\ \bar{\Omega}_3^1 & \bar{\Omega}_3^2 & \bar{\Omega}_3^3 \end{pmatrix} \cdot \bar{H}(p, y, r).$$

It is evident that  $f^1 = \bar{\Omega}_1^1, f^2 = \bar{\Omega}_2^2, f^3 = \bar{\Omega}_3^3$ , but it is also evident that *generally* they do not represent the vestibulo-oculomotor tensor  $\bar{\Omega}$  if the off-diagonal elements are not all zeros. Thus, while appealing, 'slicing' the nine-element tensor into three separate 'components' is demonstrably wrong.

The need for tensorial treatment can be made even more apparent. It should be realized that in the VOT for both  $\bar{E}$  and  $\bar{H}$  a common reference-frame may well be a desirable simplification, but one coordinate system will not do for all transformations from  $\bar{H}$  to  $\bar{E}$ . In between, other vectors, such as firing frequencies of motoneuronal axons, can also be intercepted in the vectorial channel of VOT. These vectors are expressed in different reference-frames, thus the need for reference-frame invariant treatment is obvious. For example, the internal vector of the action of six oculomotor muscles employs an intrinsic reference-frame. The oculomotor-vector  $\bar{M}^\mu$  has  $\mu = 6$  components; it is a physically existing vector and it is related to both  $\bar{H}$  and  $\bar{E}$  in a reference-frame invariant manner. The six-dimensional oculomotor space, which applies to one eye, is obviously overcomplete compared to the physical three-space. Again, a tensorial relation exists between the oculomotor and eye-displacement vectors:  $\bar{E}^j = \bar{\Upsilon}_\mu^j \cdot \bar{M}^\mu$ , where  $\bar{\Upsilon}$  is the Oculomotor Tensor. While  $\bar{\Upsilon}$  is invariant to reference-frames, of course, its expression is the simplest in the reference-frame co-centered with the eye. Employing the convenient pitch, yaw, roll reference-frame, it is once again tempting to equate the oculomotor space with the Euclidean external space and to split the vector-vector relationship into three components which 'establish' the separate  $f^1, f^2$  and  $f^3$  functions. (In this

case the difference of actions in a pair of antagonistic muscles, for example the lateral and medial recti, would constitute one coordinate axis.) While separate measurement of  $f^1$ ,  $f^2$  and  $f^3$  certainly simplifies matters with respect to  $\bar{Y}$  the tacit fundamental misconception need not be further belabored.

Indeed, it is generally felt that a direct, separable correspondence between particular eye muscles and particular eye movement directions is, at best, a simplification. This is emphasized by a scheme for the eye muscle 'cooperation' (e.g. CARPENTER, 1977, p. 133). He concludes that all eye muscles contribute to each component of motion; this implies that, in the present scheme, the off-diagonal elements of the tensor-matrix are indeed not zeros. Also, it should be noted that the weight from the  $i$ -th muscle to the  $j$ -th direction, which he denotes by  $g_{ij}$  (Fig. 7.23), could hardly come any closer to the *identification* of what this array represents. Still, the array of the matrix elements was shown apparently without recognizing that it is the matrix of the oculomotor *tensor*.

In tensorial terms, an important concern is the overcomplete character of the oculomotor space compared to the Euclidean external space. Here it must be assumed again that the extrinsic three-space is embedded into the six-dimensional internal hyperspace. This involves endowing the latter with an intrinsic geometry; by providing a contravariant oculomotor metric tensor. According to this scheme, the eye movements would be implemented, as above, in a two-step operation: the image vector of the intended eye movement would be decomposed first into covariant components (using the metric of the three-space) and then, via the matrix of the contravariant metric tensor of the oculomotor six-space, the covariant components would be transformed into contravariant components. The resulting motoneuronal firing frequencies to all six muscles would actually generate the intended movement vector. As was discussed in detail above and also in PELLIONISZ & LLINÁS (1979a), the ballistic movement of such displacements should show the individually characteristic trajectories that are determined by the geometry of the oculomotor space. Indeed, it is known that the saccadic eye movements, especially the oblique ones, do not usually move along straight lines, but show an interesting curved pattern (YARBUS, 1967; Figure 16; ROBINSON, 1972; VIVIANI, BERTHOZ & TRACEY, 1977). Since the position-dependent character of the tensorial expressions has been mentioned already, the above trajectories indicate that a metric tensor may be utilized to establish the geometry of a *curved* internal oculomotor hyperspace. Eye movement trajectories in the oblique direction would then correspond to the geodesics of this hyperspace.

Other more far reaching considerations may also be mentioned. Gaze is obviously generated not only by extraocular, but also by neck and other body muscles. In this case the head-acceleration is at least a six-dimensional vector and thus, the need for six-

acceleration sensors is immediately evident. Also, since the total tensorial system is, again, position and acceleration-dependent, the need for the otoliths and semicircular canals (i.e. additional position-sensors) is apparent. It is interesting to consider that with regard to the six-dimensional acceleration the six-dimensional oculomotor vector is *not* overcomplete. Note, however, that the *total* system is even more overcomplete than the one in the previous restricted case: the acceleration will evoke eye *and* neck movements and the dimensionality of this system is grossly overcomplete compared to a six-space and thus a metric tensor is required. This metric would provide a 'wired in' system of ratios of the neck and eye movements evoked by given accelerations. In addition, because of the *overcomplete* covariant decomposition of gaze as an intended movement vector; if one (or some) of the coordinate-axes were to be removed even during the movement in progress, target acquisition would still be possible with this scheme. This has been actually shown to be the case experimentally (BIZZI, 1974).

Some of the general implications of this tensorial viewpoint cannot be treated here; however, they will be discussed in a forthcoming publication. Suffice it to say at this junction that while for a stationary body the external three-space is embedded into a stationary intrinsic hyperspace, in the case of acceleration of the body the *external space must be embedded into the CNS hyperspace even though the two spaces accelerate relative to one another*. This latter case involves a rather serious theoretical problem. A possible way to minimize this acceleration is, for instance, to stabilize the head relative to the external space (as in a pirouette, or in the free fall of a cat). This maneuver, i.e. using compensatory neck movements, could reduce or eliminate the accelerations of the head relative to the external space. In the simplest case, intended movement vectors concern a stationary body and a stable visual image. By stabilizing the head the above procedure of covariant analysis of intended movements could be retained even in case of acceleration. Then, since the neck movement vector provides information regarding how the body-space moves relative to the stabilized visual image, the covariant-contravariant transformation may be amended by this second transformation.

## DISCUSSION

### *The geometry of brain function*

Explaining brain function *more geometrico* requires that its function must be analyzed in terms of the abstract geometry of hyperspaces (PELLIONISZ & LLINÁS, 1979a). The advantages of a geometrical explanation of natural phenomena are clear: Geometrical methods describe the properties of natural systems more suitably than engineering methods which have been developed to describe man-made systems. Moreover, this view points directly to tensors as a formal and powerful approach to the global

analysis of brain function, since the concept of tensors extends beyond the particularities of vectors and matrices incurred by reference-frames. Reference-frame expressed vectors are commonly found in CNS networks and are usually described in terms of linear algebra. In fact, it is especially important to point out the fundamental features of the tensor concept, since linear algebraic matrix- and vector representations of neuronal networks are already familiar to readers. Early applications of vector algebra to CNS modeling can be found in WIENER (1948) and, most prominently, in the work of McCULLOCH (1965), VON FOERSTER (1967), ASHBY (1967), GROSSBERG (1970), ANDERSON (1968), ANDERSON, COOPER, NASS, FREIBERGER & GRENANDER (1972), COOPER (1974), and KOHONEN, LEHTIÖ, ROVAMO, HYVÄRINEN, BRY & VAINIO (1977). As regards the cerebellum, multidimensional linear control systems have been mentioned by GREENE (1972).

In contrast to the above, the basic idea in the present set of papers (PELLIONISZ & LLINÁS, 1978; 1979a, b) is not that linear algebraic methods can be applied to CNS, but rather it is explicitly stated that these methods can be applied because *the brain is a tensorial system*.

#### *Steps of abstraction: via vectors to tensors*

To approach an understanding of global brain properties on the basis of available details two basic steps of abstraction are required:

(1) As previously postulated by many authors (see above), neuronal activity distributed over many elements is a *vectorial entity*, expressed in the reference-frame given by the neurons. Thus, the '*language*' of the brain is *vectorial*.

(2) The new consideration is that such vectors possess reference-frame invariant properties, thus they are *tensorial entities* (PELLIONISZ & LLINÁS, 1979a). This leads directly to questions regarding the properties of coordinate-free vectors, and beyond, to the space that contains them. Thus, the *brain as a system is tensorial*, i.e. it implements, by means of the neuronal circuits, tensorial solutions in the same sense that the lenses in the eye establish an object-image relation in a reference-frame-free manner.

As pointed out earlier (PELLIONISZ & LLINÁS, 1979a, pp. 344) the questions of orthogonality, the high dimensionality of CNS reference-frames and the homogeneous treatment of space-time we left untreated in our tensor network theory. Here we distinguish the two types of vectorial expressions which the cerebellar tensor  $\theta$ , acting as a metric, transforms as the CNS uses a *non-orthogonal, overcomplete* system of coordinates. It is left, however, to a forthcoming paper to provide detailed explanation to the dynamic properties of cerebellar coordination. It will be shown that the motor vectors are, in fact, expressed in *space-time* components. Thus the concept of temporal 'lookahead' by Taylor series expansion, introduced in our earlier paper is incorporated

into a unified concept of cerebellar space-time metric tensor.

#### *Tensorial responses are not separable into 'simple reflexes'*

When considering a larger system (e.g. locomotion, or vestibulo-ocular reflex) it is difficult to view the total set of variables of the system in its entirety. Thus the tendency has been to 'slice' the whole into components that are investigated separately. This simplification is particularly clear when defining the properties of the so-called vestibulo-ocular reflex.

It is noteworthy that the analytical attitude (which, when unguarded, may lead to oversimplification) is deeply Cartesian. Descartes, by decomposing complex systems into their components, laid the foundations of analytical geometry: he noted that the position of a point can be characterized by an orthogonal set of coordinates. Moreover, it was this approach that led him to develop the biological concept of 'reflexes'. By analogy from analytical geometry, brain function was thought to be characterizable by a set of separate, simple components—the reflexes. Thus the 'simple reflex' became prevalent for a three-hundred-year period. However, the idea in time has increasingly suffered from an overemphasis on the components, as separable entities. This continued even after the central figure in reflex physiology, SHERRINGTON (1906), strongly emphasized that 'a simple reflex is probably a purely abstract conception'. Re-establishing the entity of the whole vector itself, rather than considering only its components, is not conceptually easy nor is it experimentally attractive: dealing with separate components is both mathematically and experimentally much simpler. Given one component, the concepts and techniques developed for the analysis of a single scalar variable (like a control feedback loop, widely used in engineering) may appear to be applicable. Such an approach, e.g. applied for the vestibulo-ocular 'reflex', seemingly obviates the problem of treating the brain as other than a set of separate reflexes. *Nevertheless the separation of the properties of a system into parts is, in general, incorrect if complete analysis is required. If the latter is sought, a tensorial approach can treat the global entity itself, rather than its separate parts.* To further emphasize this point one may quote HEAVISIDE (1925): '... for general purposes of reasoning the manipulation of the scalar components instead of the vector itself is entirely wrong'.

#### *Coordination by covariant-contravariant transformation by a metric tensor*

The two-step procedure outlined above, i.e. establishing covariant components of an intended 'image' vector in an embedded space and then transforming these 'features' to the contravariant components of the same vector in an embedding space (by means of a contravariant metric of the latter), may be considered the central conclusion of this paper. The transformation requires a contravariant metric of the internal

space which we believe is supplied in the case of the motor system by the cerebellar matrix  $\theta$ . At present, we are only concerned with the subspace of movement vectors; other CNS subspaces will be treated elsewhere. In view of the studies of a metric employed in binocular vision (without using tensor analysis; cf. LEIBOVIC, BALSLEV & MATHIESON, 1971), it is evident that the full utilization of the tensorial approach not only in motor, but also in the visual and other sensory systems, should yield further insights. As already indicated, several properties are as yet unexplored concerning the cerebellar matrix  $\theta$  in serving as a metric tensor. For example, it is morphologically unknown (a) whether  $\theta$  is a square matrix or (b) whether it is symmetrical or (c) non-singular. Also, it was observed that the geometry is position-dependent, i.e. the CNS hyperspace is curved. Whether the curvature of the space is perturbed by the vectorial climbing fiber system, as well as whether the curvature is an intrinsic property of the inherent CNS space or is associated with the reference-frame, will be considered elsewhere.

In short, the generation of a movement (i.e. the execution of an intended vector) is produced by the covariant-contravariant vector transformation by the cerebellar tensor. Utilization of the covariant components of an intended movement is shown here, by computer modeling, to produce an ataxic movement with all of the characteristics of dysmetria and tremor generally found in cerebellar malfunction.

#### *Covariant analysis and contravariant synthesis*

Beyond coordination, we assume that *the covariant*

*feature analysis and contravariant component synthesis is applicable whenever a space is embedded into a hyperspace.* Therefore, it is suggested that this paradigm may be fundamental not only in motor but also in CNS sensory systems. Indeed, the principle of independence in establishing separate perpendicular projections of a vector seems particularly appropriate to sensory systems. Sensors work independently of each other; even ablation of some may not alter the functioning of the remainder. Thus a sensation as a vectorial entity is decomposed by them into covariant rather than contravariant components. From a non-tensorial point of view a similar conclusion was derived by MCKAY (1978) who emphasized that 'the analysis of covariation must be an ubiquitous function of the perceptual nervous system'.

Clearly, while our tentative conclusion is that the cerebellum functions as a metric tensor, and that such conception allows a formal description of the parallel and distributed properties of the central nervous system as a motor coordination device, the properties of the internal CNS hyperspace must be further explored. We consider the present paper mainly as an effort to provide insights into developing a geometrical theory of brain function.

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