

Coordination: a Vector-Matrix Description of Transformations of Overcomplete CNS Coordinates and a Tensorial Solution Using the Moore–Penrose Generalized Inverse

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Neuronal organisms express their function, such as a movement, by multi-componental actions. Thus, the problem of how the central nervous system (CNS) coordinates the elements of a single action is fundamental to our understanding of brain function. Coordinated activation of multijointed “limbs” has also become an acute problem in modern multivariable control theory and engineering, such as robotics. Thus, a coherent interdisciplinary approach is expected, one that arrives at concepts and formalisms applicable to this problem both in living and man-made organisms. By treating coordination with coordinates, tensor network theory of the CNS, which explains transformations through the neuronal networks of natural non-orthogonal coordinates that are intrinsic to living organisms, may successfully integrate the diverse approaches to this general problem. A link between tensor network theory of the CNS and multivariable control engineering can be established if the latter is formulated in generalized non-orthogonal coordinates, rather than in conventional Cartesian expressions. In general terms, the problem of coordinating an overcomplete (more than necessary) number of components of an action can be resolved by a three-step tensorial scheme. A key operation is a covariant-to-contravariant transformation executed by the Moore–Penrose generalized inverse when, in an overcomplete manifold, the covariant metric tensor is singular. In the neuronal organization of the CNS, it is assumed that the cerebellum plays this role of acting as a contravariant metric. A quantitative example is also provided, in order to demonstrate the viability of the numerical and network-implementations.

1. Problems

(A) THE GENERAL PROBLEM OF COORDINATION

The issue of coordination is central to the function of both biological and man-made organisms. It is deeply rooted in the Cartesian decomposition

of one entity into more than one components, e.g. a displacement in physical space into x , y , z . The problem of coordination, not always concisely defined in biology (Towe & Luschei, 1981), becomes explicit when the number of components is more than the minimum necessary; i.e. when the expression is *overcomplete*, so that a single solution is not unique. This is the case, for instance, when a spatial displacement of a part of the body is generated in the form of a so-called "coordinated" movement by not three, but by dozens of muscles. Clearly, the same displacement may arise as a resultant of an infinite variation of components. Any answer to the basic question of how biological systems arrive at a particular multicomponential expression from a choice of an infinite number of possibilities, must be given in terms of neuronal networks. For motor action, this calls for an explanation of how the cerebellar circuitry may perform such a function, since without the cerebellum, motor coordination is known to be absent (Holmes, 1939).

In man-made organisms, such as mechanical manipulators, the same problem emerges when the task is to control movements of kinematically redundant systems, e.g. of a limb composed of more than three joints. In engineering, it is not unusual that solutions for coordination are sought in terms of coordinates (cf. Klein & Huang, 1983). It is noteworthy, however, that at the same time that he introduced his Cartesian system, Descartes was apparently quite aware of the fact that a vectorial approach may be applicable to the brain's expression of sensory and motor events (inset diagram in Fig. 1.). For hundreds of years, however, aspects of coordination in biological and man-made organisms have hardly been dealt with via coordinates, and when done, such were scattered in separate disciplines. For example, some abstract questions have only recently been addressed in pure mathematics (cf. Albert, 1972, Ben-Israel & Greville, 1980). Descriptive aspects of the manifestation of sensorimotor actions are treated in neuroscience, most often by qualitative means (Towe & Luschei, 1981), although recently also quantitatively (Anderson & Hinton, 1981). In contrast, problems arising in the engineering of overcomplete mechanisms are analyzed in multivariable control theory (Klein & Huang, 1983). Since such separated treatises fell into divergent disciplines, it has been considered unimportant for engineering to arrive at control paradigms that were inherent in the operational principles of the brain, or to employ, in multivariable control theory, orthogonal coordinates instead of those intrinsic to neuronal network operations.

In recent years, however, it became possible to establish, on theoretical grounds, some general geometrical principles that appear common to coordination in both living and in man-made organisms (Pellionisz & Llinas, 1980). This paper elaborates a theory of coordination, as it is implemented

by transformation of usually overcomplete coordinates, used in neuronal networks such as those of the cerebellum. The paradigm is presented both in abstract tensorial terms, using the mathematical device of the Moore–Penrose generalized inverse, and is also illuminated by a particular numerical example.

(B) THE SPECIFIC PROBLEM OF COORDINATION IN SENSORIMOTOR SYSTEMS AS A CENTRAL ISSUE IN BRAIN THEORY

The issue becomes crucial when attempting to explain a sensorimotor operation, a primary model of general brain function. Indeed, striving to understand how the brain works, scientists have long turned to a single *sensorimotor system* to serve as a concise model for the function of the brain as a whole. Descartes, for example, pictured a spatial displacement projecting to the eyes, then through the brain, and finally, to the muscles of an arm to produce an identical displacement (see Fig. 1., region [ab1, 2]). However, this “sensorimotor theory” was based on the assumption, made in the absence of sufficient knowledge, that the sensory signals are transformed through the CNS into hydraulic pressures, spreading along the nerves, making the muscles move. Presently, it is not due to lack of knowledge that there is still no generally accepted unifying concept to explain even such basic operations of the brain (Crick, 1979; Lewin, 1982). The modern problem is no longer how to expand further an already unwieldy body of detailed knowledge, since e.g. the structure of neuronal pathways, the functional properties of nerve cells and the synaptic connections between them are rather well known. For instance, for the cerebellum, which is widely recognized as the organ for motor coordination, overwhelming sets of data have already been gathered, see e.g. in Ramon y Cajal (1911), Eccles, Ito & Szentagothai (1967), or Bloedel, Dichgans & Precht (1984).

The fundamental question has been for some time, how to approach conceptually the parallel organization of the CNS in general (Lashley, 1942), or the cerebellum in particular (Llinas, 1974). The subsequent challenge is how to arrive at the most fundamental principles of the operations of CNS, and then how to represent them by suitable formalisms so that both a general qualitative and a particular quantitative interpretation of the available data may become possible.

The first phase of such a program is the construction of heuristic models explaining partial aspects of the function of a neural organism. In cerebellar research (review in Pellionisz, 1984b), partial models which rely on the detailed mechanisms but do not deal with the central biological problem of coordination, are the classic “timing model” by Braitenberg & Onesto

(1961), the "lateral inhibition scheme" by Szentagothai (1963) or the "motor learning model" associated with Marr (Brindley, 1964; Grossberg, 1964; Marr, 1969) and repudiated by Marr (1982, p. 14). Theoretical modeling of the function of the neocortex faces even more fundamental problems. Some models with well-established biological relevance are not matched with suitable abstract formalism, see Edelman & Mountcastle (1977), or Eccles (1981). In other models, mathematical formalisms are extensively used, but they are not necessarily applied to the existing biological mechanisms as they are known in detail in neuroscience (Amari & Arbib, 1982).

Today, a prominent goal appears to be to integrate conceptually the most relevant aspects of the biological function, and to forge this coherent view into mathematically stated formal theory. In the case of sensorimotor systems, this goal necessitates the development of a cerebellar model that can account for the neuronal function of coordination by means of coordinate transformations as performed by cerebellar neuronal networks.

2. Methods

(A) GENERAL METHODS:

ABSTRACT AND QUANTITATIVE LEVELS OF DESCRIPTION OF SENSORIMOTOR TRANSFORMATION OF INTRINSIC COORDINATES

In this paper, it is shown that coordination may be described in terms of transformations through neuronal networks of coordinates intrinsic to the sensorimotor system, and that the problem of overcompleteness can be resolved by a covariant-to-contravariant motor transformation via the Moore–Penrose generalized inverse. The solution is presented by the use of a multi-faceted abstract model shown in Fig. 1. There, a limb, composed of three joints, is to be displaced in the two-dimensional plane of the diagram. The infinitesimal increments of the angles at the joints move the limb in an alpha, beta, gamma local coordinate system. The general question arises then, as to how the CNS expresses its action, e.g. a movement, in such intrinsic generally non-orthogonal frames of reference, where the motor system may have higher dimensions than the sensory system (two-to-three dimensions in Fig. 1).

Morphologically speaking, it is evident that the overall function that provides a solution to this problem emerges from the function of neuronal networks that connect sensory components into motor components. Considering the available neuroanatomical knowledge, such circuitry-schemes as shown in Fig. 1 (regions [c56], [ab57], [ce69]) and Fig. 3 provide only a symbolic representation of the anatomical substrates that are known to

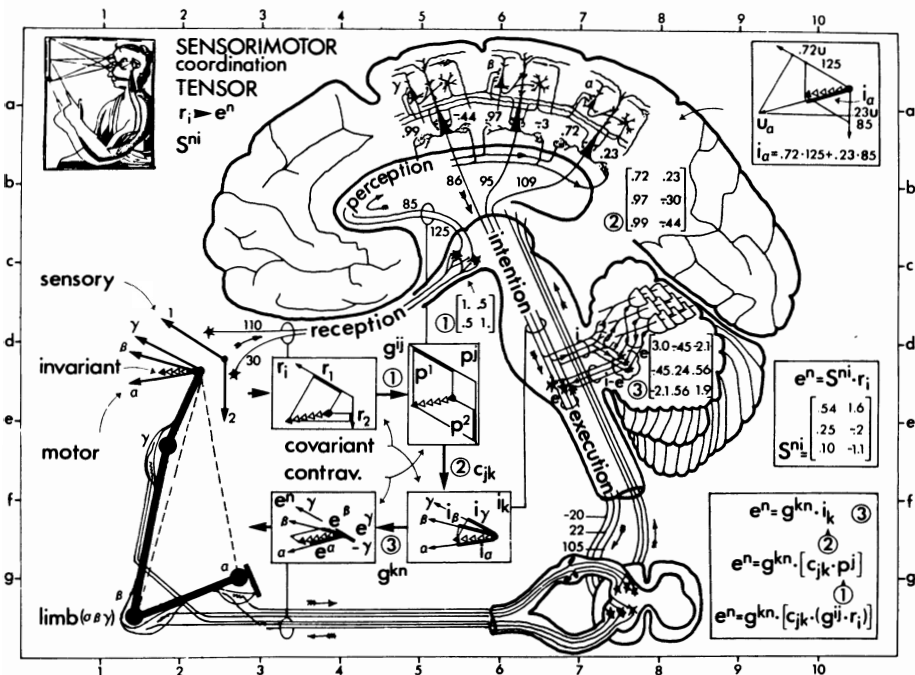


FIG. 1. A tensorial "blueprint" of a sensorimotor system. Parts of this figure are referred to throughout the text by designators (such as [de34], pointing to the r_i block). Different parts of this summary diagram are explained separately by the rest of the figures.

implement a sensorimotor act, yet an explanation of how even such simple systems work is still not trivial. It is also basic knowledge that a set of values, representing, e.g. electrical activities, arise from the sensory neurons. Similarly, a set of firing frequencies of neuronal axons arrives at the muscles of the motor system to generate a movement. Such ordered sets of quantities, as shown in [d3] and [fg7], representing frequencies, are often regarded in neuroscience as vectors ever since the work of Pitts & McCulloch (1947) or Wiener (1948). However, a vectorial approach not only invokes the concept of coordination in general, but also raises the specific question of whether the Cartesian-type orthogonal coordinates that are used in mathematical analyses are, by necessity, the ones that the CNS utilizes in its inner workings. Since there is no reason why Cartesian coordinates should be used within the CNS, a mathematical apparatus applicable to generalized coordinates, i.e. tensor analysis, had to be introduced. Figure 1 deals with such generalized coordinates, where the operations shown are characterized by five different means.

(a) *Abstract, reference-frame independent tensorial expression*

As all explanations of Nature's phenomena must ultimately be expressed at the fully abstract level, the utilization of general coordinates calls for a reference-frame-free mathematical formalism; e.g. tensor analysis. This was the fundamental argument for introducing tensor network theory of the central nervous system into neuroscience (Pellionisz & Llinas, 1979, 1980, 1982*a,b*). Such tensor notation of the transformations is shown in [dg910] of Fig. 1.

(b) *Quantitative arithmetical expression*

In order to relate the abstract theory to the functioning of particular networks, numerical expressions of the transformation of vectors through matrices in the particular example of the general functional model must be made available. This demand is to be met by computing a specific set of vectors and matrices corresponding to an exemplary 120° sensory frame and 0°–25°–37° motor frame throughout Fig. 1.

(c) *Neuronal network expression*

In brain theory, it is necessary to demonstrate how any postulated abstract function may actually be implemented by the structuro-functional reality of neuronal networks, as shown by vectors transformed through matrices of the connectivities in Fig. 1.

(d) *Didactic pictorial expression*

It is also desirable that a theory be supported by an intuitive explanation of the abstract description. This is provided in the form of two-dimensional Euclidean pictograms, [dg36], although it has repeatedly been pointed out that general tensor analysis is applicable to non-Euclidean, or non-Riemannian geometries (Pellionisz & Llinas 1982*b*).

(e) *Verbal heuristic expression*

Reception, perception, intention and execution vectors in Fig. 1 provide verbal description of the neuronal expressions in a manner that each of these intuitive words conveys well-defined mathematical meaning.

(B) SPECIFIC METHOD: TENSORIAL INTERPRETATION OF THE FUNCTION OF NEURONAL NETWORKS

Some fundamental tenets of tensor theory are demonstrated in Fig. 2. First, a set of firing frequencies of neurons, e.g. $r_i = (110, 30)^T$ or $e^n = (105, 22, -20)^T$, each representing an ordered set of quantities, is considered

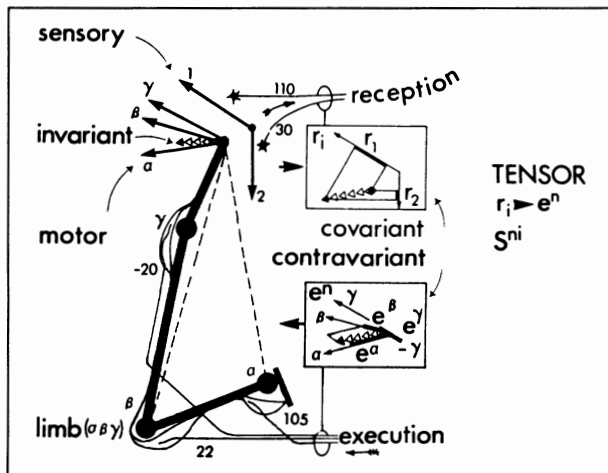


FIG. 2. An external invariant and its covariant and contravariant representation in the CNS. Invariant: arrowheads represent the spatial displacement of a three-segment limb. This invariant is expressed in two non-orthogonal systems or coordinates: a sensory and a motor. The levels of activity, measured in arbitrary units, of two schematically shown neurons provide a covariant, orthogonal projection-type sensory reception vector $r_i = (110, 30)^T$. These components, although expressed in arbitrary units, correspond to the lengths measurable in the diagram of sensory frame with a 120° angle. The motor execution vector has contravariant, parallelogram-type components: $e^n = (105, 22, -20)^T$. Since both r_i and e^n are assigned to the same invariant, they are related by an S^{ni} sensorimotor tensor.

a vector in tensor theory. It is important to note, however, that according to this generalized definition, a vector is a mathematical point in an n -dimensional hyperspace (for a more detailed discussion of this issue, see Pellionisz & Llinas, 1982b). Note that negative frequencies are also used, which refer to decreased spontaneous activity. In these terms, a motor action, such as a displacement of a limb with three degrees of freedom (alpha, beta, gamma), can be interpreted to be generated by an execution vector $e^n = (105, 22, -20)^T$. Given the structural simplicity of the "limb" in Fig. 2, it is easy to establish the unitary directions along which the hand would be displaced if the value of one of the motor angles would be changed. As seen, the measures along these directions represent a set of natural coordinates. Mathematically speaking, these are the non-orthogonal coordinates of an infinitesimal displacement. Thus, while the displacement itself is a physical entity and as such it is invariant to the existence of any system of coordinates, the motor system assigns a vector to it, which is expressed in this oblique frame of reference.

For a successful sensorimotor action, the same invariant displacement must be expressed also in a sensory frame of reference, possibly by another

mathematical vector. There is no reason to assume that in a general sensorimotor action, the natural systems of coordinates used in the CNS are orthogonal, or that sensory frames are identical to the motor coordinate system. Since a tensor is conceptually defined as a mathematical device that expresses the relation among different vectorial expressions that are all assigned to the same reference-frame invariant physical entity, a sensorimotor act is the implementation of a tensorial relation.

While this paper promulgates a general principle that is applicable to any pair of sensory- and motor frames, specific coordinate-axes can also be treated in any given sensorimotor system. For example, for the vestibulo-ocular reflex motor and sensory axes have been revealed by Volkman (1869) and Blanks, Curthoys & Markham, (1975). On this basis, a particular example of the tensorial interpretation of the vestibulo-ocular-reflex in humans can be offered (Pellionisz, 1984a). In this paper, however, it is emphasized that the investigator has to be open to accept and equipped with formalisms to handle *any* natural system of coordinates in which the CNS expresses itself. This is especially warranted because some coordinate systems inherent to CNS function are invisible, yet experimental investigation is in the process of revealing some of their features that appear to be quite far removed from the properties of traditional Cartesian coordinates (Simpson, Graf & Leonard, 1981).

Treating such natural coordinates by formal methods is possible by drawing on any of several available mathematical disciplines (see a short list in Pellionisz 1983b). The advantage of the tensor concept and formalism in brain research can be appreciated when the fact is faced that not only are the frames of reference used in the sensory- and motor systems different, but so are the types of vectors. A distinction has long been made in tensor analysis between two fundamental types of vectors, covariant and contravariant (Einstein, 1916; Levi-Civita, 1926; Synge & Schild, 1949; Coburn, 1955; Wrede, 1973). The general disregard, outside the realm of tensor analysis, of this fundamental mathematical distinction is due to the naive assumption that coordinate systems are always orthogonal, the only instance in which these vector-types are numerically identical. In general systems of coordinates, however, they may be profoundly different. The components of covariant vectors are orthogonal projections to the oblique axes; thus components arise from the invariant independently of one another. Contravariant vectors, however, are composed of interdependent, parallelogram-type components; accordingly, their most important feature is that they physically generate the invariant. The biological importance of this distinction, which is essential to understanding tensor network theory, was first pointed out by this author in Fig. 3 in Pellionisz & Llinas (1980). There it

was postulated that sensory vectorial expressions are covariant-type in the sense that the components are deduced from the invariant independently of one another, while the motor vectors are of contravariant type since the components must physically generate the invariant.

The contravariant character of motor expressions is most obvious in musculo-skeletal systems where the components physically add up to generate the physical invariant of displacement (see the parallelogram components of the motor execution vector in the e^n box in Fig. 2). For sensory systems, the covariant feature is most obvious in the vestibular semicircular canal apparatus, where it is a physical fact that each individual canal responds to the orthogonal projection (cosine component) of the acceleration to the plane of the canal, and this action of one canal is independent of the action of the others. In Fig. 2 a symbolic sensory frame of reference is used to covariantly represent the displacement in a two-dimensional oblique system of coordinates, enclosing a 120° angle. This frame may also be thought of as a rudimentary visual representation of a location by orthogonal projections to two axes forming an oblique angle. The total sensorimotor transformation is thus represented as a conversion of the covariant sensory reception vector r_i into contravariant motor execution vector e^n , by a sensorimotor tensor S^{ni} ; yielding

$$e^n = S^{ni} r_i. \quad (1)$$

In tensor notation, the covariant and contravariant vectors are sub- and superscripted, respectively, and in the equations the sub- and superscripts must balance; see the so-called Einstein-convention (1916), discussed in Pellionisz & Llinas (1982*b*).

As seen in the r_i and e^n boxes in Fig. 2, the task of a sensorimotor system is threefold: to transform a vectorial expression of an invariant in one frame of reference (sensory) to an expression in another (motor) frame, where the directions of the axes are usually different; to change the vectorial version from covariant to contravariant-type; and to perform these two changes in a manner which allows for the possibility that the number of axes in the sensory and motor system may be quite different. A particularly serious conceptual-mathematical problem of coordination is the latter, because the difference in dimensionality may mean an increased number of axes from sensory- to motor frames emerges. Not only the directions of the axes are different, but so is their dimensionality ($n > i$). Since such a conversion to an overcomplete system is not a unique mathematical expression, an explanation of how the CNS arrives at a particular solution must be found, as provided by the three-step scheme below.

3. Solution. A Three-step Tensorial Scheme of Sensorimotor Coordination

The abstract tensorial transformation which is required to convert the sensory reception into a motor execution vector is known to be physically implemented by neuronal networks in the CNS. Figure 3 shows a rudimentary scheme of pathways from sensory reception through a sensory nucleus (corresponding to the optic tectum) to the sensorimotor cortex, and via the cerebellum to the spinal motoneurons, representing motor execution. Tensor network theory states that neuronal circuitries, each different in their particular structure, may perform common general tensorial functions. While this concept has been used for electrical networks in engineering (Kron, 1939), its use in the study of neuronal networks was introduced by Pellionisz & Llinas (1979). How the different neuronal networks may represent the same tensorial function is illustrated e.g. by Fig. 2 in Pellionisz & Llinas (1982a). While vector-transformations may be mathematically represented by apparatus other than tensors (e.g. differential geometry; Spivak, 1979), tensorial treatment has the advantage of providing a *network theory*, required for any functional interpretation of neuronal connectivities.

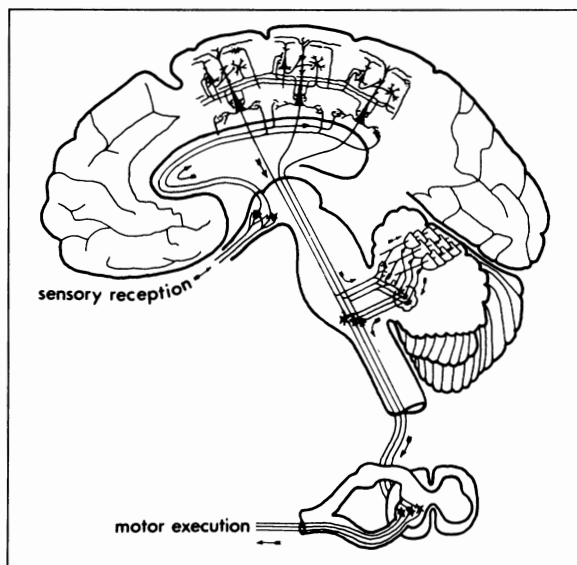


FIG. 3. Schematics of the basic neuroanatomical substrates responsible for sensorimotor transformations. Three major regions of the CNS are presented by symbolic schemes of tecto-thalamic, sensorimotor cortex and cerebellar neuronal networks. These regions take part in a preprocessing of the sensory reception, a sensorimotor conversion, and a coordination of the motor output. The output signal descends on the spinal cord, resulting in motor execution.

Tensor network theory provides a three-step explanation to sensorimotor function; a sensory metric-type transformation, a sensorimotor covariant embedding and a motor metric-type transformation. These steps, each required from abstract conceptual viewpoints, correspond to the function of the tecto-thalamic region (Pellionisz, 1983a), of the sensorimotor cortex and of the cerebellum (Pellionisz, 1984b). This scheme not only offers a solution to the problem of coordination in overcomplete systems, but also resolves other conceptual problems, e.g. how the CNS can arrive at judgments on physical entities external to it, based on their internal vectorial expressions.

(A) SENSORY METRIC TRANSFORMATION: ENABLING INTERNAL GEOMETRICAL JUDGMENTS ON EXTERNAL INVARIANTS

The first tensor-transformation must take place within the sensory system. This operation is sketched in Fig. 4 ([ce26] of Fig. 1).

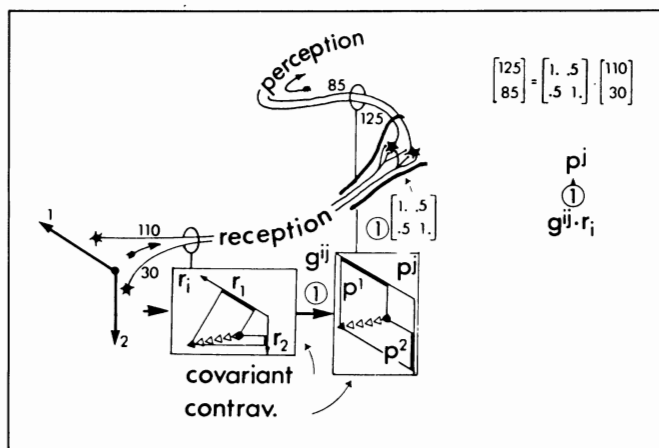


FIG. 4. Transformation of sensory reception into sensory perception. If sensory vectors are available in both covariant and contravariant versions, internal judgments are possible on the external invariant which they represent. The covariant-contravariant sensory metric transformation is implemented by the general contravariant tensor g^{ij} . This appears, for the sensory frame with axes forming a 120° angle, in the form of the matrix (1).

It is basic knowledge that a covariant sensory vector, while it is assigned to an external physical invariant, does not convey explicit information about the invariant itself (such as the length of the displacement). For example, it is impossible to establish the length of the displacement from the covariant

sensory reception vector-components themselves, such as from $r_i = (110, 30)^T$. Nor is it possible to establish this invariant from the contravariant components of the vector $p^j = (125, 85)^T$. However, it is well known that the inner product of covariant- and contravariant expressions (in the same frame of reference) yields the square of the length:

$$D^2 = r_n p^n. \quad (2)$$

Intuitively, this means that if decisions are to be made on the invariant itself within the sensory system without any motor action, *both* vectorial versions must be available there.

Based on the above considerations, it was proposed (Pellionisz & Llinas, 1982a, see elaboration in Pellionisz, 1983a) that the superior colliculus serves as a sensory preprocessor that makes both the covariant and contravariant sensory vectors available. The contravariant version, called the sensory perception vector, can be provided by a simple network that implements a

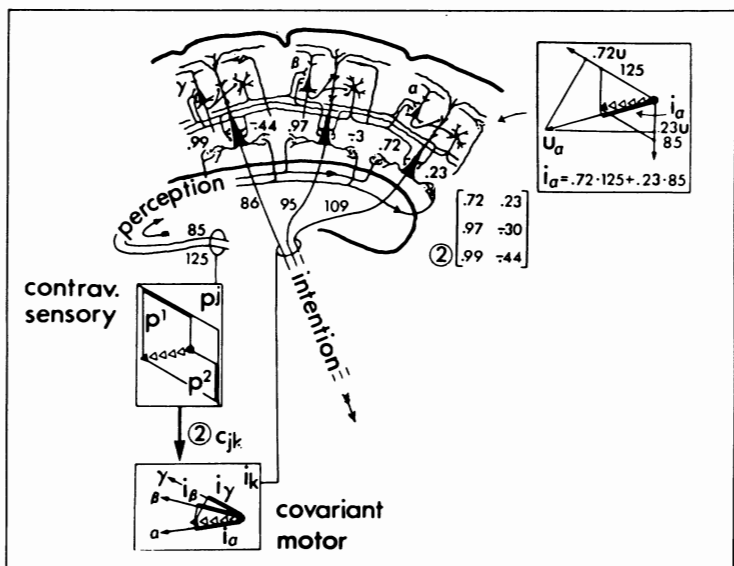


FIG. 5. Sensorimotor cortex: covariant embedding into a motor frame of the contravariant sensory vector. The mathematical principle of using a higher dimensional motor space than that of the sensory space is demonstrated in the box (upper right): a motor unit-vector along an axis u_α must be available, expressed covariantly in the sensory frame. The inner product of these coefficients and the contravariant sensory perception components will yield the covariant motor components e.g. i_α . This inner product is assumed to be taken by a large pyramidal neuron in the module alpha of the sensorimotor cortex. All modules together form the c_{jk} covariant embedding matrix (2).

metric transformation on the sensory reception vector. The cardinally important relationship of co- and contravariant vectors through the metric is shown in Fig. 3, in Pellionisz & Llinas (1980).

As seen in Fig. 4, a particular network may implement the function that is arithmetically expressed as a multiplication of the $r_i = (110, 30)^T$ vector with a matrix. This transformation can be expressed in general coordinate systems by tensorial notation as the contravariant metric g^{ji} (where g^{ji} and g^{ij} are identical, for reasons of symmetry). The numerical values of the output sensory perception vector $p^j = (125, 85)^T$ then represent the parallelogram-type contravariant components of the displacement. For obtaining the numerical values of the matrix of the contravariant metric tensor in a 120° frame of reference, consult e.g. Fig. 2 in Pellionisz & Llinas (1982a). The metric tensor in Fig. 4 can thus be expressed by matrix (1). Its neuronal implementation is a network where the cross-connections are only half as strong as the direct input-output connections. Both the size and the numerical components of the sensory metric depend on the particular features of the sensory frame of reference (e.g. the number of axes and their angle). Thus, while the network-implementation is different in each particular case, the transformation may still be described in an abstract manner by the coordinate-system-independent tensor notation as:

$$p^j = g^{ji} r_i. \quad (3)$$

(B) SENSORIMOTOR COVARIANT EMBEDDING. TRANSFORMATION FROM THE SENSORY COORDINATES TO MOTOR COORDINATES

The second step in the sensorimotor transduction is the changing of the sensory vector into an expression using the motor frame of reference. Such an operation is shown schematically in Fig. 5. The intuitive justification of this step is that the execution of a movement requires that the invariant be expressed in the motor frame. Thus, somewhere along the sensorimotor path, a transformation must take place that converts a vector expressed in sensory coordinates into a vector expressed in motor coordinates. Furthermore, the transformation must be made in such a manner that it can be performed even if the number of dimensions in the sensory and motor systems are not the same, including an increase of dimensions from the sensory to the motor system.

Covariant embedding of the contravariant sensory perception vector into the covariant motor intention vector fulfills the above requirements (Pellionisz & Llinas, 1982a, and Fig. 5 in Pellionisz, 1984a). The mathematical principle of covariant embedding is shown in the upper right box of

Fig. 5 (part [a910] of Fig. 1), and can be verbally expressed as follows: If the covariant sensory components of the unit-vector of a motor axis are available, e.g. $u_{\alpha} = (0.72 u, 0.23 u)$, then the inner product of these components with those of the contravariant sensory perception vector p^j will yield the required orthogonal projection-component of the invariant to the given motor axis, i_k . For this operation, a transformation-matrix is needed (containing the values of covariant projections of each motor unit vector to all sensory axes). If this "covariant embedding matrix" is denoted by c_{kj} , then

$$i_k = c_{kj} \cdot p^j \quad (4)$$

This covariant embedding procedure can evidently be implemented for each motor axis independently of one another by a neuronal network-module that is mathematically expressed as a row-vector of the embedding matrix, and that performs an inner-product vectorial operation with the perception vector. An example of this type of function is shown in Fig. 5, by the "pyramidal neuron"-type cells in the cortical region, the k th of which

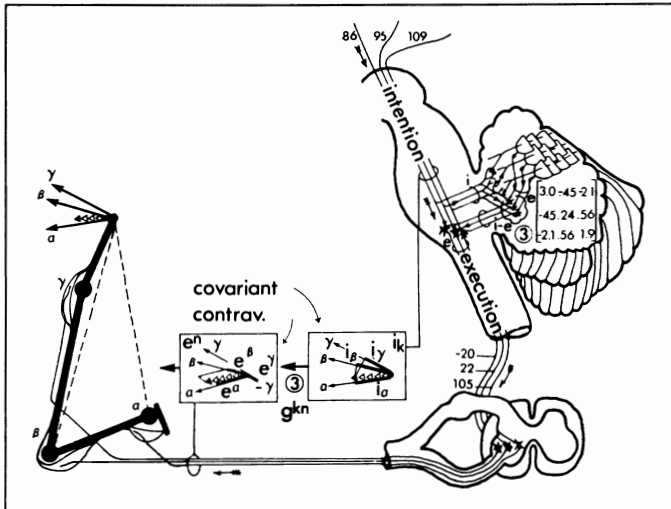


FIG. 6. Cerebellar motor coordination: transformation of covariant intention to contravariant execution by the neuronal network acting as the Moore-Penrose generalized inverse of the covariant metric tensor of the motor space. The covariant motor intention (i) is converted to contravariant motor execution (e) by the network of the cerebellum. Matrix 3 yields the numerical components of the generalized inverse of the covariant metric tensor of the 0-25-37 degree motor frame. The boxes e^n and i_k show that both vectors are assigned to the same invariant displacement (arrowheads), yet the difference is that the contravariant expression executes the movement, while the covariant vectorial version cannot physically generate it.

sums the products of the paired p^j and c_{jk} components. For instance, the covariant motor embedding module for the alpha motor axis (upper right box) produces $i_{\text{alpha}} = 109$ component of the outgoing motor intention signal. The "small pyramidal cell-type" neurons and inhibitory interneuron-type cells of the cortex are not assumed to take part in the covariant embedding procedure. A description of the role of these network-elements in the process of generating the required transformation matrices (a problem discussed in Pellionisz & Llinas, 1981; Pellionisz, 1983b) is not necessary for the understanding of this paper, and will be explained in a forthcoming publication.

While this sensorimotor transformation satisfies the requirements mentioned above, it yields a covariant motor intention vector. This type of vector cannot be used directly to properly execute movements. For a detailed discussion and demonstration by computer modeling of the difference in execution of covariant versus contravariant vectors, see Pellionisz & Llinas (1980). The covariant character of the motor intention vector necessitates the existence of the key element in the overcomplete sensorimotor transformation, presented below, which could not have been offered, however, without the elaboration of the previous two steps.

(C) CEREBELLAR COORDINATION. TRANSFORMATION OF COVARIANT MOTOR INTENTION INTO CONTRAVARIANT MOTOR EXECUTION THROUGH THE MOORE-PENROSE GENERALIZED INVERSE OF THE COVARIANT METRIC TENSOR OF OVERCOMPLETE MANIFOLDS

Acting in a metric tensor-like manner in the motor hyperspace, is assumed to be the role of the cerebellum (Pellionisz & Llinas, 1980). Via this transformation, shown in Fig. 6, the covariant motor intention i_k is converted by the matrix g^{kn} , implemented by the cerebellar connectivity, into a contravariant-type (physically executable) expression in the motor frame e^n . This motor execution vector e^n , arriving at the alpha, beta, gamma executor muscles, is capable of generating the required displacement.

The cerebellar metric-type transformation is explained in more detail in Fig. 7. Indeed, tensor network theory was developed, in the first place, to interpret the structuro-functional properties of the cerebellar network so that the overall cerebellar function of motor coordination could be precisely explained in a formal mathematical manner. The numerical values of the matrix elements in the matrix representation of both the sensory metric and of the sensorimotor embedding were mathematically uniquely determined. Thus, the quantitative example given in Figs 2-6 can be numerically checked on the basis of the geometrical relationship among the sensory and motor axes. In contrast, because of the overcompleteness of the motor frame, there

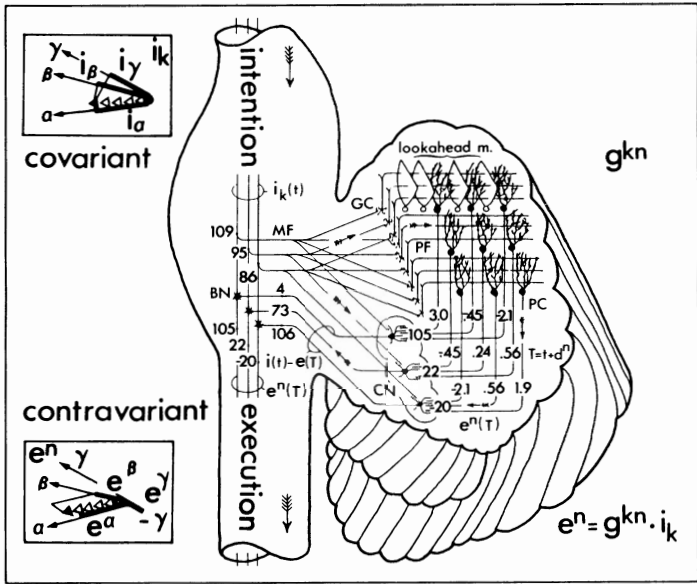


FIG. 7. Detailed scheme of the cerebellum acting as a space-time metric tensor of the motor hyperspace. The network, shown in a more concise form in Fig. 6., is elaborated into a quantitatively traceable scheme of the covariant-contravariant transformation. MF, mossy fibers; GC, granule cells; PF, parallel fibers; PC, Purkinje cells; CN, cerebellar nuclei; BN, brain stem nuclei. The $i_k(t)$ motor intention components refer to time-point t , while the $e^n(T)$ motor execution components refer to time-point T , where $T = t + d^n$. The matrix-elements in the array between Purkinje cells and cerebellar nuclei show the coefficients by which the mossy fiber information must be multiplied to yield the components of the execution vector expressed in summed firing frequencies of Purkinje axons arriving at cerebellar nuclear cells; $e^n = (105, 22, -20)^T$. The Purkinje-cell arrangement along a parallel fiber beam represents a "temporal lookahead module": implying that some supernumerary Purkinje cells take first, or second order time derivative of the input.

is an infinite number of choices for a motor metric-type matrix whenever a motor system is employed that has a higher number of dimensions than the sensory. (For the presentation of this problem, see Pellionisz & Llinas (1980) for a brief introduction of the use of the Moore-Penrose generalized inverse in overcomplete systems, see Pellionisz (1983a,b).) The multiple solution arises from the physical fact that a lower dimensional space can be embedded into a higher dimensional space in many different ways (cf. embedding a point into a line). It is important to point out, however, that once an embedding is *physically* accomplished, e.g. by the structure of a

given musculoskeletal system (e.g. Fig. 1), the geometry of both the embedded and embedding spaces, and thus their relationship, can be uniquely expressed.

The issue of cerebellar coordination-matrix is given central importance because it can be discussed not only from the above intuitive-physical point of view, but also from a mathematical, biological and technical vantage point.

From a mathematical point of view, the problem of uniqueness is in the forefront. For a given set of axes, even if it is overcomplete, the components of the covariant metric tensor are the cosines of the angles between the axes. Thus, the covariant metric is a uniquely determined symmetrical matrix with real-valued components. Its inverse can also be uniquely established either by regular inversion or, in the event of singularity, which is the case in overcomplete embedding, by the Moore-Penrose generalized inverse (Albert, 1972; Ben-Israel & Greville, 1980). Such a solution ensures that in both the non-overcomplete and overcomplete case the eigenvectors of the covariant-to-contravariant (and opposite) transformation-matrices are identical. This generalized inverse is calculated from the cosine-matrix of the depicted 0° - 25° - 37° motor frame, as shown in matrix (3) in Fig. 6.

The biological importance of the overcompleteness is given by the fact that for a particular musculoskeletal system, the above coordination-paradigm requires only the availability in the CNS of a suitable matrix, implemented by a neuronal net.

Such covariant-to-contravariant transformation is an exact basis for a theory of cerebellar coordination. An answer to the question beyond the explanation of coordination, i.e. how such networks are generated by the CNS or in man-made organisms, will be provided elsewhere.

From a technical viewpoint, a theory of the cerebellum using the generalized covariant-to-contravariant metric-type transformation provided by the Moore-Penrose inverse, immediately lends itself to an ultimate technical beneficiary of neuroscience, robotics, by providing a natural control paradigm for multivariable coordination (Pellionisz, 1983b).

Although a more detailed account is given elsewhere Pellionisz (1984b), some important features of the cerebellar network implementation of the paradigm can be pointed out in the scope of this paper. With regard to the *functional architecture* of the cerebellum, as seen in Fig. 7, it is stressed that this organ is an "add on" system so that its extirpation results in a direct throughput of the covariant intention vector arriving at the muscles to execute the movement. This is in good agreement with the clinical findings that movements can be made in the absence of the cerebellum, but they

are uncoordinated (Holmes, 1939). This condition, by definition, would result in "dysmetric", ataxic movements in the model, as demonstrated by the computer graphics in Pellionisz & Llinas (1980), and in its accompanying computer movie display (for reviews, see Llinas, 1981; Llinas & Simpson, 1981). The "add on" character of the cerebellar system is satisfied in the scheme of Fig. 7 in the following way. The covariant-contravariant transformation occurs via the mossy fiber—granule cell—Purkinje cell—cerebellar nucleus path in the network of the cerebellum. This network transforms the intention vector i_k , carried by the mossy fibers, into the execution vector e^n , which arrives at the deep cerebellar nuclei. The mossy fiber collaterals to the cerebellar nuclei, together with the inhibitory Purkinje cell vector, yield the output vector of the nuclei, $i_k - e^n$. In turn, this vector forms, together with the direct intention vector i_k , the e^n contravariant motor execution vector in the brain stem nuclei, which descends upon the spinal cord and drives the motor apparatus.

Additional details are shown in Fig. 7, which, because of their complexity, could not be displayed in Figs 1–6. From the point of view of the *result* of the vector-transformations, it is immaterial which part of the mossy fiber—granule-cell—Purkinje cell chain implements e.g. a given multiplication factor of 3.0 from a mossy fiber input to yield a particular Purkinje cell output. It may be provided by the strength (number and synaptic efficacy) of mossy fiber endings, the number (or sensitivity) of granule cells, or their synaptic efficacy to Purkinje cells, or the electroresponsiveness of the Purkinje cell itself. While such details are important from the viewpoint of morphogenesis and functional modification of the metric, insufficient evidence is available at this time to locate each exact site of such numerical transformations.

The main point of importance here is, that any plasticity required for generating and modifying these matrix-components serves, in this interpretation, to make the network act more precisely as a metric tensor. Thus, plasticity needs to be interpreted as the development of the basic coordination-function. This is in contrast to views that if plasticity is found, it is, *per se*, the function of the cerebellum ("motor learning", cf. Ito, 1982). A similar interpretive issue may be raised concerning the actual spinal mechanism where the signals from the cerebellum and the motor cortex converge. The micromorphological and electrophysiological mechanisms of the spinal cord, however, are much less clear than those of the cerebellum. Nevertheless, the point of "neuronal schematics", as in Fig. 7, is to demonstrate the ease by which the cerebellar-type neuronal networks may yield a matrix-transformation required from a conceptual point of view. For further exposition of the tensorial model of the cerebellum, see Pellionisz (1984b).

4. Discussion

(A) TENSORIAL INTERPRETATION OF THE USE OF GENERAL COORDINATES, INTRINSIC TO CNS: e.g. SPACETIME COORDINATES

Since tensors are capable of expressing the relationship among the vectorial versions belonging to physical objects in a general, reference-frame-free manner, it is possible to interpret the use of any system of coordinates, even those that are highly unusual. This is necessary in a description of CNS function since it has been pointed out, for example, that within the CNS the separation of space and time information is impossible because of the lack of a simultaneity-agent (Pellionisz & Llinas, 1982a). Thus, the cerebellar neuronal network, for instance, cannot use pure space-coordinates as depicted in the didactic example in this paper, but it must work with spacetime coordinates. It is, as a matter of course, likely that the CNS uses other unorthodox (e.g. torque-time) coordinates, that make a particular expression much less straight than the given example of using pure space coordinates. Nevertheless, it is claimed that the need to formally express brain function in such general coordinates is eminently fulfilled by a tensorial approach.

The scheme in Fig. 7 shows some aspects of this spacetime operation in the cerebellar function, not featured in Figs. 1-6. The scheme (Pellionisz & Llinas, 1982a) unifies the "timing" aspect (cf. Braitenberg & Onesto, 1961) and the metric-type "coordination" aspects of the function of cerebellum (Pellionisz & Llinas, 1979, 1980), suggesting that the cerebellum serves as a space-time metric. Such function provides a prediction of a future value of each contravariant component (for details of the "temporal lookahead module" see Fig. 1 in Pellionisz & Llinas, 1979). The principle of generating a prediction of the components in e^n requires that some Purkinje cells that are "in register" along a beam of parallel fibers produce responses proportional not just to the mossy fiber input itself, but also to its first and second order time derivatives. Further, the numerical distribution of the Purkinje neurons taking such derivatives must conform with the requirements of a Taylor-series expansion. In Fig. 7 such a "lookahead module" is shown schematically, outlining only a few Purkinje cells. The "lookahead-module" is a functional redefinition of the role of "stacks" of Purkinje cells, although it is not incompatible with the original morphological "lateral inhibition scheme" (Szentagothai, 1963).

From a closer observation of the detailed structure of the network it becomes clear that there is a wide range of possible variations in how the matrix-multiplication and temporal prediction can be achieved by a particular network. For example, an identical matrix-component may be imple-

mented either by the value of synaptic efficacy of parallel fiber-Purkinje cell connections, or the number of Purkinje cells executing the same function or by a combination of both features. Likewise, the same quantitative effect may be achieved by the strength of the projection of a Purkinje cell onto a nuclear neuron. Finally, since the temporal derivation is a distributive operation, the sum of the output of several Purkinje cells (yielding the same derivative) would be functionally equivalent to the output of a single Purkinje cell taking a derivative of a summed input. The most timely questions in interpreting cerebellar function, however, concern not so much the details of these differences between such possible variations, but the general principles of the solution that must be inherent in all variations of the scheme.

(B) OVERVIEW OF SENSORIMOTOR TRANSFORMATIONS

Summarized quantitative representations of sensorimotor coordination are provided by Fig. 8. In a manner which complements Fig. 3, the three consecutive transformations are shown here by the matrices of the "sensory metric", of the "covariant embedding" and the cerebellar "motor metric". While Fig. 8. provides a variety of representations of the transformations in verbal, visual, vector-matrix and tensorial forms, it is clear that in the absence of anatomically elaborate network-representations such as in Fig. 3, this scheme would probably amount to a barrier in communicating with most experimental neuroscientists. The vector-matrix formalism provides the actual quantitative features of a particular set of transformations. A solely numerical representation may be of high practical value when dealing only with a particular aspect of the tensorial function; when one reduces the scope of treatment to the quantitative tracing of a given vector-matrix operation (Robinson, 1982). On the other hand, the abstract symbolism of tensor analysis can be combined with the heuristic pictograms and with a numerical vector and matrix expression, to yield a general understanding, in addition to practical guidance to the investigation of, the VOR mechanism (Pellionisz, 1984*b*). Nevertheless, the main power of the abstract representation of sensorimotor and other neural function by tensor formalism lies in the fact that it encompasses the functional essence of all particular neuronal embodiments regardless of the peculiarities of a given set of frames of reference. Offering both an abstract and a numerical treatment, based on a general formalism, brain theory can serve as a bridge (cf. Pellionisz, 1983*b*) leading from detailed knowledge of the CNS, through abstract understanding of brain function, to technological utilizations.

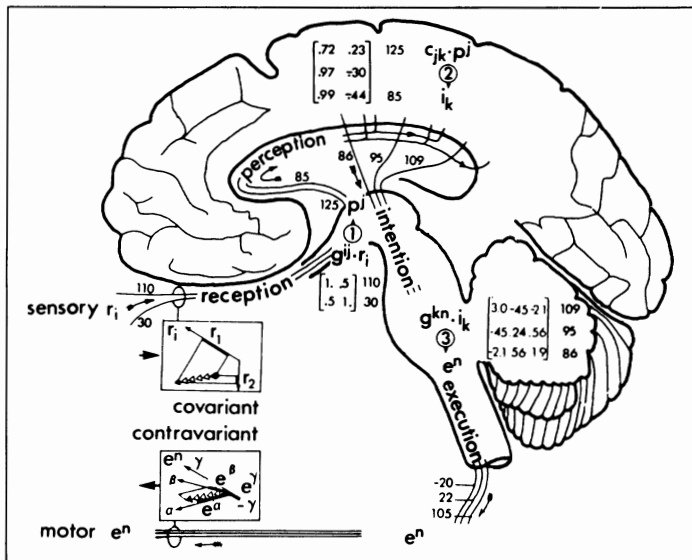


FIG. 8. Vector-matrix and tensorial expressions of sensorimotor transformations. The transformation matrix expressing the sensory metric tensor (1), the matrix of sensorimotor covariant embedding tensor (2) and the matrix expressing the motor metric tensor (3) are shown symbolically. The vector-matrix transformations can be numerically traced from the covariant sensory reception vector r_i to contravariant motor execution vector e^n . Comparison of vector-matrix and tensorial formalisms reveals the practical features inherent in numerical (arithmetical) expressions and the general character and abstract power of reference-frame-independent tensorial expressions. r_i : covariant sensory reception vector, p^j : contravariant sensory perception, g^{kn} sensory metric, c_{jk} : covariant sensorimotor embedding, i_k : covariant motor intention vector, g^{ij} motor metric tensor, e^n : contravariant motor execution vector.

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