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The Olivocerebellar System in Motor Control
Tensor Network Model of the Cerebellum and Olivary System
Quantitatively Elaborated for the Optokinetic Reflex

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Introduction: A Theory of Olivocerebellar Function?

Ever since the discovery (Szentágothai and Rajkovits 1959) that the cerebellar inferior olive is the source of climbing fibers which intimately connect to the Purkinje cells of the cerebellar cortex, it has been physically evident that the function of olivary neurons is inseparable from that of the rest of the cerebellar system (e.g., cerebellar cortex and deep cerebellar nuclei). By the same token, the question has long been posed - although hitherto rarely heeded - "can we make a real system approach to cerebellar function without modeling the whole motor system?" (Arbib et al. 1968). One could carry this argument further, insisting that a motor plant cannot be considered out of the context of a sensorimotor apparatus, and further, that sensorimotor reflexes are only the most rudimentary primitives of the hierarchy of internal cognitive representations by the CNS of the external world. Ultimately, such chain questions lead to the overriding issue of whether our qualitative and quantitative system of understanding of brain function (or even the philosophy underlying brain theory) is appropriate for us to start, within the framework that a theory provides, "putting the pieces together." Leery of either possibility that the answer is (a) "no", or at least "not yet" (and thus an investment in synthesis would be too risky) or (b) "yes", the continuous expansion of the body of data is untenable unless a theoretical infrastructure consolidates (but then such a frame would exert a strong influence on data gathering), only the most forward-looking neuroscientists raise their sights from what can be safely known from experimental investigation. Yet experimentation is always a testing of theories (even if they are implicit or incomplete), and if a theory underlying a specific question from nature is ill defined or inappropriate, then nature's answer will be ill defined or inappropriate, too. Thus, meeting the challenge of coming forth with attempts at theoretical synthesis is an absolutely inevitable task for modern experimentation - if not for reasons of intellectual responsibility then simply for cost-efficiency. Yet, presently, this duty (and the risk it entails) is largely left to professional brain modelists and theorists (one reason for their scarcity).

Although we are still in the early dawn of the era marked by brain theory, the profound impact of its emergence is beginning to be widely felt (cf. Churchland 1985). Theory, at the least, is closely watched by pioneering neuroscientists who have long recognized that the ever-widening base of experimental knowledge, though absolutely necessary, is alone totally insufficient for neuroscience to succeed as a discipline. Experimentalists of this stature are not satisfied
with extending the available body of data, but aim at arriving at theoretical frameworks. For instance, classic cerebellar experimental schools such as that of Eccles, having established the electrophysiological properties of most cerebellar neuronal types, or that of Ito, having revealed the inhibitory nature of Purkinje cells, or that of Szentágothai, having discovered the origin of climbing fibers in the inferior olive, summarized their achievements in a volume (Eccles et al. 1967). Yet, when coming to a theoretical interpretation, they concluded on the last page: "It is essential to be guided by the insights that can be achieved by communication theorists and cyberneticists who have devoted themselves to a detailed study of cerebellar structure and function... The enlightened discourse between such theorists on the one hand and neurobiologists on the other will lead to the development of revolutionary hypotheses... and... these hypotheses will lead to revolutionary developments in experimental investigation." Indeed, cerebellar research has already distinguished itself by at least one outstanding theoretical construct: Marr's theory (1969, rooted in the idea by Brindley 1964). As reviewed elsewhere (Pellionisz 1986a), this theory, which has kept cerebellar research in the limelight for almost two decades, withered away only with Marr's last word "...the study has disappointed me, because even if the theory was correct, it did not much enlighten one about the motor system - it did not, for example, tell one how to go about programming a mechanical arm" (Marr 1982, p. 15).

As discussed at length in a broader overview and tabulation of different cerebellar modeling schools (Pellionisz 1985a), this is only one of the insufficiencies of the vintage Marr theory - from the point of view of utilization. From the point of view of knowledge, that early idea acknowledged neither basic cerebellar function (said nothing about coordination - which is considered its chief role since Flourens 1842), nor structure (said nothing about a sensorimotor or motor system and left even central structures such as the cerebellar nuclei unaccounted for). From the point of view of understanding CNS function, the Marr model has been used to explain a single dimensional amplification "gain" change (of, e.g., the vestibulo-ocular reflex; Robinson 1968; Ito 1970) - although the presently most unanimously held view is that the brain is a massively parallel distributed processor (cf. Rumelhart 1986; Eckmiller and Malsburg 1988) that calls for multidimensional concepts and formalisms.

A multidimensional concept and formalism was established in cerebellar research, both in modeling and theory as well in experimentation. In modeling, cerebellar function was conceived as the transfer of large activity patterns (Pellionisz 1970; Pellionisz and Szentágothai 1973). In experimental analysis it was discovered that the function of the olivary system is expressed by firings of assemblies of neurons rather than single cells (Sotelo et al. 1974), and the case was made for the inevitability of multielectrode recordings (Llinás 1974). In theory, tensor analysis for network transformations of multidimensional intrinsic coordinates was introduced and elaborated (Pellionisz and Llinás 1979, 1980, 1982, 1985, Pellionisz 1983, 1984a,b, 1985b, 1986, 1987, 1988b). Present efforts are intensive in all areas; experimentation, theory and application. (For multielectrode experimentation see Bower and Llinás 1982; Carman et al. 1986; Fukuda et al. 1987). On the theoretical side, not only is the development of tensor network theory being furthered (Pellionisz 1987), but concepts are being introduced for the geometrical interpretation of multidimensional recordings (Pellionisz 1988a). Applications of tensor theory have been pursued in neurobiology (Simpson and Pellionisz 1984; Pellionisz and Peterson 1985, 1986, 1988a,b;
Peterson and Pellionisz 1986; Peterson et al. 1985, 1988; Pellionisz and Graf 1987; Daunicht and Pellionisz 1987), and also lately in neurobotics, neurocomputer and functional neuromuscular stimulation techniques (Pellionisz 1983, 1984, 1986b, 1988a,c). These latter utilizations became possible because the axiom that the CNS operates with natural coordinates that are intrinsic to the sensorimotor apparatus led to tensor geometry, the formalism of general coordinates, as a unifying mathematical language describing both neuronal network transformations and coordination of man-made (robotic) systems.

While attempts at synthesis are already eminently possible in system neuroscience and in its forefront, sensorimotor coordination and gaze research, it is predicted that brain theory will, before long, become a major rejuvenating factor in neuroscience at large. In this paper, attention is focused on a concise quantitative model of the optokinetic sensorimotor reflex, incorporating the cerebellar and olivary subsystems. The intent is to show that some obvious theoretical axioms - that CNS networks, including the cerebellum, use general coordinates intrinsic to nature - already not only yield a framework for understanding CNS function, but also lead to experimental paradigms for independent or collaborative projects (Simpson and Pellionisz 1984; Peterson et al. 1985, 1988; Gielen and Zuylen 1986; Peterson and Pellionisz 1986; Daunicht and Pellionisz 1987; Laczkó et al. 1987, 1988; Lestienne et al. 1987; Pellionisz and Graf 1987; Berthoz et al. 1988; Bloedel et al. 1988; Pellionisz and Peterson 1988a,b).

Tensor Network Model of the Cerebellum: Coordination by Coordinates

As it is impossible to consider the role of the cerebellar olivary system without a treatment of the cerebellum as a whole, the fundamental task is to establish its broadest general functional features. The classical textbook understanding that the cerebellum coordinates movements (Flourens 1842; Holmes 1939; Dow and Moruzzi 1958; Bloedel et al. 1985) is formally restated here: its role is to yield the right set of motor coordinates. This assumption is in concert with general observations that movements do occur even in the absence of the cerebellum, but with the wrong components that do not properly construct displacements (acerebellar dysmetric ataxia; cf. Holmes 1939), and also with specific findings that the cerebellar climbing fibers carry direction-specific information, revealing an underlying coordinate system (Simpson and Alley 1974; Simpson et al. 1979).

Once coordination is treated in terms of coordinates, a fundamental axiom that needs to be recognized relates to the nature of the reference frames used in the CNS. As established earlier (Pellionisz and Llinás 1980), there is no reason to assume that the CNS is limited to the utilization of traditional (Cartesian, x,y,z,t orthogonal) reference frames, but it is an axiomatic fact that it uses those coordinate systems that are intrinsic to nature. This truism is well recognized in neuroscience (cf. Simpson et al. 1981; Simpson and Graf 1985), as natural frames of reference have been quantitatively documented since Helmholtz's (1896) measurements of the extraocular muscle frame in which motoneurons express eye movements. Lately, the quantitative computerized measurement of oculomotor, vestibular, retinal, climbing fiber, neck-muscle, limb-muscle systems has opened up a whole new field of active research (see, among others, Oyster et al. 1972; Blanks et al. 1975; Ezure and Graf 1984; Simpson et al.
The question is not whether such natural intrinsic frames exist, but (a), for experimentalists, how to experimentally reveal them and (b), for theory and modeling, how to formally handle such natural (general, nonorthogonal, typically overcomplete) coordinate systems. The subtlety of the axiom of moving from Cartesian \((x,y,z, t)\) orthogonal frames to general vector formalism can be appreciated from the following fact: Volkmann (1869) and Helmholtz (1896) measured that the axes of eye rotation by superior and inferior rectus muscles are not identical, but lie as far apart as 36° (see Robinson 1975), and thus in fact the extraocular muscle system is not an (orthogonally) paired arrangement. Still, only because of the lack of availability of a formalism to treat nonorthogonal coordinates, were these quantitative data ignored for more than a hundred years and an orthogonal, \(x,y,z\) (paired) arrangement of the oculomotor mechanism was pretended. Likewise, the widely held belief that the arrangement of vestibular semicircular canals is orthogonal flies in the face of precise quantitative data. There is no evidence that in any species such orthogonality would be the case—it is only assumed for lack of an alternative. Instead of 90°, one finds in the human vestibular apparatus an angle of 117.8° (Blanks et al. 1975). The sizable investment of experimentally procuring meticulous quantitative anatomical measurements is wasted if, in the absence of a methodology suitable for non-orthogonal coordinates, such data are shortchanged with convenient orthogonal frames.

Neuroscience is free to use any coordinate system that experiments reveal with the availability of the tensor formalism of general coordinates (Pellionisz and Llinás 1980). The extra investment necessary to turn this freedom into opening new dimensions is only to acquire some intuition and mathematical detail about general frames. This is in short supply, since all of us, especially engineers, have been trained to use the simplest—Cartesian—coordinates. Most important is to recognize the long-established distinction between the two basic versions of vectors in nonorthogonal coordinates (co- and contravariant expressions, Levi-Civita 1926) and the metric tensor that transforms one vector to another. Since the orthogonal projection (sensory-type) and parallelogram (motor-type) components are identical in orthogonal frames, the neurobiological importance of such dual representations, and the transformation between sensory and motor-type vectors by the metric tensor, was pointed out only with the introduction of the theoretical axiom of general intrinsic coordinates (Pellionisz and Llinás 1980, Fig. 3).

By means of this tensorial formalism, it became possible to work out models of various motor systems. For appendages such as limbs, the establishment of intrinsic coordinates and the complexity of modeling the use the CNS makes of them poses special problems (such as dealing with various multidimensional connected spaces; joint space, muscle space, neuronal space). These issues are treated elsewhere (Gielen and Zuylen 1986; Pellionisz 1988a,b). This paper focuses on a special class of sensorimotor systems, gaze reflexes, where neuronal networks transform one intrinsic multidimensional vectorial expression of an invariant (e.g., displacement) to another, operating on a rather simple "limb of one joint", the eye and/or the head, that can also be considered at first approximation to rotate around one center (Peterson et al. 1985). (For a tensorial model of the vestibulo-ocular reflex in man, rabbit, cat and rat, see Simpson and Pellionisz 1984; Pellionisz 1985b; Pellionisz and Graf 1987; Daunicht and Pellionisz 1987; for a tensorial model of the vestibulo-colic reflex in the cat see Peterson and Pellionisz 1986; Peterson et al. 1986; Daunicht and Pellionisz 1987; Peterson et al. 1985; Gielen and Zuylen 1986; Laczkő et al. 1987).
Fig. 1. Retino-ocular (optokinetic) sensorimotor reflex as a tensorial transformation, via neuronal networks, of sensory coordinates that are intrinsic to retinal ganglion cells and of motor coordinates that are intrinsic to extraocular muscle motoneurons. A, Sensory frame, intrinsic to mammalian retinal ganglion cells (data shown in table originate from Oyster et al. 1972). The four-axis frame (of maximal on-off type direction sensitivities of retinal ganglion cells) lies in the 2D plane of the retina. These exemplary axes are displayed in the extrinsic pitch, yaw, roll frame. A corresponding frame in the cat is yet to be established and put into the context of this conceptual model. Dor, ganglion-sensitivity axis along a mostly dorsal direction, lat, lateral; ven, ventral; med, medial direction. B, Motor frame, intrinsic to the extraocular muscles in the cat (data shown in table originate from Ezure and Graf 1984). The six eye muscles (MR, medial rectus; LR, lateral rectus; IR, inferior rectus; SR, superior rectus; IO, inferior oblique; SO, superior oblique) rotate the eye in this six-dimensional frame that is intrinsic to the anatomy. Central inset: the scheme of the cat head shows a retinal (A) and an oculomotor (B) apparatus. Vestibular semicircular canals and several neck muscles are displayed here only to indicate that the hierarchy of gaze reflexes employs at least two sensory and two motor systems (see Pellionisz 1986). ROR, To act as an optokinetic (retino-ocular) reflex (ROR), neuronal networks have to transform a shift of the visual image, passively measured in retinal coordinates, into an active eye movement that is physically executed in oculomotor coordinates. Transformation of vectors within and among general coordinates can be described by tensors.
A Sensory Frame:
Axes intrinsic to retinal ganglion cell sensitivities (4 axes in 2D)

B Motor Frame
Axes intrinsic to eye-rotations by extracocular muscles (6 axes in 3D)

Method (1896). The xyz and x'y'z' origin and insertion points of a muscle, together with the x'',y'',z'' rotation point of the eye, determine a plane whose normal will be the axis along which the eye turns (right-hand rule for the right eye, left-hand rule for the left eye is assumed; cf. Pellionisz 1985b). This method has been utilized by Ezure and Graf (1984) to anatomically measure the oculomotor coordinates shown in Fig. 1B. It is evident that the oculomotor neurons must express eye movements using this frame that is intrinsic to the physical geometry of the arrangement of muscles.

The retinal sensory frame (Fig. 1A), although it consists of a simple four-axis arrangement, constitutes yet another kind of intrinsic frame. As established by Oyster et al. (1972) for the rabbit - a comparable set of measurements for the cat remains a challenge for experimentalists - the retinal ganglion cells carry directional information on the displacement (velocity) of retinal image, in effect constituting a "neuronal" intrinsic frame similar to the one displayed by cerebellar climbing fibers (Simpson et al. 1981). This class of frames intrinsic to CNS function (and not to the anatomical structure) are, of course, much more difficult to experimentally establish than skeletomuscular intrinsic coordinates; nevertheless,
Four-Stage General Tensorial Sensorimotor Transformation Scheme

1. Covariant reception
2. Contravariant perception
3. Covariant intention
4. Contravariant execution

Tensorial Scheme of the Retino-ocular (Optokinetic) Reflex in the Cat
With retinal sensory and eye movement motor frames quantitatively established, the reflex of tracking the retinal image displacement of a moving target by ocular rotation can be mathematically stated as a tensor transformation between two vectors that express the identical image displacement in the retinal sensory frame and in the oculomotor system of coordinates. Fig. 2 encapsulates a general tensorial scheme (valid for any coordinate system) of how the primary measurement is transformed into final execution. The scheme provides solutions for three necessities: (a) the change of frame from sensory to motor; (b) a resolution of the mathematical problem that the number of motor axes is larger than the number of the sensory axes (this overcompleteness permits an infinite number of variations in motor expression; cf. Pellionisz 1984); (c) change of the vectorial version used in sensory and motor frames. This latter problem (explained in more detail in Pellionisz and Llinás 1980; Pellionisz 1984, 1985b) concerns the fundamental fact that primary sensory measurements, (most obviously the vestibular canal excitations) are expressed in orthogonal projections (sensory-type, so-called covariant) vectorial components, while the physical motor execution (resultant of muscle actions) has to be expressed in parallelogram components (motor-type, mathematically so-called contravariant vectors, since the sum of covariant components does not physically add up to generate the invariant; cf. Pellionisz and Llinás 1980). These different versions are depicted in the upper row of Fig. 3. Both the sensory and motor frames are displayed in this row in an exemplary manner, the motor frame being overcomplete compared with the sensory frame (three motor axes versus two sensory axes) similar to the overcompleteness of the ROR (making a transformation from four retinal axes to six eye muscles). The proposed tensorial scheme uses three transformation matrices (A, B, C, shown by patch diagrams, cf. Figs. 3-4) that transform the initial covariant reception vector into a contravariant version expressed in the same frame, and to a covariant intention vector that already uses the motor frame, but yields projection-type, "naive" components that are unsuitable for direct execution and thus have to

Fig. 2. Tensorial scheme of the retino-ocular (optokinetic) reflex in the cat. The theoretically required four stages (1-4) of a general tensorial sensorimotor transformation scheme are shown in the upper row, using simple exemplary coordinate systems (two-axis nonorthogonal sensory frame and three-axis nonorthogonal motor frame). For readability, the frames shown are simplifications of those used in Fig. 1. For calculating A, B and C, however, the actual retinal and oculomotor frames (Fig. 1) were used; cf. also Fig. 3. It should be noted that if a general (tensorial) transformation solution is valid for one unrestricted set of frames, it is valid for all. Diagrams (2-4) demonstrate that in nonorthogonal frames of reference the orthogonal projection type (covariant) and physically executable parallelogram component (contravariant) vectorial expression are different. In order for an optokinetic reflex to work, an invariant (such as the position change of a target) has to be both measured (by covariant components in the retinal frame, \( u^i \)) and executed (by contravariant components expressed in the oculomotor frame, \( v^m \)). The proposed solution (Pellionisz 1984) implements this transfer by means of a three-tensor network transformation (A, B, C), employing two interim vectorial expression s: \( u^j \) and \( v_n \).
Tensor formalism

Verbal expression

Contravariant metric tensor of the coordinate system of retinal ganglion neurons

Matrix expression of tensors

- .257 .053 -.251 .022
- .053 .260 -.029 -.252
- .251 -.029 .247 .000
- .022 -.252 .000 .247

Patch-diagram representation of the matrices

Theoretical hypothesis

Retinal sensory metric tensor: function of superior colliculus
Retino-ocular sensorimotor coordinate transformation
Metric tensor of motor space: function of cerebellar network
be turned into contravariants first (cf. Figs. 3-5 in Pellionisz and Llinás 1980).

A quantitative elaboration of the sequence of three multidimensional tensor transformations is shown in Fig. 3 (the steps follow procedures given in Pellionisz 1984, 1985b). Tensors are presented in abstract formalism (generalized for all coordinate systems), verbally, by numerical matrix expressions, patch diagrams, and also by putting forward the theoretical prediction for their site of implementation. Since tensor network theory claims that such tensor operations are incorporated by networks, it may be particularly important to show, in Fig. 4, how a "tensor network module" (which is a set of interconnections among input axons and a column of output neurons) may embody not just a particular matrix, but a general tensor transformation, or even a functional geometry. It is easy to conceive that the i input fibers, each carrying a firing frequency, constitute a multidimensional (here, four-dimensional) vector, whose components will be multiplied, to yield the scalar product, by the components of one row of the matrix of interconnection strengths. The sum of these products (altogether a scalar product) will yield the firing frequency of one output cell (neurons are symbolized in Fig. 4. and throughout the paper by exemplary dendritic trees). The output vector of firing frequencies of all neurons will be the product of the input vector with the matrix of interconnections. While the particular matrix of interconnections and the values and dimensions of input and output vectors may vary, a class of a given tensor network module (e.g., representing the superior colliculus of different specimens or even species) may embody one and the same general tensor. For instance, if the component values of the connection matrix are such that the network transforms an input vector with covariant components to a vector expressed in the same frame but with contravariant components (cf. transformation of \( u_i \) to \( u^j \) by \( A \) in Fig. 2), then the network performs the operation of the metric tensor, which in effect comprises the geometry of the space spun over the axes of the coordinate system. Speaking of generalizations, it must be emphatically stressed here that the notion of general coordinates is not limited to space coordinates only. While - for the sake of simplicity of exposition - only space coordinates are used in this paper, the cerebellum is conceived (and elaborated, e.g., in Pellionisz and Llinás 1982) as a metric tensor of the unified space-time domain, such that coordination and timing functions are inseparable.

Fig. 3. Tensors of the optokinetic reflex. The three transformations necessary for a sensorimotor transfer are shown at five different levels of abstraction. The quantitative matrix expressions are calculated from data shown in Fig. 1. The sensory- to motor-frame conversion (middle column) is a 4 x 6 table of cosines among the four retinal and six oculomotor axes. The sensory and motor contravariant metric tensors (first and third columns) are the Moore-Penrose generalized inverses of the covariant metric tensors (which are, again, the tables of cosines among axes of the sensory and motor frames, respectively). The patch-diagram representation of these matrices is used for illustrating throughout the figures the network implementations of these transformations. Filled and empty circles represent +/- components of the matrix, with the area of each patch proportional to the numerical value of the matrix component. For more detail, see Pellionisz 1984, 1985.
Tensor Network Module

Input n-vector expressed in an intrinsic frame

$u_i$

Column of output neurons

$g_{ij}$

Output m-vector (product of input vector with a transformation matrix), expressed in the same, or in a different intrinsic coordinate system

$d^2 = u_j^* u_i$

A tensor module may implement a metric tensor transformation:
connecting covariant (sensory-type) and contravariant (motor-type) expressions e.g., in the functional space spun by the sensory axes:

$u_j = g_{ij} u_i$

Implementing the geometry enables decisions on the external invariant "distance" $d$:

Hypothesis for the function of colliculus superior

Fig. 4. Tensor network module. Diagram illustrates how a neuronal network can be conceived of (at different levels of abstraction) as implementing (a) a matrix, (b) a tensor, (c) a functional geometry. The visual symbolism of a tensor network module is composed of (1) a bundle of input axons, whose firing frequencies constitute an ordered set of quantities, a vector; (2) a bundle of axons of output neurons which carry another vector (the number of fibers in the input and output pathways need not be equal); (3) a set of interconnections among the axons of input fibers and the dendritic trees of the output neurons. Such compact arrangement of heavily interconnected neurons is similar to the structure of a nucleus along a neuronal pathway. A matrix: Components of the interconnections matrix may be implemented, e.g., by synaptic strengths, and/or of the number of synapses; the diagram shows such effect by means of patches (cf. Fig. 3). A tensor: If for the shown case the input vector carries a covariant vector of retinal measurements ($u_i$) and the numerical values of the transformation matrix components correspond to the contravariant metric tensor of the retinal space ($g^{ij}$), then the vector of output neuron firing frequencies will carry the product of the input vector with the transformation matrix, which is the contravariant retinal vector ($u_j$). A geometry: By comprising the metric tensor, a simple neuronal connectivity in effect establishes the functional geometry of the retinal space.
With the visual symbolism of tensor network modules, the "evolution" of a multidimensional sensorimotor reflex can be put forward (Fig. 5). Part A presents the most essential element, the transformation tensor matrix from a four-axis retinal sensory frame to a six-axis oculomotor frame. The components of this matrix easily arise if each motor axis is projected, one by one, to all sensory axes (such a procedure is shown in Fig. 5 of Pellionisz 1985b). Mathematically speaking, the components are the cosines among sensory and motor axes. While this is an utterly simple transformation, it is inadequate, in itself, to represent a sensorimotor reflex for several reasons. First, neuroanatomy demonstrates that sensory detectors never connect in a single step to the motor apparatus (thus, a single brain-stem matrix would lump an entire three-neuron reflex arc into a single matrix; Robinson 1982, versus Pellionisz 1985b). Second, the single table of cosines (a projection matrix) would mathematically do if the input sensory vector were contravariant and the output would have to be covariant. However, in sensorimotor transformation vectors of the opposite types occur: the sensory input is covariant and the motor output has to be contravariant (cf. Fig. 2). Thus, the single transformation matrix of A alone would, indeed, yield a motor vector but with wrong component values, an approximation at best. A further deficiency of such a primitive sensorimotor transfer shown in A is that no decisions can be made on the external invariants (distances) without actually performing the movement (a life or death question when jumping a ditch).

Section B of Fig. 5 shows that with the introduction of a sensory preprocessing, incorporating the sensory geometry, two of the above problems are eliminated. First, network A of Figs. 2-3, serving as the metric tensor of the retinal frame, would make available the contravariant counterpart of the covariant retinal sensory vector. As shown in Fig. 4, with both representations available, their inner product yields a measure of the invariant distance itself. Thus, no actual motor performance ("jumping of the ditch") would be necessary to decide if it is appropriate to attempt a movement; such decisions are possible entirely within the sensory domain (for further elaboration of inferring invariants from dual representation, see Pellionisz and Linás 1982; Pellionisz 1987). Second, such a metric tensor (mathematically, the matrix of Moore-Penrose generalized inverse of the table of cosines among sensory axes; cf. Albert 1972; Pellionisz 1985b) will yield the proper contravariant sensory vector transformed from the input. However, the third deficiency remains: schemes A and B in Fig. 5 yield the motor output in improper (covariant) vectorial coordinates.

Section C of Fig. 5 shows that these two transformation tensors are predicted to be embodied by the neuronal networks of the optic tectum (and pretectum), in accordance with the findings that its input is sensory, its output is motor, and that it converts retinotopic measurements to a vectorial version that yields distances (Sparks and Pollack 1977). Since the brain-stem core of the ROR in section C consists of the same transformations as in section B (the oculomotor tensor module is only a "transmitter", a unit matrix with diagonal elements of 1 and off-diagonals of 0), in the absence of the cerebellum the oculomotor response would be executed with covariant (dysmetric) components. Again, specific quantitative experimental tests of the theoretical prediction of dysmetric eye movements (which are easily modeled) would be most valuable.

Section D of Fig. 5 complements the brain-stem core of the ROR with an "add-on" cerebellar circuit - corresponding to the fact that the
Fig. 5. Tensor network model of the stages of "evolution" of the optokinetic reflex (ROR), including the essential cerebellar network. 

A, The absolute necessity for a sensorimotor performance is a conversion from a sensory coordinate system to a motor frame. This is accomplished by a tensor network which incorporates the matrix of the cosines among sensory and motor axes (cf. Fig. 3B). While such a network is easily constructed by the CNS, it yields an approximative, projection-type (covariant intention) motor output. Also, the eye displacement, necessary to compensate a shift of the retinal image, can be judged only by actually performing the movement. B, A tensor-network module, implementing the metric tensor of the sensory space (cf. Fig. 3A), complements the system in such a manner that with the availability of both the covariant and contravariant retinal expres-
The Olivary-Climbing Fiber System: Ongoing Correction of the Cerebellar Metric Tensor to Make It Position-Dependent (Change the Curvature of the Motor Hyperspace)

The tensor network diagram of Fig. 5 predicts an optokinetic reflex which may function in the total absence of the cerebellum (with quantitatively predictable ataxic performance). It also predicts that decisions can be made on the movement amplitudes within the sensory domain. When a movement is made, it is still with intentional components. C, It is predicted that the two operations described above are implemented by networks of the colliculus superior. If the brain-stem core of the ROR is not complemented by a cerebellar circuit (corresponding to the case of cerebellar ablation: see its removal along the dotted line), intentional motor commands are transmitted through the oculomotor nuclei, which network consists of straight connections of input and output fibers, mathematically, a unit matrix, to result in an ataxic (naive) motor performance. D, The cerebellar tensor network provides the metric of the motor system (cf. Fig. 3C). Mossy fibers (MF), carrying a motor intention vector, are transformed through the granule cell (GC)-parallel fiber (PF)-Purkinje cell (PC) pathway to the cerebellar nuclei. If the corticonuclear system of projections of Purkinje cells forms the matrix shown in Fig. 3C, then it will transform the mossy fiber covariant input to contravariant motor output, and with a negative sign since Purkinje cells are inhibitory. The mossy fiber collaterals to the cerebellar nuclei provide a direct (excitatory) intention vector. Therefore, the vector leaving the cerebellar nuclei (CN) will carry the i-e intention-execution (coordination) vector. This negative vector, projecting to the oculomotor nuclei, will result in the i-(i-e)=e contravariant execution vector.
Fig. 6. The olivary-climbing fiber system updates the cerebellar motor metric tensor in an ongoing manner to correct for position-dependence (changing the curvature of the motor hyperspace). A fixed matrix, acting as a metric tensor, provides a perfect covariant-contractive transformation only if the intrinsic coordinates do not change with the position of the eye. Since such a change is a fact, in secondary positions of the eye the metric will be only approximative; thus, an error will occur in the optokinetic reflex. This error vector can be produced by the neuronal network of the olive acting as a "comparator" of the motor execution signal e and the change that actually occurred in the position of the retinal image. Comparison is possible only if the accessory optic system (AOS) transforms the retinal vector into one expressed in oculomotor coordinates. The olive thus receives the oculomotor error vector. Its output is a climbing fiber correction vector that is the error vector expressed in eigenvector components (for this operation, the olive must store the eigenvector of the oculomotor system). The climbing fiber vector reaches the cerebellar nuclei in two ways: directly, via climbing fiber collaterals to the nuclei, and indirectly, via Purkinje cells that also project to the nuclear neuronal array. Thus, the external (matrix) product of the climbing fiber vector with itself can momentarily arise over the array of nuclear cells. This complementary matrix functionally updates the wired-in cerebellar metric tensor, such that the cerebellum can act as a metric not in a position-independent "flat" but in a position-dependent "curved" motor hyperspace.

Once the cerebellum is fully developed, the olivary-climbing fiber system is not part of the essential cerebellar network. The network diagram of Fig. 5 therefore provides a quantitative framework for data about an experimentally accessible and technically duplicatable entire multidimensional coordinated sensorimotor apparatus, within which the specific function of the olivary-climbing fiber system is proposed as shown below below (see Fig. 6). It is hoped that such explanations might bring closer the day when cerebellar modelists first explain (and perhaps even check by implementation) cerebellar coordination of multidimensional sensorimotor systems (that actually works in the absence of climbing fibers) before attributing a single dimensional gain-control role, attained by a Purkinje cell-climbing fiber-parallel fiber heterosynaptic junction, or postulating an associative memory role that will not coordinate a movement.

The proposed role of the olivary-climbing fiber system has two facets (the elements were shown in Pellionisz and Llinás 1985). One is played in the genesis of the cerebellar metric tensor network (see the metaorganization principle and procedure in the above paper), the other is exerted in the ongoing modification of the metric tensor function (Llinás and Pellionisz 1985). It is obvious from Fig. 6, that these functions are inherently multidimensional, corresponding to findings that olivary neurons fire in assemblies of electrotoneically coupled neurons (Sotelo et al. 1974; Llinás 1974). Mathematically speaking, the model interprets information carried by bundles of climbing fibers (vectors) to cerebellar zones of Purkinje cells (cf. Voogd and Bigaré 1980), rather than interpreting a single climbing fiber as communicating a scalar value ("gain") to a single Purkinje cell.

The function of the olivary-climbing fiber system as an ongoing modifier of the cerebellar metric is necessitated by the mathematical
fact that the fixed matrices of Fig. 5, without climbing fiber modification of the electroresponsive properties of Purkinje cells, would yield a perfect mathematical result only if the coordinate systems intrinsic to the retinal ganglion cells and to the eye rotations by extraocular muscles were fixed (did not depend on the position of the eye). This is only approximately true, however, (Figs. 4, 8, 9 in Ostriker et al. 1985 provide quantitative measures of how the frame intrinsic to the oculomotor apparatus changes with the position of the eye; the position dependency is not dramatic but certainly perceptible). Therefore, if the cerebellar metric tensor is perfectly calibrated to yield exact contravariants from covariant components in the primary eye position, the "wired-in" matrix connections of the cerebellum perform only an approximative metric transformation when the eye is in a secondary position. The model therefore predicts a quantifiable error shift of the retinal image during optokinetic tracking in climbing fiber-deprived preparation (another prediction for quantitative experimental tests).
As for the function of olive, it has been suggested (Oscarsson 1969; Armstrong 1974) that in this system, being connected both to the downgoing executor pathways as well as ascending pathways reporting on the motor performance, the olive may serve as a "comparator". It is also experimentally known that such retinal error shifts are reported to cerebellar Purkinje cells by means of climbing fiber-evoked complex spikes expressed in an intrinsic coordinate system (Simpson and Alley 1974; Simpson et al. 1981; Simpson and Graf 1985). This experimental knowledge is represented in Fig. 6 by the postulates that the olivary network computes the error vector of the performance, expressed in oculomotor coordinates (by comparing, in this case, the oculomotor execution vector with the retinally detected displacement of the image of the target). Such a comparison, however, of one vector expressed in retinal frame with another expressed in motor frame, would not be possible if they were not converted into a common frame. Thus, conclusion of the experimentation that the function of the accessory optic system (AOS) is to convert retinal coordinates to another frame that appears to be an oculomotor coordinate system (Simpson et al. 1979, 1981) is a strong basis for this model. Since the analysis of this question in depth is presently a focus of active research, in this paper the retino-ocular conversion is only tentatively represented, using matrix B from Fig. 2.

The above-elaborated ongoing modification of the cerebellar metric accords well with the observation that a "phasic" grouped firing of climbing fibers occurs whenever errors or obstacles are encountered in motor coordination function (Llinás and Volkind 1974). It is also worthwhile to point out that the anatomy of cerebellar pathways, specifically, the direct projection of climbing fiber collaterals to the nuclei together with the indirect projection to the same array via Purkinje cells of the cerebellar cortex, enable the olivary system to construct an external (matrix) product of the climbing fiber error vector on the array of cerebellar nuclear cells (see more detail in Pellionisz and Llinás 1985, Fig. 4). Thus, when the optokinetic reflex operates in an off-primary position, climbing fiber assemblies (reporting on the error of the metric) functionally update the cerebellar metric tensor by inducing an ongoing modification of the array of nuclear cells.

Mathematically, the above function is equivalent to having in the multidimensional motor space a position-dependent metric tensor, in effect predicting sensorimotor operations to take place in a curved functional space (where the curvature of the operational region is adjusted by the climbing fiber system). Electrophysiologically, such a dynamic ongoing alteration is predicted to be much more distinctly detectable on the array of cerebellar nuclear cells (where a double - direct and indirect - projection of climbing fibers occurs) than on Purkinje cells, which transmit this climbing fiber action only to the nuclei, although from modeling studies it is clear that the deep depolarization may undoubtedly exert some residual influence (Pellionisz and Llinás 1977). Moreover, given that the quantitatively predictable ongoing modification is an inherently multidimensional function, occurring on an array of neurons (and corresponding to the positive and negative components of the error matrix), the alteration is bimodal, positive or negative (or zero) on different particular neurons. Therefore, it is not entirely surprising that single-cell electrophysiological studies looking into modifiability (when interpreted within an entirely different, single-dimensional theoretical framework) are apparently inconclusive (having found both a "depression" detected by Ito et al. 1982 and an "enhancement", reported by Bloedel et al. 1983). It is rather likely that such bimodal ongo-
ing modifications evoked by the olivary-climbing fiber system will be revealed over an array of neurons, using multi-unit recording techniques from which data the effect of the multi-unit signals on the intrinsic functional geometry can be calculated (cf. Pellionisz 1988a). If an experimental paradigm is combined with a quantitative model of those coordinates that are intrinsic to coordinated (and erroneous) motor performance, theoretical predictions of this multidimensional climbing fiber-induced adjustment of the metric will become testable.

Some more subtle aspects of the predicted function of the olivary-climbing fiber system can also be mentioned here, although a more detailed discussion (illustrated by a quantitative example) is offered elsewhere (Pellionisz 1984a; Pellionisz and Llinás 1985). Namely, in order for the climbing fiber vector to mathematically produce the error-correction matrix, the olive has to send a climbing fiber vector expressed in the eigenvector coordinates of the motor system (see mathematical elaboration in Eq 17 in Pellionisz and Llinás 1985). This issue is connected to the other facet of the predicted function of the olive (not in the focus of this paper) — its role in the genesis of the cerebellar motor metric tensor. As proposed by the metaorganization principle and procedure (Pellionisz 1984; Pellionisz and Llinás 1985), such a process is based on reverberative oscillations of proprioceptive and motor executive commands, which tremor stabilizes in the eigenvectors of the motor plant (see Fig. 3 in Pellionisz and Llinás 1985). These eigenvectors need to be (a) sent via climbing fiber vectors to imprint the cerebellar corticonuclear network to serve as the Moore-Penrose generalized inverse, and (b) stored in the olive, such that it can decompose an oculomotor error vector into eigenvector components. A likely neuronal mechanism of storing eigenvectors in the olive may be the experimentally revealed electrotonic coupling of olivary neurons (Sotelo et al. 1974; Llinás and Volkind 1973; Llinás and Yarom 1981). The issue of expressing internal CNS vectors not in structural intrinsic frames, but in such functional derivative frames as the one composed of eigenvectors of the oculomotor frame has also been raised in connection with saccadic burster neurons (in the monkey; Pellionisz 1988b).

Cerebellar Theory: the Challenge of Verification

The above tensor network model of the cerebellar-olivary system, presented in a multidimensional quantitative framework of a sensorimotor mechanism, may indicate to the reader a need to proceed from an overly simplistic basic model of cerebellar function to a much more complex scientific account. If advancing toward increasing complexity (e.g., from single- to multi-dimensionality) leaves one with an uneasy feeling, one may wish to recall that if scientific theories are based on charmingly simplistic assumptions (e.g., that planets rotate around us), then models (e.g., of planetary trajectories) are hopelessly complicated, and experimental verification of such pontification may result in wasted or frustrated science. Based on a much more complex axiom (that we observe planetary trajectories centering around an object that we also rotate around), surprisingly elegant explanations may emerge, leading to perhaps even simpler but certainly more progressive verification.
Verification of theory in neuroscience will be twofold in the future. In addition to experimental scrutiny (e.g., of predictions presented in this paper), the very recent emergence of neurocomputer-related applications has begun to exert a new influence on neuronal (cerebellar) modeling and brain theory. Neurocomputing and neurorobotics industries will become testing workshops for brain theories (Pellionisz 1983, 1988c; Eckmiller and Malsburg 1988). As a result, neuronal modeling and brain theory will no longer be an ivory-tower exercise. No longer will prestige or political clout supremely arbitrate which theory is more advanced; natural selection through survival of actual tests will guarantee evolution. Theories that the earth is flat, or that the cerebellum serves as an associative memory, become untenable when means are available to verify that one reaches an eastern location by traveling all around westward, or when it becomes evident that one cannot program a robotic arm for coordinated movement based on the fiction that the cerebellum is an associative memory.

Cerebellum: Homework for Brain Theory

In a larger sense, one might mention that the basic paradox of analysis vis-a-vis synthesis is not at all unique for cerebellar research. It arises in this domain since sensorimotor research in general and cerebellar coordination research in particular constitute a leading edge of system neuroscience. However, it is a general law that natural science progresses from the initial stage of gathering experimental (phenomenological) knowledge toward the goal of attaining a theoretical (conceptual) understanding. It has been amply demonstrated, e.g., in physics, how the richness of interdisciplinary phenomenology yields in time to the elegance of disciplined theory. Neuroscience, not being an exception among natural sciences, is presently scrambling to generate its own theoretical foundation, although, metaphorically speaking, its body can still be likened to "a well-dressed gentleman with no shoes." There is no doubt, however, that our time is marked by the emergence of brain theory (Churchland 1985). The challenge is immense, and heretofore has been only partially met. A classical, modest approach is based on the philosophy of making brain theory a chapter in control-system engineering by conceiving brain function as an amplification-gain controller (Robinson 1968; Marr 1969; Ito 1970). Lately, modern brain theories, promulgated by physicists, excel in abstract simplification but connect rather loosely to the biological knowledge base (e.g., the Nestor model by Cooper, 1974, or the spin-glass theory by Hopfield, 1982). Others, put forward by biologists, are strongly based on experimental data but are devoid of abstract mathematics (group selection theory by Edelman, 1979, attentional "searchlight" hypothesis by Crick, 1984). It is believed (see review in Pellionisz 1983) that mature neuroscience will demand and insist on theories which are not borrowed from other disciplines (either from engineering or physics) but are of neuroscience, for neuroscience and by neuroscience. Cerebellar research has led for more than 20 years with such theoretical consolidation. It also provides a much-scrutinized testing ground to check if lofty brain theories pass the simple tests of explaining basic CNS functions such as that of a three-neuron arc or of the cerebellum. One may wish, and indeed expect, therefore, that cerebellar research will be among the first to benefit if breakthroughs are truly achieved in brain theory.

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References


Brindley GS (1964) The use made by the cerebellum of the information that it receives from sense organs. IBRO Bull 3:80


Flourens P (1842) Recherches experimentales sur les proprietes et les fonctions du systeme nerveux dans les animaux vertebres, Edn 2, Bailliere, Paris


Helmholtz H von (1896) Handbuch der physiologischen Optik, zweite Aufl. Voss, Leipzig

Holmes G (1939) The cerebellum in man. Brain 63:1


Marr D (1982) Vision. WH Freeman, San Francisco


Rumelhart D (1986) Parallel distributed processing V. I-II. MIT Press, Boston


