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Tensorial aspects of the multidimensional massively parallel sensorimotor function of neuronal networks

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Quantitation and mathematization of experimental neuroscience leads to the establishment of brain theory. Progress is spearheaded by system neuroscience and sensorimotor research, yielding computational paradigms of neural nets, to be utilized by neurocomputing and neurobotics. A mathematical concept and formalism using natural (general) coordinate systems that are intrinsic to the CNS is presented by a detailed elaboration of a computerized tensor network model for the vestibulocollic reflex in the cat, involving the cerebellum. The use of intrinsic coordinates is also shown for the multidimensional frames inherent in neuronal firings, and joint and muscle hyperspaces of the musculoskeletal apparatus of head movements. Tensor theory leads towards a quantitation and geometrization of concepts of motor strategies, trajectories, posture and style.

Introduction

Progress in brain research is characterized today by two main trends. One is the well-known, ceaseless growth of the body of data gathered on the structure and the functioning of the CNS. The other trend is perhaps less noticeable, and is underrepresented in the literature. Experimental neuroscience, just like any other maturing branch of natural science, is irrevocably advancing from a qualitative data-gathering stage (phenomenology) to a disciplined research. Brain science is going to stand on its own philosophical, conceptual, and most of all mathematical-theoretical basis.

Quantitation of the parallel organization of the brain

The progress towards quantitation and mathematization is led by system neuroscience in general, and sensorimotor research in particular. This is the natural proving ground of any mathematical brain theory, since invariants of the external world, such as displacements, directions, forces etc., represented by the CNS in both sensory and motor manner, can be physically measured. This is not necessarily true for higher order but less accessible brain functions, e.g. consciousness. Therefore, in the modern era Hering [29], Mach [42], Helmholtz [28], Högyes [31], Lorente de Nó [40], Szentágothai [82] and others envisioned the understanding of brain function as based on the strategy of first concentrating on simple sensorimotor function (most particularly, the oculomotor reflex), basically following the age-old approach set by Descartes. This cautious and prudent strategy is particularly profitable today as robotics and the emerging neurocomputer industry are looking on neuroscience as the resource of proven natural sensorimotor paradigms for coordinated, vision- and tactile-equipped, and ultimately.

Abbreviations: AOS, accessory optic system; CF, climbing fibre; CNS, central nervous system; GC, granule cell; IO, inferior olive; MF, mossy fibre; PC, Purkinje cell; VCR, vestibulocollic reflex.
intelligent organisms [18, 19, 38, 49, 54, 55].

The present task is to make sure that neuroscience's own theoretical concepts and mathematical formalisms facilitate an advancement in experimental brain research. It is not that neuroscience has been without concepts of quantitation or mathematical techniques. The problem is that such approaches have been borrowed from other disciplines (mostly from engineering) and thus were applied to the brain in a manner that is axiomatically not necessarily appropriate. One example of this is that 19th century philosophy considered the brain to be a machine. Thus, feedback control analysis, as used in electrical engineering, was employed until very recently to characterize, by single-dimensional gain–phase description of the amplification, the function of neuronal networks that underlie movements, e.g. oculomotor activity. Lately, the field of eye movement research has rebounded from such a single-dimensional representation and a multidimensional approach has taken hold [30, 58, 76].

The limitations inherent in concepts that consider the brain as an amplifier and thus, in effect, reduce brain theory to a chapter in control engineering are a subject of a newly established field, neurophilosophy [14]. Here, suffice to illuminate them by pointing out two major inadequacies. First, the automatic assumption that the brain is a machine, implies that the underlying laws are based on the well-known Newtonian classical mechanics with a separation of the space and the time domain (e.g. [12]). It is a fact, however, that lacking a simultaneity agent in the CNS, space and time information cannot be separated, and thus the brain uses non-Newtonian mechanics [59]. A second automatic, but not at all necessarily true assumption is that the brain is a serial processor—a computer. This belief is an undue generalization of the fact that virtually all man-made (electronic) machines are serially organized (they perform one operation at a time, albeit in ultra-fast sequence). As a result, concepts taken from engineering without scrutiny often imply that the CNS is also a serially organized machine, or at most, a device where several (e.g. x, y, and z) processors work in parallel, but are separable to independent systems (e.g. horizontal, vertical and torsional).

Modern scientists, especially computer experts [84] emphasize, however, that the serially organized computers (so-called von-Neumann machines) created by them are very much unlike the CNS, since the brain is a massively parallel system (high number of neurons perform their operations at once). This notion, which is an axiomatic understanding in neurocomputer research [18, 19] was, in fact, well expressed already in Sherrington's intuition [77] which characterized the CNS as an ‘enchanted loom’, where flickerings of myriads of neurons in parallel express the operandum. The same idea of parallelism is inherent in a number of other classic concepts. ‘Synergies’ [6] describe movements in terms of co-activation of several muscles. ‘Schemas’ [72] also imply that the CNS expresses its action by collective terms. ‘Patterns’ and ‘assemblies’ [21, 27, 48] are also terms introduced to represent a parallel action of arrays of neurons.

Formalisms for parallel sensorimotor function

Today, the belated acceptance of the fact that the CNS is a massively parallel processor necessitates multidimensional approaches both to represent and interpret multichannel EMG signals [39], multi-unit electrophysiological recordings of neurons [11, 54, 75], and ultimately also to conceptualize highly intuitive but hitherto qualitative notions implying multicomponental action, such as ‘motor strategies’, ‘trajectories’, or ‘posture’, in a quantitative and formal mathematical manner.

Given the virtual consensus today that CNS function is expressed by parallel action of a multitude of components, it is only natural that oculomotor research, as one of the most advanced sensorimotor fields where the arrays of individual motor elements (eye muscles) and sensory detectors (vestibular canals) are plainly visible, has embraced multidimensional approaches [30]. Beyond this major conceptual advancement, a key technical issue concerns the question of suitable mathematical formalism. Since the time of Pitts and McCulloch [73] and
Wiener [85], vector–matrix formalism, using multidimensional arrays, has been extensively applied in particular in the research of posture and gaze [3, 5, 46, 49–51, 53, 56, 58, 63–68, 76, 79] and in sensorimotor research in general [22, 25, 26]. One central issue that is presently still unsettled about such vector–matrix formalisms concerns the nature of the coordinate systems in which CNS vectors are expressed. While the choice of convenience of frames is the well-known Cartesian (3-dimensional orthogonal x, y, z) system, it is an undeniable fact that the CNS is not limited to the use of such special frames. In fact, brain function is expressed in coordinate systems that are intrinsic to the organism [58] and our task is simply ‘letting the brain speak in its own terms’ [78].

The multidimensional approach to the CNS that explores parallel function in terms of intrinsic coordinate systems presents two main classes of problems. One is the anatomical establishment of coordinate systems. This field of activity, originated by Helmholtz’ [28] measurement of the rotational axes of human extra-ocular muscles has produced a good number of quantitative data lately on the vestibular system [8, 9, 15], oculomotor apparatus [16, 17, 20, 80] and neck musculature [4, 71]. Eventually, this new field of quantitative computerized anatomy is expected to grow into a major area of research with its own computerized (graphical) data-gathering technology and retrieval system.

The second major item on the agenda is research establishing how to mathematically interpret the CNS’ use, by means of neuronal networks, of the intrinsic coordinates. Both issues will be exposed in this paper through the example of a tensorial model of the vestibulocollie reflex in the cat [61, 62, 64–69].

Sensorimotor function by multidimensional transformations of intrinsic coordinates: a tensorial model of the VCR in the cat

The problem faced by sensorimotor systems is how to transform information about the environment, measured by a diverse set of sensors, into appropriate responses executed by multiple muscles acting in concert. When one focuses attention to the spatial (kinematic) properties of the transformation, the geometrical arrangement of sensors and muscles are critical since they define the intrinsic biological coordinate frames in which the stimulus and response are expressed. The nervous system in turn must transform stimuli expressed in one frame into responses expressed in the other, perhaps by stages involving additional coordinate frames (cf. section ‘Generalized functional intrinsic coordinates’).

The basis of tensorial modelling of the VCR

As for data by quantitative anatomy, such intrinsic frames of reference are shown in Fig. 1. The sensory apparatus is shown in Fig. 1B: the rotational axes of vestibular semicircular canals were established by Blanks et al. [8]. The anterior, horizontal and posterior (pairs of) semicircular canals constitute a three-dimensional frame in which head movements are physically measured as the orthogonal projections of the head movement to these axes. A compensatory head movement is physically generated by the motor apparatus, using a 30-axis motor frame, in the form of the sum of the motor vector components. Having such a dual expression, both in a sensory and motor frame, of a physical entity, the VCR can be analysed as a primary sensorimotor system. This is unlike the vestibulo-ocular reflex, where reflex output is not directly sensed by the semicircular canals [51]. Moreover, for the VCR both the tenfold overcompleteness of the motor intrinsic frame over the sensory (from three components to thirty) and the nonorthogonality of the frames (especially that of the motor axes) are self-evident.

As for the basic mathematical concepts of how to represent such intrinsic vectorial expressions and their transformations by networks, a key consideration is that Nature’s frames of reference and transformations between and among them can be described by generalized vectorial (tensorial) formalism. The proposal that neuronal networks should be considered as tensors [57] was based upon the conceptual definition that tensors are
mathematical operators expressing entities (i.e. the event that the sensory inputs arise from and the response that the motor activity generates) in any possible frame of reference in a generalized mathematical manner (cf. [7, 36]). Tensorial operations which, in simplest cases, take the form of matrices, could thus express, via neuronal networks, the stages of transformation of stimulus to response. Fig. 1A shows a general scheme (valid any case of sensory and motor frame [50]), applicable for a set of

Fig. 1. Tensor network model of the vestibulocollic reflex arc in the cat (after Pellionisz and Peterson [62]). (A) A general sensorimotor transformation scheme of the vectorial expression of a goal in a nonorthogonal sensory system to an overcomplete, nonorthogonal motor frame. The sequence is an orthogonal projection-to-parallelogram component transformation in the sensory frame, projection of the motor axes on the sensory, and projection-to-parallelogram components in the exemplary motor frame, which will yield a performance of the goal. (B) Neuronal networks of this head-stabilization reflex use coordinates intrinsic to the structure of vestibular semicircular canals (A, anterior; P, posterior; H, horizontal). The rotational axes of these canals have been anatomically measured [8] and the paired canal directions are displayed here in a pitch–roll–yaw frame. (F) For the head-movement system, the rotational axes of neck muscles have been measured [4] and displayed here in the same pitch–roll–yaw frame as the vestibular directions. Data and abbreviations of the 15 muscles (of each side) follow the nomenclature of [62]. (C, D, E) Tensor network modules, schematically displaying tensor transformation matrices implemented by neuronal networks. Arrays of patches display the tensor-matrix elements (corresponding to strengths of connections among input and output lines). One cell in a ‘stack’ of output neurons is visualized. Such a module multiplies the vector of firing frequencies arriving through the input lines by the tensor matrix implemented by the patch interconnections, to yield the vector of firing frequencies of the output neurons. The $3 \times 3$ sensory metric tensor (C), $3 \times 30$ sensorimotor covariant embedding transformation (D) and $30 \times 30$ motor metric tensor (E) have been calculated from data shown in B and F, according to the method shown in detail in [51].
three transformations with four different vectorial expressions. Fig. 1C, D, E show the tensor matrices, shown by dot diagrams, that represent the transformations implemented by means of neuronal networks.

Adoption of this general formalism enables one to discern an important difference between the types of vectorial representations of sensory input and motor output in their respective coordinate frames (even if these frames were identical). The response of a sensor, such as a semicircular canal (see Fig. 1A, stage 1), to a stimulus is independent of the responses of other sensors and is proportional to the cosine of the angle between the sensor’s axis of maximum sensitivity and the axis of the applied stimulus (or equivalently to the projection of the stimulus vector upon the sensor axis). On the other hand, the muscle activations that generate the motor response are not independent of one another since the forces or torques they generate must sum in a parallelogram fashion to produce the desired movement (see Fig. 1A, stage 4). The projection-type vectorial representations are termed covariant in tensorial nomenclature, while the parallelogram-type representations are termed contravariant (cf. Fig. 1 in [7]). The CNS can thus be conceived of as a neuronal network performing tensorial transformations converting a covariant sensory input in one frame into a contravariant motor output in another frame [58].

When constructing a tensorial model of the VCR, one must consider an additional conceptual problem raised by the overcompleteness in sensorimotor systems. A system is overcomplete when the number of independent effectors (muscles) exceeds the number of controlled degrees of freedom of the apparatus they control. The simplest example of overcompleteness of a motor system is shown in Fig. 1A, where the exemplary motor frame is 3-dimensional, compared to the 2 sensory axes in the two-dimensional plane. The difficulty posed by an overcomplete motor system is that it can generate the same movement using an infinite number of different patterns of muscle activation. The modeller must then find the type of criterion that the CNS uses in ‘choosing’ the particular pattern observed experimentally. The tensorial modelling scheme [50], utilizes the difference between covariant intention and contravariant execution representations of the desired movement. These vectorial versions, both given in the motor frame, are determined by the muscle geometry. The covariant presentation can always be found uniquely by projecting an invariant to the axes of a frame. The problem is then to find a unique contravariant representation. In a non-overcomplete system this is just the inverse of the covariant metric tensor. In an overcomplete system the problem is not that such an inverse does not exist but that there are an infinite number of inverses. It was hypothesized [49, 50] that the nervous system chooses a unique solution equivalent to the Moore-Penrose generalized inverse of the covariant metric [1]. Beyond the fact that this inverse minimizes the sum of squares of activity of the muscles during any movement, it should be noted that it may be implemented by a network (matrix) that could be constructed by the plausible biological process of reverberative oscillations in the developing nervous systems [60]. As it is shown in detail elsewhere [62], it is this choice of an optimal inverse that gives the VCR model its predictive power. Related models have been prepared for the vestibuloocular reflex [79] and tested in the case of voluntary arm movements [23]. The deviation of maximal EMG directions from muscle rotation axes can be calculated from the Moore-Penrose generalized inverse, and this allows one to make predictions of patterns of motor activation, on the basis of the geometry of the receptors and effectors. In fact, this tensor model predicts the actual VCR activation of the 6 neck muscles tested within the range of experimental precision [62].

Sensorimotor tensor transformations

The above-characterized theoretical solution is based on the four-stage (three-tensor) scheme of sensorimotor transformation shown in Fig. 1A. The transformation tensors are not shown in this figure by matrices, but schematically by ‘tensor net-
work modules' (C, D, E). In such modules, elements of the calculated matrices are represented by patches, symbolizing the strengths of connections among input and output arrays of axons. The firing frequencies of such a bundle of \( n \) axons are mathematically represented as \( n \)-dimensional vectors. The task performed in this scheme is threefold: (a) to change the sensory frame into motor, (b) to change the measured, covariant type vector to an executable contravariant version, and (c) to increase dimensions from three to thirty. The central, covariant embedding tensor (Fig. 1D) accomplishes both (a) and (c), simply by projecting the 3 sensory (i subscripts) upon the 30 motor axes (j subscripts) which can be mathematically expressed as

\[
c_{ij} = u_i v_j,
\]

where \( u \) and \( v \) are the coordinates of the (normalized) sensory and motor axes, respectively, and each matrix element of \( c_{ij} \) is the inner (scalar) product of the vectors of coordinates of the \( i \)th and \( j \)th axis.

The reason that the \( c_{ij} \) covariant embedding tensor is necessary but not sufficient in converting the covariant sensory reception vector \( u_i \) into contravariant motor execution \( v^j \) is that \( c_{ij} \) is a projective tensor. It turns a physical-type (contravariant) input vector into an output that is provided in its projection components (covariants). However, our task is the opposite; to turn the available sensory input (which is covariant), into the output required (which should be contravariant). This is why the other two conversions in the tensorial sensorimotor scheme are necessary. The sensory metric tensor \( g^{ii} \) (Fig. 1C) converts the covariant sensory reception into contravariant sensory perception, and the motor metric \( g^{ii} \) (Fig. 1E) turns covariant motor intention into contravariant motor execution. This general function of transforming covariant nonorthogonal versions into contravariant ones by metric tensors can be accomplished for any given set of axes by a matrix implemented by a divergent–convergent set of neuronal connections, often reporting on different sensory modalities, so characteristic for the CNS, e.g. among primary and secondary vestibular neurons \([2, 3, 44, 74]\), and among brainstem premotor neurons and neck motoneurons.

Mathematically, the required contravariant tensor \( g^{ii} \) can be established as the inverse of the covariant metric tensor \( (g_{ii}) \):

\[
g^{ii} = (g_{ii})^{-1}
\]

where components of \( g_{ii} \) are the inner (scalar) products of the arrays of coordinates of the (normalized) axes:

\[
g_{ii} = u_i v^i
\]

Two important questions arise regarding such metric transformations; a biological and a mathematical one. First of all, even if such transformations are implemented by matrices of neuronal networks, the CNS does not arrive at them by mathematical computation, but by some procedure feasible for a biological system. The question relates to the nature of this unknown procedure. Second, at the level of pure mathematics, a problem occurs with overcomplete coordinate systems. In such cases \( g_{ii} \) is singular (its determinant is zero), thus \( g_{ii} \) has an infinite number of inverses. The question is how CNS neuronal can arrive at a unique covariant-to-contravariant transformation (even in case of overcompleteness).

An attempt, aimed at answering both questions jointly, led to the proposal of a metaorganization principle and procedure which utilizes the Moore-Penrose generalized inverse \([49, 50, 60]\). Biologically, the proposed solution is based on arriving at special vectors whose covariant and contravariant expressions have identical directions (so-called eigenvectors of the system). This can be performed by the CNS in the form of a reverberative oscillatory procedure, where muscle proprioception recurs as motoneuron output, setting up tremors stabilizing in the eigenvectors. These special activation vectors would imprint a matrix of neural connections that can serve as the proper coordination device (implemented, for example, by the cerebellar neuronal circuit). Mathematically, this unique inverse of \( g_{ij} \) can
be obtained from the outer (dyadic matrix) product (symbolized by \( > < \)) of the eigenvectors \( E_m \), weighted by the inverses of the eigenvalues \( L_m \), where \( 1/L_m = 0 \) if \( L_m \) was 0:

\[
g^{ij} = \Sigma_m \frac{1}{L_m} \cdot (E_m > < E_m)
\]

Once the Moore-Penrose generalized inverse is calculated by the above formula for the third transformation, the model predicts for each neck muscle a unique direction of head rotation for which that muscle should be maximally activated. Muscle activation during rotation about other axes is predicted to decline as the cosine of the angle between these axes and the optimal axis. As shown in detail elsewhere [62] the predicted optimal activation direction should typically differ quite significantly from muscle pulling directions, but can be readily tested experimentally with confirmatory results [62, 70].

Although pulling and activation directions are quite widely separated in this nonorthogonal system, the model predicts the activation directions within 4 to 11°. Thus the hypothesis that the CNS determines neck-muscle activation patterns in a manner corresponding to the Moore-Penrose generalized inverse is supported by the fact that the model predicts the pattern of muscle activity, produced by the VCR in decerebrate cats, within the limitations of experimental error.

**Elaborations: tensor network models**

The modelling approach described here opens avenues for substantial developments. First, while the data used in this paper are for the VCR of a traditional experimental animal, the cat, the problem addressed is applicable to many forms of motor control in a broad range of species including humans. Software is now available to construct similar models for any sensory–motor system where the geometry of sensors and muscles is made available by quantitative anatomical studies.

Second, investigators may wish to experimentally evaluate some quantitative predictions of such simple tensorial models. Gielen and Zuylen [23] have recently reported successful prediction of patterns of human arm muscle activation using a tensorial model. The experimental approach of recording EMG responses to multidirectional stimuli is also broadly applicable and could yield useful information about principles underlying motor control in a variety of species.

A third possibility is to further explore the neuronal network embodiments of such general coordinate transformations. The manner of how this challenge is addressed is indicated in Fig. 2. This multidimensional network scheme is the neuroanatomical elaboration of the rudimentary four-stage sensorimotor transformation shown in Fig. 1. The scheme in Fig. 2 introduces two refinements. One is based on the fact that the motor metric transformation is not implemented in a simple throughout manner (as shown in Fig. 1) but via a ‘add-on’ organ, the cerebellum (cf. [10]. This principle of organization is presented in detail elsewhere [50–52, 60].

The parallelly organized multidimensional neuronal network shown in Fig. 2 performs the motor metric function via the connection matrix of PCs with MFs collaterals to the cerebellar nuclei. Given that the execution vectors (PC projections) are inhibitory, the nucleofugal output will be the difference of motor intention and execution vectors, which will yield in the neck motor nuclei the required execution-vector output. The second aspect of elaboration is the path of multidimensional visual error signals to the PCs (via the AOS to the IO and to CF analogous to [43, 81]). As elaborated in [52] the CF vector, by projecting to the cerebellar nuclei both directly (through collaterals) and indirectly (via the PCs), in effect changes the motor metric tensor function of the cerebellum: altering the curvature of the motor functional space in an ongoing manner. While the rapprochement of such multidimensional quantitative parallel network models to neuroanatomical realities will require much further studies, it seems evident already at this stage that representation of such circuits as loops of single axons with nuclei merely serving as relay stations will no longer suffice.

A fourth important direction of studies is the ex-
ploration of intrinsic coordinates of more abstract nature than those embedded in skeletomuscular structure.

**Generalized functional (other than structural) intrinsic coordinates**

The fact that brain function is expressed by multidimensional intrinsic coordinates is most obvious in the case of anatomically explicit sensory and motor systems. Neurons connected to the peripheries of sensorimotor systems (e.g., vestibular canals and neck muscles) must use structural frames. Their rotational axes have been quantitatively established for several species. Typically, they are nonorthogonal overcomplete multidimensional frames (Fig. 1). In this light it is surprising to find claims in the literature that central neurons of this system apparently use an orthogonal frame: the paramedian pontine reticular formation reportedly contains medium-lead burst cells, whose firing rate is tightly related to eye velocity in either horizontal or vertical saccades [13, 24, 32, 33, 41].

The possibility that the CNS employs intrinsic coordinate systems in its operation that are different from the ones at the sensory and motor ends, of course, cannot be excluded. In fact, it has been shown that functionally and not structurally determined directional preferences (in our terms, intrinsic coordinates) do exist in the visual system, both at the retina [47] and in its relayed form to the cerebellum [43]. There are two main tasks: one is to experimentally identify such internal intrinsic frames, and the other is to theoretically interpret their functional significance. It is shown below that this paradox between a nonorthogonal structural frame and an orthogonal functional frame may receive an explanation in tensor theory with important implications to both theory and experimentation.

**Tensorial relationship between structural and functional reference frames of brain function: saccade neurons in the monkey utilize frames composed of the eigenvectors of the frame of extra-ocular muscles**

Tensor network theory of the CNS centers around the general question of transformations among intrinsic coordinates [50]. An even more profound problem is, however, how different (structural and functional) geometries are connected [60]. When attempting to relate the nonorthogonal structural frame with the apparently orthogonal functional frame, the question emerged as to whether the apparently orthogonal functional frame is, in fact, aligned with the eigenvectors of the nonorthogonal extra-ocular structural frame [53].

Availability of the rhesus monkey oculomotor frame (Fig. 3A; data from [80]) permits calculation of its eigenvectors (Fig. 3B). The procedure of this calculation is given in [51, 56, 60]. Comparison of
Figs. 3A and B reveals that the above hypothesis meets an affirmative answer: Functional and structural geometries are connected in a manner that the frame in one utilizes the eigenvectors of the frame in the other. This finding may have both important theoretical and experimental implications. From a theoretical viewpoint, it was shown in the meta-organization of networks [60], that neurons must utilize the eigenvectors of the metric tensor of the motor frame to enable independent adaptive modifications, since eigenvectors form an orthogonal set. Experimentation could help by further investigating this issue. Data would be desirable in other species that have different motor frames and eigenvectors (see [51, 56], where such eigendirections are calculated for the human and the cat). Quantitative properties of adaptive coordination along eigenvectors could also be experimentally explored. The paradigm of eigenvector connection of structural and functional frames therefore illustrates that a theory of CNS function expressed with multidimensional intrinsic coordinates can provide not only mathematical explanation of certain features of parallel brain function, but also yield specific suggestions for experimental investigation.

Geometrization of complex descriptions of sensorimotor function: motor strategies, trajectories, posture

Tensorial modelling of the CNS's use of structural and functional intrinsic coordinates is likely to pre-

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**Fig. 3.** Saccadic burster neurons in the monkey may use a functional frame of reference that is the eigenvector system of the structural frame of reference of the oculomotor muscles (after [53]). (A) Data by quantitative morphology (from [80]) showing the rotational axes, in a pitch–roll–yaw frame, of the six extra-ocular muscles in the rhesus monkey. Data refer to the left eye, data and visualization uses the right-hand rule. LR, lateral rectus; MR, medial rectus; SR, superior rectus; IR, inferior rectus; SO, superior oblique; IO, inferior oblique. This diagram is used here to display obvious features of this structural frame: (a) the overcompleteness, (b) the non-orthogonality, (c) the gross deviation of the axes from pure horizontal and vertical directions. (B) The eigendirections, calculated from the structural frame presented in A. The table of E1-E3 eigenvectors (with L1-L3 eigenvalues) has been calculated as shown in [51, 56]. The D1-D3 eigendirections are both tabulated and displayed in a frame identical to the one in panel A. As shown, the D2 and D1 eigendirections (preferred functional directions, since they are orthogonal, and thus separable) are aligned with an almost pure vertical and horizontal retinal shift, within 5.4° precision. Thus, the experimentally observed ‘vertical’ and ‘horizontal’ saccadic burster neurons [13, 24, 32, 33, 41] may well utilize an abstract functional intrinsic frame that is the eigenvector frame of the structural intrinsic coordinate system.
sent both major difficulties and new possibilities. One of the biggest hindrances at present is the meager availability of quantitative data on intrinsic structural frames (and the shortage is even more serious for functional neuronal frames). While quantitative computerized anatomy is likely to become an abundant source of data in the future, techniques are already explored that could alleviate the present shortage of quantitation. For instance, anatomical measurements of cat neck muscles [4] are only available for a fixed-head animal (where it is a good approximation that the head rotates around the single C1/C2 joint-point). However, with more complex head movements this approximation is not satisfactory, and thus data gathered by the ‘Helmholtz method’ (fixed origin and insertion points of muscles, fixed single rotational centre) no longer yield sufficient approximation.

A graphics-based computer software technique has been developed [34, 35, 37, 54] that removes the above bottlenecks, although this new method is not without limitations itself and is extraordinarily labor-intensive. Once a graphical rendering of the skeletomuscular system is available in the form of photographs, X-rays, drawings, etc., this information is scanned into a graphical computer. Fig. 4 provides examples of the display of the cat’s head skeletomuscular system (cf. [71, 83]). Once (any number of) joint rotation points, relative stiffness values, muscle origin and insertion points are established by the operator, relative to the (movable) skeletal parts, the intrinsic movement coordinates belonging to individual muscles are computed, together with the covariant metric tensor (table of cosines among muscle axes) and its Moore-Penrose generalized inverse. This computation can be re-

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**The Epiphenomenon of Apparently Different "Motor Strategies" Arising from a Single Motor Paradigm**

Head-Shift and Head-Tilt Arise from the Same Tensorial Model of Motor Coordination Using the Moore-Penrose Generalized Inverse of the Covariant Metric of the Frame Intrinsic to Neck Muscles

---

**A** Head-Shift "Strategy"

- **movement intention**
  - 1 obliquus c.c.
  - 2 rectus c.m.
  - 3 biventer/1

---

**B** Head-Tilt "Strategy"

- **movement intention**
  - 4 biventer/2
  - 5 cleidomast.
  - 6 sternomast.
  - 7 occipitoscap.

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Fig. 4. Still pictures from a tensorial model movie of the head movements in the cat, using graphics-based establishment of the intrinsic coordinates of the skeletomuscular system consisting of the skull, all cervical vertebrae and 7 exemplary neck muscles. The head-shift movement strategy and head-tilt strategy arise from an identical model, where only the command of the movement is different (an 'intention' specified by the operator). While the movement intentions are straight displacements, the model predicts curved trajectories (an expression of the curved geometry of the functional motor space). Also, both the head-movement display as well as the predicted activations of 7 muscles with time (right side of panels) can be dramatically different with somewhat different intentions. Software that extracts the structural intrinsic coordinates from graphical input and calculates the Moore-Penrose generalized inverse of the motor metric in a dimension-free (tensorial) manner can be applied to several sensorimotor systems of many species.
freshed during a movement if desired. Thus, to any intention movement specified by the operator, the corresponding execution components of the muscles are computed, and the resulting movement is displayed (also by a computer movie). Motor behaviour of such systems can be studied restricted to the joint space (without muscles), or in muscle space and, with high enough resolution in the future, approximating the motoneuron space. Some applications of this model, capable of quantitating the functional behaviour of complex skeletomuscular systems, already yielded insights to sensorimotor function.

The display shown in Fig. 4 demonstrates that the identical model may yield remarkably different ‘motor strategies’ (a shift in A, utilizing several cervical rotational points, while a tilt in B basically around a single rotation point) if somewhat different motor intention is imposed by the operator. Thus, it is expected that this method will be helpful for studies by quantitative modelling also those systems, already yielded insights to sensorimotor function.

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References


