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Chapter 14. In: Control of head movement,
Peterson BW, Richmond FJ

1988, Oxford University Press: 178-186

Control of Head Movement

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New York Oxford
OXFORD UNIVERSITY PRESS
1988

A Tensorial Model of Neck Motor Activation

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The data presented in the previous chapter provide a detailed description of how the central nervous system organizes neck muscle activation in the context of a well-defined sensorimotor task—the vestibulocollic reflex (VCR). The fact that the geometrical alignments of both the sensory receptors (the 3 semicircular canals, Curthoys et al., 1977) and motor effectors (the 30 neck muscles, see Chapter 13 and Baker et al., 1984c) have been measured opens the possibility of modeling the VCR using the tensorial methodology described by Pellionisz and Llinás (1979) and Pellionisz (1984). This approach allows one to predict patterns of motor activation, such as those described in Figure 13.5, from the geometry of the receptors and effectors. This chapter describes the properties of the tensorial model of the VCR and shows that it predicts quite closely the actual VCR activation of the six neck muscles tested to date. The possibility of extending the model to other neck motor activities such as voluntary movement is also discussed. As an introduction to these issues, the next section will briefly discuss the conceptual problems presented by complex sensorimotor systems and review the rationale behind the development of the tensorial modeling approach.

CONCEPTUAL BASIS OF TENSORIAL MODELING

The problem faced by a sensorimotor system is to transform information about the environment, measured by a diverse set of sensors, into appropriate responses executed by multiple muscles acting in concert. When the spatial (kinematic) properties of the transformation are considered, the geometrical arrangements 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. The proposal by Pellionisz and Llinás (1979) that neuronal networks should be considered as tensors was based upon the conceptual definition that tensors are mathematical operators expressing the relationships among mathematical (vecto-

rial) representations, in different frames of reference, of physical entities such as sensory events and the responses they generate (cf. Levi-Civita, 1926; Coburn, 1955). Tensorial operations that, for any particular frame of reference, take the form of matrices could thus express the stages of transformation of sensory stimulus to motor response.

Adoption of the tensorial concept and formalism emphasized an important difference between the representation of sensory input and motor output in their respective coordinate frames. The response of a sensor, such as a semicircular canal, 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). Such projection-type representations are termed *covariant* in tensorial nomenclature (cf. Bickley and Gibson, 1962). On the other hand, the muscle activations that generate the 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. Such parallelogram-type representations are termed *contravariant*. The central nervous system (CNS) can thus be conceived of as a tensorial network that converts a covariant sensory input given in one frame into a contravariant motor output expressed in another frame (Pellionisz and Llinás, 1980).

Before constructing a tensorial model of the VCR, we must consider the conceptual problem raised by *overcompleteness* in motor systems. A motor system is overcomplete when the number of independent effectors (muscles) exceeds the number of controlled degrees of freedom of the appendage they control. As indicated in earlier chapters, it is difficult to be certain if the neck motor system is overcomplete in this most general sense. However, we can also consider the head-neck system to be *functionally overcomplete* in a given behavioral context when the number of muscles exceeds the number of *behaviorally relevant* degrees of freedom (three rotational angles of the head for the VCR). In this case we assume that the system does not independently control internal degrees of freedom (such as all angles of individual joints) as long as the required head movement is properly generated.

The difficulty posed by an overcomplete motor system is that it can produce the same movement using an infinite number of different patterns of muscle activation. Theory must then propose some type of optimality criterion that the system uses in "choosing" the particular pattern observed experimentally. The solution proposed by Pellionisz (1984) in the form of a tensorial modeling scheme utilizes the difference between covariant and contravariant representations of the desired movement, both expressed in the motor frame determined by the muscle geometry. The covariant presentation can always be found uniquely by projecting the movement vector upon each of the muscle axes. The problem is then to find an optimal contravariant representation. In a nonovercomplete system this is just the inverse of the covariant metric. In an overcomplete system the problem is not that such an inverse does not exist, but that there are an infinite number of inverses. Pellionisz (1983, 1984) hypothesized that the nervous system chooses an inverse equivalent to the Moore-Penrose generalized inverse of the covariant metric (Albert, 1972). This inverse has several attractive features. It minimizes the

sum of squares of activity of the muscles during any movement. It may also be implemented by a network (matrix) that could plausibly be constructed by a developing nervous systems (Pellionisz and Llinás, 1985). As will be seen below, 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 (Simpson and Pellionisz, 1984) and voluntary arm movement system (Gielen and van Zuylen, 1986).

GENERATION OF A TENSORIAL MODEL OF THE VESTIBULOCOLLIC REFLEX

The sensorimotor frames of the vestibulocollic reflex in the cat are illustrated in Figure 14.1. As shown, the anterior, horizontal, and posterior (pairs of) semi-circular canals constitute a three-dimensional nonorthogonal frame in which head movements are physically *measured* as the orthogonal projections (covariant components) of the head movement. In turn, the compensatory head movement is physically *generated* in the 30-axis motor frame, as a result of the sum of the (contravariant) motor vector components. Having such a dual relationship with a given physical entity, the vestibulocollic reflex is a primary sensorimotor system. Moreover, in this case both the 10-fold overcompleteness of the transformation (from 3 components to 30) and the nonorthogonality of the frames (particularly that of the motor axes) are self-evident.

The proposed theoretical solution is based on the three-step scheme of sensorimotor tensor transformation shown in Figure 14.2. The task is (1) to change the sensory frame into motor, (2) to change the measured, covariant type vector to an executable contravariant version, and (3) to increase dimensions from 3 to 30. The three steps of the transformation do not accomplish these goals one-by-one. The central, covariant embedding tensor accomplishes both (1) and (3) simply by projecting the 3 sensory (i subscripts) upon the 30 motor axes (p subscripts), which can be mathematically expressed as

$$\mathbf{c}_{ip} = \mathbf{s}_i \cdot \mathbf{m}_p$$

where \mathbf{s} and \mathbf{m} are the coordinates of the (normalized) sensory and motor axes, respectively, and each matrix element of \mathbf{c}_{ip} is the inner (scalar) product of the vectors of coordinates of the i th and p th axis.

The reason that the \mathbf{c}_{ip} covariant embedding tensor is necessary but not sufficient in converting the covariant sensory reception vector \mathbf{s}_i into contravariant motor execution \mathbf{m}^e is that \mathbf{c}_{ip} 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 case is the opposite; the available sensory input is covariant, whereas the output required is contravariant. This is why the other two conversions in the tensorial sensorimotor scheme are necessary; the sensory metric tensor \mathbf{g}^{pr} (the small 3×3 matrix in Fig. 14.2) that converts covariant sensory reception into contravariant sensory perception, and motor metric \mathbf{g}^{ie} (the large 30×30 matrix in Fig. 14.2) that turns covariant motor intention into contravariant motor execution. This general function of transforming covariant nonorthogonal

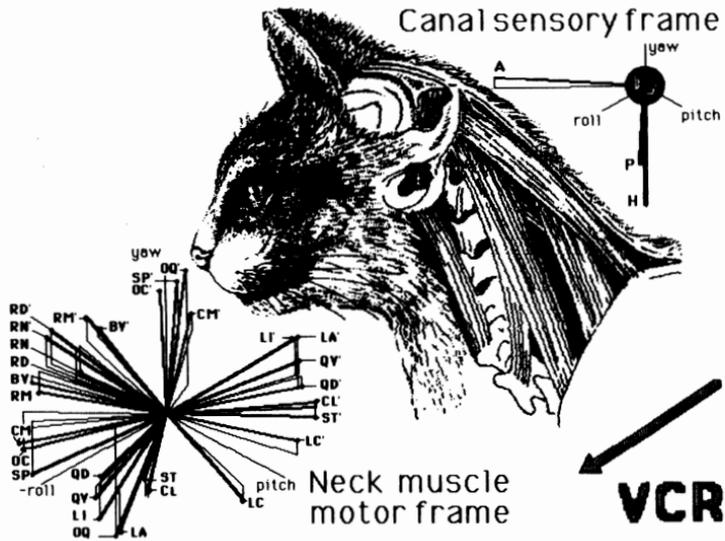


Figure 14.1. Illustration of the quantitatively established 3-axis vestibular frame of reference (data from Blanks et al., 1972) and the 30-axis collicular frame of reference (data from Peterson et al., 1985a). The heavy lines represent rotational axes of the head around which the semicircular canals measure changes in head angular orientation and axes around which the individual neck muscles generate head rotations. The vestibular apparatus and some representative neck muscles are visualized in the central schematic diagram, in which the cervical column is shown close to a vertical orientation (cf. Vidal et al., 1986). The task for tensor network theory is to explain how neuronal nets in the CNS accomplish the required overcomplete covariant-to-contravariant transformation of canal input to muscle output. A, P, and H refer to anterior, posterior, and horizontal canals, respectively. Abbreviations for muscles: BV, biventer; CL, cleidomastoid; CM, complexus; LA, longus atlantis; LC, longus capitis; LI, longissimus; OC, occipitoscapularis; OQ, obliquus capitis inferior; QD, obliquus capitis superior (dorsal division); QV, obliquus capitis superior (ventral division); RD, rectus capitis medialis; RM, rectus capitis major; RN, rectus capitis minor; SP, splenius; ST, sternomastoid. Primes indicate rotational axes of contractions of contralateral muscles.

versions into contravariant ones by a metric tensor can be accomplished for any given set of axes by a matrix of divergent-convergent neuronal connections among primary and secondary vestibular neurons and among brain stem premotor neurons and neck motoneurons (Markham and Curthoys, 1972; Baker et al., 1984b).

Mathematically, the required contravariant metric tensor \mathbf{g}^{pr} can be established as the inverse of the covariant metric tensor \mathbf{g}_{pr} :

$$\mathbf{g}^{pr} = (\mathbf{g}_{pr})^{-1}$$

where \mathbf{g}_{pr} is the inner (scalar) product of the vectors of coordinates of the (normalized) axes s_i :

$$\mathbf{g}_{pr} = s_i s_i$$

Two important questions arise regarding such metric transformations: a math-

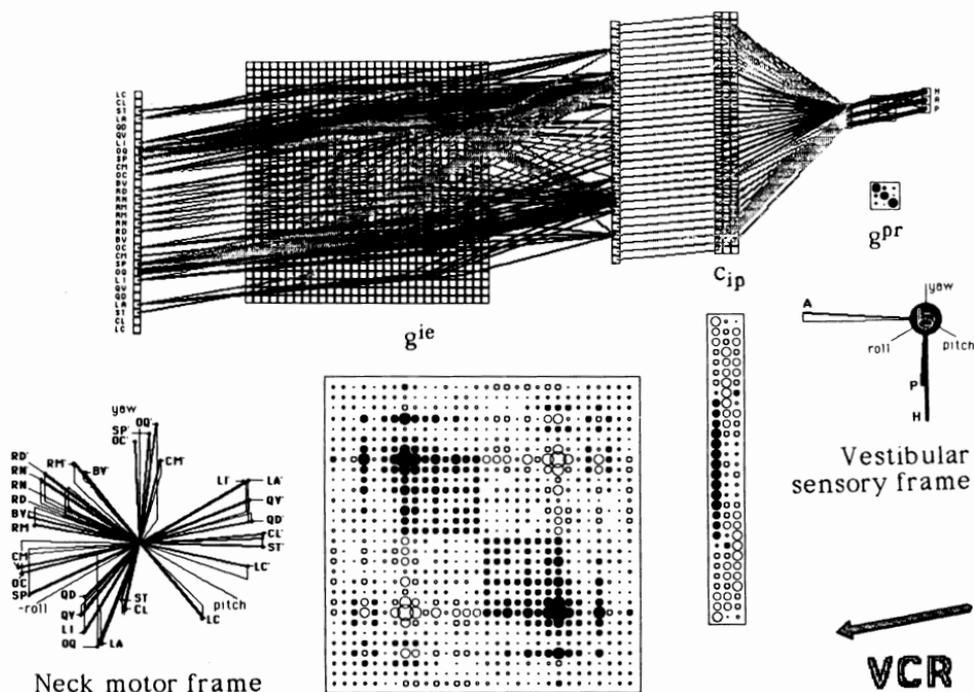


Figure 14.2. Illustration of the tensor network model of the VCR in the cat (cf. Pellionisz and Peterson, 1985). The sensorimotor transformation occurs in three stages: \mathbf{g}^{pr} , sensory metric tensor, \mathbf{C}_{ip} , sensorimotor embedding tensor, and \mathbf{g}^{ie} , neck motor metric tensor. These general tensorial operations are expressed in the particular frames of reference of the VCR by matrices, which are here represented by patch diagrams in which positive and negative components are shown by filled and open circles whose surface area is proportional to the size of the component. The CNS can implement these matrices by neuronal networks as indicated in the upper part of the diagram. There the strengths of connectivities from H, A, P canals to the 30 neck muscles are represented by line shadings (black for excitation, grey for inhibition) and by line thickness proportional to the value of the interconnecting matrix element.

emational and a biological one. First, even if such transformations are implemented by matrices corresponding to neuronal networks, the CNS does not arrive at them by mathematical computation, but by some unknown procedure feasible for a biological system. Second, at the level of pure mathematics, a problem occurs with *overcomplete* coordinate systems. In such cases \mathbf{g}_{pr} is singular (its determinant is zero), thus \mathbf{g}_{pr} has an infinite number of inverses. The question of how CNS neuronal networks can arrive at a unique covariant-to-contravariant transformation (even in case of overcompleteness) led to the proposal of a metaorganization principle and procedure that utilize the Moore–Penrose generalized inverse (Pellionisz, 1983, 1984; Pellionisz and Llinás, 1985). 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) by a reverberative oscillatory procedure (muscle proprioception recurring

as motoneuron output, setting up stabilizing tremors). These special activation vectors would imprint a matrix of neural connections that could serve as the proper coordination device (e.g., cerebellar neuronal circuit). Mathematically, a unique inverse of \mathbf{g}^{ie} can be obtained from the outer (dyadic matrix) product (symbolized by \gg) of the eigenvectors \mathbf{E}_m , weighted by the inverses of the eigenvalues λ_m (the inverse is taken as 0 if $\lambda_m = 0$, cf. Albert, 1972):

$$\mathbf{g}^{ie} = \sum 1/\lambda_m (\mathbf{E}_m \gg \mathbf{E}_m)$$

The tensor network model of the vestibulocollic reflex, based upon the above theoretical considerations, emerges from the preliminary data (presented in Chapter 13) in the form shown in Figure 14.2. Each of the three matrices in the model is represented by a box in which the size and sign of each matrix element are indicated by filled (positive) and open (negative) circles. Four columns represent canal inputs (H, A, P), motor nerve outputs (LC), and two intermediate neural stages. Once the model has been set up we can compare its properties to those of the VCR.

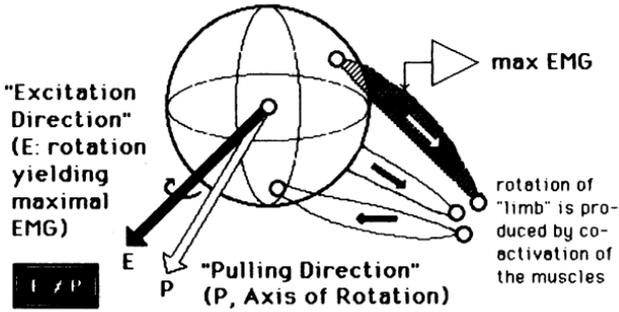
MODEL PROPERTIES

The model attempts to predict semicircular canal actions upon neck muscles. It therefore deals with the high-frequency VCR responses described in Chapter 13. One feature of those responses is that they vary sinusoidally with the angle between the animal and the stimulus axis. Semicircular canals are known to respond in this way (Estes et al., 1975). Since the three matrices of the model perform simple spatial transformations, they do not alter this sinusoidal behavior. The model therefore predicts such behavior at the neck motor output and at all intermediate stages.

The other key feature of the VCR data was that muscles were maximally activated by rotations in planes other than their pulling planes. This feature turns out to be the consequence of the nonorthogonality of the muscle axes. As shown in Figure 14.3, it can be demonstrated in a simple two axis, 135° coordinate frame. As illustrated, the contravariant activation of the muscle lying along the 0° axis is 1.0 if the desired movement is along that axis. Generation of the same sized movement in a direction that is *different* from the 0° axis (perpendicular to the second axis, i.e., at 45° with respect to the muscle being measured), however, requires a 1.4 unit activation of that muscle in order to produce forces that produce the correct parallelogram sum.

Although the divergence of activation and pulling directions is to be expected according to the above analysis, the actual activation directions that were consistently chosen in the five cats from the infinite number of possible directions must reflect an algorithm employed by the VCR to resolve the overcompleteness of the VCR system. How closely does this algorithm resemble the Moore–Penrose generalized inverse incorporated in the model? To answer this question the model's responses to the same stimuli used in the experiments were calculated and used to produce predicted activation vectors, which are plotted with the label $-\mathbf{M}$ in

① Experiment Pulling & Excitation Directions Differ



② Theory: in Non-Orthogonal Frames this Difference is Expected and its Magnitude can be Calculated

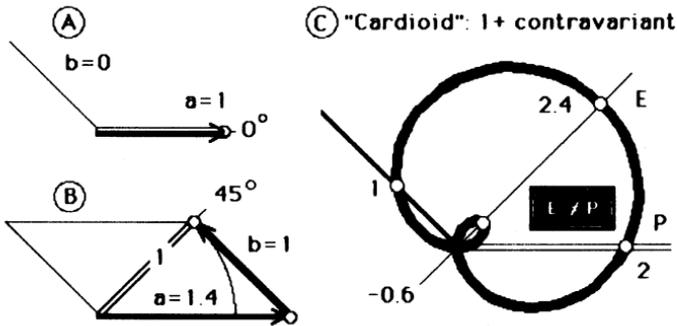
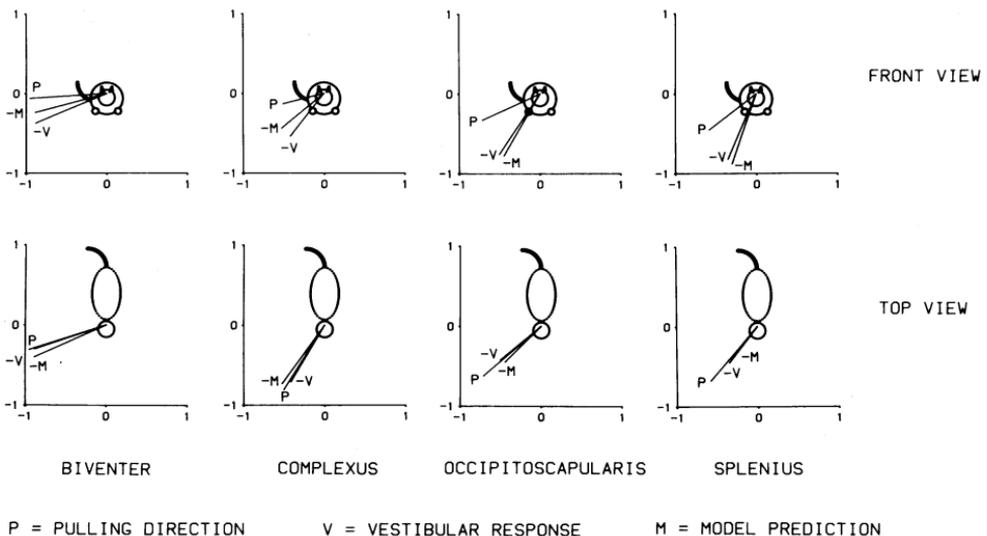


Figure 14.3. Difference between anatomical pulling directions and maximal excitation directions of a neck muscle (1) and its geometrical explanation (2). (1) If an appendage, such as the head, is rotated by coactivation of (neck) muscles, the rotation axis (pulling direction) of each muscle can be determined by anatomical measurements of the points of origin, insertion, and center of rotation (cf. Fig. 13.5). As also illustrated in Figure 13.5, axes of head movements that are accompanied by maximal activation of each muscle (E) are typically not aligned with the pulling directions (P). (2) The observed divergence between P and E can be explained by using the distinction between covariant (projection) and contravariant (parallelogram) representations in nonorthogonal coordinate systems. In the frame illustrated, in which two muscle axes are at an angle of 135° , a unitary displacement in the direction of axis a is generated by muscle activation $a = 1$, $b = 0$ (2A). However, as shown in inset 2B, a unitary displacement in the 45° direction (deviating from the axis direction itself) requires muscle activation of $a = 1.4$, $b = 1$ for the parallelogram sum of a and b to generate the required unitary displacement. The relationship of the contravariant component to the displacement direction can be visualized in a "cardioid" diagram in which $1 + a$ is plotted against displacement direction in polar coordinates. The plot in 2C clearly shows that activation of a reaches its maximum value not for displacements along its own axis but rather for displacements at an angle of 45° with respect to that axis. Thus, contrary to our intuitions that have been honed for orthogonal systems, in nonorthogonal coordinate frames the pulling directions and optimal activation directions of muscles can be expected (and predicted) to differ by large angles from one another.

Figure 14.4. As shown, these predictions are always rotated away from the muscle pulling directions (**P**) in the direction of the measured VCR responses (**-V**) and are typically quite close to the latter. Differences between **-V** and **-M** are small enough to be accounted for by the variability in existing measurements of the pulling directions (upon which the model is based) and of the actual responses. Thus a tensorial model based solely upon the anatomy of the canals and neck muscles is able to predict with remarkable accuracy the spatial properties of the VCR.

The successful approximation of overall input/output properties of the VCR (measured in six muscles) should be regarded as only an initial stage of the modeling effort (see also Pellionisz and Peterson, 1985). More muscles need to be tested and the experiments generalized to other species. The VCR model also predicts neural signals at intermediate stages of the sensorimotor transformation. These should be compared with actual neural recordings and the model altered if necessary to incorporate the actual coordinate frames found in the CNS. Finally, the model can be generalized to predict neck motor responses to visual, somatosensory, or other inputs. The tensorial method should therefore be useful in advancing and testing hypotheses concerning neural processes that generate volun-

Figure 14.4. Comparison of pulling directions (**P**), maximal excitation directions during VCR (**V**), and model predictions of VCR direction (**M**) for four neck muscles in decerebrate cats. As in Figure 13.5, pulling and optimal response axes are indicated by unit vectors aligned with the axis. Vectors indicated by **P** are as in Figure 13.5. Vectors **V** and **M** are plotted with their signs reversed to facilitate comparison of them with the pulling directions. Assuming that the VCR generates attempted head movements in the direction opposite to the rotation applied by the turntable, the reversed vectors **-V** and **-M** therefore indicate the direction of head motion for which each muscle is maximally activated. Whereas the angles between **P** and **-V** in the muscles illustrated ranged from 18° to 31°, model predictions were within 4° to 10° of **-V**.



tary tracking or orienting head movements, which involve motor patterns that differ from those observed in the VCR (see Chapter 2).

SUMMARY

This chapter describes a tensorial model of the VCR that predicts the muscle activation patterns that are generated when a cat is rotated in three-dimensional space.

The treatment begins with a description of two types of representation in nonorthogonal coordinate frames: covariant (sensory or projection type) representations and contravariant (motor or parallelogram type) representations. The issue of overcompleteness that occurs when the number of muscles exceeds the number of degrees of freedom of movement is also discussed. In overcomplete systems an infinite number of motor patterns can be used to generate a movement.

The VCR model has three transformation stages consisting of matrices that represent tensorial operations. Stage 1, a 3×3 matrix representing the vestibular metric tensor, converts vestibular sensory input from covariant to contravariant form. Stage 2, a 3×30 matrix representing the sensorimotor embedding tensor, converts the signals from vestibular to neck motor coordinate frames. Stage 3, a 30×30 matrix representing the neck motor metric tensor, converts the neck motor command from covariant to contravariant form. Because the system is overcomplete (30 muscles generating head movements in 3 rotational degrees of freedom), an infinite number of stage 3 matrices could be chosen. The model incorporates the matrix corresponding to the Moore–Penrose generalized inverse of the covariant motor metric.

Choosing the Moore–Penrose inverse for stage 3 causes the model to predict a particular pattern of neck muscle activation in response to vestibular stimulation. Comparison of this predicted pattern with the experimentally measured patterns presented in Chapter 13 indicates that the model is quite effective at reproducing the spatial properties of the VCR.

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