

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

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

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

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

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

$$\vec{E} = \vec{\Omega}_i^j \cdot \vec{H}^j$$

where  $\vec{\Omega}_i^j$  is the vestibulo-oculomotor tensor (VOT).

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

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

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

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

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

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

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

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

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

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

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