

$v_i$  do not simply encode the position of the target at time  $t$ , but rather, each  $v_i$  component represents the position of the target at the time-point of  $t - d_i$ , where each delay  $d_i$  may be different.

From an experimental point of view, the schemes in Figs 3 and 4 also include a temporal display of the activities of the neurons in the transformation-network (bottom of both figures). Note, that all neurons are activated sinusoidally, only their amplitude and phase are different. This scheme illustrates how formidable is the problem of inferring, from such single cell data, the global functional properties which emerge from the compound activity of single elements. In Fig. 4A (bottom), the covariants and contravariants are shown together both for the case of simultaneity (comparable to Fig. 3C: the signals shown by dotted lines) and for the case of delayed, non-simultaneous signals (shown by continuous lines). Again, the difference between the simultaneous and non-simultaneous cases would only be detectable experimentally in the phase of the sinusoidal time functions.

In contrast to displaying single cell activities, a visualization of the 'assembled' vectorial output itself (right side of Fig. 4A) makes it clear that if the metric transformation in such an asynchronous system were performed directly on the delayed components, the contravariants would yield a distorted, elliptical movement instead of the circular one. Here, the existence of some kind of interaction between space and time information in neuronal systems is clearly indicated: *temporal dispersion* may be transformed into *spatial distortions*. Such a functional interdependence of space and time is well known in psychophysics. For example, the Pulfrich illusion (cf. ref. 36) demonstrates that temporal differences in the detection, by the right and left eye, of a planar pendular movement make the movement appear to follow a spatially distorted elliptical path. On a motor level, there is a similar relationship between the temporal spike responses of cerebellar neurons to spatial precision of saccadic eye movements.<sup>10</sup> In the field of psychophysics the mismatch of the subjective perception of objective temporal sequences is generally known.<sup>9,32</sup> A manner in which the CNS may establish a relation between space-time coordinates is proposed below.

*Predictive space-time metric: reestablishing the relation by temporal lookahead between an event and its asynchronously delayed coordinates*

The present solution to the problem of establishing space-time coincidences *via* asynchronous CNS function is based on the predictability of the future values of vectorial components (Fig. 4B). Such a 'temporal lookahead' scheme was elaborated earlier,<sup>20</sup> based on experimental evidence indicating that the activity of Purkinje cells shows zero-, first-, and even the second-order time derivatives of the velocity-stimulus (cf. Fig. 12 in ref. 11). The basis of the principle of prediction is that a set of derivatives (according to the coef-

ficients in a Taylor-series-like expansion) of the input time-function can be produced by a 'stack' of Purkinje cells which are activated by a 'beam' of parallel fibers. If the activity of these Purkinje cells is summed on a cerebellar nuclear neuron, then a temporal lookahead of the input signal can be obtained (for a detailed explanation of the functioning of such a 'lookahead module' see Fig. 1 in ref. 20). We have suggested there that such 'prediction' could be the neural basis for coordinated motor actions when body movements have to anticipate the location of fast moving targets. Recently, features of temporal extrapolation in CNS have been corroborated with experimental evidence.<sup>15,33</sup>

It is proposed that the metric network utilizes the 'lookahead modules' as follows: the sensory part of the scheme in Fig. 4B is initiated by a set of delayed covariant components. Then, if a 'lookahead-module' is incorporated by a network (shown symbolically by a few Purkinje cells at the center of Fig. 4B) then both  $v_1$  and  $v_2$  can be processed in a manner such that the individual delays  $d_1$  and  $d_2$  are compensated by an identical 'temporal lookahead'  $d_1$  and  $d_2$ , respectively. As a result, the synchrony of covariant components may be reestablished in the CNS so that a simple space-metric is then usable.

A space-time metric tensor in the brain, therefore, must serve two simultaneous purposes: (a) to provide a procedure by which each of the temporally-dispersed covariants are augmented by a suitable 'temporal lookahead' so that they all refer to the same external time-point, and (b) to assemble the invariant from such temporally-extrapolated covariant components.

The space-time metric in Fig. 4B achieves these goals by (a) containing 'lookahead-modules' for each covariant space-time component in order to compensate for the delay involved in the individual coordinate, and (b) providing a connectivity-matrix (just as in Fig. 4A) which serves as a metric.

However, a space-time metric tensor may not be as simple as shown in Fig. 4. Firstly, in some particular expressions of the network, individual neurons in the first set may not be separable from the neurons in the latter. Thus, in general, a space-time metric may be implemented by a morphologically-unified network. Second, since the matrix of the metric tensor in an oblique frame contains non-zero off-diagonals, a network expression of such matrix will have cross-connections from the  $i$ th input to  $j$ th output line ( $i \neq j$ ). Therefore, a 'slicing' of the network implementing the space-time metric into separate input-output loops is also inapplicable in the general case. But before a more detailed discussion of such general features of morphologically-unified metric networks, we have first to elaborate further the basic scheme of the space-time metric.

*'Explicit' and 'implicit' space-time metrics*

The fundamental scheme in Fig. 4B is expanded