

## Sensori-Motor Transformations in the Brain (with a Critique of the Tensor Theory of Cerebellum)

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Section 1 lists 12 points which must be addressed by neural models of sensorimotor coordination. Section 2 addresses the problem of extrapolating motor output from noisy data or from sensory input. The Pellionisz-Llinas cerebellar lookahead module addresses this problem for the noise-free case, and we suggest theoretical and experimental tests of the model; we then suggest the investigation of neural analogs of the Kalman-Bucy filter. Section 3 offers a brief exposition of mechanics in a tensor framework to provide the irreducible minimum of mathematical machinery to evaluate the Pellionisz-Llinas tensor theory of brain function and to suggest fruitful new hypotheses. Our critique of this theory in section 4 leads us to conclude that what they offer is based on metaphorical use of terminology from Euclidean tensors, not on rigorous application of the mathematics of tensor analysis. The central claim of their theory—that the input is a covariant intention vector transformed by a metric tensor encoded in the cerebellum to a contravariant execution vector—has not been substantiated and probably cannot be substantiated. However, we do point the way to further use of tensor analysis in the study of neural control of movement. The concluding section then returns to the points raised in section 1 with a highly selective survey of models of cerebellum and tectum.

### 1. A General Perspective on Sensorimotor Coordination

Elsewhere (Arbib, 1981) we have offered an analysis of "perceptual structures and distributed motor control" which stresses that action and perception are intertwined in a continuing *action-perception cycle*. In general, the organism does not simply emit a response after some delay to a single

sensory stimulus. Rather, it continually acts on the basis of a program of action, this program depends on a representation of the animal's relation to its environment, and as the animal moves the consequent sensory stimulation enables it to update this environmental model. The animal acts to perceive, and perceives to act. We suggested the relevance of certain concepts of Artificial Intelligence, and introduced the notions of *perceptual schema*, *motor schema* (analogous to a synergy in the sense of Bernstein), *schema-assemlage*, and *coordinated control program*. We will not rehearse this analysis here, but rather note a set of problems of sensorimotor coordination.

*Point 1.* The nervous system must work with different coordinate systems. For example, a target might be represented in sensory terms by a pair of two-dimensional coordinates (corresponding to the projection of the target on the left and right retinas), and in motor terms by the joint angles which will enable the arm to grasp the target. Note that each of these representations takes 4 coordinates (assuming a 2-segment arm) to specify a point in 3-dimensional space.

*Point 2.* Note that the representations above are not of a point in absolute space, but of a point relative to the body. Moreover, the retinal representation is relative to the eyes, while the motor representation is relative to the shoulder. Thus the brain must solve the *remapping problem* not by implementing a fixed map from sensory to motor coordinates, but rather a map which is itself dependent on such factors as eye vergence and accommodation, and turning of the head.

*Point 3.* Much successful biological control theory offers lumped models of neural activity which treat such coordinates as if they corresponded directly to neural activity. However, the first visual code of a target is not a pair of coordinates, but rather a localized peak of activity in the two-dimensional manifold of each retina. In some models we can usefully reduce this peak to its angular coordinates, but this does not imply that there exists a pair of neurons whose firing rate directly encodes these coordinates. Again, to maintain a given joint-angle, the brain must specify a complex set of alpha- and gamma-neuron firing of agonist and antagonist, and there may be no single neuron whose firing rate encodes the angle.

*Point 4.* In catching a target, delays within the brain, movement of the target and inertia of the arm all conspire to force the brain not to compute arm-coordinates on the basis of simultaneous eye-coordinates but rather to use prior sensory data to extrapolate where the arm should be in the future to intercept the target's trajectory.

*Point 5.* But the moving target problem shows that, even at the level of lumped coordinates, the task of the brain is not simply a transformation from eye-coordinates to position-coordinates, even with delays. To extrapolate the target's position, we need other parameters of its position, such as velocity. Moreover, the control signals to move the arm to a desired position may well differ from those required to maintain that position; e.g. they may be force signals based on comparing feedback on arm position and velocity with visually-based signals on target position and velocity.

*Point 6.* However, the moving target problem is deceptive in that it suggests relevant sensory information can be lumped into signals encoding the motion of a single point. Consider the problem of walking down a street while inspecting shop windows and avoiding bumping into other pedestrians, or consider a toad detouring around a paling fence to get a worm on the other side. In both cases, the relevant stimuli involve complex spatiotemporal patterns of retinal stimulation which encode objects in dynamic interrelationship. The brain may or may not have to recognize these objects as part of the consequent navigation problem. The paper (Arbib, 1981) analyzes these issues in more detail.

*Point 7.* It is a common mathematical assumption that a function (and certain derivatives) is continuous, if not linear. However, this assumption is often inappropriate in defining a sensori-motor transformation. Given the navigation problem of deciding whether to go through a gap of width  $d_1$  or another of width  $d_2$ , it is clear that if we start with a situation in which the first gap is the unequivocal choice, and then continually decrease  $d_1$  and increase  $d_2$ , there will come a point at which the chosen direction of movement changes *discontinuously*. Moreover, the system will exhibit *hysteresis*—if we now reverse the changes of  $d_1$  and  $d_2$ , the switchover point will differ, with larger  $d_1$  and smaller  $d_2$  than in the switchover first observed.

*Point 8.* Different tasks require different control systems, and the coordination and interwoven activation of these systems. We must understand how each such system is anatomically localized (or distributed), and how the parameters of its mathematical description are neurally encoded.

*Point 9.* A control system may need both *short-term memory* (of parameters related to the current situation; e.g. the mass and moment of inertia of any object being manipulated), and *long-term memory* (e.g. improved coordination and "polishing" of a skill). What processes make the necessary changes? How are they neurally encoded and stored? We shall use the term

*identification algorithm* which provides the controller with estimates of the parameters of the system currently being controlled.

*Point 10.* There are many unresolved issues concerning the relation between ballistic and tracking movements, and of the relation between feedback and feedforward.

*Point 11.* Complicating the remapping problem of Point 2 is what might be called the *hierarchical control problem*. To visually fixate an object may require eye movements alone, or head movements, trunk movements, locomotion to approach the object, and even manipulation of the object. This involvement of many motor systems is extremely complex, yet may be controlled by simple visual feedback: has an interesting feature of the object been brought into focus?

*Point 12.* We close this list with the *postural stability problem*: in controlling even a small movement, the brain commonly has to first adjust muscles all over the body to provide a stable posture for the given movement.

This list is clearly not exhaustive, but it should serve to provide sufficient perspective for the analysis in the following sections.

## 2. Lookahead in the Nervous System

Biological control theory received major impetus from Wiener's (1948) book on cybernetics, and Wiener's view of such systems was based on his earlier study of extrapolation, interpolation and smoothing of stationary time series. This was motivated by the problems of World War II anti-aircraft gunnery. The problem is twofold: (a) Because an airplane is moving fast, sightings of its position will be "noisy," and (b) because the plane is moving fast, it will have moved beyond its present situation by the time a shell can intersect its trajectory. (a) yields the problem of *interpolation and smoothing* of stationary time series—given a model of the statistical distribution of errors in measurement, to infer the "best" (by least-mean-square error criterion) trajectory compatible with the data. (b) yields the problem of *extrapolation* of a future point on the trajectory from past values.

If we ignore all problems of measurement errors, the extrapolation or lookahead problem is easily solved by classical methods of the calculus. Suppose that  $f: R \rightarrow R$  is a real-valued function for which  $f$  and its first  $n+1$  derivatives are defined and continuous on an interval  $(a, h)$ . Then the theorem of the *Taylor's series with a remainder* tells us that

$$f(a+h) = f(a) + hf'(a) + \frac{h^2}{2!} f''(a) + \dots + \frac{h^n}{n!} f^{(n)}(a) + R_n \quad (1)$$

where the remainder

$$R_n = \frac{h^{n+1}}{(n+1)!} f^{(n+1)}(a + \theta h) \quad (2)$$

for some  $\theta$  with  $0 < \theta < 1$ . Clearly, if  $|f^{(n+1)}(x)| \leq M$  on the interval  $(a - \eta, a + \eta)$ , we have

$$|R_n| \leq \frac{|h|^{n+1}}{(n+1)!} M \quad (3)$$

so long as  $|h| < \eta$ . Thus the truncated Taylor series

$$f(a) + hf'(a) + \frac{h^2}{2!} f''(a) + \dots + \frac{h^n}{n!} f^{(n)}(a) \quad (4)$$

is a good approximation to  $f(a + h)$  if  $M$  is not too big, i.e. if  $|h|^{n+1} M / (n+1)!$  is less than the allowable error in the approximation.

If all the derivatives involved are continuous at  $a$ , then the derivatives can be estimated with arbitrary accuracy from values of  $f(x)$  for  $x < a$ , and so may be assumed known, on the basis of observations made prior to  $a$ . In summary:

#### THE TAYLOR LOOKAHEAD METHOD

If  $f$  and  $n$  have the property that  $\eta$  can be so chosen that

$$|h|^{n+1} M / (n+1)! < \epsilon \quad (5)$$

then the *lookahead formula* (4) will estimate  $f(a + h)$  for any  $h$  with  $|h| < \eta$  with error at most  $\epsilon$ .

Of course, if we had an explicit formula for  $f(x)$  with  $x$  in  $(a, a + h)$ , we would not need the lookahead formula. But if we do not know  $f$ , how can we be sure that the condition (5) holds? Let  $F_n$  be the set of functions for which equation (5) holds. All the polynomials in  $x$  of degree less than  $n + 1$  surely belong to  $F_n$ . Hence some further argument will be needed to justify sufficient confidence that a signal belongs to  $F_n$ .

Pellionisz & Llinás (henceforth, PL) note that neural delays ensure that the motor output is delayed relative to the sensory input (assuming, apparently, a direct stimulus-response relationship), and Wiener's example reminds us that the effect of a motor command may itself be delayed relative to the time of the command itself. Thus if we consider a neural system at time  $t$  computing the transformation of an input  $u$  to an output  $v$ , it should

compute *not*

$$v(t) = f(u(t)) \quad \text{but rather}$$

$$v(t+d) = f(u(t+d)) \quad \text{using values of } u \text{ for times up to } t - \delta \quad (6)$$

for suitable delays  $d$  and  $\delta$ . PL essentially adopt the Taylor lookahead method for solving equation (6), save that  $u$  and  $v$  are now vector-valued, rather than real-valued. The formula they use for the multi-dimensional form of (4) is also complicated by their tensor theory (Section 4), but we believe that this complication is not necessary for our analysis in this section.

Llinás, Precht & Clarke (1971) studied cerebellar Purkinje responses to physiological stimulation of the vestibular system in the frog, and found that different Purkinje cells show zero-, first-, and even second-order time derivatives of the velocity stimulus. This leads PL to the hypothesis:

#### THE CEREBELLUM AS A LOOKAHEAD MODULE

The cerebellum implements a sensorimotor transformation with lookahead

$$v(t+d) = f(u(t+d)) \quad \text{based on values of } u \text{ for times up to } t - \delta$$

by taking an appropriate linear combination of Purkinje cell firing representing the zero-, first-, and second-order derivatives of  $f$  with respect to  $u$ .

This is an interesting scheme, and deserves careful further analysis. However, we note that this hypothesis *has not been tested*. Leaving aside the complications posed by multidimensionality, we simply note the problems posed by the one-dimensional case:

(a) PL view the total transformation as given by summing of Purkinje cell output on cerebellar nucleus (CN) neurons. We *do not have experimental evidence* that the mossy-fibre to CN transformation implements a meaningful sensorimotor transformation  $f$  and so, *a fortiori*, we have no evidence that cerebellar connectivity represents the Taylor coefficients of  $f$ . Again, lacking such an  $f$ , we do not know whether the remainder term  $R_n$  is sufficiently small, as in equation (5), to justify a second-order Taylor approximation.

(b) The Purkinje cell "derivatives" in (Llinás *et al.*, 1971) are very noisy. In fact, it is not clear from the records that they are derivatives with any quantitative precision, even with the reliability afforded by redundancy. It seems, then, that a careful parametric analysis is required to show that this lack of precision does not vitiate the lookahead formula.

Clearly, the PL lookahead module should receive much further study. However, it is worth noting that the use of the Taylor series has three theoretical disadvantages:

- (i) It uses differentiators, which are highly noisy operators and amplify disturbances. (This can be answered by resolving the issues in (b) above.)
- (ii) It assumes noise-free data, and does not address Wiener's "smoothing of time series" problem.
- (iii) It corresponds to an instantaneous dependence of  $v$  on  $u$  (the derivatives of  $u$  only being used to solve the lookahead problem). By contrast, motor control usually involves a dependence on the prior history of  $u$ :

$u$  and  $v$  are related by a functional  $F$  such that

$v(t)$  depends on  $u(\tau)$  for any and only values of  $\tau$  with  $\tau \leq t$ .

The classic Wiener-Hopf technique answers all three objections, and thus offers a technique for providing the least-mean-square estimate of the whole trajectory of  $v$  by applying a kernel to the data on  $u$ . The Wiener-Hopf technique assumes that signals  $u(t)$  have a certain stationary stochastic property  $S$  on the average, instead of assuming that they belong to  $F_n$ . The Kalman-Bucy filter is mathematically equivalent under the stationary environment, but is dynamic. It works when the stochastic property  $S$  is unknown or even changing slowly: at each time  $t$ , it receives  $u(t - \delta)$  as input, uses it to update an internal state which encapsulates stochastic information about the past history of  $u$  relevant to the extrapolation of  $v$ , and then provides its current estimate of  $v(t + d)$  as output. It is adaptive in this sense.

[*Bibliographical Note:* Hopf & Wiener (1931) developed their factorization method to solve a problem of radiative equilibrium in stars; Wiener modified the method to apply to problems in smoothing and prediction in a classified report of 1942, released in 1949; Levinson (1947) provides an excellent exposition of Wiener's theory, accessible to readers with a knowledge of complex variables and Fourier integrals (Wiener, 1933). For original presentations on the Kalman-Bucy filter, see Kalman (1960), Kalman & Bucy (1961); a useful exposition may be found in Rhodes (1971).]

Clearly, the theoretical advantages of the Kalman-Bucy filter do not imply that it provides the operating principle for any region of the brain. It thus seems reasonable that future research on the neural lookahead problem should both further analyze the PL cerebellar lookahead module—both theoretically and experimentally as in (a) and (b) above—and also look into possible neural analogues of the Kalman-Bucy filter for realistic motor control problems. For other neural approaches to lookahead, see Fujita (1982*a,b*) and Sutton & Barto (1981). They are related to the technique

of adaptive systems in which the system can be modified on the basis of supervision in terms of signals from a teacher.

### 3. A Brief Outline of Mechanics in a Tensor Framework

PL have offered a "tensor theory of the cerebellum" (Pellionisz & Llinás, 1979, 1980*a,b*, 1981, 1982*a,b*). PL speak of the neural encoding of spatial coordinates as constituting a hyperspace whose geometry is largely unknown, but certainly non-Euclidean. One would thus expect their theory to rest on the tensor analysis of manifolds ("smooth" geometric spaces) which are not Euclidean. However, we are convinced that their entire theory rests on *analogies* with (not applications of theorems from) the restricted theory of tensors on *Euclidean* spaces. Thus their "tensor theory of the cerebellum" would be better named "the Euclidean tensor metaphor for cerebellum". As such, it is a theory in its own right. However, our critique in section 4 will show that this theory has serious gaps and is not supported by experiment. Nonetheless, a theory may be valuable if it stimulates further work. In this case, the PL theory stimulates us to consider what a theory of cerebellum (or, more generally, neural control of movement) would look like that does use the powerful machinery of (non-Euclidean) tensor analysis. We thus devote the present section to a general exposition of tensor analysis. This account may seem to unduly burden the mathematical patience of the reader of the *Journal of Theoretical Biology*. However, it provides the irreducible minimum of mathematical machinery which must be understood if the reader is to evaluate the PL tensor metaphor of brain function, and see the possibilities for further use of tensor analysis in brain theory.

With this, we now look at the mechanics of a system whose state-space is a manifold rather than a Euclidean space. In classical mechanics, we distinguish the configuration of a system from its state. For example, the configuration would specify the position of each component of the system, while the state would specify both the configuration of the system and the momentum of each component. The point is that the future states of a system are completely determined by its present state (for specified external forces)—clearly, the present position of a car does not determine its position 5 seconds later, unless we also know its velocity, subject to specified external forces. We thus have a space  $S$  of states, a space  $M$  of configurations, a map

$$\pi: S \rightarrow M \quad (1)$$

such that  $\pi(s)$  is the configuration of a system in state  $s$ , and we have that for each state  $s_0$  and time  $t_0$  there exists a unique trajectory  $s: T \rightarrow S$  which assigns a state  $s(t)$  in  $S$  to each time  $t$  in  $T$  and which has the property



that  $s(t_0) = s_0$ . Newtonian mechanics not only gave us the concept of state-determined trajectories, but also showed us that these trajectories could be obtained by integrating differential equations

$$\dot{s}(t) = f(s(t), F(t)) \quad (2)$$

expressing the rate of change of state  $\dot{s}(t)$  at time  $t$  as a function of the state  $s(t)$  at time  $t$  and the external force  $F(t)$  applied to the system at time  $t$ .

In the early development of mechanics, the state space was a (subset of) some Euclidean space, i.e. every point in  $S$  could be given a sequence  $(x_1, \dots, x_n)$  of real numbers as its coordinates, and the distance between two points  $x = (x_1, \dots, x_n)$  and  $x' = (x'_1, \dots, x'_n)$  was given by the formula

$$d(x, x') = \left( \sum_{i=1}^n (x_i - x'_i)^2 \right)^{1/2}. \quad (3)$$

Let us denote by  $E^n$  this Euclidean  $n$ -space. The derivative  $\dot{s}(t)$  could then be seen as also being a vector in  $E^n$ , given by the formula

$$\dot{s}(t) = \lim_{h \rightarrow 0} \frac{s(t+h) - s(t)}{h}. \quad (4)$$

Representing the force  $F$  as an  $m$ -dimensional vector, then, the function  $f$  of the differential equation (2) is of the form  $f: E^n \times E^m \rightarrow E^n$  which assigns to each state  $s$  in  $E^n$  and force  $F$  in  $E^m$  another value,  $f(s, F)$ , which is in the state space  $E^n$  but which can also be regarded as a rate of change of state.

This notion that  $\dot{s}(t)$  lies in the state space proves to be *grossly misleading*, an artifact of the use of a Euclidean state-space. To see this we must give a brief account of mechanics on a manifold. Since our aim is to provide the necessary background for the critique of the cerebellum as a metric tensor in the next section, the discussion will be selective, aiming to introduce the concepts of covariant tensor, metric tensor, and contravariant tensor. (More modern approaches to mechanics on a manifold use the theory of linear differential forms, see, e.g. Loomis & Sternberg, 1968. For useful side-by-side exposition of the modern and the tensorial treatment, see Spivak, 1970.)

Suppose that the constraints on the system are such that the states do not "fill out" a region of Euclidean space but rather lie on a "curved space" or manifold. (In Fig. 1, we represent such a manifold as a curved surface embedded in Euclidean 3-space, but relativity theory has taught us the importance of considering manifolds which are intrinsically curved but

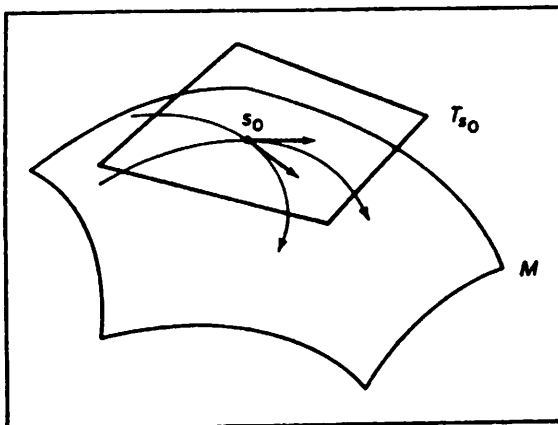


FIG. 1. Here we see two examples of the fact that the derivative at  $s_0$  of a trajectory  $s: I \rightarrow M$  is not an element of  $M$  but an element of the tangent space  $T_{s_0}$  at  $s_0$ .

which are to be viewed as “full spaces” in their own right rather than as subspaces of a Euclidean space.) Consider any trajectory passing through the point  $s_0$ . It is clear from Fig. 1 that the  $\dot{s}(t)$  for the trajectory lies *not in the manifold but in the tangent plane* at  $s_0$ . It is a “coincidence” that for flat (i.e. Euclidean) manifolds the tangent space can be identified with the manifold as in our discussion of  $S = E^n$ .

Let us consider a patch  $U$  of manifold  $M$  in the neighborhood of  $s_0$ . We can set up a *local coordinate system* as shown in Fig. 2 so that each point

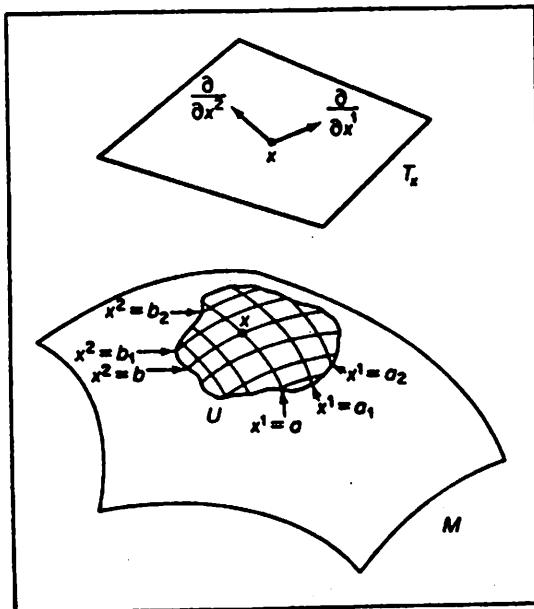


FIG. 2. The local coordinate system in the neighbourhood  $U$  of  $x$  induces a pair of unit vectors which provide a basis for the tangent space  $T_x$  at  $x$ .

in  $U$  is uniquely specified by a pair of coordinates  $(x^1, x^2)$ , the values there of the variables  $x^1$  and  $x^2$  respectively. (Note: We could just as well have chosen a different coordinate grid around  $U$ ; the important point is that once the grid is chosen, each point in  $U$  is uniquely specified by its coordinate values, and different coordinate vectors in the chosen system cannot describe the same point of  $U$ .) We see that the choice of coordinates near  $x$  induces a corresponding set of coordinates on the *tangent space*  $T_x$ —here  $\partial/\partial x^1$  is the unit vector tangent to the curve through  $x$  in the direction of increasing  $x^1$ ; similarly  $\partial/\partial x^2$  is the tangent vector for a unit increase in  $x^2$ . These vectors provide a basis for  $T_x$  as a vector space, though clearly they need not be orthogonal.

The situation generalizes (though we omit many of the mathematical niceties). We say a *manifold*  $M$  is *n-dimensional* if each point  $x$  of  $M$  lies in a neighborhood  $U$  in which points are uniquely specified by an irredundant  $n$ -dimensional vector  $(x^1, \dots, x^n)$  of real numbers. Then with each point  $x$  we associate a tangent space  $T_x$  and (given the choice of coordinates near  $x$ ) we set up a basis  $\partial/\partial x^1, \dots, \partial/\partial x^n$  where  $\partial/\partial x^i$  is the unit vector tangent to the curve of increasing  $x^i$  through  $x$ .

We have an important restriction: it may be that two “charts” (neighborhoods)  $U$  and  $\bar{U}$  with coordinates  $(x^1, \dots, x^n)$  and  $(\bar{x}^1, \dots, \bar{x}^n)$ —note that  $n$  must be the same in the two charts—overlap. We then require that the change of coordinates be smooth and unequivocal on the overlap  $U \cap \bar{U}$ . Let  $x$  be a point in the overlap. Then we can express its  $\bar{U}$  coordinates as a function of its  $U$  coordinates, writing  $\bar{x}^i(x^1, \dots, x^n)$ . We require that at each such point, the  $n^2$  partial derivatives

$$\frac{\partial \bar{x}^i}{\partial x^j}(x^1, \dots, x^n)$$

exist, and that the determinant of the matrix  $|\partial \bar{x}^i / \partial x^j|$ , called the *Jacobian*, be non-zero. (We say that *the Jacobian is non-singular*.) This implies that the change of coordinates in *both* directions is well-defined, so that given the coordinates of a point in one system we can solve uniquely for its coordinates in the other system.

Note that if  $x$  is in  $U$  and  $\bar{U}$ , we have the same  $T_x$  considered as an abstract space, but the  $U$ -coordinates induce a basis  $\partial/\partial x^1, \dots, \partial/\partial x^n$ , while the  $\bar{U}$ -coordinates induce a basis  $\partial/\partial \bar{x}^1, \dots, \partial/\partial \bar{x}^n$ .

Now let us return to mechanics. Leaving implicit the specification of forces (as we may do if the force is dependent on the state rather than time or an external control), we may write the differential equation for a system whose state-space is the manifold  $M$  in the form

$$\dot{s}(t) = f(s(t))$$

where  $s(t)$  is a point in  $M$ , and  $\dot{s}(t)$  is thus a vector in  $T_{s(t)}$ , the tangent space at  $s(t)$ . Thus  $f$  assigns to each point  $x$  in  $M$  a value  $f(x)$  in  $T_x$ . We call such a map a *flow* on  $M$ . In coordinate form the value  $f(x)$  is a vector in  $T_x$ , and so can be written in terms of the basis  $\partial/\partial x^1, \dots, \partial/\partial x^n$ , say as

$$f(x) = f^1(x) \frac{\partial}{\partial x^1} + \dots + f^n(x) \frac{\partial}{\partial x^n}. \quad (6)$$

Note that it is important that *the set of coordinates be irredundant*, that the tangent space be  $n$ -dimensional for the same  $n$  as the number of coordinates, and that  $\partial/\partial x^1, \dots, \partial/\partial x^n$  then form a basis for  $T_x$ . It is this property of being a basis that lets  $f(x)$  *uniquely determine* the coordinates  $f^1(x), \dots, f^n(x)$  in equation (6).

We may make the dependence on the choice of coordinates in  $U$  explicit in equation (6) by writing

$$f(x) = f^1(x^1, \dots, x^n) \frac{\partial}{\partial x^1} + \dots + f^n(x^1, \dots, x^n) \frac{\partial}{\partial x^n}. \quad (6')$$

Suppose, though, that we had chosen a different set of coordinates  $(\bar{x}^1, \dots, \bar{x}^n)$  in some neighborhood  $\bar{U}$  of  $x$ . Then we could express  $f$  in these coordinates as

$$f(x) = \bar{f}^1(\bar{x}^1, \dots, \bar{x}^n) \frac{\partial}{\partial \bar{x}^1} + \dots + \bar{f}^n(\bar{x}^1, \dots, \bar{x}^n) \frac{\partial}{\partial \bar{x}^n} \quad (6'')$$

where we use  $\bar{f}^i$  to stress the different numerical dependence of the components of  $f$  with respect to these new coordinates.

How are these two coordinate systems related? We have

$$\frac{\partial}{\partial x^i} = \sum_{j=1}^n \frac{\partial \bar{x}^j}{\partial x^i} \frac{\partial}{\partial \bar{x}^j} \quad (7)$$

and then

$$\begin{aligned} \sum_{j=1}^n \bar{f}^j(\bar{x}^1, \dots, \bar{x}^n) \frac{\partial}{\partial \bar{x}^j} &= f(x) \\ &= \sum_{i=1}^n f^i(x^1, \dots, x^n) \frac{\partial}{\partial x^i} \\ &= \sum_{i=1}^n \sum_{j=1}^n f^i(x^1, \dots, x^n) \frac{\partial \bar{x}^j}{\partial x^i} \frac{\partial}{\partial \bar{x}^j} \\ &= \sum_{j=1}^n \left( \sum_{i=1}^n \frac{\partial \bar{x}^j}{\partial x^i} f^i(x^1, \dots, x^n) \right) \frac{\partial}{\partial \bar{x}^j}. \end{aligned}$$

Then, since the  $\partial/\partial\bar{x}^j$  form a basis, we may conclude that

$$\bar{f}^j(\bar{x}^1, \dots, \bar{x}^n) = \sum_{i=1}^n \frac{\partial \bar{x}^j}{\partial x^i} f^i(x^1, \dots, x^n). \quad (8)$$

We thus conclude that a flow on a manifold is a contravariant vector where

*Definition.* A set of  $n$  functions  $A^i$  of the  $n$  coordinates  $(x^1, \dots, x^n)$  are said to be the components of a *contravariant vector* if they transform according to the equation

$$\bar{A}^j = \sum_{i=1}^n \frac{\partial \bar{x}^j}{\partial x^i} A^i \quad (9)$$

(when  $\bar{A}^j$  and  $A^i$  are evaluated at coordinates corresponding to the same point  $x$  of the manifold) on change of coordinates from  $(x^1, \dots, x^n)$  to  $(\bar{x}^1, \dots, \bar{x}^n)$ .

Note that the change of coordinates *maintains the dimensionality*  $n$  of the manifold. Correspondingly, we have the definition

*Definition.* A set of  $n$  functions  $B_i$  of the  $n$  coordinates  $x^i$  are said to be the components of a *covariant vector* if they transform according to the equation

$$\bar{B}_j = \sum_{i=1}^n \frac{\partial x^i}{\partial \bar{x}^j} B_i \quad (10)$$

on change of coordinates from  $x^i$  to  $\bar{x}^i$ .

Such vectors are the coordinate representation of cotangent fields. A cotangent field assigns (in an appropriately smooth way) a cotangent  $p_x$  to each point  $x$ . Here cotangent is not used in the trigonometric sense. Rather,  $p_x$  is a linear map from  $T_x$  to the real line  $R$ . Thus if  $f_x$  and  $f'_x$  are two tangents at  $x$ , and  $\lambda$  and  $\lambda'$  are arbitrary real numbers, we have

$$p_x(\lambda f_x + \lambda' f'_x) = \lambda p_x(f_x) + \lambda' p_x(f'_x).$$

Let  $(B_1, \dots, B_n)$  be the coordinate representation of a cotangent  $p_x$  at  $x$  with respect to the coordinates  $x^i$ . When a tangent  $f(x)$  at  $x$  has the coordinate representation  $(A^1, \dots, A^n)$ , where  $A^i = f^i(x)$  as is shown in equation (6), the cotangent  $p_x$  operating on  $f(x)$  yields a scalar  $p_x(f_x)$  by

$$p_x(f_x) = \sum B_i A^i.$$

If we represent  $p_x$  as a row vector  $B = (B_1, \dots, B_n)$  and  $f(x)$  as a column vector  $A = (A_1, \dots, A_n)^T$ , where  $T$  denotes the transposition,  $p_x(f_x)$  is the inner product  $BA$  of these vectors. It is easy to check that, when the components of  $f_x$  transform in the contravariant manner, equation (9), the

components of  $p_x$  do indeed transform in the covariant manner, equation (10), retaining the inner product  $p_x(f_x) = \sum B_i A^i = \sum \bar{B}_i \bar{A}^i$  invariant.

Note well that with respect to general transformation of coordinates, the coordinate vectors  $(x^1, \dots, x^n)$  do not themselves form either a covariant or contravariant vector. For example, we have

$$\bar{x}^j = \sum_{i=1}^n \frac{\partial \bar{x}^j}{\partial x^i} x^i \quad (11a)$$

only for linear transformations, not for the general changes of coordinates that define contravariance.

However, there is a *restricted* form of tensor analysis used for Euclidean (vector) spaces (Bowen & Wang, 1976; Coburn, 1955). In this case, a coordinate system is obtained by choosing a *basis* (a set of  $n$  linearly independent—but not necessarily orthogonal—vectors) for the  $n$ -dimensional vector space under consideration. If the basis comprises the vectors  $b_1, \dots, b_n$  then the corresponding coordinates of a vector  $x$  comprise the numbers  $(x^1, \dots, x^n)$  such that

$$x = x^1 b_1 + \dots + x^n b_n \quad (11b)$$

In this Euclidean tensor theory, the only admissible change of coordinates is to give a new basis  $\bar{b}_1, \dots, \bar{b}_n$ —and then there exists a non-singular matrix  $A = [a_i^j]$  such that the new coordinates  $(\bar{x}^1, \dots, \bar{x}^n)$  of a vector  $x$  are related to the old ones by

$$\bar{x}^j = \sum_{i=1}^n a_i^j x^i \quad (11c)$$

In this case, it is clear that  $\partial \bar{x}^j / \partial x^i = a_i^j$  and that with respect to this restricted set of linear transformations, the coordinate vector  $(x^1, \dots, x^n)$  does form a contravariant vector.

We next turn to the notion of a metric tensor [see, e.g. Spain (1953) for further details]. We know that in Euclidean space the distance  $ds$  between two points  $(x^1, \dots, x^n)$  and  $(x^1 + y^1, \dots, x^n + y^n)$  (where the  $y^i$  are infinitesimal) is given by [recall equation (3)]

$$ds^2 = (y^1)^2 + \dots + (y^n)^2.$$

More generally, there are many manifolds  $M$  with the property that the distance  $ds$  between neighboring points with coordinates  $x^i$  and  $x^i + y^i$  (where the  $y^i$  are “infinitesimal”) is given by the quadratic differential form

$$ds^2 = \sum_{i,j} g_{ij} y^i y^j \quad (12a)$$

where the  $g_{ij}$  ( $1 \leq i, j \leq n$ ) are functions of  $x^i$  subject only to the restriction that  $g$ , the determinant of the matrix  $|g_{ij}|$ , is never zero. If such  $g_{ij}$  exists, we say  $M$  is a *Riemannian manifold* and call  $g_{ij}$  the *metric tensor* for  $M$ .

Returning to the Euclidean case, suppose that our coordinates  $(x^1, \dots, x^n)$  are taken with respect to a basis  $b_1, \dots, b_n$ , and that  $b_1, \dots, b_n$  are themselves expressed as coordinate vectors

$$b_j = (b_j^1, \dots, b_j^n)$$

with respect to an orthogonal basis  $e_1, \dots, e_n$ . We then know that

$$x = \sum_{i=1}^n x^i b_i = \sum_{k=1}^n \left( \sum_{i=1}^n x^i b_i^k \right) e_k$$

But we know from vector space theory that the square of the length of a vector is just the sum of the squares of its components with respect to any orthonormal basis

$$\begin{aligned} |x|^2 &= \sum_{k=1}^n \left( \sum_{i=1}^n x^i b_i^k \right)^2 \\ &= \sum_{i,j} \left( \sum_{k=1}^n b_i^k b_j^k \right) x^i x^j. \end{aligned}$$

Hence, in this Euclidean case  $g_{ij}$  is independent of  $x^i$ , and is given by

$$g_{ij} = \sum_{k=1}^n b_i^k b_j^k \quad (\text{Euclidean}) \quad (12b)$$

In the Euclidean case, then, a vector  $x^i$  is of unit length (a meaningless concept in a general manifold) if  $\sum_{i,j} g_{ij} x^i x^j = 1$ , and two vectors  $x^i$  and  $y^j$  are orthogonal if  $\sum_{i,j} g_{ij} x^i y^j = 0$ . More generally we know from the theory of Euclidean vector spaces that if  $e^i$  are the coordinates of a vector  $e$  of unit length, and if  $x^i$  are the coordinates of a vector  $x$  (with respect to the same basis) then the length of the projection of  $x$  upon the ray defined by  $e$  is given by the *scalar product*

$$x \cdot e = \sum_{i,j} g_{ij} x^i e^j \quad (\text{Euclidean}). \quad (12c)$$

More generally, of course,

$$x \cdot y = \sum_{i,j} g_{ij} x^i y^j = |x| \cdot |y| \cos \theta, \quad (12d)$$

where  $\cos \theta$  is the angle between the two vectors  $x$  and  $y$ .

Returning to the general case, manipulations akin to those preceding equation (8) verify that  $g_{ij}$  is a *covariant tensor of the second order*, i.e. that

it transforms according to the rule

$$\bar{g}_{ij} = \sum_{k,l} \frac{\partial x^k}{\partial \bar{x}^i} \frac{\partial x^l}{\partial \bar{x}^j} g_{kl}. \quad (13)$$

Since  $\det(|g_{ij}|) \neq 0$ , we may form the *inverse*, which we write  $g^{ij}$ , so that

$$\sum_{j=1}^n g_{ij} g^{jk} = \delta_i^k \quad (14)$$

where  $\delta_i^k$  is the Kronecker delta:  $\delta_i^k = 1$  if  $i = k$ , else  $\delta_i^k = 0$ . We also refer to  $g^{ij}$  as the metric tensor—the use of superscripts preventing ambiguity. It is readily checked that  $g^{ij}$  is a *contravariant tensor of the second order*, i.e.

$$\bar{g}^{ij} = \sum_{k,l} \frac{\partial \bar{x}^i}{\partial x^k} \frac{\partial \bar{x}^j}{\partial x^l} g^{kl}. \quad (15)$$

We next note the process of “lowering the superscript” or “raising the subscript,” respectively. If  $A^j$  is a contravariant vector we define the *associate* of  $A^j$  to be the covariant vector

$$A_i = \sum_{j=1}^n g_{ij} A^j. \quad (16)$$

Similarly, we define

$$B^i = \sum_{j=1}^n g^{ij} B_j \quad (17)$$

and say that the contravariant vector  $B^i$  is associate for the vector  $B_j$ . Note that these operations are inverse to one another:

$$\begin{aligned} \sum_{j=1}^n g^{ij} A_j &= \sum_{j=1}^n g^{ij} \left( \sum_{k=1}^n g_{jk} A^k \right) \\ &= \sum_{k=1}^n \left( \sum_{j=1}^n g^{ij} g_{jk} \right) A^k = \sum_{k=1}^n \delta_k^i A^k = A^i. \end{aligned}$$

We see that this association generalizes the passage between a column (contravariant) vector and its (covariant) transpose (row) vector in a Euclidean vector space [set  $g^{ij} = \delta^{ij}$  and recall the discussion following equation (10)]. In fact, if we associate with  $g_{ij}$  the inner product  $T_x \times T_x \rightarrow R$  defined by  $\langle A|B \rangle = \sum g_{ij} A^i B^j$ , then we see that  $A$  induces a covariant vector, that is, a linear map  $T_x \rightarrow R$ , whose components are given by the right-hand side of equation (16a). This covariant vector operates on  $B$  to yield  $\langle A|B \rangle = \sum A_i B^i$  so that it is precisely the associate of  $A$ .



Equation (12c) deserves more attention in the Euclidean case. Suppose that  $(x^1, \dots, x^n)$  are the coordinates of the vector  $x$  with respect to a basis of  $n$  vectors  $e_1, \dots, e_n$ . Then, with respect to that same basis, the vector  $e_i$  has coordinates  $(0, \dots, 1, \dots, 0)$  with the 1 in the  $i^{\text{th}}$  position. Then equation (12c) becomes

$$x \cdot e_i = \sum_{j=1}^n g_{ij} x^j. \quad (16b)$$

Thus if the basis is composed of unit vectors, the components of the associate of  $(x^1, \dots, x^n)$  is made up of the lengths  $x_i = x \cdot e_i$  of the normal projections of  $x$  upon the basis vectors. Clearly, this geometrical interpretation is meaningless in the general, non-Euclidean, case.

One more point about equation (16) in the Euclidean case. If we define a change of basis by the matrix  $A_j^i = g_{ij}$  then we can see the numbers which define the associate, covariant, vector as also defining a contravariant vector

$$x^i = \sum_{j=1}^n A_j^i x^j = \sum_{j=1}^n g_{ij} x^j$$

with respect to a new basis. Let  $b_1, \dots, b_n$  be the old basis, and  $\bar{b}_1, \dots, \bar{b}_n$  be the new basis. Then, the coordinates of the  $\bar{b}_j$ 's are  $\bar{b}_j^i$  in the old coordinates, and  $\delta_j^k$  in the new coordinates so that

$$\delta_j^k = \sum_i g_{ki} \bar{b}_j^i$$

so that we conclude that  $\bar{b}_j^i = g^{ij}$  (the inverse of the  $g_{ij}$  matrix). Thus, applying equation (12d) in the old coordinates, we deduce that

$$\begin{aligned} \bar{b}_l \cdot b_k &= \sum_{ij} g_{ij} g^{ik} \delta_j^l \\ &= \delta_l^k. \end{aligned}$$

In other words, the basis  $\bar{b}_1, \dots, \bar{b}_n$  is uniquely defined by the requirement that  $\bar{b}_l \cdot b_l = 1$  for each  $l$ , while  $b_l$  is normal to  $b_k$  for  $k \neq l$ . This basis is called the *dual basis*, or *reciprocal basis*, of  $b_1, \dots, b_n$ . Hence we conclude that the *covariant* associate of a given vector  $x$  is in fact the *contravariant* expression of the same vector with respect to the dual basis.

PL have argued that it is an important question to ask, given a vector, whether it is covariant or contravariant. Our above exposition shows this to be mistaken. In general tensor analysis, a coordinate vector is *not* a tensor at all, either covariant or contravariant. In Euclidean tensor theory a vector is *both* covariant and contravariant, all depending on the choice of basis.

Of course, there are many ways of mapping a flow field (associating a tangent—expressed in coordinates as a covariant vector—with each point of the manifold) with a cotangent field. Some, such as the above method of association, can be thought of as a “change of coordinates” for the field, but as we have seen in discussing equation (11), the coordinates of the manifold cannot be regarded as covariant or contravariant vectors, and thus change of coordinates on a manifold is a *completely different* operation from the association of equations (16) and (17).

We close this section by outlining very briefly how the above machinery is used to develop mechanics on a manifold. Given a manifold  $M$  which is to serve as the configuration space for the mechanical system under study, the cotangent bundle  $T^*(M)$  serves as the state space. Here, a typical point of  $T^*(M)$  comprises a point  $x$  of the manifold  $M$  and a cotangent defined at  $x$ . In coordinates, this might be written  $(q^1, \dots, q^n, p_1, \dots, p_n)$ , with  $(q^1, \dots, q^n)$  the configuration-coordinates and  $(p_1, \dots, p_n)$  the momentum-coordinates of this state of the system.

The dynamics of the system is then given by a flow on  $T^*(M)$ . Often (though not always) the flow is induced by a function  $H: T^*(M) \rightarrow R$  called the *Hamiltonian* which can be written as a sum  $H = K + U$ , where  $U$  is called the *potential energy* and  $K$  is called the *kinetic energy*. To choose a kinetic energy  $K$ , we choose a Riemannian metric  $g^{ij}$  on the *configuration manifold*  $M$ , and then (essentially) define  $K$  in coordinate terms by

$$K(q^1, \dots, q^n, p_1, \dots, p_n) = \frac{1}{2} \sum_{i,j=1}^n g^{ij} p_i p_j.$$

Again,  $U$  is simply given by a function  $U: M \rightarrow R$ . The Hamiltonian equations

$$\frac{dq^i}{dt} = \frac{\partial H}{\partial p_i} \quad \text{and} \quad \frac{dp^i}{dt} = -\frac{\partial H}{\partial q_i}$$

then reduce to the form

$$\frac{dq^i}{dt} = \sum_{j=1}^n g^{ij} p_j \quad \text{and} \quad \frac{dp^i}{dt} = -\frac{\partial U}{\partial q_i}. \quad (18)$$

Modern approaches (e.g. Loomis & Sternberg, 1968) develop this theory using coordinate-free methods, without appealing to the terminology or techniques of tensor analysis. But the PL theory, reviewed in the next section, does not even take account of the tensorial form of mechanics. Clearly, a fully developed theory of motor control will make contact with these modern developments in mechanics. Particular interest will then inhere

in the notion (cf. Einstein's concept of matter as curvature in space-time) that potential energy is represented by a metric on configuration space.

#### 4. A Critique of the Metric Tensor Model of the Cerebellum

Einstein's relativity theory abandons the traditional separation of a Euclidean space from a time axis, merging them into a single Riemannian manifold, called space-time. PL seek to emulate this. We agree with their overall aim, that behavioral goals (such as physical displacement of parts of the body) be "vectorally expressed in the CNS in various frames of reference such that the different expressions still represent the same physical entity which is, by its nature, invariant to the existence of coordinate systems," and that we must thus re-examine our ideas about the space-time representation in the brain. We have already analyzed what PL have to say about lookahead in section 2. In their papers, they claim this study as part of a theory of simultaneity inspired by the goal of a neural "theory of relativity." In fact, far from introducing space-time, their model simply offers an account of how "lookahead" could enable the system to compensate for delays in a time separated from the other coordinates.

Our analysis will lead to the conclusion that PL have made *no case* for more than a Euclidean tensorial metaphor for brain function. Thus we interweave the non-Euclidean extension of their metaphor with our critique. We believe that this is constructive for further work, and that general tensor concepts will prove useful in brain theory as they have in various other fields [see, e.g. Amari (1982), Brockett (1976) and Kron (1934)].

Briefly, our criticism of the PL theory is as follows:

1. Modern mathematics has developed many techniques for coordinate-free analysis of structures. PL write as if the use of tensor analysis were the only such technique. In particular, some of their examples suggest that a change of coordinates involves a tensor transformation, whereas we have seen in section 3 that coordinates are *not* covariant or contravariant at all, save in the Euclidean case—and this is too restrictive for the study of sensory and motor coordinates.

2. PL speak of a CNS hyperspace  $F$  but never prove that  $F$  is a Riemannian manifold, or that there is a choice of coordinates with respect to which the cerebellum encodes the metric tensor of  $F$ .

3. PL wrongly assert that every array of numbers must be the coordinates of either a covariant or contravariant vector, thus wrongly insist that the input and output of cerebellum must be one or the other, assert without foundation that the cerebellum implements a metric tensor, and "conclude"

that the output is the contravariant associate of the input, which is posited to be a covariant vector.

4. Their analysis makes no use of tensor theory, beyond a metaphorical use of the terms "covariant," "contravariant," and "metric tensor" based on Euclidean tensors. PL make no use of the general tensor analysis required for analysis of nonlinear manifolds of movement. In particular, PL offer no discussion of the dynamics which motivated our exposition in section 3. We offer one possible "salvage operation" in the possible response to our Caveat 6, but this approach seriously undermines the idea that the tensorial theory explains sensory to motor transformations.

5. The tensor theory is grounded in *no* data on cerebellar anatomy, physiology or function (beyond the scant data for the lookahead theory discussed in section 2).

We now turn to the more detailed analysis which should enable the reader to evaluate the above assertions, and their import for the future employment of (general) tensor analysis in brain theory.

PL distinguish the representation of an event-point in a Newtonian frame by a vector  $p_M = (x, y, z, t)$  from another representation  $p_F = (x^1, \dots, x^n)^\dagger$ . We could imagine  $(x^1, \dots, x^n)^\dagger$  as a pattern of neural firing. Neither is pre-eminent, and each can be derived from the other.

*Caveat 1.* A pattern of neural firing rarely codes an  $(x, y, z, t)$  in any external reference frame, but may well encode the position of the event-point *relative* to the current time and the current position of the body. Moreover, as noted in section 1, event-points have less import, in general, to the animal than whole configurations of the environment relative to the animal's present state. PL usually speak as if the spatio- or event-temporal pattern represented by a vector  $v$  encodes an  $(x, y, z, t)$  of a single object. However, in general motor control the brain must encode event-times of a number of objects  $(x_i, y_i, z_i, t)$ , or  $s_i(t)$ , the trajectories of the  $i$ -th object.

PL then speak of the space  $F$  of all coordinates of the form  $p_F = (x^1, \dots, x^n)$  as the CNS hyperspace, and note that its geometry is largely unknown, but *certainly non-Euclidean*.

*Caveat 2.* We may note three approaches to the status of  $F$ .

(i) To posit a map  $\phi$  which assigns to each  $(x, y, z, t)$  in  $M = E^4$  a unique neural encoding  $\phi(x, y, z, t) = (x^1, x^2, \dots, x^n)$ —though we saw the ill-defined nature of such a  $\phi$  in Caveat 1—so that  $F$  is defined to be the image of  $M$ . In this case,

$$F = \phi(M) = \{\phi(x, y, z, t) \mid (x, y, z, t) \in E^4\}.$$

<sup>†</sup> PL use the coordinates  $f_1, \dots, f_m$  but we use  $(x^1, \dots, x^n)$  to avoid confusion with the flows of section 3.

(ii) To make  $F$  the image of some restricted subset  $S$  of observable event-points. In this case  $F = \phi(S) \cap \phi(M)$ .

(iii) To make  $F$  the manifold of all possible neural firings (of some designated set of neurons).

In cases (i) and (ii),  $F$  is a 4-dimensional manifold,  $\phi$  is a manifold isomorphism, and the coordinates  $(x^1, \dots, x^n)$  are highly redundant ( $n$  may be as big as  $10^3, 10^6, 10^9$  or even greater). In case (iii),  $F$  is an  $n$ -dimensional manifold, and  $\phi$  is not an isomorphism, but an embedding, e.g. of the form

$$\phi: M \rightarrow [0, a]^n$$

where  $[0, a]$  is the image of neural firing rates for each neuron (suitably normalized if necessary).

Let us merge cases (i) and (ii) above by simply using  $M$  for the observable part of  $E^4$ , whether it is equal to all of  $E^4$  or not. Note that cases (i) and (ii)—that  $F = \phi(M)$  and that  $\phi: M \rightarrow F$  is a manifold isomorphism—seem closer to the tensor analysis of section 3 than the embedding of case (iii). However, PL explicitly choose (iii).

*Caveat 3.* PL assert that  $M$  and  $F$  are tensorially related to one another, and that this consideration provides the basis for a tensorial treatment of the space-time representation in the brain. Leaving aside the problem that the  $F$ -coordinates are redundant, we note the aberrant terminology in saying that  $M$  and  $F$  are tensorially related unless one assumes a Euclidean theory with only linear transformations—hardly appropriate, e.g. for the change from eye to hand coordinates. We saw that any smooth and invertible change of coordinates is acceptable in the non-Euclidean case, and we saw in equation (11) that there is then nothing tensorial about changing coordinates.

We saw that a tensor is a coordinate-dependent function of the points on the manifold that transforms in certain ways. For example, the coordinate-representation of a *flow* (which assigns a tangent vector at every point) transforms as a *contravariant vector*, equation (9), while a *cotangent field* has a coordinate representation that transforms as a *covariant vector*, equation (10). We may summarize this for future reference:

$$\text{contravariant vector} \sim \text{field of column vectors} \sim \text{tangent field (flow)} \quad (19a)$$

$$\begin{aligned} \text{covariant vector} \sim \text{field of row vectors} & \quad \sim \text{cotangent field} & (19b) \\ & \quad \quad \quad \text{(linear functional} \\ & \quad \quad \quad \text{on flows).} \end{aligned}$$

In the formal analysis that follows, PL view the cerebellar network as acting as a metric tensor which transforms a covariant intention into a

contravariant execution, both given in a particular frame of reference. Yet as an example of the role of the cerebellum they cite the transformation of the position of a target from eye-coordinates to arm-coordinates, which is more like  $\phi$  above than the purely Euclidean covariant-contravariant transformation shown in Fig. 3. Here, PL fix a basis for a Euclidean space and

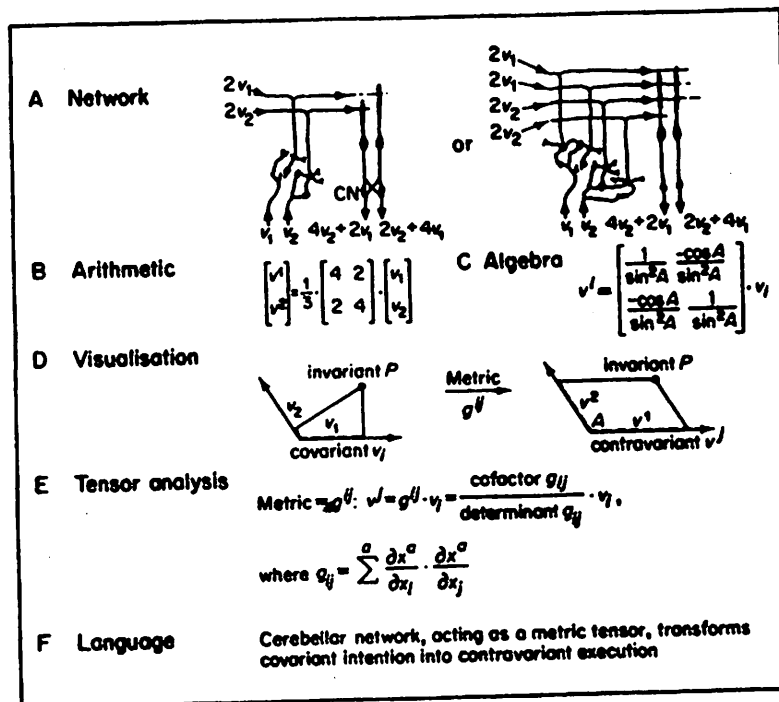


FIG. 3. Networks, vectors, matrices and tensors. A concise demonstration of how a set of neuronal networks (A) can perform a transformation to be described by a general tensor, such as the metric (F). The arithmetical (B) or algebraical (C) vector-matrix approaches represent intermediate levels of abstraction from the level of network representations (A) to the full generality of coordinate system free description by tensor analysis (E, F); from Pellionisz & Llinas (1982).

use equation (11) which associates with any covariant vector, say  $v_i$ , a contravariant vector, denoted  $v^j$ , by the rule

$$v^j = \sum_{i=1}^n g^{ji} v_i \quad (20)$$

(PL use the summation convention to omit the summation sign, and use the symmetry of  $g^{ij}$  to write  $g^{ij}$ ), where  $g^{ij}$  is the inverse of the metric tensor  $g_{ij}$ .

*Caveat 4.* The linear expression of Fig. 3(a) for the output of cerebellar nucleus (CN) neurons is suspect because of the inherent nonlinearities of

neurons, because of the effects of climbing fibres, because of collateral inputs and because of the fact that the Purkinje inputs to CN neurons are inhibitory.

*Possible Response.* An analysis of the linear range of the *MF-CN* transformation, taking such effects into account.

In any case, let us temporarily model the cerebellum as a linear operator  $G$  transforming an intention vector  $v$  to the associated execution vector  $u$ ,

$$u = Gv.$$

By taking appropriate bases for the spaces of intention  $I$  and execution  $E$  we have

$$u^j = \sum_{i=1}^n G_i^j v^i \quad (21)$$

in the component form, where we assume the  $I$  is an  $n$ -dimensional vector space, and  $E$  is  $m$ -dimensional.

We may take the dual basis in  $I$  such that an intention vector  $v$  is represented by a covariant vector  $v = (v_i)$ . We have in this case

$$u^j = \sum_{i=1}^n G^j_i v_i \quad (22)$$

Equations (21) and (22) are general tensorial forms of linear transformations, but so far this is just standard linear algebra, with  $G$  just a linear transformation. But PL theory further assumes (1) that  $I$  and  $E$  are the dual versions of the same linear space (hence  $m = n$ ) and (2) that intention and execution vectors are connected by the metric tensor  $g_{ij}$ . We then have

$$v^i = \sum g^{ij} v_j \quad (23)$$

where the execution vector ( $u^i$ ) is identified with the contravariant form of the intention vector ( $v^i$ ). The above two assumptions seem to be very problematic: (i) Why take  $m = n$ , in spite of the fact that the mossy fibre inputs have higher dimensionality than the Purkinje cells do? (ii) How can one introduce a metric tensor  $g_{ij}$  in the network of the cerebellum? The metric tensor is usually positive-definite and symmetric, so that the linear transformation is restricted to a special form, equation (23), compared with general equations (21) or (22).

*Caveat 5.* In tensor analysis, the metric tensor  $g_{ij}$  (of which  $g^{ij}$  is the inverse) is obtained with respect to the given coordinate frame on a Riemannian manifold by providing the distance on the manifold via equation (11),

$$ds^2 = \sum_{i,j} g_{ij} y^i y^j.$$

But the  $g_{ij}$  of Fig. 3 has *not* been related in any way either to the intrinsic geometry of  $F$  or (if  $F$  is to be compared to the state space of the exposition of mechanics at the end of section 3) to a potential energy plausibly related to the control of movement.

*Possible Response.* To answer this objection, it would have to be shown that the intrinsic geometry (or the dynamically plausible choice of potential energy) for the manifold underlying the neural space is indeed given by  $g_{ij}$  as metric tensor, but PL have not even told us what the manifold  $F$  is (cf. Caveat 1) let alone given any evidence that its structure is captured in the connectivity of cerebellar cortex.

PL have offered no such evidence that the cerebellum implements a metric tensor. But if the  $g^{\psi}$  of equation (20) does not constitute some intrinsically appropriate metric tensor, then there is no reason to call  $v_i$  a covariant intention and  $v^j$  a contravariant execution.

Moreover, note that in Fig. 3(e), PL write

$$g_{ij} = \sum_a (\partial x^a / \partial x_i) (\partial x^a / \partial x_j).$$

When  $(x_i)$ -space is embedded (as a curved submanifold) in a higher-dimensional Euclidean space with Cartesian coordinate system  $(x^a)$ , this  $g_{ij}$  is the Riemannian metric induced by the embedding. However, PL do not specify the role and meaning in the cerebellum of this higher-dimensional Euclidean space.

We would agree with PL that "in multidimensional, *non-Euclidean* hyperspace ... non-rectilinear (or even nonlinear) non-orthogonal reference frames may be used [our emphasis]" and that, subject to the subtleties discussed in section 1, "sensorimotor coordination can be conceptualized as a transformation from a sensory to a motor vector within general (non-orthogonal) systems of coordinates." But then they argue that the first vector representation of Fig. 3(d) is covariant because  $v_2$  and  $v_1$  are obtained "independently" by normal projection, whereas the second is contravariant because  $v^2$  and  $v^1$  are obtained by parallel projection. As we saw in section 3, this is acceptable only if the vectors in the basis have unit length. Let us, for the moment, make the suspect assumption that neural coordinates are computed with respect to a basis of (not necessarily orthogonal) unit vectors in a Euclidean space. Then there is a sense in which contravariant components are generated "dependently", since parallel projection to one basis vector requires the plane determined by the other basis vectors, while the covariant vectors are generated "independently", simply by projection to the specific basis vector.

This leads PL to their basic identification: "Components of sensory information are established independently, i.e. if sensory information is



expressed vectorally, it is of the covariant type," while "motor execution is expressed as the resultant of physical components, i.e. a vectoral expression of motor execution is of the contravariant type." However, with respect to the dual basis, the components of the motor vector are as "independent" as the sensory components. Even worse, the vector of firing of retinal neurons is a vector of million-fold dimension, and so can hardly be the representation of a point in 3-dimensional space or 4-dimensional space-time with respect to a basis of (3 or 4, respectively) linearly independent vectors. And if motor execution is expressed as a pattern of, e.g. supraspinal commands to alpha and gamma neurons controlling a hierarchy of effectors, in what sense do the components of this neuronal firing pattern correspond to summable physical components?

The effectors are usually so coupled that a complicated execution pattern is necessary even to execute a single task. Assume that, for the execution command  $u$ , the effectors realize its linear transform  $Hu$ , or  $\sum H_j^i u^j$  in component form, where  $H$  is determined by the dynamics of muscles, bones, joints, etc. In order that the intention  $v$  is realized by  $Hu$ , it is necessary to apply the execution command  $u$  such that  $Hu = v$  holds. If  $u$  is obtained from the intention by a linear transformation  $u = Gv$ , it is necessary that  $HGv = v$  holds for every  $v$ . This can indeed be satisfied when  $G$  is the *generalized* inverse (recall our caveat that  $m \neq n$  in general!) of  $H$ , satisfying

$$\sum H_k^i G_j^k = \delta_j^i.$$

This  $G$  is not necessarily symmetric or positive definite. Hence, the tensorial theory neither implies nor requires that  $G$  is a transformation between covariant and contravariant vectors.

*Caveat 6.* A covariant vector corresponds to a cotangent field on a manifold, equation (19b), and a particular numerical representation of that vector corresponds to a particular choice of coordinates for that manifold. Since PL do not use general tensor analysis, it is not surprising that they give no argument for covariance of this kind.

*Possible Extension.* If we identify the CNS hyperspace  $F$  with the configuration space  $M$  of our exposition of mechanics at the end of section 3, we may note that the left half of the Hamiltonian equation

$$\frac{dq^i}{dt} = \sum_{j=1}^n g^{ij} p_j \quad \text{and} \quad \frac{dp_i}{dt} = -\frac{\partial U}{\partial q^i} \quad (18)$$

is much like the transformation PL postulate for the cerebellum—the covariant momentum vector is transformed into the contravariant velocity vector by applying the metric (potential energy) tensor. But then why use

“intention” to refer to “momentum,” and “execution” to refer to “velocity”? Where in the brain is  $(q^1, \dots, q^n)$  encoded, and where and how is the right-side of equation (18) computed? Even if the brain evaluates  $dq^i/dt$  and  $dp_i/dt$  (and the fact that a quantity is convenient for mathematical analysis does not guarantee its explicit representation, by neural firing, in the brain), how are these derivatives integrated to actually change the total coordinates  $(q^1, \dots, q^n, p^1, \dots, p^n)$  if these are represented in the brain, and how do these values affect the motoneurons? Unfortunately, the “tensorial blueprint” for the amphibian brain offered by Fig. 5 (section 5) does not seem to fit well with our attempt to provide an extension of the PL theory which makes some reasonable contact with modern mechanics. Note that with our interpretation, the intention is *not* a sensory vector but is a motor control vector. In particular, this undermines the tensorial view of the tectum as a sensory-perceptual transformer in Fig. 5 (the next section offers other interpretations of the tectum).

*Caveat 7.* In Fig. 3, and in our discussion so far, we have treated  $g^{ij}$  as if it were constant, i.e. as if it did not depend on position on the manifold. But, in fact, we must recall that in the non-Euclidean case a tensor is a *field* and assigns a (possibly different) value to each point of the manifold. Thus the form of equation (20) is really

$$v^j(x^1, \dots, x^n) = \sum_{i=1}^n g^{ji}(x^1, \dots, x^n) v_i(x^1, \dots, x^n) \quad (20')$$

where we make explicit the dependence of each component, including  $g^{ji}$ , on the actual point of CNS hyperspace given by coordinates  $(x^1, \dots, x^n)$  in the chosen reference frame.

*Possible Response.* Show that  $g^{ji}$  does not depend on  $(x^1, \dots, x^n)$ —i.e. that the chosen coordinates exhibit a uniform Riemannian structure—for then (20') is still implementable by networks like those of Fig. 3(a). Otherwise, some scheme must be found (e.g., by *short term* synaptic modulation) to adapt  $g^{ji}$  to values appropriate to the current  $(x^1, \dots, x^n)$ .

In line with the original motivation from relativity theory, PL extend the analysis of the cerebellum presented so far to one in which the cerebellum is viewed as a *space-time metric*. We have presented what we consider the essentials of this approach in the theory of lookahead modules in section 2. There we explicitly dropped all reference to tensor notions, for the formulas given in section 2 gain no functional efficacy by being expressed in tensor notation, and the arguments given in the present section apply just as much against viewing the space-time transformation as providing the components of a metric tensor. But even if it were a metric tensor, PL

would seem to be in error in writing it as  $g^{i\Omega T}$  where  $i$  and  $j$  index space-coordinates and  $\Omega$  and  $T$  index time-coordinates. Surely the approach of space-time geometry is to still write  $g^{ij}$  but now each of  $i$  and  $j$  index the coordinates of a unified space-time, and not just those of space alone.

In summary, the above arguments make it highly unlikely that the PL tensorial metaphor for cerebellum

input = covariant vector

transformation = metric tensor

output = contravariant vector

can be substantiated. However, in our possible response to Caveat 6, we have offered a direction for future research, by showing that (while raising many questions), there is a mechanical interpretation for

input = momentum vector

transformation = potential energy tensor

output = velocity vector.

Of course, there is no guarantee that such a transformation must take place in the cerebellum, even if such mechanical computations are eventually shown to be embedded explicitly as the input-output function of a specific region of the brain. In any case, the appeal to mechanics seems inconsistent with those examples (e.g. eye-coordinates  $\rightarrow$  arm-coordinates) in which PL take

input = sensory vector

output = motor vector.

Yet each of these hypotheses needs careful analysis in view of the fact that cerebellum receives input from collaterals of cerebral motor commands and spinal feedback as well as sensory input, and that it has output that is routed to cerebral association cortex, as well as descending pathways to the spinal cord.

We close by reiterating our remark at the end of section 3 that, whatever the fate of the current PL theory, "a fully developed theory of motor control will make contact with... modern developments in mechanics." If this critique of the PL theory can stimulate such contact, it will have served its purpose. We also stress that remapping is a vital function of the brain, but note that, since neural firings provide highly redundant non-Euclidean coordinates, the study of such remapping is not tensorial in the sense espoused by PL.

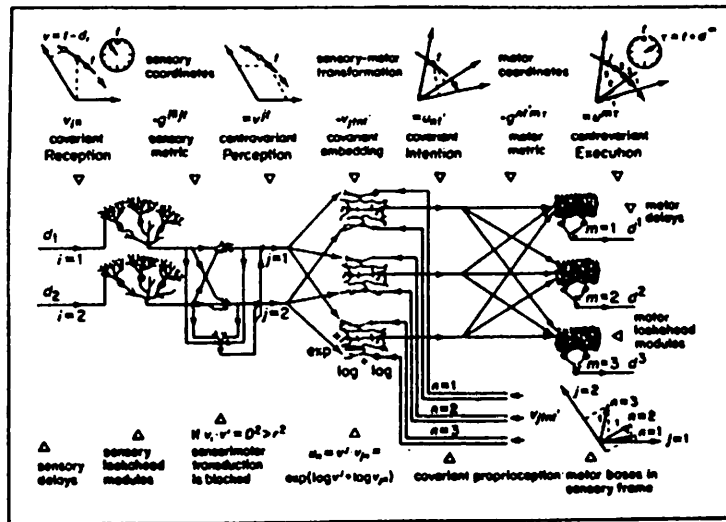


FIG. 4. Tensorial scheme of a sensorimotor system. Two different (sensory and motor) frames of reference are used with two different vectorial expression in each. Thus, the transformation from asynchronous covariant (sensory reception) vector to asynchronous contravariant (motor execution) vector is implemented through a contravariant sensory vector (perception) and a covariant motor vector (motor intention). At the levels of visualization, verbal description, network representation and tensor notation those minimum necessary transformations are shown, necessary for a two-to-three dimensional system (Pellionisz & Llinas, 1982).

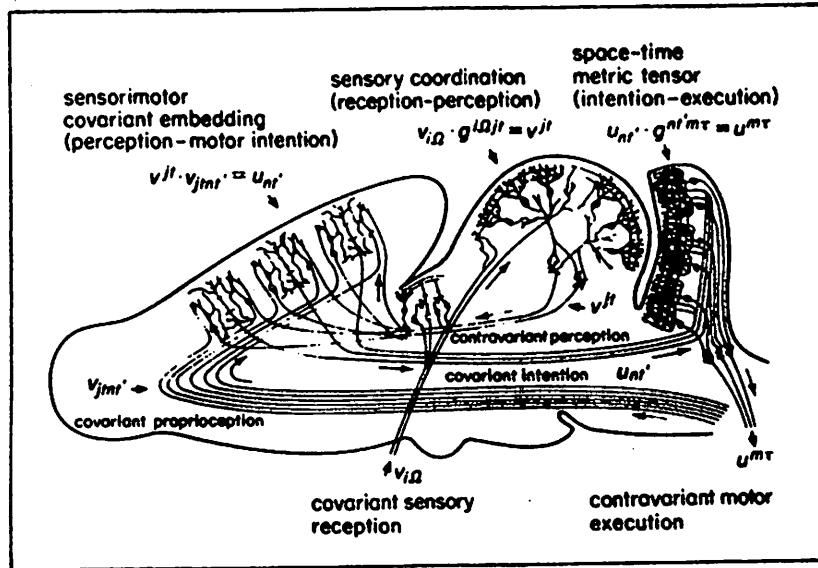


FIG. 5. Tensorial "blueprint" of the amphibian brain. The neuronal networks shown implement tensor transformations from a two-dimensional covariant sensory reception vector into a higher, three-dimensional contravariant motor execution vector. The cerebellum is featured as the motor metric, the superior colliculus as the sensory metric, while the cortical network is a tensor-transformer implementing a sensorimotor covariant embedding (Pellionisz & Llinas, 1982).

### 5. Models of Sensorimotor Coordination

In two elegant diagrams (Figs. 4 and 5), PL offer a general scheme for a sensorimotor neuronal network, based on the ideas reviewed in sections 2 and 4. Examining the figures, we see that the amphibian sensorimotor system is conceived as having three divisions: the *tectum* transforms a covariant sensory vector, using sensory lookahead modules, into a contravariant perception vector; the *forebrain* combines the contravariant perception vector with a covariant proprioception vector to produce a covariant intention vector; and the *cerebellum* transforms this covariant intention vector into a contravariant motor execution vector. Since sections 3 and 4 provide tools for the analysis of these systems, we do not here provide a further critique, but rather outline a number of neural models, relevant to the points made in section 1, which offer radically different views of tectum and cerebellum. A new generation of sensorimotor models should incorporate the valid features of these models, but much further work, both experimental and theoretical, is required to determine just what those features are.

#### MODELS OF THE CEREBELLUM

1. Boylls (1975, 1976) emphasizes that cerebellar cortex cannot be modelled in isolation, and instead takes as the unit of modelling a network involving cerebellar cortex, a cerebellar nucleus, and a reticular nucleus. Input is provided via reticular nuclei as mossy fibres and via inferior olive as climbing fibres, and output travels from cerebellar nuclei via brainstem nuclei. Reverberatory loops between reticular and cerebellar nuclei can build up firing levels which encode parameters for adapting spinal motor circuitry which is modulated by brainstem nuclei. Anatomy of Voogd and Oscarsson suggests how the brain may be divided into strips corresponding to "identification algorithms" which adjust the parameters for different "motor schemas." This adjustment is short-term, corresponding, e.g., to adjusting the stride to the current terrain.

2. Marr (1969) and Albus (1971) view the single Purkinje cell of cerebellar cortex as the basic unit of analysis. Marr suggests how other circuitry may act to provide "gain control" for Purkinje cell input; both stress a view of the cell as a "Perceptron," a linear threshold unit for which a "reinforcement" signal applied on climbing fibre input could adjust parallel fibre synapses. Marr postulated increased parallel synaptic weights with coincident activity; Albus postulated a decrease. Tsukahara & Kawato (1982) proposed a global model involving cerebral cortex, red nucleus, inferior olive and cerebellum. They assumed that plasticity of red nucleus is responsible for improving the motor schemas of the cerebellum.

3. Ito (1982) supports the applicability of the heterosynaptic interaction hypothesis for neural plasticity adopted in the Marr-Albus model to the floccular control of the vestibulo-ocular reflex by neuronal circuit analysis, lesion experiments and unit recording from Purkinje cells. The plasticity of parallel fibre-Purkinje cell synapses seems to accord with the Albus hypothesis in sign, but a large part of the plastic change recovers within 10 minutes accompanied by slow recovery thereafter. The experiments do not yet demonstrate whether or not the synaptic changes are stable enough for permanent memory in which the internal model of the cerebellum is stored (Ito, 1970), or whether it maintains only a short- or intermediate-term memory concerning the present situation of the properties of signals (cf. the Kalman-Bucy filter).

4. Robinson [see, e.g. (Robinson, 1981) for a review] has demonstrated that many phenomena in the neurophysiology of eye movements can be analyzed by the use of *lumped* control systems analysis. This corresponds, e.g. to the situation in which we re-present a single peak of activity across the retina by the coordinates of this peak. In behaviorally simple tasks, such lumped coordinates can provide a meaningful short-hand notation for the activity in a number of neural structures. Then the interaction of these structures can be represented by a low-dimensional nonlinear control system. Such models have great value, and have recently provided the basis for the demonstration of a cerebellar involvement in adaptive control of the primate saccadic system. However, such models cannot address the spatial distribution of firing across the cells of the structures implicated. A fruitful task for brain theory is to integrate such lumped models with the analysis of interacting layers as in the work of Boylls (above) and Lara & Arbib (below).

5. Fujita (1982*a,b*) combines the Marr-Albus theory with methods of stochastic approximation which yield a general theory of self-organizing neural nets (1982). The model uses adaptive filtering to meet some of the desiderata of "lookahead" discussed in section 2 (but without recourse to Taylor series or tensors); locates learning in a "microzone" including Golgi cells as well as Purkinje cells, and is integrated with a control system model of the vestibulo-ocular reflex. The model is also related to Ito's experimental findings. However, the theory does not yet account for processing of spatio-temporal patterns. See the following models of tectum where spatial pattern processing is modelled.

#### MODELS OF TECTUM

1. Ewert (1976) summarizes data on the implication of both tectum and pretectum in the discrimination of prey from predator in frog and toad.

Ewert & von Seelen (1974) gave a lumped model (one cell for pretectum, two cells for tectum) to explain the data on worm-antiworm-square discrimination. Cervantes, Lara & Arbib (1984) provide an explanation of the phenomena in terms of posited spatiotemporal activity in interacting layers of neurons in tectum and pretectum, building on the studies discussed in 3 and 4 below.

2. Pitts & McCulloch (1947) modelled the superior colliculus as a distributed controller of eye movements, in which spatial distribution of activity—rather than localized decision-making based on a lumped variable—provided the appropriate transformation from retinal activity to muscle contraction.

3. Didday (1976), continuing the Pitts-McCulloch tradition, gave a distributed neural network model of tectum to solve the following nonlinear problem: Given a pattern of retinal activity representing several "flies", how can the tectum suppress all but one of the peaks of activity in its output to yield an output pattern whose peak will direct brainstem controllers to release a snap at just one of the flies? Amari & Arbib (1977) have developed a more general theory of competition and cooperation in neural nets which embraces both Didday's model of prey-selection and Dev's (1975) model of stereopsis.

4. Ingle (1975) has demonstrated facilitation of prey-feeding in the frog: a short stimulus will not elicit feeding, but re-presentation of that stimulus within 2 seconds of a first presentation will. Following the anatomy of Szekely & Lazar (1976), Lara, Arbib & Cromarty (1982) have isolated a unit of tectal circuitry, the tectal column, and shown by computer simulation that, with suitable choice of parameters, this unit can support facilitation. Later studies (Arbib & Lara, 1982; Lara & Arbib, 1982) studied one dimensional arrays of such columns (with and without pretectal interaction) to extend the work of Didday and of Ewert and von Seelen cited above.

5. Frogs and toads exhibit subtle detour behavior to approach a worm that is visible behind a barrier of vertical palings (Collett, 1979; Ingle, 1976). House (1982) has extended the Dev model to provide a model of depth perception using cooperation between disparity and accommodation cues; and Arbib & House (1983) are building on this to model the interaction of worm and barrier cues in the amphibian brain to determine complex patterns of interaction between several motor schemas.

This list is a small sample of both lumped and neurally distributed models of sensorimotor coordination. It serves to indicate the wealth of phenomena to be addressed, and the diversity of techniques available for that analysis. The proper evaluation of these models still poses major challenges, and much work remains to be done to incorporate their viable features in ever

more powerful models of the neural mechanisms of sensorimotor coordination.

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