Sensory prediction as a role for the cerebellum

RC Miall, M Malkmus and EM Roberston
University Laboratory of Physiology,
Parks Road,
Oxford, U.K.
Electronic mail: *chris.miall@physiol.ox.ac.uk*

We suggest that the cerebellum generates sensory or 'state' estimates based on outgoing motor commands and sensory feedback. Thus, it is not a motor pattern generator (**Houk et al.**) but a predictive system which is intimately involved in motor behaviour. This theory may explain the sensitivity of the climbing fibres to both unexpected external events and motor errors (**Simpson et al.**), and we speculate that unusual biophysical properties of the inferior olive might allow the cerebellum to develop multiple asynchronous sensory estimates.

Houk et al (HBB) have developed an extensive set of ideas of the cerebellum as an adjustable pattern generator, in which the key role for the cerebellar cortex is to modulate and terminate motor commands being driven by positive feedback within brainstem circuits. They dismiss the suggestion of the cerebellum as a sensory predictor or state estimator (Paulin, 1993; Miall et al, 1993) with little comment on the data that supports such theories. We think the weight of these data point towards sensory predictions and are difficult to reconcile with a role of adjustable pattern generator. However, it is worth pointing out that a sensory predictor is not a sensory analyser (Bower & Kassel, 1990). We do not claim the cerebellum is concerned with processing sensory information per se, but is vital for the processing of sensory inputs by other brain structures, in the context of movement.

Perhaps the first point to make is one stressed by Paulin (1993) – that the comparative anatomy of the cerebellum is difficult to explain if its role is that of generating motor commands. It seems that those species with advanced sensory-motor abilities, in which reafference resultant on motor behaviour must be analysed, have larger cerebellar cortices than their body or brain mass would predict. Cetaceans have greatly extended paraflocullar nodes (Riley, 1928); echolocating bats and electric fishes also have large cerebellar volumes. The primates have a massive expansion of lateral cerebellar cortex, in parallel with the expansion of neocortex, but this occurs without an increase in joints or muscles. Thus there is poor correlation between cerebellar size and the complexity of the motor apparatus. **Thach** follows Flourens (1824) in suggesting that the cerebellum is particularly involved in co-ordinated movement of many different joints, and there is data implicating its role in coordination between different motor structures (hand-eye co-ordination, for example). The APG model (**HBB**) does not seem to have a role here – fits output cannot easily be used for coordination, unless it holds separate APGs for every co-ordinative structure or synergy.

Our hypothesis is that the cerebellum provides an estimate of the current state of the motor system, which the proprioceptive and teleceptive systems cannot do because of their intrinsic processing and conduction delays. State estimation has many uses (Miall & Wolpert, 1996); thus all neural functions which depend on state estimation (motor planning, mental imagery, internal feedback control, cancellation of reafference, coordination) could be linked to the cerebellum, and these multiple uses explain the expanded area of the primate cerebellum.

Of course it is only in man that one can properly address questions of cognitive function, and of the mental planning or imaging of movements without execution. Again, suggestions that the cerebellum may have a key role in these processes (**Thach**) are difficult to account for on the basis of motor command generation. And it is striking that the output of the cerebrocerebellum is not restricted to 'downstream' motor executive areas, as one would predict from Houk's theory. Instead there are extensive connections to frontal areas and to parietal areas.

Let us turn to some specific features of **HBB's** theory. The APG model is based on positive feedback, which can be difficult to control. Positive feedback loops can be easily pushed into excessive activation. For a motor command, a graded response is sought, and yet small changes in the responses of the neurons in the loop would be magnified into larger and larger variations in the loop output. Thus brainstem positive feedback loops would be rather unreliable, and the task of inhibitory modulation by the cerebellar cortex difficult. However, if it is accepted, the APG hypothesis makes a strong prediction: mass stimulation of the cerebellar cortex (e.g. with transcranial magnetic stimulation) should halt all movement in its tracks. We do not know if there is data to support this. Finally, the APG model suggests a reciprocal relationship between Purkinje cell responses and motor commands. This can indeed be seen, but in many, many papers there is quite powerful activation of P-cells throughout movement, rather than just at its termination.

We believe, like **Simpson et al. (SWZ)**, that a key to understanding the function of the cerebellum is given by the climbing fibres. If the climbing fibres provide a sensory rather than motor signal, as **HBB** accept, and if this signal is used to train the cerebellum, then it seems much more likely that the cerebellum learns within a sensory rather than motor framework. Kawato and colleagues (1992a,b) have

accepted that one should use a motor error signal to generate a motor output; yet one sees pronounced somatosensory sensitivity of olivary cells in the absence of movement.

So let us now address the response properties of the IO, which as **SWZ** describe, remain a puzzle. They can not easily be characterised as simple error signals, nor do they have a straightforward relationship to movement. The theory that the cerebellum makes estimates of sensory states requires a teacher, that can signal mismatches between present estimates and reality. The climbing fibres may do that. They signal something like an error during motor tasks (see **SWZ**), but this may reflect the mismatch in expected and actual sensations when the motor task changes. They also signal purely sensory events, for example the passive stimulation of the skin (Gellman et al., 1985) which cannot be a movement error. It can, however, be a sensory prediction error. The cerebellar predictor may function continually, predicting the sensory consequences of movement, and the sensory consequences of not moving. Thus any unexpected external event is a failure of sensory predictions. Given the low levels of sensory inputs expected during rest, these externally generated sensory discrepancies may be large relative to the sensory errors that external stimulation causes during active movement. Hence the apparent sensitivity during rest. The recent report of time-locked climbing fibre activity during rhythmic movement (Welsh et al., 1995) might reflect the sensory differences from moment-to-moment when licking a feeding tube that delivers a water drop.

In our original model of the cerebellum (Miall et al., 1993) we suggested one or more predictors, operating in exteroceptive (visual) and proprioceptive co-ordinates. Malkmus (in preparation) has suggested that the cerebellum could generate multiple asynchronous predictions, families of predictions at many different temporal offsets from the current state of the motor system. Some of these might be long-lead predictions used in motor planning, others shorter lead for internal error correction, and some even synchronous with reafference, to allow its cancellation.

Of course, we have implicitly accepted that the climbing fibres carry a training signal, and this remains an assumption. However, one can ask what training signal would be best to allow the development of a sensory prediction? Malkmus suggests that the inhibitory output from the cerebellum might be propagated and delayed through serial connections within the inferior olive, so that multiple asynchronous comparisons between cerebellar output and reafference take place. The appropriate cerebellar outputs would be trained by the combination of Hebbian learning at the parallel fibre/Purkinje cell synapse with LTD in response to CF activation. Simulations have shown that the combination of these two learning rules provides a powerful learning paradigm. These simulations also suggest that even after successful training, the maintenance of that prediction requires a constant level of IO activation (constant over a long time scale), and that individual climbing fibre responses can be expected to follow episodes of higher than average P-cell activity; this again differs from Welsh's interpretation of CFs (Welsh et al., 1995). It does not seem to be necessary to actually store the complete pattern belonging to a given prediction. Rather cerebellar cortex could store the difference between the current state and the predicted state, thus considerably reducing the amount of information stored. The deep nuclei would then use this difference information to create the prediction. Finally, sagittal microzones within the cerebellar cortex would hold similar but temporally shifted patterns of information. If these ideas hold up, they provide an exciting explanation for the well known but purely understood relationship between the inferior olive and the cerebellum.

References:

Bower, J.M. & Kassel, J. (1990) Variability in tactile projection patterns to cerebellar folia Crus IIA in the Norway rat. Journal of Comparative Neurology, 302, 768-778.

Flourens, P. (1968) Recherches experimentales sur les proprietes et les fonctions du systeme nerveux dans les animaux vertebres. Paris 1824. Translated, 1968. In The human brain and spinal cord. eds. E. Clarke & CD. O'Malley, (pp. 657-661). Berkeley.L.A.: U. California P..

Gellman, R., Gibson, A.R., & Houk, J.C. (1985) Inferior olivary neurones in the awake cat: Detection of contact and passive body displacement. Journal of Neurophysiology, 54, 40-60.

Kawato, M. & Gomi, H. (1992a) A computational model of four regions of the cerebellum based on feedback-error-learning. Biological Cybernetics, 68, 95-103.

Kawato, M. & Gomi, H. (1992b) The cerebellum and VOR/OKR learning models. Trends in Neurosciences, 15, 445-453.

Miall, R.C. & Wolpert, D.M. (1996) Forward models in physiological motor control. Neural Networks, 9, 1265-1279.

Miall, R.C., Weir, D.J., Wolpert, D.M., & Stein, J.F. (1993). Is the cerebellum a Smith Predictor? Journal of Motor Behavior, 25, 203-216.

Paulin, M.G. (1989) A Kalman filter theory of the cerebellum. In: Dynamic interations in neural networks: Models and data. eds. M.A. Arbib & S. Amari, Springer-Verlag.

Paulin, M.G. (1993) The role of the cerebellum in motor control and perception. Brain Behavior and Evolution, 41, 39-50.

Riley, H.A. (1928) Mammalian cerebellum: Comparative study of abor vitae and folial patterns. Archives of Neurology and Psychiatry, 20: 898, 1-34.

Welsh, J.P., Lang, E.J., Sugihara, I., & Llinas, R. (1995). Dynamic organization of motor control within the olivo-cerebellar system. Nature, 374, 453-457.