The cerebellum and visually controlled movements.

RC Miall
University Laboratory of Physiology, Parks Road, Oxford OX1 3PT, UK
Email: rcm@physiol.ox.ac.uk

Abstract

I will review some of the data from human and animal models pointing to a critical role for the cerebellum in the control of visually-guided movements. There are now several contrasting theories that suggest what this role may be; evidence from functional imaging, lesion studies, anatomy, and computational modelling supports the theory that the cerebellum forms a forward model of the motor system. This may be used for control (as suggested by the 'Smith Predictor' hypothesis); it may also underlie a cerebellar role in co-ordination, motor planning and in predicting the sensory consequences of movements.

The role of the cerebellum

The cerebellum is clearly an important neural structure, both because its dysfunction leads to pronounced disturbances in movement, posture and balance, but also because it is a relatively massive structure in higher vertebrates. In man, it represents about 10% of the volume of the brain, and even more striking, it has been estimated to hold more than half of all the neurones in the central nervous system. Such massive processing power must have a vital purpose, but it has been extraordinarily difficult to pin down precisely what the cerebellum actually does.

I believe that one of the fundamental functions of the cerebellum is to act as a sensory predictor, responsible for generating predictions about the sensory consequences of motor acts. Sensory predictions which are available in advance of the normal delayed reafferent signals can be used to control motor systems (Miall et al. 1993). Sensory predictions are also important for other functions more removed from motor control (Miall & Wolpert 1996). There is now a growing body of evidence that suggests the cerebellum is involved each of these different functions, and thus the implication is that the cerebellum is concerned with processing or generating sensory predictions.

Physiological aspects of the cerebellum

Comparative anatomical studies show that the cerebellar cortex an old structure, in phylogenetic terms, and is particularly large in the primates. The cerebellar cortex can be simply described by its anterior-posterior and its lateral dimensions. The log of the anterior-posterior length is very strongly correlated with log body mass raised close to the power of 2/3 (Sultan & Braitenberg, 1993). This suggests the number of ‘beams’ within the parallel fibres of the cortex, a plausible measure of the parallel processing power of the cerebellum, correlates with body surface area. The skin is a vital but undervalued sensor affecting motor control. Any motor action must distort the skin, and the skin of course is the interface between our actions and the external environment. Thus motor acts have important consequences for sensory input to the skin. The role of the cerebellum in processing sensory reafference from human movements has recently been demonstrated in an fMRI experiment by Blakemore et al. (1998). A ‘forward model’ (Jordan, Rumelhart, 1992) is a key component in systems that uses motor outflow (also called efference copy) to anticipate and cancel the sensory effects of movement. Thus evidence for a role in predicting sensory reafference is evidence for the cerebellum being a forward model of the motor system.

Cerebellar control of movement

The cerebellum is, of course, vital for visually guided movements and seems particularly important in movements made under visual feedback. Paradoxically, patients with pronounced cerebellar motor problems can actually do better without visual feedback (Beppu et al , 1984; Haggard et al. 1995; Liu et al, 1997). The most likely reason for this is that visual feedback pathways are slow, with delays of around 200 ms. Thus fast motor acts need to be controlled by a feedforward mechanism, but must also deal with this slow reafferent signal. Cerebellar dysfunction can lead to visually guided tracking that is strikingly similar to that seen when visual feedback is artificially delayed by 200-300 ms and this highlights its normal role in dealing with feedback delays. Hence the role of the cerebellum in controlling movement is compatible with its role in processing reafferent information.

It is also clear that during rapid reaching movements, information about the initial location of the hand is essential for accuracy. Miall & Wolpert (1996) have described the computations involved in integrating sensory and motor information to provide an estimate of the state of the arm (e.g. arm position and velocity). This framework based on observer models consists of a state estimation process, the observer, which monitors the motor commands sent to the arm and the returning sensory feedback. Using a forward model and taking both sensory and motor input sources, the observer can estimate the arm's state, integrating the multiple sources of information to reduce the overall uncertainty in its estimate. A state estimate is not identical to the reafferent signals mentioned above, but is closely related. Cerebellar patients show deficits in performance consistent with this model.

Such a state estimator could also be used in motor coordination. Temporal delays in the sensory and motor pathways suggest that for many human movements, coordination needs to depend on a predictive state estimate, rather than on feedback signals. There is strong evidence for the cerebellum’s role in coordination, and this again supports its role as a forward model. Vercher & Gauthier (1988) have shown that monkeys, like humans, can make eye movements to follow movement of a cursor controlled by the hand with very low latency. However, inactivation of the cerebellum impaired this ocular-manual coordination, so that the latency of the eye movements rose to a level normally seen when tracking an external, unpredictable, target. They have also recently demonstrated that sensory afferents are not required for the temporal linking of ocular and manual systems, whilst motor outputs are required (Vercher et al. 1996). This confirms that efferent copy is an important part of the coordination process. fMRI experiments have confirmed increased cerebellar activation in coordinated eye and hand movement (Miall et al, submitted).

Forward models can also assist in feedforward control. By including the forward model within an internal negative feedback loop, it provides an neural control system that can generate near optimal motor outputs. We have proposed a particular form of this control strategy, known as a Smith predictor, as a model for the cerebellum (Miall et al. 1993). This includes a forward model, servicing a rapid high-gain internal feedback loop whose output can drive the arm towards the desired state. The feedback controller therefore compares the reference value of a controlled variable with an estimate of the state of the motor system, as provided by the forward model, and corrects the estimated error signal. As the internal forward model avoids the feedback delays in the real motor apparatus, this internal feedback loop can have a high open-loop gain, and function as a near-optimal feedforward controller. Note that the output is equivalent to that of an inverse model (Gomi & Kawato, 1992; Kawato & Gomi, 1992). The Smith predictor also includes an explicit delay mechanism, that delays a copy of the rapid sensory estimate to allow temporally synchronous comparison with the actual sensory consequences of the movement. This is important to allow any errors in the internal estimate to be detected and corrected. By ensuring synchrony between the delayed output of the forward model and the actual feedback, the Smith predictor effectively isolates the feedback delays from the control loop. Current fMRI experiments have again suggested that the cerebellum has a crucial role in timing, and its activity correlates with artificial delays in the sensory feedback from movement (SJ Blakemore et al, in preparation).

Fitting the forward model to physiology

Two major inputs to a forward model would be a set of state inputs from the sensors throughout the body, necessary to update the forward model, and also the efferent copy of motor commands, from which the new state estimate is generated. The cerebellum certainly receives both these. It receives a large projection from fibres descending from the motor cortex and it is thought that these represent the efferent copy of outgoing motor commands. The cerebellum also receives a vast amount of proprioceptive information directly from the ascending spinocerebellar tracts, which provide an update on the state of the motor apparatus. These sensory signals are delayed and in different co-ordinate systems from the required information of current state; hence they cannot be used directly instead of the forward model.

The outputs of a forward model should correlate with the expected state of the motor apparatus. This is rather difficult to test, as one needs to distinguish between internal predicted state signals arising from the model, the external sensory signals from the periphery, and motor commands. We are currently recording the neural activity in the cerebellar cortex in a visually guided task in which these signals can be separated, and initial results look promising (Liu et al, 1998).

Finally, Gellman et al. (1985) have shown that climbing fibre inputs to the cerebellum are activated by cutaneous inputs on the paws of a walking cat, but are inactive if the animal actively used that foot. Andersson & Armstrong (1987) have reported similar results. This is exactly what would be expected of a sensory error signal. If the main teaching signal reaching the cerebellar cortex is concerned with the errors in sensory predictions, this strongly suggests that the cerebellum is instructed by this input into development of a forward model. If the climbing fibres were a motor error signal responsible for training an inverse model (Kawato, Gomi, 1992; Gomi, Kawato, 1992), this sensitivity to passive stimulation would be difficult to explain.

Conclusions

I have shown that several lines of evidence point to the cerebellum as the most probable site of a forward model for limb movement (Miall et al, 1993). This forward model is probably used for motor control, co-ordination and for coping with sensory feedback during movement. The challenge now is to discover the neural mechanisms that support this forward modelling function.

Acknowledgement

This work was supported by a Wellcome Senior Research Fellowship.

References

Andersson G, Armstrong DM (1987) Climbing fibre input to b zone Purkinje cells during locomotion in the cat. *J Physiol (Lond) 385*: 107-134

Blakemore SJ, Wolpert DM & Frith CS (1998) Central cancellation of self-produced tickle sensation. *Nature Neurosci. 1*: 635-640

Beppu H, Suda M, and Tanaka R (1984) Analysis of cerebellar motor disorders by visually guided elbow tracking movement. *Brain 107*: 787-809

Gellman RS, Gibson AR, Houk JC (1985) Inferior olivary neurones in the awake cat: Detection of contact and passive body displacement. *J Neurophysiol 54*: 40-60.

Gomi H, Kawato M (1992) Adaptive feedback control models of the vestibulocerebellum and spinocerebellum. *Biol Cybern 68*: 105-114

Haggard PN, Miall RC, Wade DT, Fowler S, Richardson A, Anslow P, Stein JF (1995) Damage to cerebellocortical pathways following closed head injury: an MRI and behavioural study. *J Neurol Neurosurg Psychiatry 58*: 433-438

Jordan MI, Rumelhart DE (1992) Forward models: Supervised learning with a distal teacher. *Cogn Sci 16*: 307-354

Kawato M, Gomi H (1992) A computational model of four regions of the cerebellum based on feedback-error-learning. *Biol Cybern 68*: 95-103

Liu X., Miall R.C., Aziz T.Z., Haggard PN., Palace J.A. & Stein J.F. (1997) Analysis of action tremor and impaired control in movement velocity in multiple sclerosis by visually-guided wrist tracking tasks. *Movement Disorders, 12:* 992-999.

Liu X. & Miall R.C. (1998) Neurons specifically related to visual representation of arm movements in the lateral cerebellar cortex. *Soc. Neurosci. Abstr.* 24: 555.4

Miall RC, Weir DJ, Wolpert DM, Stein JF (1993) Is the cerebellum a Smith Predictor? *J Motor Behav 25*: 203-216

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

Miall R.C., Imamizu H., Miyauchi, S. (submitted) Activation of the cerebellum in co-ordinated eye and hand tracking movements: an fMRI study. *Hum. Brain Map.*

Sultan F, and Braitenberg V (1993) Shapes and sizes of different mammalian cerebella. A study in quantitative comparative neuroanatomy. *J. Hirnforsch. 34*: 79-92

Vercher J, Gauthier GM, Guedon O, Blouin J, Cole J, Lamarre Y (1996) Self-moved target eye tracking in control and deafferented subjects: roles of arm motor command and proprioception in arm-eye coordination. *J. Neurophysiol 76*: 1134-1144

Vercher JL, Gauthier GM (1988) Cerebellar involvement in the coordination control of the oculo- manual tracking system: effects of cerebellar dentate nucleus lesion. *Exp Brain Res 73*: 155-166