Behav. Brain Sci. ***20(2): p.258, 1997.***

Sequences of sensory predictions

RC Miall
University Laboratory of Physiology,
Parks Road,
Oxford, U.K.

Electronic mail: *chris.miall@physiol.ox.ac.uk*

I argue that the role for the cerebellar cortex is in the generation of sensory predictions, not motor sequences. This proposal may explain the allometric relationship described in the target article. I also point out that the parallel beam organisation may have a non-temporal basis.

Braitenberg, Heck and Sultan (**BHS**) suggest a single function for the whole of the cerebellum, that it generates neural sequences used for motor commands. I am also tempted by the simplicity of one function for all regions the cerebellar cortex, but I take issue with them over what that singular operation might be. I believe that the cerebellum is a sensory predictor, responsible for generating predictions about the sensory consequences of motor acts (Miall et al. 1993). Paulin (1989) and Darlot (1993) have suggested similar functions. Sensory predictions which are available in advance of the normal delayed reafferent signals can be used to control motor systems (Miall et al. 1993) and for other functions more removed from motor control (Miall & Wolpert 1996). There is a growing body of evidence that suggests the cerebellum is more 'sensory' than 'motor'. For example, Gao et al. (1996) have demonstrated that the dentate nucleus is highly activated during sensory discrimination tasks, whether or not the task involves movement. Diener et al. (1993) and Nawrot & Rizzo (1995) have shown perceptual deficits in cerebellar patients. Bell et al. (in press) have evidence of the generation of sensory predictions in 'cerebellum-like' structures in fish. The cerebellum is also increasingly implicated in non-motor behaviours (Leiner et al. 1993), although by itself this does not mean that its output is sensory.

I would suggest that the best predictor of a large cerebellar cortex (relative to body weight) is the ecological need for movement-related sensory analysis by each species. **BHS** are puzzled why cattle have such an extended cerebellum in the sagittal axis (**BHS** Section 9 & Fig. 2); bovines do not appear to have an expanded motor apparatus, and anthropomorphically, its difficult to imagine a cow having a need for many more motor sequences than other quadrupeds! However, BHS suggest that a major input to the cerebellum is from cutaneous receptors (Section 27), and if we assume that more cerebellar cortex is required to predict the cutaneous consequences of movement, then this odd fact and the relationship given in BHS Figure 4 become more clear. In Sultan and Braitenberg (1993), they show that vermal length has a 0.54 power relationship with body weight across many species. For a spherical body, surface area scales with mass with a power of 0.66. Thus, vermal length increases with body surface, but with an exponent of less than unity: one can imagine that motor actions do not affect the whole body surface, or that a common sensory prediction can made for a large number of cutaneous inputs. But small animals deviate more from a spherical shape than larger ones because their weight-bearing limbs can be relatively slim and long. Thus the slope of the relationship between log vermal area and log body weight should be shallower for smaller body weights, and indeed it is (Sultan & Braitenberg 1993, Figure 19). Then in converting from vermal length to cerebellar width, and plotting against cerebellar area, one achieves the declining curve in **BHS** Fig 4 (see also Sultan & Braitenberg 1993, Figure 15). I agree that the cerebellar width is likely to be related to the complexity of the inputs and duration of predictions, and am happy to believe that humans generate sensory predictions that are longer and more complex than those of other animals.

Finally, I would also point out that although their suggestions of a sequence detector system are elegant and are well borne out by Heck's electrophysiological data, there are alternative schemes that in principle would be equally effective in sequence detection and yet would look nothing like the cerebellum. For example, Abbott & Blum (1996) have shown that a simulation of overlapping neurons can both generate and predict motor sequences because of the temporal asymmetry of the rule governing LTP, but the neurons need no special geometry. Other network models for aspects of timing (Miall 1989; 1993) show that simulated neurons may not display any clear timing function individually, and thus one would not know simply from single unit recordings that they were involved in timing. So there may be other reasons for the dramatic orthogonal organisation of the cortex. One reason may be that the parallel inputs represents an efficient way to get the maximum number of different inputs onto the dendritic tree of each Purkinje cell, while allowing neighbouring P-cells to share significant subsets of the input array.

In conclusion, I would propose that the cerebellar cortex generates sensory predictions about the outcome of movement. This may involve a timing scheme like the one proposed in the target article; it is certainly important that predictive signals have the correct temporal relationship to what they predict.

Supported by the Wellcome Trust & MRC.

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