

Cerebellar function: On-line control *and* learning

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[JRB] The first part of **Bloedel's** target article reviews evidence for the organization of the cerebellum into sagittal zones and suggests that the functioning of the cerebellum is through sagittally organized units of cells. Bloedel proposes that Pur-

kinje cells in these units can have responses to mossy fibre inputs selectively enhanced through signals from climbing fibres. He suggests that under his "dynamic selection hypothesis" the climbing fibres will determine the populations of sagittally aligned Purkinje cells that would most dramatically modify the activity of cerebellar nuclear neurones. Bloedel supports this speculation with recent, to-be-published data from recordings in an identified cerebellar zone (Bloedel & Kelly 1992). But what does this "dynamic selection" accomplish? A characteristic feature of climbing fibre responses, repeatedly stressed in the target article, is that climbing fibres fire in response to perturbation. Whatever these responses do in terms of modulating Purkinje cell output, they do so after the event. The spectacularly massive cerebellar structure is relegated to assisting with compensatory movements after a motor error. Also, the proposal does not require some of the key features of cerebellar circuitry, in particular, the large numbers of parallel fibres synapsing with each Purkinje cell.

Bloedel claims that his hypothesis provides a unifying view of cerebellar integration that implements the circuitry and organizational features of the sagittal zones. He states that "there is virtually no other functional concept that integrates these features into a general view of cerebellar cortical processing." These claims can be disputed. First, as indicated above, this does not seem to be a particularly convincing explanation of the cerebellar circuitry. Second, it is incorrect to claim that it is the only theoretical proposal to take account of the sagittal organization of the cerebellum: One of us has shown how sagittally organized units of cells could be used in the learning of movements (Gilbert 1974; 1975).

The key test of cerebellar theories and hypotheses is the extent to which they account for empirical data and make testable predictions. On this score, **Bloedel's** hypotheses are lacking. In particular, the results of Thach and associates (Gilbert & Thach 1977; Thach 1970b) in recording from Purkinje cells of performing animals offer little support for the gain change or dynamic selection proposals.

In contrast, there is a large volume of evidence (Gilbert & Thach 1977; Ito 1984) to support learning in the cerebellum, much of which is not discussed in **Bloedel's** review (e.g., long-term depression caused by conjunctive stimulation of climbing and parallel fibres; Ito 1989). A major strength of the cerebellar learning hypothesis is that it makes sense of the response properties of the olive. Responses to perturbation, in addition to any immediate corrective function, can be used by the system as an instructor to modify transmission in active synapses for future benefit. **Bloedel** claims that there is substantial evidence against learning in the cerebellum on the basis of an experiment from his laboratory. He claims that decerebrate, cerebellectomized rabbits can learn eyeblink responses (Kelly et al. 1990b) but fails to point out that there has already been substantial criticism of this experiment. Using **Bloedel's** protocols, normal rabbits cannot learn an eyeblink response (Nordholm et al. 1991), and using conventional protocols cerebellectomy abolishes conditioned eyeblink responses in decerebrate rabbits (Yeo 1991a).

In any case, the most compelling evidence for cerebellar plasticity has not been from eyeblink conditioning experiments. The very substantial body of experimental evidence for such plasticity is from work on gain and phase modifications of the VOR, primarily by Ito and his colleagues (see Ito 1984; 1989). **Bloedel** demonstrates an extremely limited view of work in this area when he cites only the review by Lisberger (1988a; 1988b) that suggests a brainstem *and* cerebellar engagement in VOR modification.

In his final section, **Bloedel** puts forward his Vermittler hypothesis:

The cerebellum serves as a active mediator whose output provides the CNS with an optimized integration with the relevant features of external execution space, internal intention space, . . . As a consequence of this integration the cerebellar output can modify activity in

central pathways responsible for motor execution to ensure the specification of the appropriate kinematic and dynamic characteristics of the movement.

This hypothesis is a very general one that is similar to what many others have proposed for the role of the cerebellum. It should be noted that the hypothesis does not have many implications for the detailed functioning of the cerebellar circuitry. In fact, some of the early theories that proposed learning in the cerebellum also hypothesized that the cerebellum would perform in a way similar to that suggested by **Bloedel's** Vermittler hypothesis (Albus 1971; Marr 1969).

A useful theory of cerebellar function would be one that makes more sense of perturbation response properties of the olive. We suggest that the cerebellum must engage in processes of on-line control based on calibrations and learning that have gone before.