Supplementary information S5 (box): Alternative models of cerebellar microcircuitry

CMACs
As explained in Text Box 4, cerebellar cortex is often regarded as a gigantic memory or look-up table (LUT) which stores the desired response to a given set of inputs, so that it functions as a pattern classifier or feature detector. The most widely used LUT is based on the Cerebellum Model Articulation Controller (CMAC) of Albus. The CMAC's mode of operation can be illustrated by a simplified example. For the vestibulo-ocular reflex (VOR), head velocity at a given instant activates a small number of granule cells, whose weights have the correct values to drive the floccular PCs to counter-rotate the eyes at the appropriate velocity. At the next instant, if head velocity changes, a new set of granule cells are activated and a new set weights ensures the correct response. For real control problems the CMAC typically associates particular combinations of coarsely coded position, velocity and acceleration inputs (as signalled by granule cells) with the appropriate control outputs. Since the learning rule used by the CMAC for adjusting its weights is of the same form as the covariance rule used by adaptive-filter models, the key difference between the two lies in input coding. To continue the VOR example, head-velocity in an adaptive filter would most naturally be coded as a continuous variable by granule cell firing rate (as recently demonstrated by Arenz et al.). In the CMAC, as indicated above, a given value of head velocity is coded by which population of granule cells fire. Any explicit temporal structure in mossy fibre inputs is discarded.

It has been argued that LUTs cannot handle time varying signals, e.g. Fujita has written that "Albus (1971) proposed spatial pattern-classifier models ... . However these models do not account satisfactorily for processing of time-analog signals conveyed by frequency-modulated nerve impulses" (p195). However, a better way of expressing the difference is that the adaptive filter is the convenient way to interpret a time varying output synthesised from time varying inputs, and so is particularly relevant for controlling mechanical systems. These systems have properties such as inertia, viscosity and elasticity, which are naturally described in terms of operations such as differentiation and integration. These operations require knowledge of not just the current value of an input signal, but of its past values also (although the CMAC could in principle be configured to respond to delayed inputs, in practice this appears not to have been carried out.) The advantages of the adaptive-filter are especially apparent for control problems where inputs that vary along many dimensions, where outputs depend on the past history of the system (hysteresis), and for the analysis of control stability.

In summary, to the extent that the appropriate input coding depends on the nature of the signal-processing problem to be solved, CMACs can be seen as a subclass of adaptive filter rather than as a totally separate model (Text Box 4).

Perceptrons
A special case of an LUT, where inputs and outputs can only take two values (0 or 1), is equivalent to a Perceptron and is closer to Marr's contribution to the Marr-Albus framework. However, as Marr himself commented "the cerebellar study ... disappointed me, because even if the theory were correct, it did not enlighten one about the motor system - it did not, for example, tell one how to go about
programming a mechanical arm. It suggested that if one wishes to program a mechanical arm so that it operates in a versatile way, then at some point a very large and rather simple type of memory will prove indispensable. But it did not say why, nor what that memory should contain\(^7\), p.15. Marr's scheme would in fact be very difficult to apply in a control context\(^8\), as indeed is the case for Perceptrons in general. Thus, although Perceptrons can be used in theoretical investigations, for example to analyse certain kinds of optimal coding scheme e.g.\(^9\), their relevance to cerebellar function may be limited.

References