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Title: Computational analysis of the eligibility trace in cerebellar learning

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Both experimental evidence and computational analysis suggest that the cerebellum uses a learning rule which combines LTD and LTP to decorrelate parallel fibre (PF) from climbing fibre (CF) inputs (Jorntell & Ekerot 2002, Coesmans et al. 2004, Dean et al 2002). However, the implementation of this rule by spiking neurons is not well understood. A central issue is the shape of the 'eligibility trace', which describes the amount and direction of learning at PF/PC synapses as a function of the time elapsing between PF and CF discharge.
Here we investigate the eligibility trace mechanism by computational analysis of a rate based covariance-learning law and by computer simulation of a spike-timing-dependent-plasticity formulation.
Experimental evidence provides two constraints that help to determine the shape of the eligibility trace. One is that CF signals are delayed by a period that varies from ~10 msec (C1 zone, tactile) to ~100 msec (flocculus, retinal slip). The second is that even with a 100 ms delay, learning is still possible with CF inputs modulated at frequencies up to 5 Hz (Raymond & Lisberger 1998), whereas without an eligibility trace it would be restricted to an upper bound of 2.5 Hz.
Since it is generally assumed that the cell-signalling processes generating the eligibility trace (e.g. Wang et al. 2000) are uniform over cerebellar cortex we have looked for a single profile satisfying these constraints. We show that an alpha-function eligibility trace with a peak at 40ms can cope with delays between 10 and 100ms for CF inputs modulated at frequencies up to 5.5Hz. This trace differs from those proposed by Kettner et al (1997), who used an alpha-function with a peak at 100ms, and by Raymond & Lisberger (1998) who used an Gaussian profile with peak at 100ms and a sigma of 25ms. In both these cases the trace was designed to cope specifically with the 100 ms delay of retinal slip, rather than with an unknown delay that could vary between 10 and 100 ms.
Our analysis provides support for the uniformity assumption above in that a single eligibility trace can cope with the range of delays found in climbing fibre inputs to the cerebellum without unduly restricting the frequency range over which learning can operate. However these results indicate the necessity of obtaining direct experimental evidence for this assumption given its importance in computational models of cerebellar learning.

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