COMMENT

Comments on 'Hebbian learning is jointly controlled by electrotonic and input structure'

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Abstract. It is argued that simulations presented by Tsai, Carnevale and Brown do not agree with their theoretical predictions and that their mathematical derivation contains a major flaw. The origin of these misunderstandings is traced to the application of a special case of an equation whose general version is given here.

I would like to correct a number of errors that crept into Tsai, Carnevale and Brown (1994).

Equation (10) and the remainder of the paper do not follow from equation (9). Equation (9) retains the decay term from Oja's rule (1982) in the non-isopotential situation, where it loses its desirable mathematical properties, making equation (10) incorrect. If the weights are to converge to the principal eigenvector of C, a decay term like that of Yuille *et al* (1989) must be used (Miller and MacKay 1994, Goodhill and Barrow 1994). This accounts for the failure to use equation (10) in a predictive fashion, for in the simulations shown the weights do not converge to the principal eigenvector of C.

In remarks following equation (12), it is stated that this decoupled form of the equation supplies 'less useful neurophysiological insight' than equation (10). Fortunately the insights to be had are computational, not neurophysiological. When it holds, equation (12) shows that the input's only important property is its pairwise correlational structure. Equation (12) is also interesting because of its potential applications. Just as Oja's equation for the instantaneous isopotential case was used to account for receptive fields in the visual system (Miller *et al* 1989), this equation can extend such analysis to non-isopotential neurons. And just as Chernjavski and Moody (1990) used an identical equation to predict the length scale of cortical columns, one might predict the length scale of clusters of synaptic facilitation along a dendritic shaft.

The last paragraph on page 8 says that the instant at which Hebbian modulation occurs is both simultaneous with the instantaneous presynaptic activity and subsequent to the presynaptic activity's postsynaptic effect. This would have delighted Bishop Berkeley (1734). Equation (9) is a special case of

$$\frac{\mathrm{d}m_i}{\mathrm{d}t} = \eta \int_0^\infty \xi_i(t-\tau) \,\psi_i(\tau) \,\mathrm{d}\tau \,v_i(t) - \mathrm{decay}$$

where $v_i(t) = \sum_j w_j \int_0^\infty \xi_j(t-\tau) \tilde{v}_{ij}(\tau) d\tau$ is the postsynaptic potential, $\xi_i(t)$ is the input to synapse *i* at time *t*, $\tilde{v}_{ij}(\tau)$ is the neuron's voltage response to a unit current injection at

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synapse j as measured τ seconds later at synapse i, and we introduce $\psi_i(\tau)$ as the time course of opportunity for modulation of synapse i following presynaptic activity. This leads to

$$\langle \mathrm{d}m/\mathrm{d}t \rangle = \eta \mathbf{C}m - \langle \mathrm{decay} \rangle$$

in which **C** is defined by the more general

$$C_{ij} = \int_0^\infty \tilde{v}_{ij}(\tau) \left(Q_{ij} * \psi_i \right)(\tau) \, \mathrm{d}\tau$$

where $Q_{ij}(\tau) = \langle \xi_i(t) \xi_j(t-\tau) \rangle$ (Pearlmutter 1994). To get the special case of Pearlmutter and Brown (1992), one considers $\psi(\tau)$ to be a Dirac delta pulse and takes the limit as this pulse is moved towards 0+.

Brown, Carnevale and Tsai had access to a preliminary draft of Pearlmutter (1994). That mansucript, and the short abstract Pearlmutter and Brown (1992), suffered from an overly terse mathematical formulation. The more leisurely exposition in the final publication should reduce the possibility of this sort of confusion.

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