

## *Editorial* **Hebb in perspective**

It is more than half a century ago since Donald Hebb published his classic book on the organization of behavior (Hebb 1949). Though highly readable, it has been cited in the computational/theoretical neuroscience literature much more often than it has been read. Why is this? On p. 62 of the book one finds the now-famous neurophysiological postulate: “When an axon of cell A is near enough to excite a cell B and *repeatedly* or *persistently* takes part in firing it, some growth process or metabolic change takes place in one or both cells such that A’s efficiency, as one of the cells firing B, is increased”. This simple and self-explanatory hypothesis to explain synaptic “learning” also aroused considerable debate, because the mechanism was local. “Locality” is the appealing idea that a synaptic efficacy is determined by the information that is available to pre- and postsynaptic neurons both in space and in time – but nothing else.

One then may wonder, of course, where the above “metabolic change” might take place. Hebb directly continued by suggesting that “synaptic knobs develop”, and on p. 65 he states very explicitly: “I have chosen to assume that the growth of synaptic knobs, with or without neurobiotaxis, is the basis of the change of facilitation from one cell on another, and this is not altogether implausible”. No, it is not. We even perceive the assertion as a commonplace, though in Hebb’s time it was a breakthrough.

Since its original formulation in English (but none other), the central question implied by Hebb’s postulate has been how to implement it. Most of the information that is presented to a neuronal network varies in space *and* time, and thus requires a *common* representation of both the spatial and the temporal aspects of the input. As neuronal activity changes, the responding system should be able to measure and, if necessary, store this change. How can it do so?

By now we know the Hebb rule works by means of a *learning window* in the context of spike-timing-dependent synaptic plasticity. Through the learning window a temporal mechanism “looks” at the arrival of a presynaptic spike in relation to the postsynaptic firing time. If a spike arrives at, for example, an excitatory synapse not too long *before* the postsynaptic neuron fires, the synapse strengthens; otherwise, if the spike is “too late”, the connection is weakened. Locality in space was a hypothesis clearly formulated by Hebb himself (Hebb 1949). Locality *in time* is an exciting and recent development.<sup>1</sup>

Why focus on time-resolved synaptic plasticity in Biological Cybernetics? An important reason for doing so is that our journal is devoted to advances in computational neuroscience. The above mechanism has been predicted theoretically (Gerstner et al. 1996) well in advance of any experimental verification. There is, meanwhile, a plethora of them (Bell et al. 1997; Bi and Poo 1998, 1999; Debanne et al. 1998; Feldman 2000; Holmgren and Zilberter 2001; Markram et al. 1997; Zhang et al. 1998). This underlines the novel role that computational neuroscience plays in prediction as well as verification of new experimental developments. We are therefore very pleased to count several experimentalists who contributed to the experimental verification among our authors. Time playing a key role, we think it is more than timely to focus on the Hebb rule in its novel generality that naturally allows the storage of spatio-temporal activity patterns.

The present special issue devoted to “Hebb in perspective” aims at presenting both theoretical and experimental foundations of spike-timing-dependent synaptic plasticity. Some of the essays have a review character so as to allow both a thorough but readable introduction and a comprehensive overview of the subject. We think the developments

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<sup>1</sup> As for temporal locality we could quote James (1890): “When two elementary brain processes have been active together or in immediate succession, one of them, on re-occurring, tends to propagate its excitement into the other.” However, the temporal order of the two processes, though at present the key issue, is unspecified. Furthermore, Hebb’s argument (Hebb 1949) was the first truly modern explanation.

one-half century after Hebb finally put his work in a proper perspective. Moreover, it is our expectation that, in view of the richness of data supporting time-dependent synaptic plasticity through a learning window, locality in time will lead to novel perspectives hitherto unimagined.

**J. Leo van Hemmen**  
**Walter Senn**

### **Background material**

- Bell CC, Han VZ, Sugawara Y, Grant K (1997) Synaptic plasticity in a cerebellum-like structure depends on temporal order. *Nature* 387: 278–281
- Bi G-Q, Poo M-M (1998) Synaptic modifications in cultured hippocampal neurons: dependence on spike timing, synaptic strength, and postsynaptic cell type. *J Neurosci* 18: 10464–10472
- Bi G-Q, Poo M-M (1999) Distributed synaptic modification in neural networks induced by patterned stimulation. *Nature* 401: 792–796
- Debanne D, Gähwiler BH, Thompson SM (1998) Long-term synaptic plasticity between pairs of individual CA3 pyramidal cells in rat hippocampal slice cultures. *J Physiol (Lond)* 507: 237–247
- Feldman DE (2000) Timing-based LTP and LTD at vertical inputs to layer II/III pyramidal cells in rat barrel cortex. *Neuron* 27: 45–56
- Gerstner W, Kempter R, van Hemmen JL, Wagner H (1996) A neuronal learning rule for sub-millisecond temporal coding. *Nature* 383: 76–81
- Hebb DO (1949) *The organization of behavior – a neurophysiological theory*. Wiley, New York
- Holmgren CD, Zilberter Y (2001) Coincident spiking activity induces long-term changes in inhibition of neocortical pyramidal cells. *J Neurosci* 21: 8270–8277
- James W (1890) *The principles of psychology*. Henry Holt, New York
- Markram H, Lübke J, Frotscher M, Sakmann B (1997) Regulation of synaptic efficacy by coincidence of postsynaptic APs and EPSPs. *Science* 275: 213–215
- Zhang LI, Tao HW, Holt CE, Harris WA, Poo M-M (1998) A critical window for cooperation and competition among developing retinotectal synapses. *Nature* 395: 37–44