

Editorial: Cell Assemblies¹

The nature of cortical representations is central for an understanding of how memory and cognitive operations are implemented by the brain. In his seminal book “The Organization of Behavior”, the canadian psychologist Donald O. Hebb (1904-1985) outlined a comprehensive biological theory of psychological function (Hebb, 1949). His theory relates psychological phenomena as various as learning, perception, motivation, and emotion to anatomical structures and physiological processes in the brain. The connection made by Hebb’s theory was truly groundbreaking when it was published in 1949 and it defined the program of theoretical neuroscience, that is prevailing to the current day.

Hebb built his theory on the definition of a new concept that he called the “cell assembly”. A cell assembly is comprised by a group of neurones with strong mutual excitatory connections. Thus, the definition relies on the interrelation of structural and physiological properties of nerve cells. Since a cell assembly, once a subset of its cells are stimulated, tends to be activated as a whole, it can be considered as an operational unit in the brain. Hebb related cell assemblies to the psychological level by proposing that they represent “objects” (or more abstract entities of thought). In the framework of Hebb’s theory, a number of phenomena described by psychology can be explained by simple mechanisms: An “association” is nothing but the activation of an assembly by a stimulus or another assembly. Short-term memory is persistent activity that can be maintained by reverberations within or between assemblies, even if the primary stimulus is withdrawn. Long term memory, in contrast, corresponds to the formation of new cell assemblies: According to the principle “what fires together, wires together” Hebb postulated a simple synaptic mechanism how new cell assemblies can be formed by groups of cells that are often coactivated: Hebb’s synaptic learning rule prescribes a strengthening of synapses between coactivated cells (by some metabolic or structural changes).

Hebb’s ideas have influenced the research of many experimental and theoretical neuroscientists. Various “brain theories” realized aspects of Hebb’s work or incorporated his concepts, e.g., Abeles (1991); Amit (1995); Braitenberg (1978); Damasio (1989); Edelman (1992); Marr (1971); McGregor (1993); Mesulam (1998); Miller (1996); Milner (1996); Wickelgren (1992);

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Palm (1982); Palm and Aertsen (1986); Pulvermüller (1992); Shaw et al. (1985). Parts of Hebb’s ideas have also been formalized mathematically: For instance, the main properties of assemblies can be well studied in formal associative memories (Steinbuch, 1961; Willshaw et al., 1969; Palm, 1982; Hopfield, 1982; Amit, 1988; Bienenstock, 1994). To track down the traces of cell assemblies in physiological data, however, turned out to be difficult. For a long time the required techniques of multiple single-unit recording and multivariate data analysis were just unavailable. Nonetheless, advanced techniques to validate the cooperation of cells have been developed meanwhile (Nicolelis and De Schutter, 2001), such that evidence for Hebbian cell assemblies and associated learning mechanisms is now accumulating. Indeed, multiple single-unit recordings revealed that the coordination of cell firing in cortical networks is more intricate than expected. Cell assemblies could manifest themselves, at least in principle, in covariances between firing rates. However, as it turned out, also the precise relative firing times and temporal correlations in neural ensembles seem to be important for coding and synaptic plasticity (Abeles, 1991; Aertsen et al., 1989; Gerstein et al., 1989; Singer and Gray, 1995; Eckhorn, 1999; van Hemmen and Senn, 2002). These observations led to a shift in paradigm from the study of rate coding mechanisms to spike based coding in the neurosciences during the last 15 years. Still, also in this quickly developing new field of research, cell assemblies provided a background for a multitude of studies on, for instance, synchronized oscillations as a tentative solution for the “binding problem” in perception (for reviews, cf. Singer and Gray (1995); Eckhorn (1999)) or, more recently, spike-time dependent synaptic plasticity as a variant of the Hebbian learning rule (cf., van Hemmen and Senn (2002); Bi and Poo (2001)).

Nonetheless, it seems that the various fields of research dealing with subjects related to cell assemblies –formal associative memories, synchronized oscillations, and synaptic learning rules– went separate ways, and the goal of an integrative neurobiological brain theory gradually disappeared from their foci. The purpose of this special issue of *Theory in Biosciences* is to provide a survey of recent results in the different mentioned fields with respect to developing a brain theory of cell assemblies. A collection of papers is presented that discuss cell assemblies in conceptual or integrative frameworks. Several of the contributions concentrate on biologically motivated associative networks for perception and memory processes in large scale cortical systems. Complementary works target on a diversity of topics, such as formal aspects of spatio-temporal correlations in assemblies, the impact of attention on recognition processes and behavior, and the realization of basic neural

mechanisms for grammar and language. Part of the contributions have been presented at a workshop on cell assemblies, organized by the editors at the 12th Computational Neuroscience Conference, CNS 2002, Chicago, IL. The incentive for this special issue was to convey recent theoretical and experimental work investigating and elaborating theories of cell assemblies. We hope the compiled studies can inspire those thinking about how brain function and mechanisms relate and that, ultimately, the results presented may contribute to a neurobiological theory of cognition.

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