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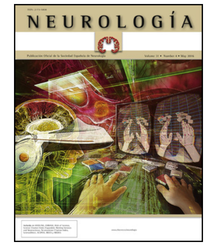

REVIEW ARTICLE

Structural synaptic plasticity in the hippocampus induced by spatial experience and its implications in information processing☆

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Mossy fibres

Abstract
Introduction: Long-lasting memory formation requires that groups of neurons processing new information develop the ability to reproduce the patterns of neural activity acquired by experience.
Development: Changes in synaptic efficiency let neurons organise to form ensembles that repeat certain activity patterns again and again. Among other changes in synaptic plasticity, structural modifications tend to be long-lasting which suggests that they underlie long-term memory. There is a large body of evidence supporting that experience promotes changes in the synaptic structure, particularly in the hippocampus.
Conclusion: Structural changes to the hippocampus may be functionally implicated in stabilising acquired memories and encoding new information.

PALABRAS CLAVE
Plasticidad sináptica;
Hipocampo;
Experiencia espacial;
Memoria a largo plazo;
Ensambles neuronales;
Fibras musgosas

Plasticidad sináptica estructural en el hipocampo inducida por la experiencia espacial y sus implicaciones en el procesamiento de información

Resumen
Introducción: Para formar memorias perdurables, es necesario que los grupos de neuronas encargados de procesar la información que adquirimos desarrollen la capacidad de reproducir los patrones de actividad que se forman a través de la experiencia.
Desarrollo: Los cambios en la eficiencia sináptica permiten que las neuronas se organicen en «ensambles» y reproduzcan una y otra vez estos patrones de actividad. Entre los cambios en la eficiencia sináptica están las modificaciones en la estructura, las cuales tienden a perdurar

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por mucho tiempo y por ello se les vincula con la memoria a largo plazo. En la literatura existe amplia evidencia de que la experiencia promueve modificaciones en la estructura sináptica, particularmente en regiones como el hipocampo.
Conclusión: Las implicaciones funcionales de estos cambios en el hipocampo incluyen un posible papel en la estabilización de los recuerdos adquiridos y en la codificación de nueva información.

Memory and its underlying neuronal mechanisms

One of the most remarkable features of humans and other animals is their ability to learn and remember. Humans can recognise stimuli encountered long before, such as the face of someone we met years ago. We can also establish long-lasting associations between stimuli such that we are consistently startled by car horns and are able to recognise our childhood surroundings and still find the small shop where we used to buy sweets.

The information that we obtain and keep in our memory is represented in the central nervous system by the coordinated activity of groups of neurons that develop the ability to repeat activity patterns acquired through experience. This idea shows that the information underlying cognitive processes, including memory, is represented in the central nervous system by groups of neurons called 'ensembles'.[1] This is known as population coding.[2] A graphic way to explain this concept is to compare neuronal units with the letters of the alphabet: it is not letters that convey information but rather the combination of letters and the order in which they are combined that creates meaningful words and sentences.

Plasticity and neuronal ensembles

Renowned neuroanatomist Santiago Ramón y Cajal introduced the hypothesis that changes in synaptic connectivity of the CNS could provide the substrate for memory.[3] It was not until the middle of the past century that Donald Hebb (1945) formally introduced what is known today as 'Hebb's 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''.

Lorente de Nó's concept of the 'reverberating circuits' became Hebb's empirical basis for explaining that the reverberation in 'neuronal ensembles' was the mechanism strengthening synaptic connections within the ensemble, which resulted in the ability to repeat activity patterns generated through experience. Ensembles can repeat activity patterns generated either without external stimuli (off-line activity patterns) or with partial stimulation using information related to the event that motivated memory creation (on-line activity patterns).

There are several types of changes in synaptic efficacy and some are more long-lasting than others. More specifically, changes in the structure of synaptic connections tend to last longer and may therefore be involved in long-term memory.[4]

Where can population coding and ensemble dynamics be studied?

The hippocampus has shown itself to be the most suitable localisation for identifying and studying neuronal ensembles due to its anatomical location, the physiological characteristics of the neurons forming it, its plasticity, and its role in memory creation.

For more than 50 years now, we know that the hippocampus is essential for memory creation.[5] We also know, thanks to subsequent studies in animal models, that the hippocampus is involved in processing episodic information, which includes both spatial and temporal information.[6,7] The mechanisms underlying synaptic plasticity, such as long-term potentiation (LTP), can also be studied in the hippocampus using animal models. In this model of plasticity, postsynaptic response to low-frequency pulses increases in the long term after applying trains of high-frequency stimulation.[8,9] With this experimental model, synaptic efficacy has been shown to vary depending on the pathway's activity history, more specifically in the synapses of the stimulated pathway.[9,10] This finding, which served as the empirical basis for Hebb's postulate, was suggested as the mechanism underlying spatial memory consolidation in the hippocampus.[11] However, according to Hebb's original idea, the growth processes that may take place can be interpreted as changes in the structure of synaptic connections.

Does experience change cerebral synaptic structure?

Empirical evidence of the changes in neuronal structure as a consequence of experience began to be published in the early 1960s, when Rosenzweig et al. introduced the paradigm of the 'enriched environment'.[12] Initially, these authors found that enriched environments had an effect on gross parameters, including brain weight and brain protein and nucleotide content.[12] In subsequent studies, environmental enrichment was proved to increase dendritic branching and the number of dendritic spines.[13] The key lesson is that since then, a connection between structural changes and improved learning skills has been described.