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Autor: Eccles, J.C.

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Learning and Memory in the Mammalian Brain

by J.C. ECCLES, Contra (Locarno)

The simplest concept of learning and forgetting is that excess usage of synapses leads to hypertrophy and enhanced function, whereas disuse leads to regression and diminished function. This theory can be criticized because it is now recognized that almost all cells at the highest levels of the nervous system are discharging impulses continuously. One can imagine therefore that there would be overall hypertrophy of all synapses under such conditions of continued activation, and hence but little possibility of any selectivity in the hypertrophic change. Evidently, frequent synaptic excitation alone could hardly provide a satisfactory explanation of synaptic changes involved in learning. SZENTAGOTHAI (1968) and MARR (1969) have proposed that synaptic learning is a dual or dynamically linked happening; namely that activation of a special type of synapse provides instructions for the growth of other activated synapses on the same dendrite. This may be called the "conjunction theory of learning". It was originally suggested that the unique operation of climbing fibres (CF) on the Purkyně dendrites of the cerebellum was to give "growth instructions" to the spine synapses that about the same time were activated by the parallel fibres. Otherwise activation of the spine synapse did not result in growth and the long-term memory coded thereby.

There is a very ancient part of the cerebellum that controls the eye movements when the head is turned. One can think that the function of this part of the cerebellum is to maintain, as far as possible, a fixed position of the visual image on the retina. The movements of the head are sensed by the semicircular canals of the vestibular system. For our present purpose we have only to consider the horizontal canal because in the experiments of ITO (1975) the head of the rabbit was subjected to a sine wave horizontal rotation with a standard amplitude of 10^{o} and a frequency of 0.15 Hz. It was of great interest that, when the head rotation was continued for many hours, there was a progressive increase in the compensation, which after several hours became almost perfect for eliminating retinal image slip.

These observations provide clear evidence of a learning process that over some hours tends to improve the stability of the retinal image. Two experiments define the neural pathway concerned in this learning. Firstly, with ablation of the flocculus, it fails to occur. Two possible explanations remain: it could be by the mossy fibre return circuit to the flocculus from the visual system. That was disproved by finding that learning did not occur, or at most only in a minor, late form when the inferior olive was destroyed. Thus we have good evidence that the CF input to the cerebellar Purkyně cells of the flocculus is effective in causing a learned cerebellar modification that gives improvement in the stabilization of the retinal image over and above that achieved by the vestibulo-ocular reflex.

But it is not enough simply to postulate this potential influence of single CF impulses in sharpening the response to a mossy fibre (MF) input. It is required to show that the CF inputs have themselves a degree of refinement that matches their potentiality for refining the MF responses by selecting a class of the MFs that represents the context of the CF input and that can effectively operate in the absence of this CF input, as postulated by MARR (1969). The CF input to a Purkyně cell instructs it to increase the potency of those parallel

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fibre synapses that *are selected by the conjunction in time* from the existing multitude of synapses. This potentiation is the plastic influence of the CF input. It is highly selective. Perhaps no more than a few thousand of the 100.000 parallel fibre synapses on that cell form the MF context of its CF input.

This hypothesis of learning brings it into relationship with Jerne's selection theory of immunity. The action of the antigen is to select from the vast array of lymphocytes those with the correct antibodies and to call forth an immense clonal multiplication of these specific lymphocytes that in turn shed their antibodies into the blood stream. JERNE (1967) suggested that the learning processes in the brain similarly might be by selection rather than by instruction.

The aim of this theoretical paper has been to give an account of the general principles involved in the conjunction-potentiation theory of learning for the cerebellum. There is already a wealth of detailed anatomical knowledge with precise study of the climbing fibre and mossy fibre pathways. There is evidence of trophic interaction and the studies of ITO and associates provide the first experiments on mammals where there has been an analytical investigation of the neural machinery involved in learning. Important corroborative evidence for the role of the cerebellum flocculus in the adaptive changes of the vestibulo-ocular reflex (GONSHOR and MELVILL JONES, 1976) has recently been reported by ROBINSON (1976), but the possible role of the climbing fibres has not yet been investigated. Much more experimental evidence is urgently needed on this extremely important problem of learning in the cerebellum. It now appears likely that the climbing fibre – mossy fibre conjunction that is involved in the neural mechanism of cerebellar learning may provide a paradigm for a conjunction theory of cerebral learning (ECCLES, in course of publication).

References

GONSHOR, A., and MELVILL JONES, G.: Extreme vestibulo-ocular adaptation induced to prolonged optical reversal of vision. J. Physiol. *256,* 381–414 (1976).

ITO, M.: Cerebellar learning control of the vestibulo-ocular mechanisms. 26. Int. Physiol. Congr. New Delhi 1975.

JERNE, N.K.: Antibodies and learning: Selection versus instruction. In: QUARTON, G. C., MELNECHUK, T., and SCHMITT, F.O. (Eds.): The neurosciences: A study program, 200–205. Rockefeller Univ. Press: New York 1967.

MARR, D.: A theory of cerebellar cortex. J. Physiol. (London) *202,* 437–470 (1969).

ROBINSON, D.A.: Adaptive gain control of the vestibuloocular reflex to the cerebellum. J. Neurophysiol. *39,* 954–969 (1976).

SZENTAGOTHAI, J.: Structure–functional considerations of the cerebellar neuron network. Proc. I.E.E.E. *56,* 960–968 (1968).