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Abstract

Examples of how LTP and LTD can control adaptively timed learning that modulates attention and motor control are given. It is also suggested that LTP/LTD can also play a role in storing memories. The distinction between match-based and mismatch-based learning may help to clarity the difference.

Text

Our neural modeling work has also led us to conclude that "all forms of synaptic modifications related to learning and memory are not equivalent" (p. 6). Calling the study of these changes "the search for the engram" does create a strong impression to the contrary. I will first review results relevant to their claim "that LTP is the neural equivalent of an arousal or attention device" (p. 23).

For definiteness, I will initially consider learning of the rabbit nictitating response, although the mechanisms are of broader significance. Both the hippocampal dentate-CA3 circuit and the cerebellar Purkinje cell-subcerebellar nucleus circuits are implicated in this process. We have proposed that both circuits carry out adaptively timed learning. Neither learned change "stores an engram", however.

The hippocampal circuit is proposed to maintain attention upon salient cortical representations for a task-relevant duration while also inhibiting orienting responses that could otherwise reset attention and trigger exploratory behaviors (Grossberg and Merrill, 1992, 1996; Grossberg and Schmajuk, 1989). This process enables a learning subject to cope with the fact that many associations, notably with rewarding and punishing events, are made over variable time delays. Without an adaptive timing process, an animal could not learn to wait for delayed consequences, and would instead relentlessly explore the world searching for immediate gratification. The adaptive timing process influences other learning processes as well, including the encoding of declarative memories, by holding in short-term memory cortical representations that could not otherwise be associated with delayed environmental contingencies. We have shown how paradoxical data about declarative and procedural memories, including hippocampal amnesias, may be clarified by such an adaptive timing process. I should hastily add that it is not proposed to be the only type of LTP/LTD that the hippocampal system supports.

The hippocampal dentate-CA3 circuit enables an animal to focus attention quickly upon behaviorally salient cues, both positive and negative, yet also maintain attention upon such cues task-determined durations. Drawing attention rapidly to salient cues can be a matter of life or death, as when a predator is rapidly approaching. On the other hand, fast attention could also prematurely release motor responses in a task-unappropriate way. We have proposed that cerebellar learning enables conditioned motor responses to be released with an appropriate delay even if attention is quickly deployed. In particular, we have modeled LTD of Purkinje cells as an adaptively timed gate. When this gate opens throughout a learned interval, it enables conditioned motor gains to be released via a subcortical pathway (Fiala, Grossberg, and Bullock 1996; Grossberg and Merrill, 1996). We have developed a detailed biochemical model of how the metabotropic glutamate receptor (mGluR) system may mediate the slow adaptive timing process. We have also summarized data showing that this system may be old phylogenetically , and may have evolved to deal with a general problem of maintaining cell sensitivityto variable intensities and durations of stimulation.

Using these distinct hippocampal and cerebellar models, we have suggested how the three properties of fast attention, task-appropriate attentional maintenance, and properly delayed release of motor behaviors are all achieved, even though neither of the LTD/LTP adaptively timed processes encodes a declarative memories. In both cases, the slower learning processes modulate faster learning processes that may encode cognitive, emotional, or motor memories.

Another distinction that is useful to keep in mind is the difference between mismatch-based learning and match-based learning. Mismatch-based learning is often used to learn spatial and motor skills, match-based learning for learning sensory and cognitive representations. The former is easily extinguished. In particular, our biochemical cerebellar model suggests how LTD can be extinguished due to the presentation of a conditioned stimulus without an unconditioned stimulus. This is adaptive because there is no reason to remember the spatial and motor maps, delays, and gains that are appropriate to our smaller bodies as we grow up. Match-based learning can persist for many years, as we accumulate more knowledge about the world (Carpenter and Grossberg, 1993; Grossberg, 1976). I believe that the evidence does support a role for LTP in this sort of learning as well. In particular, our models anticipated the type of Hebbian and anti-Hebbian mixture of effects that are used to model recent data about NMDA receptors (Artola and Singer, 1993). It remains to be seen how match-based and mismatch-based learning mechanisms compare on the biochemical level.

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