Theta Rhythm and Memory

The recent report by Landfield, McGaugh, and Tusa (*1*) presented good evidence that rats which had the greatest incidence of theta activity in the electroencephalogram (EEG) immediately after a footshock and during retention tests were also the ones that were most likely to show retention for the footshock. One reasonable conclusion that Landfield and his co-workers made was that "the amount of theta in the EEG can also apparently be used as a measure of retention . . ." (*1*). However, the conclusion that theta may be specifically related to, or involved in, the brain processes of memory storage should have been balanced with equally plausible alternative explanations. For example, the theta activity could have been a secondary effect that was caused, not by neurons involved in memory processing, but by neurons that caused increased muscle activity, both immediately after footshock training and during retention testing.

Within certain limits, rats that show the best retention are those which perceive the most pain and have the greatest affective response to footshock. Recall of that unpleasant experience, either immediately after training or when placed in the footshock environment during the retention test, would increase both the general level of arousal and the tension of the skeletal muscles of the rat. A growing array of recent studies (*2*), which the authors did not cite, clearly indicates the possibility that the amount of theta activity (not necessarily its frequency content) is correlated nonspecifically with muscular activity, independently of any learning or memory processes.

I suggest that the observations by Landfield, McGaugh, and Tusa could be explained in terms of the well-accepted view that neurons in the brainstem reticular formation can cause not only theta rhythm but also generalized muscle activity (*3*). Immediately after footshock, the intense sensory experience would most certainly have activated the brainstem reticular formation, triggering a presumed muscle activation and the observed theta activity. During retention tests, those rats that showed retention for the unpleasant experience could have been receiving brainstem reticular formation–activating influences through the readout of memories in higher brain centers in the cortex and the limbic system, again causing a presumed increase in muscle activity and the observed theta activity.

The final conclusion by Landfield and his co-workers seems especially pertinent, "Under these conditions, theta may be a correlate of a brain state which is optimum for memory storage." I suggest, as many others have, that this brain state is one of general alertness.

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Klemm makes two main points regarding the interpretation of our recent report (*1*). He is quite correct in pointing out that theta rhythms have been correlated with alertness (*2*) and with some forms of motor activation. Klemm cites several important papers, including his own rather elegant work, which are consistent with the latter view.

Since there is growing evidence that some aspects of arousal are important for memory storage (*3*), it seems reasonable, as Klemm notes, to suggest that alertness (or arousal) may be the primary correlate of memory storage, and that theta activity may be merely a secondary correlate of alertness. However, the experimental value of this hypothesis seems somewhat limited since it is not very precise. Arousal processes are a poorly defined complex of many biological mechanisms (*4*), only some of which are likely to be *directly* relevant to memory processes. Presumably, these relevant aspects are arousal-related changes in electrical and biochemical activity of the brain rather than arousal-induced peripheral changes in, for example, circulation (although peripheral effects can, of course, influence brain activity). We have focused on brain electrical patterns in an attempt to dissect out possible memory-related aspects of arousal processes. In this context, our views on cortical theta activity (one of the elements of alertness) are simply a more specific version of Klemm's suggestion, rather than an alternative.

The complexity of arousal is relevant to Klemm's other point regarding theta activity, muscular activation, and reticular formation activity. Judging from the extensive connections and internal structure (*5*) of the reticular formation, it seems likely that many systems interact within the reticular formation, and that its activity is a correlate of many aspects of arousal, including those possibly involved in memory storage. For instance, it has been found that stimulation, after a training trial, of the reticular formation (which drives theta, as Klemm notes) can also facilitate learning (*6*). Moreover, theta has been shown to be quite prominent in the absence of movement or electromyographic activity (*7*). One way to resolve this issue would seem to be to manipulate specific aspects of arousal and to determine whether or not memory storage is directly influenced by such manipulations. Although Klemm's points are quite reasonable, we feel that our findings, as well as those of other studies, justify the suggestions of a possible relation of theta activity to memory storage.

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