Contextual Memory

by Richard H. Hall, 1998

Time

Explicit and implicit memories are independent both behaviorally and neurologically. One of the principal characteristics of explicit memory, and one of the ways that researchers know that it's independent is through the verbal response of humans with brain damage. For example, HM demonstrates memory when he improves on explicit tasks, but when asked, he reports that he has no (explicit) memory of those tasks. Obviously this presents some challenges for non-human animal models of explicit memory since these animals are incapable of verbal report. However, another fundamental characteristic of explicit memory is its contextual nature. More specifically, explicit memory involves the memory for a combination of factors, a holistic sort of memory. For example, HM's memory for a given explicit task involves very specific stimulus-response memories, but his conscious memory would involve the memory of the time the previous learning took place, the environment the task took place in and other contextual cues. For this reason, animal researchers have focused on the contextual, multi-cue, nature of explicit memories to represent this type of memory in experiments with non-human animals.

The **radial maze experiment** is one example of an experiment that can serve to test contextual memory in animals (see Figure 1). In a radial maze experiment food is placed at the end of certain arms of the maze and the rat goes to the end of various arms to pick up the food. Implicit, or non-contextual memory, can be tested by always placing the food at the end of certain arms of the maze (for example, A, B,C, & D in figure 1). After some time the rat will remember to always search these arms for food. Implicit memory in this case would be assessed by noting how long it takes for the rat to recognize that it only receives food at the end of certain arms of the maze. Explicit memory, on the other hand, can be measured by assessing the number of times a rat goes back to an arm where it has already received food. So, although a rat may learn that arm A always contains food, it is a more complex task to remember whether it has already gotten the food from arm A, because the rat must take into account, first, where the food is located and, second, the time at which the food was last eaten. Due to the fact that this type of memory involves a memory for multiple cues it can be considered explicit/contextual memory. Consistent with the theory that the hippocampus is important in explicit memory, rats with lesions to the hippocampus are able to find the arms that consistently have food, but they are unable to remember which arms they have been to previously.

Figure 1. Radial Maze Experiment

Space

A second example of an experimental test of contextual memory in animals is the **milk maze** experiment (see Figure 2). In this experiment a tub is filled with water mixed with powdered milk and a platform is placed just below the surface in a certain location in the tub. Since the water is opaque the platform cannot be seen. When a rat is placed in the tub it will instinctively swim until it finds the platform where it can stand without swimming. When a rat is placed in the same location in the tub several times until it remembers which direction to swim to find the platform, implicit memory is being tested since the rat only has to remember one cue, direction. However, when the rat is placed in a different location after each trial explicit/contextual memory is being tested because the rat must remember where the platform is located relative to external cues outside the tub. So the rat must remember, first, that the platform is located a certain distance from the edge of the tub, and, second, that the platform is located on the side of the tub where the experimenter is standing, or where the wall of a certain color is, or some other external cue. Again, the second case is an example of explicit memory because multiple cues must be remembered in combination. The difference between this experiment and the radial maze experiment is that in the case of the milk maze additional spatial, as opposed to temporal cues, must be remembered. Consistent with the radial maze experiment, the rat with a hippocampus lesion can learn the task when always placed in the same location (implicit memory), but cannot learn when placed in different locations (explicit memory).

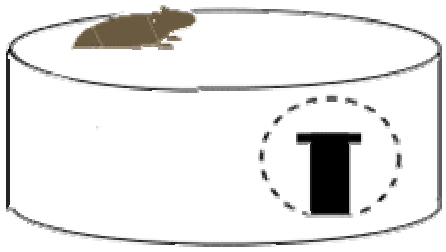

Figure 2. Milk Maze Experiment

“Complex” classical conditioning

One of the most dramatic demonstrations of the role of the hippocampus in contextual vs non-contextual memory comes from, yet another, classical conditioning/conditioned fear experiment. In this unique experiment conditioning was measured in response to a single-cue conditioned stimulus (implicit memory) and a multi-cue-contextual (explicit memory) conditioned stimulus. So, although conditioned fear is usually used to represent implicit memory, in reality a conditioned fear paradigm can be created such that the acquisition of a conditioned response can represent explicit memory.

In this experiment rats were randomly divided into three groups. In one group the amygdala was lesioned. (As discussed in previous modules, the amygdala is important in learning of implicit memories.) In a second group the hippocampus was lesioned. In a third, control group, the rats only received a "sham" lesion, meaning that they were exposed to the operating procedure but no brain areas were lesioned. All of the rats were then conditioned by pairing foot shock with a tone. The unconditioned/conditioned response was "freezing" behavior. Rats with the control lesion exhibited a conditioned fear response when they were placed in the chamber where the conditioning occurred. Thus, the chamber itself is serving as a conditioned stimulus. The memory for the chamber is a memory for the context in which the conditioning occurred, and as such the control rats were exhibiting contextual memory. They also exhibited a conditioned fear response to the tone when it was presented. The rats with an amygdala lesion did not exhibit a fear response to the context or to the tone. Most importantly, rats with the hippocampus lesion exhibited a fear response to tone (implicit/non-contextual memory), but not to the chamber (explicit/contextual memory). (Figure 3 illustrates the findings of this experiment).

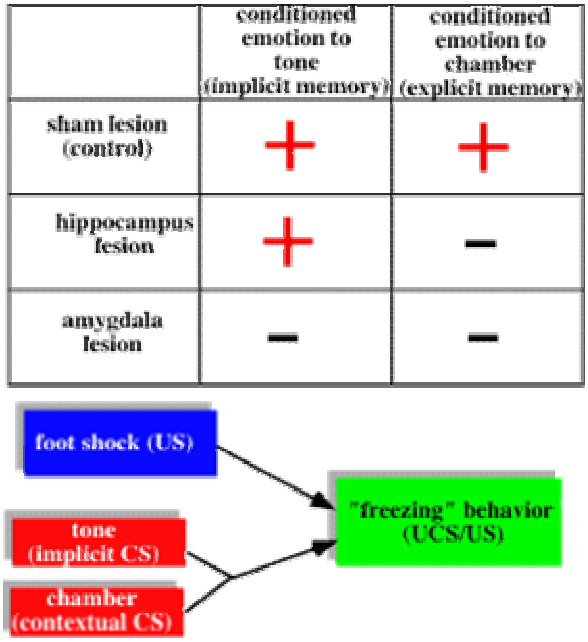

Figure 3. Multi vs Single Cue Conditioned Response Experiment Results.

Cellular Basis of Contextual Learning

There is also evidence that specific cells may be especially important in the types of contextual learning described in this module. More specifically, **pyramidal cells** in the hippocampus appear to be specialized for various contextual cues. For example, pyramidal cells have been identified that respond to: a) specific locations, such as a certain arm in a radial maze; b) general locations, such as the arm of a radial maze that points south; and c) the direction in which a rat is moving, such as movement to the right or left. Presumably, the combination of the firing of all of these cells accounts for a rats ability to form an explicit/contextual memory.

There is also evidence that **long term potentiation,** which has been identified as important in more basic memories, is also the phenomenon that underlies contextual memories. After rats have demonstrated learning in the milk maze experiment, long term potentiation can be found in the dentate gyrus. That is, the response of individual cells in the dentate gyrus in response to a pulse in the entorhinal cortex, is now greater than it was before the learning. In addition, when rats' genes are altered such that NMDA receptor formation is inhibited, performance in the milk maze experiment significantly declines. The NMDA receptors have been identified as playing a crucial role in the formation of long term potentiation.