

Question 1: If you try to recall how many windows there are in your house by mentally walking from room to room, are you using declarative memory, procedural memory, or both?

Answer: In trying to recall the number of windows in your house by mentally walking from room to room, you are using your declarative memory. In this case, the memory is a conscious effort pertaining to a fact. These features are typically associated with declarative memories.

Question 2: What evidence is there that declarative and nondeclarative memory use distinct circuits?

Answer: Studies support the idea that declarative and nondeclarative memories use distinct circuits. Most of these are lesion studies. For example, animals with lesions of the hippocampus or temporal lobe are unable to form declarative memories, but procedural memory is intact. Animals with lesions of the striatum are unable to form procedural memories, but declarative memory is intact. A very dramatic example of the disassociation between structures subserving the two types of memory is the renowned case of amnesia resulting from temporal lobe damage in the subject H.M. At the age of 27, H.M. had an operation in which an 8-cm length of medial temporal lobe was bilaterally excised to control seizures, including cortex, the underlying amygdala, and the anterior two-thirds of the hippocampus. The surgery controlled his seizures, but left him unable to form new declarative memories (he has remained hospitalized for over 40 years), yet his procedural memory is intact.

Question 3: What abilities and disabilities do you think a person completely lacking working memory would have?

Answer: Working memory is a temporary form of information storage that is limited in capacity and requires rehearsal. It is information held in the mind—keeping a memory alive through repetition is a hallmark of working memory—like remembering a phone number until you dial it. Working memory is commonly tested by measuring digit span. If a person lacks working memory, his inability to retain recently acquired information may cause him to duplicate the same actions over and over again. If a person is searching for some document in a set of files, the lack of working memory may cause him to keep checking the same files again and again because he cannot remember where he has already looked, and he may not be able to remember what he is looking for while he is searching the files.

Question 4: Why did Lashley conclude that all cortical areas contribute equally to learning and memory? Why was this conclusion later called into question?

Answer: American psychologist Karl Lashley conducted experiments to study the effects of brain lesions on learning in rats. He trained rats to run through a maze from start to finish without entering blind alleys. He then systematically lesioned larger and larger areas of cortex and looked at its effect on learning. He found that greater areas of cortical destruction were associated with more errors made while the rats learned to run the maze. The rats with larger lesions had difficulty remembering which arms of the maze were blind alleys. Based on these findings, he speculated that all cortical areas contribute equally to learning and memory because no single area caused a specific deficit. This conclusion was later questioned because the lesions were so large that they each damaged several cortical areas involved in learning the maze task. Another problem was that the rats may solve the maze in several different ways—by sight, feel, and smell—and the loss of one memory may be

compensated for by another. Subsequent research in this area had proven Lashley's conclusions to be incorrect.

Question 5: What evidence indicates that long-term memories are stored in neocortex?

Answer: Short-term memories are initially held in a particularly fragile form. For example, when we try to remember a phone number, an interruption can make us forget. However, long-term memory is much more robust. It can survive interruption, anesthesia, and the normal bumps and traumas that life involves. Because of this robustness, it is believed that memories are ultimately stored in structural changes in neocortex. Hebb suggested that the brain can use cortical areas for both the processing of sensory information and the storage of memories. This notion is supported by single unit recordings in area IT where neuronal responses to the presentation of monkey faces changes with repeated presentations. In addition, people with expertise distinguishing birds or cars show extrastriate visual areas that are significantly more activated by stimuli that match their expertise, as if the visual cortex is used not only to decode the information but also to store the long-term memories essential for developing expertise.

Question 6: If you were using a microelectrode to record from the brain and you suspected that a neuron you encountered was involved in storing long-term memories, how would you test that hypothesis?

Answer: If you were recording from an awake, behaving monkey, you could test the animal in a long-term memory paradigm and correlate his behavior with the output of the neuron. You could also remove the brain area and test the animal's ability to form long-term memories after the surgery. It might also be useful to apply a molecule that temporarily disabled the

neuron. The animal could be tested while the neuron was disabled and again when the molecule's effects were reversed. The behavior could then be correlated with the two conditions to determine the contribution of the neuron of interest.

Question 7: If a neuron in visual cortex responds to faces, how could you determine whether it is involved in perception or storing memories for faces?

Answer: One way to distinguish perception from memory is to watch the response pattern of the neuron after repeated presentations of the faces. If the neuron's responses are always the same, regardless of how often the stimuli are presented, it is likely to be only involved in perception. However, if the response properties of the neuron change with repeated presentations, perception cannot be its only function. If the changes are systematic, you may discover a pattern that is consistent with the formation of memories. For example, a single neuron in area IT was recorded while a subject monkey was presented with pictures of other monkeys. At first all the faces produced the same level of neuronal activity, but over time, the cell became selectively active only for certain faces. This dynamic aspect of responses in area IT supports the view that the brain can use cortical areas for both the processing of sensory information and the storage of memories. Therefore, if a neuron in visual cortex responds to faces, it may be involved in both perception and storing memories for faces.

Question 8: What are place cells, and where are they found? In what ways are the response characteristics of place cells different from the receptive fields of sensory neurons?

Answer: Place cells are found in the hippocampus. They fire maximally when an animal is in a specific location in the environment, such as the northwest corner of a box, but not when the animal is elsewhere in the box. This is the cell's place field. Other hippocampal neurons fire

maximally when the animal is elsewhere. Place cells are unlike receptive fields of sensory neurons because they fire when the animal returns to the place field even if the visual cues are absent. In addition, place cells are dynamic; that is, they change in ways to suit the current environment.

Question 9: What role does the hippocampus play in spatial memory, working memory, and relational memory?

Answer: Spatial memory is the ability to create a spatial map of the environment. Recordings from hippocampal place cells suggest a role for the hippocampus in spatial memory as these neurons fire maximally when the animal is in a specific location in his environment (northeast corner of the box). Working memory is the ability to retain recently acquired information, such as the arms of a radial arm maze in which a food reward has already been retrieved, and to use it for efficient navigation (never go down the same arm twice). The notion of relational memory tries to integrate these two processes by suggesting that highly processed sensory information comes into the hippocampus and nearby cortex, and memories are formed in a manner that links all the things happening at the time. In relational memory, neurons encode information about place as a series of simple associations between nearby objects and concurrent sounds and smells. Such memories can provide an understanding of the layout of the environment without having a complete organized map of space in the hippocampus. Eichenbaum and colleagues did odor discrimination experiments to study relational memory in rats and showed that the response of the hippocampal neurons related the specific odors, their spatial locations, and the fact that they were presented separately or together.

Question 10: What is working memory, and in what brain areas have neural correlates of working memory been observed?

Answer: Working memory is a temporary form of information storage that is limited in capacity and requires rehearsal. It is often referred to as information held “in mind.” Different digit spans in different modalities suggest the presence of multiple temporary storage areas in the brain (probably cerebral cortex)—depending on the sensory system. Hippocampal lesions cause a deficit in working memory (as tested in the radial arm maze) and so do lesions of the prefrontal cortex (as tested in the Wisconsin card-sorting test). Six areas in the frontal lobe showed activity during the delay period in an fMRI study of working memory. The active areas could be separated into three groups: those active during the facial identity task alone, those active during both the facial identity and spatial memory tasks, and those active during the spatial memory task alone.