Consequently, investigations of the origins of basal groups of modern pollinating insects must explore more completely assemblage 3 [panel (A) of figure], of which there is tantalizing but still incomplete evidence. These investigations will require extensive examination of Middle Jurassic to earliest Cretaceous compression deposits. Although there has been considerable effort toward characterizing the insect constituents of Cretaceous amber, the oldest insect-bearing amber is about 125 million years old and thus too recent to address the origin of the basal clades of modern insect pollinators.

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NEUROSCIENCE

Memory and Awareness

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When we remember our past experiences, we typically invoke a previous conscious awareness of these events. But memory for some aspects of the past can be expressed without any awareness that one is "remembering." These two kinds of memory are described as explicit or declarative memory (when we consciously recollect previous experiences) (*1*) and implicit or nondeclarative memory (when past experiences influence current behavior or performance even though we do not consciously recollect them). Recent advances in cognitive neuroscience are beginning to reveal the brain systems underlying the two forms of memory. Clark and Squire's (*2*) article on page 77 of this issue, which examines classical conditioning in healthy volunteers and amnesic patients, provides a striking example of the role of awareness in remembering that is best understood in the broader context of explicit and implicit forms of memory.

Amnesic patients, who have selective damage to the inner (medial) regions of the temporal lobes (including the hippocampus and related structures) perform poorly on tests for explicit memory that require them to recall or recognize recently presented information. But the same patients often show normal performance on implicit memory tests, in which they are simply asked to carry out a task and are not required to recollect any past experiences (*1*). Consider, for example, a type of implicit memory known as priming: a change in the ability to identify or produce an item as a result of a previous encounter with the item. In tests for priming, participants are asked to complete fragmented words or identify a word or picture after a brief exposure. Priming has occurred when individuals can complete or identify items that they have recently studied faster or more accurately than novel, nonstudied items. Amnesic patients exhibit normal priming effects on a variety of tasks (*3*). Thus, the medial temporal lobe (MTL) regions that are damaged in amnesiacs are crucial for explicit memory but are not needed for priming and related forms of implicit memory (*1*, *3*).

Amnesic patients show normal delay conditioning of an eyeblink response, as reported in previous studies and by Clark and Squire (*2*). This result fits well, because the delay conditioning paradigm does not require any explicit memory. In delay conditioning, participants simply listen to a tone followed immediately by an air puff that elicits an eyeblink response; after a number of such pairings, the tone alone elicits the eyeblink response.

More puzzling are findings from earlier research and from Clark and Squire (*2*) indicating that amnesic patients do not develop normal trace conditioning, which involves the same procedures as delay conditioning with one difference: in delay conditioning the tone and air puff overlap temporally and terminate at the same time, whereas in trace conditioning there is a brief interval after the offset of the tone and onset of the air puff. Why would this brief delay (which falls within the preserved immediate memory span of amnesic patients) produce a conditioning deficit? A key finding from Clark and Squire's new study—that trace conditioning in healthy volunteers occurs only in those who exhibit awareness of the contingency between tone and air puff, whereas delay conditioning occurs independently of such awareness—provides a neat answer. Amnesic patients cannot call on the explicit or declarative memory used by healthy volunteers to develop awareness of the contingency that is necessary for trace but not delay conditioning.

Memory phenomenon	Awareness necessary?	MTL necessary?
Delay conditioning	No	No
Trace conditioning	Yes	No
Word completion priming	No	No
Associative completion priming	Yes	Yes
Sequence learning	No	No

These results may help in understanding data from a recent study (*4*) in which brain activity was examined in healthy volunteers during delay conditioning with positron emission tomography (PET), which provides an index of local neuronal activity by measuring changes in regional cerebral blood flow. The medial temporal lobes were activated during delay conditioning. In light of Clark and Squire's data, it seems likely that this activation is associated with incidental awareness of the tone–air puff relation on the part of some experimental par-

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ticipants, even though such awareness is not necessary for delay conditioning to occur. Interestingly, a similar pattern has been observed during eyeblink conditioning in the rabbit where, as noted by the authors, delay conditioning is accompanied by hippocampal cell activity—even though hippocampal lesions do not abolish delay conditioning. Might such activity indicate some form of incidental awareness in the conditioned animals? In view of the fact that trace conditioning in the rabbit is impaired after hippocampal lesions, and the observed dependence of trace conditioning on awareness in humans, Clark and Squire's results raise the intriguing possibility that delay and trace conditioning could be used to study aspects of awareness in nonhuman animals.

Data from conditioning experiments in humans in some respects parallel earlier findings from priming experiments and a different type of awareness. After studying a list of common words (for example, *garden*), amnesic patients show intact priming of the studied items when asked to complete three-letter word stems (*gar__*) with the first word that comes to mind (*5*). The magnitude of this word-priming effect in healthy participants who become aware during the test that they are producing words from the study list and those who do not (*6*). In contrast, in a variation of this test amnesic patients exhibit impaired priming of new associations between unrelated words (*3, 6*). For example, after studying an unrelated word pair (for example, *shirt-garden*), healthy volunteers—but not severely amnesic patients—are more likely to complete the word stem "*gar__*" with "*garden*" when the stem is paired with "*shirt*" than when it is paired with another unrelated word from the study list. However, healthy volunteers tested under similar conditions exhibit priming of new associations on the test only when they are aware that they are producing words from the study list (*6*). Thus, just as awareness of the relation between tone and air puff appears necessary for trace conditioning, awareness of the relation between study and test appears necessary for associative priming of stem completion. Both phenomena depend on the medial temporal lobe system that is damaged in amnesia.

During word priming, neural activity is reduced in regions of extrastriate visual cortex involved in perceptual analysis and in regions of left inferior frontal cortex involved in conceptual analysis (*3, 7*). Surprisingly, one study that used the stem completion task also reported a small increase in medial temporal lobe activity during word priming (*8*). However, this activation likely occurred because participants spontaneously became aware that they were completing stems with words they had studied earlier (*9*).

Awareness has also emerged as a central issue in sequence learning, in which people respond rapidly to a series of visual stimuli that appear in various locations on a screen. Participants are unaware that the series contains a recurring sequential pattern, but both healthy volunteers and amnesic patients learn the pattern (*10*). Neuroimaging studies reveal consistent activations of motor cortex and basal ganglia during sequence learning (*10*). Several brain regions (left premotor area, left anterior cingulate, and right ventral striatum) showed increased activity when the sequence was changed across trials—even though participants were unaware of the change (*11*). Thus, neuroimaging data are consistent with the idea that sequence learning without awareness relies on brain regions outside the medial temporal region (*10*).

Evidence from the three types of learning—classical conditioning, priming, and sequence learning—converges on the conclusion that several phenomena of memory and learning that do not require the medial temporal region also do not require particular types of awareness (see figure). Defining and measuring awareness presents a formidable challenge (*12*). Nonetheless, by contrasting "unaware" expressions of memory with situations in which awareness does play a vital role, and by combining data from brain-injured patients, neuroimaging studies, and even nonhuman animals, it should be possible to gain even greater insight into the neural processes that support memory, learning, and awareness (see figure).

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ATMOSPHERIC CHEMISTRY

Photochemistry of Ozone: Surprises and Recent Lessons

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The highly reactive hydroxyl radical OH is nature's atmospheric detergent; among other things, it initiates the oxidation of pollutants, cleansing them from the atmosphere. Hydroxyl formation in the lower atmosphere begins with the solar photolysis of ozone, which produces the electronically excited oxygen atom $O(^1D)$. In general, the reactions of electronically excited species are of negligible importance in the chemistry of the lower atmosphere, but the case of $O(^1D)$ is a notable exception: Its role is pivotal. Even though most of the $O(^1D)$ is deactivated to the ground state, $O(^3P)$, the small fraction that survives to react with H_2O and CH_4, turns out to be the major source of OH. Knowledge of how $O(^1D)$ is formed in the atmosphere is therefore critical in understanding the creation of OH. Recent surprising findings from several laboratories, including our own, are beginning to reveal the importance of the longer wavelength "tail" in the chemistry of $O(^1D)$ formation. The longer wavelengths are important because stratospheric ozone screens most of the shortwave ultraviolet from the lower atmosphere.

The weakness of the chemical bond in ozone and the existence of low-lying electronically excited states of both atomic and molecular oxygen lead to a number of energetically allowed dissociation channels. The

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