the term ‘procedural knowledge’, sometimes called implicit memory, denotes knowledge of how to accomplish a task, and often pertains to knowledge which unlike ‘declarative knowledge’ cannot be easily articulated by the individual, or knowledge that is nonconscious.
co-activity rules for synaptic efficacy change depend on neuromodulatory systems

- **no ACh, no NE (as in NREM sleep)**
  - spike-timing (pre-post)
  - spike-timing (post-pre)

- **ACh + NE (as in waking)**
  - spike-timing (pre-post)
  - spike-timing (post-pre)

- **NE, no ACh (??)**

- **ACh, no NE (e.g., REM sleep)**
  - spike-timing (pre-post)
  - spike-timing (post-pre)
learning 101: Pavlovian fear conditioning – association of an initially neutral tone (CS) with a foot-shock results in ‘freezing’ responses when the tone alone is played – this type of memory may be implicit or explicit.
rats learn, across days, to efficiently reach and grasp a small sugar pellet over those days, the muscle patterns used in grasping adapt over those days, the area of primary motor cortex taken up by neurons associated with the reaching limb grows if ACh inputs to the primary motor cortex are removed, neither the learning nor the changes in motor cortex occur

Kargo and Nitz, JNS, 2003
mod. from Conner et al., Neuron, 2003
implicit/procedural learning II: perceptual skill learning - ‘more is better’ – ACh helps

Rats trained to make a nosepoke if they detect a 4 kHz tone show improvements in detection over days of training.

Over the same time period the topographic representation of pitch in primary auditory cortex changes such that more neurons respond to 4 kHz tones.

In separate experiments, pairing of a 9 kHz tone with stimulation of ACh neurons in the basal forebrain changes the topographic representation in primary auditory cortex such that more neurons respond to 9 kHz tones.

Kilgard et al., Science, 1998

Polley et al., JNS, 2006
implicit/procedural learning III: basal ganglia versus hippocampus – an ACh-based competition

in training (below), the rat is taught to move to the goal to obtain reward

subsequently, on test trials (above), the maze is turned upside-down and the rat demonstrates whether he has learned to ‘make a left’ at the ‘T’ (a response strategy) or to ‘move to that place in the room’ (a place strategy)

if the rat is asked this question early in training (within the first couple of days), one tends to see a ‘place’ strategy and ACh is high in the hippocampus

if the rat is asked this question late in training, one tends to see a ‘response’ strategy and ACh is high in the basal ganglia

early in training, when one would normally expect a ‘place’ strategy, inactivation of the hippocampus (the home of ‘place cells’) results in the emergence of a response strategy

late in training, when one would normally expect a ‘response’ strategy, inactivation of the basal ganglia (proposed to select responses via the direct pathway) results in the emergence of a place strategy

thus, the animal has learned two separate strategies which compete for expression
episodic memory (memory for events and their ordering - a form of explicit memory):  

hippocampal cell activity in a ‘place’ often depends on the places previously or subsequently visited (this is termed retrospective and prospective place coding)

for one block of trials, the animal must travel to the west end when placed at either the N or S start point
for the next block, the animal must travel to the east end when placed at either the N or S start point

some hippocampal neurons fire in a certain place, but only if they reached that place from the N as opposed to the S side – their activity depends on the character of the full episode and is termed ‘retrospective’

other hippocampal neurons are ‘prospective’ – they fire in a certain place depending on where the animal will go from that place – they too have activity dependent on the full episode

about half of all hippocampal neurons fire spikes (green dots) when the animal is in a certain part of the maze (here the S arm) – this is seen irrespective of the direction taken after reaching the middle

adap. from Ferbinteanu and Shapiro, Neuron, 2003
working memory: holding items in memory (7+/−2) is achieved through interaction of the prefrontal and parietal cortex

Adapted from Chafee and Goldman-Rakic, JNP, 1998
an example: prefrontal ‘top-down’ influences on parietal cortex during an oculomotor delayed response task – inactivation of prefrontal cortex via cooling depresses ‘working memory’ responses of parietal cortex neurons and increases errors

error rate (percent saccades to wrong site) for each of 8 directions used increases when prefrontal cortex is inactivated

delay-period activity for the same neuron is depressed when prefrontal cortex is inactivated

Chafee and Goldman-Rakic, JNP, 2000