MECHANICS OF MEMORY – A REVIEW

Pampori, Z. A. and Malla, W. A
Division of Veterinary Physiology, SKUAST-Kashmir, Alusteng, Srinagar, Kashmir, J&K State, India.
Email - drzap64@gmail.com

Abstract: The interaction of living organisms between themselves and with the environment is essential for survival. The communication among different living species involves the integrity of central nervous system which generates brain activity such as arousal, attention, learning and memory. Moreover, face perception and recognition of faces are fundamental brain processes for human relationship. The ability to hold objects in memory is essential to intelligent behavior, but its neural basis still remains poorly understood. Advances in neuroscience research for past two decades have contributed to clarify the intricate puzzle about brain recognizing objects.

Key words: Biology of memory, Construction of memory, Neurophysiology of memory, Types of memory.

INTRODUCTION:

Memory provides an organism the competence to learn and adapt from previous experiences as well as build relationships. Memories make you feel comfortable with familiar people and surroundings, tie your past with your present, and provide a framework for the future. Most people talk about memory as if it is a thing or part of a body, like bad eyes or a good head of hair. But it does not exist as a "thing" that you can touch. It is a concept that refers to the process of remembering. The most difficult problem in discussing memory and one of the mysteries of the brain is neural basis of memory. Earlier many experts described memory as a sort of tiny filing cabinet full of individual memory folders in which information is stored away. Others equate memory to a neural supercomputer wedged under the human scalp. But today, experts believe that memory is far more complex and elusive and that it is located not in one particular place in the brain but is a brain-wide process instead. Physiologically memories are generated by changes in capability of synaptic transmission from one neuron to the next as a result of previous neuronal activity. These changes in turn develop new neuronal pathways for transmission of these signals which are called memory traces. Once established these memory traces can be activated and memories reproduced by the thinking mind. Memory in biological terms is the processes by which information is *encoded*, *stored*, and *retrieved*.

A. ENCODING OR REGISTRATION

It allows information, which is perceived from the outside world by our senses in the form of chemical and physical stimuli, to get processed by the nervous system and converted into a construct, stored in the brain and later recalled from short term or long term memory. All perceived and striking sensations travel to the brain’s thalamus where all these sensations are combined into one single experience[1]. The hippocampus is responsible for analyzing these inputs and ultimately deciding if they will be committed to long-term memory. Encoding can be visual, elaborative, acoustic, organizational and semantic.

Visual encoding is the process of encoding images and visual sensory information into mental pictures[2]. Visual sensory information is temporarily stored within our iconic memory and working memory before being encoded into permanent long-term storage. The visual information is stored in the visuo-spatial sketchpad[3]. The amygdala plays an important role in visual encoding. It accepts visual input in addition to inputs from other systems and encodes the positive or negative values of conditioned stimuli[4].

Elaborative encoding is the process of actively relating new information to the information that is already in memory. Thus the nature of any particular memory depends as much on the old information already in our memories as it does on the new information coming in through our senses. Many studies have shown that long-term retention is greatly enhanced by elaborative encoding[5].

Acoustic encoding is the encoding of auditory inputs. When we hear any word, we do so by hearing to individual sounds, one at a time. Hence the memory of the beginning of a new word is stored in our echoic memory until the whole sound has been perceived and recognized as a word[6]. Studies indicate that lexical, semantic and phonological factors interact in verbal working memory. This emphasizes that verbal working memory performance cannot exclusively be attributed to phonological or acoustic representation but also includes an interaction of linguistic representation[7]. However, it needs clarification whether linguistic representation is expressed at the time of recall or it has a fundamental role in encoding and preservation.

Organizational encoding is the course of classifying information permitting to the associations amid a sequence of terms.

Semantic encoding is the encoding of sensory inputs that have particular meaning or can be applied to a context. Words studied in semantic or deep encoding conditions are better recalled as compared to both easy and hard groupings of non-semantic or shallow encoding conditions with response time being the deciding variable[8]. Brodmann's areas 45, 46, and 47 (the left inferior prefrontal cortex) showed significantly more activation during semantic encoding conditions compared to non-semantic encoding conditions.

Encoding is achieved using a combination of chemicals and electricity. Neurotransmitters are released when an electrical pulse crosses the synapse which serves as a connection from nerve cells to other cells. Positron emission tomography (PET) demonstrates a consistent functional anatomical blueprint of hippocampal activation during encoding and retrieval. Activation in the hippocampal region associated with memory encoding has been shown to occur in the rostral portion of the region[9]. PET studies have shown increased cerebral blood flow in the right hippocampus and the left prefrontal and temporal cortices during encoding and in the right prefrontal and parietal cortex during recognition[10]. Amino acid neurotransmitters, glutamate and GABA, are intimately implicated in the process of factual memory registration, whereas amine neurotransmitters, norepinephrine and serotonin, are involved in encoding emotional memory[11]. Encoding begins with any novel situation, as the brain will interact and draw conclusions from the results of this interaction. These learning experiences have been known to trigger a cascade of molecular events leading to the formation of memories[12]. These changes include the modification of neural synapses, modification of proteins, creation of new synapses, activation of gene expression and new protein synthesis. However, encoding can occur on different levels. The first step is formation of short term memory followed by conversion into long term memory and memory consolidation. The process of encoding is known to be a heritable trait that is controlled by more than one gene. In fact studies suggest that genetic differences are responsible for as much as 50% of the variance seen in memory tasks[12].

B. STORAGE

It is the second stage or process of memory in which encoded information is maintained over periods of time. It refers to the retention of information, which has been achieved through the encoding process, in the brain for a prolonged period of time until it is accessed through recall. Modern memory psychology differentiates the two distinct type of memory storage: short-term memory and long-term memory. In addition, different memory models have suggested variations of existing short-term and long-term memory to account for different ways of storing memory.

1. Sensory memory

Sensory information is being taken in by sensory receptors and processed by the nervous system, stored in sensory memory and is just long enough to be transferred to short-term memory[13]. Sensory memory (SM) allows individuals to retain impressions of sensory information after the original stimulus has ceased[14]. SM is considered to be outside of cognitive control and is instead an automatic response. The information represented in SM is the "raw data" which provides a snapshot of a person's overall sensory experience. SM is not involved in higher cognitive functions such as consolidation of memory traces or comparison of information. Winkler and Nelson[15] reported that the capacity and duration of SM cannot be influenced by top-down control; a person cannot consciously think or choose what information is stored in SM, or how long it will be stored for. The role of SM is to provide a detailed representation of our entire sensory experience for which relevant pieces of information can be extracted by short-term memory and processed by working memory[14]. SM corresponds approximately to the initial 200–500 milliseconds after an item is perceived. The ability to look at an item, and remember what it looked like with just a second of observation is an example of sensory memory. Participants often report that they seem to have "seen" more than they could actually report after a short presentation. The first experiments exploring this form of sensory memory were conducted by Sperling[16] using the "partial report paradigm". Subjects were presented with a grid of 12 letters, arranged into three rows of four. After a brief presentation, subjects were then played either a high, medium or low tone, cuing them which of the rows to report. Based on these partial report experiments, Sperling was able to show that sensory memory capacity was approximately 12 items, but it degraded very quickly (within a few hundred milliseconds). This form of memory degrades so quickly that the participants would see the display but unable to report all of the items. There are many types of sensory memories; *Iconic memory*, *Echoic memory*, *Haptic memory*.

Iconic memory is a type of sensory memory that briefly stores an image which has been perceived for a small duration. Visual information is detected by photoreceptor cells in the eyes which is then sent to the occipital lobe in the brain. Iconic memory was the first sensory store to be investigated with experiments dating back as far as 1740 by Johann Andreas Segner (1704 - 1777), a German physicist and mathematician.

Echoic memory is another type of sensory memory that briefly stores sounds which have been perceived for a small duration. Auditory information travels as sound waves which are sensed by hair cells in the ears and directed to and processed in the temporal lobe. Echoic Memory is a fast - decaying store of auditory information and it will get shortened in case of damage to or lesions developing on the frontal lobe, parietal lobe, or hippocampus[17].

Haptic memory represents sensory memory for the tactile sense of touch. Sensory receptors all over the body detect sensations such as pressure, itching, and pain which get carried to post-central gyrus of parietal lobe through afferent neurons in spinal cord. Evidence for haptic memory has only recently been identified resulting in a small body of research regarding its role, capacity, and duration[18].

Winkler and Nelson[15] identified four common features for all forms of SM;

a. The formation of a SM trace is independent of attention to the sensory stimulus.
b. The information stored in SM is modality specific, i.e. echoic memory is for the exclusive storage of auditory information or haptic memory exclusive storage of tactile information.
c. Each SM store represents an immense amount of detail resulting in very high resolution of information.
d. Each SM store is very brief and lasts for a very short period of time. SM trace once decayed or replaced by a new memory, the information stored is no longer accessible and is ultimately lost.

2. Short-term memory

Short-term memory also referred as primary or active memory, is the capacity for holding a small amount of information in mind in an active, readily available state for a short period of time. The duration of short-term memory (when rehearsal or active maintenance is prevented) is believed to be in the order of seconds with its capacity very limited. George[19] showed that the store of short-term memory was 7±2 items. Modern estimates of the capacity of short-term memory are lower, typically of the order of 4–5 items. However, memory capacity can be increased through a process called chunking. For example, in recalling a ten-digit telephone number, a person could chunk the digits into three groups: first, the area code (such as 123), then a three-digit chunk (456) and lastly a four-digit chunk (7890). This method of remembering telephone numbers was far more effective than attempting to remember a string of 10 digits; because of the chunking of information into meaningful groups of numbers. This may be reflected in some countries in the tendency to display telephone numbers as several chunks of three numbers, with the final four-number group generally broken down into two groups of two. Short-term memory is believed to rely mostly on an acoustic code for storing information, and to a lesser extent on visual code. Conrad[20] found that test subjects had more difficulty recalling collections of letters that were acoustically similar (e.g. E, P, D). Confusion with recalling acoustically similar letters rather than visually similar letters implies that the letters were encoded acoustically. Conrad's[20] study, however, deals with the encoding of written text, thus while memory of written language may rely on acoustic components, generalizations to all forms of memory cannot be made. Short-term memory is supported by transient patterns of neuronal communication, dependent on regions of the frontal lobe (especially dorsolateral prefrontal cortex) and the parietal lobe.

Atkinson and Shiffrin[21]. developed a memory model referred as “modal model” which proposed that all memories pass from short term to long term store after a small period of time. However, the exact mechanism, by which this transfer takes place, whether all or only some memories are retained permanently, remains controversial among experts. Anterograde amnesia, the inability to learn new facts and episodes, is evidence in favour of separate stores for short term and long term memories. Since the subjects with this type of amnesia have intact ability to retain small amounts of information over short period of time (up to 30 seconds) and are unable to form long term memories. Davelaar et al.[22] experimented distractor tasks and arrived at the conclusion that short term and long term memories have separate stores and can vary independently of each other. However, all researchers do not agree with the hypothesis of separate stores of memory rather propose that memory is unitary over all time scales, from milliseconds to years[23]. The limited duration of short-term memory quickly suggests that its contents spontaneously decay over time. The decay assumption is usually paired with the idea of rapid covert rehearsal. In order to retain information for longer, information must be periodically repeated or rehearsed that can be either by articulating it out loud or by mentally simulating such articulation. In this way, the information will re-enter the short-term store and be retained for a further period. Lewandowsky et al.[24], however, disputed that spontaneous decay plays any significant role in forgetting over the short-term, and the evidence is far from conclusive. Authors doubting that decay causes forgetting from short-term memory offer an alternative form of interference. They propose that when several elements (such as digits, words, or pictures) are held in short-term memory simultaneously, their representations compete with each other for recall, or degrade each other. Thereby, new content gradually pushes out older content, unless the older content is actively protected against interference by rehearsal or by directing attention to it[25].

Mongillo et al.[26] have proposed that stimuli are coded in short-term memory using transmitter depletion, a stimulus activates a spatial pattern of activity across neurons in a brain region and the available neurotransmitters in their store are depleted and this pattern of depletion is iconic, represents stimulus information and functions as a memory trace. The memory trace decays over time as a consequence of neurotransmitter reuptake mechanisms that restore neurotransmitters to the levels that existed prior to stimulus presentation.

2. Working memory

Baddeley and Hitch[27] proposed an alternative model of short-term memory which they called **working memory,** which replaced the concept of general short term memory with specific, active components. Working memory holds and manipulates multiple pieces of transitory information for a short period of time, before it is either forgotten or encoded into long term memory. Alloway[28] defines working memory as brain’s Post-it note. Working memory involves a short-term use of memory and attention. It is a set of skills that helps us keep information in mind while using that information to complete a task or execute a challenge. A child uses this skill when doing math calculations or listening to a story. Working memory is a broad and deep group of mental processes that allow doing things like plan ahead, solve problems, organize and pay attention. Working memory helps us stay involved in something longer and keep more things in mind while approaching a task.

Instead of all information going into one single store, there are different systems for different types of information. Working memory consists of a central executive which controls and coordinates the operation of two subsystems; the phonological loop and the visuo-spatial sketch pad (Fig. 2).

The central executive is the most important component of the model, responsible for monitoring and coordinating the operation of the slave systems (i.e. visuo-spatial sketch pad and phonological loop) and relates them to long term memory (LTM). The central executive decides which information is attended to and to which part of the working memory that information is sent, to be dealt with. The central executive decides what working memory pays attention to, directs attention and gives priority to particular activities when two activities sometimes come into conflict. It drives the whole system (the boss of working memory) and allocates data to the subsystems (phonological loop and the visuo-spatial sketch pad). It also deals with cognitive tasks such as mental arithmetic and problem solving.

Visuo-Spatial Sketchpad (*inner eye*), stores and processes information in a visual or spatial form. It is likely that the visuo-spatial sketch pad plays an important role in helping us keep track of where we are in relation to other objects as we move through our environment i.e. used for navigation. The sketch pad also displays and manipulates visual and spatial information held in long-term memory.

The **phonological loop** is the part of working memory that deals with spoken and written material. It is assumed to be responsible for the manipulation of speech based information and can be **used to remember a phone number. It consists of two parts;**

Phonological Store (*inner ear*) – Linked to speech perception, holds information in speech-based form (i.e. spoken words) for 1-2 seconds.

Articulatory control process (inner voice) – Linked to speech production, used to rehearse and store verbal information from the phonological store. It circulates information round and round like a tape loop. This is how we remember a telephone number we have just heard. As long as we keep repeating it, we can retain the information in working memory. Written words must first be converted into an articulatory (spoken) code before they can enter the phonological store.

Evidence suggests that working memory uses two different systems for dealing with visual and verbal information. A visual processing task and a verbal processing task can be performed at the same time. It is more difficult to perform two visual tasks at the same time because they interfere with each other and performance is reduced. The same applies to performing two verbal tasks at the same time. This supports the view that the phonological loop and the sketch pad are separate systems within working memory. Those with weak working memory are likely to have learning disorders, too. In a government-funded study, Alloway[29] tested more than 3,000 high grade school and junior children in the U.K. They found that one in 10 had very poor working memory. Working memory turned to be a reliable and more powerful predictor than IQ when it comes to learning. Ninety-eight percent with poor working memory had very low scores in standardized tests of reading comprehension and math.

In brain, working memory selectively maintains a limited amount of currently relevant information in an active state to influence future perceptual processing, thought and behavior. Electrophysiological, pharmacological and brain-imaging studies demonstrating that prefrontal cortex shows sustained activity during acquisition of information in working memory tasks; that indicates that this area maintains on-line representations of stimuli after they are removed[30].

3. Long-term memory

The storage in sensory memory and short-term memory generally has a strictly limited capacity and duration, thus cannot be retained indefinitely. However, long-term memory can store much larger quantities of information for potentially unlimited duration (sometimes a whole life span). Remembering telephone numbers for many years through repetition is said to be stored in long-term memory. Long-term memories are maintained by more stable and permanent changes in neural connections widely spread throughout the brain. While short-term memory encodes information acoustically, long-term memory encodes it semantically. Atkinson and Shiffrin[21] proposed multi-store model for long-term memory i.e. memory is actually made up of multiple subcomponents (Fig. 1). It also states that rehearsal is the only mechanism by which information eventually reaches long-term storage. It also shows that all the memory stores are a single unit. However, it does not hold much evidence because many examples contradict with this model and is being criticized for being too simplistic. A patient with brain damage, having problems with his short term memory of spoken numbers, letters and words and with significant sounds (such as doorbells and cats meowing), whereas visual (pictures) short term memory was unaffected. Similarly, it now stands established that the sensory store is split up into several different parts such as taste, vision, and hearing.

Anderson[31] divided long-term memory into

a. ***Declarative (explicit) memories*** and
b. ***Procedural (implicit)* memories**

Declarative memory requires conscious recall, in that some conscious process must call back the information. It is also referred as explicit memory, since it consists of information that is explicitly stored and retrieved. Declarative memory can be further sub-divided into *Semantic memory, Episodic memory, Autobiographical memory and Visual memory.*

Semantic memory concerns facts taken independent of context. It allows the encoding of abstract knowledge about the world, such as "Paris is the capital of France".

Episodic memory concerns information specific to a particular context, such as a time and place. Episodic memory attempts to capture information such as "what", "when" and "where" and enables individuals to recall specific events such as birthday parties and weddings. It is used for more personal memories, such as the sensations, emotions, and personal associations of a particular place or time.

Autobiographical memory is a memory for particular events within one's own life. It is generally viewed as either equivalent to, or a subset of, episodic memory.

Visual memory is a part of memory preserving some characteristics of our senses pertaining to visual experience. One is able to place in memory information that resembles objects, places, animals or people in sort of a mental image. Visual memory can result in priming and it is assumed that some kind of perceptual representational system underlies this phenomenon.

Procedural memory is also referred as *implicit memory* and is not based on the conscious recall of information, but on implicit learning. Implicit memory is a type of memory in which previous experiences aid in the performance of a task without conscious awareness of these previous experiences. This type of memory is displayed when one does better in a given task due to repetition without formation of any new explicit memories, but unconsciously accessing aspects of previous experiences. Procedural memory is primarily employed in learning motor skills that depends on the cerebellum and basal ganglia.

C. RETRIEVAL

It is the third process of memory which involves the retrieval or recollection of stored information that must be located and returned to our consciousness in response to some cue for use in a process or activity.

Memory has been classified by some researchers as *Recognition memory* and *recall* memory. Recognition memory tasks require individuals to indicate whether they have encountered a stimulus before (such as a picture or a word). Recall memory tasks require subjects to retrieve previously learned information (e.g. individuals might be asked to produce a series of actions they have seen before or to say a list of words they have heard before). Some have classified memory on the basis of type of information into *Topographic memory* and *Flashbulb memory*. Topographic memory involves the ability to orient oneself in space, to recognize and follow an itinerary, or to recognize familiar places. While travelling alone if one gets lost, is because of failure of topographic memory and is often reported among elderly patients who are evaluated for dementia. Flash bulb memory is clear episodic memory of unique and highly emotional events. Remembering where you were or what you were doing when you first heard the news of about 9/11 are examples of flashbulb memories. While on the basis of temporal direction memory has been classified into *Retrospective memory* and *Prospective memory.* In retrospective memory the content to be remembered is in the past. Thus, retrospective memory as a category includes semantic, episodic and autobiographical memory. In prospective memory the content to be remembered is in the future or memory of future intentions or remembering to remember. Prospective memory can be further broken down into event-based and time-based prospective remembering. Time-based prospective memories are triggered by a time-cue, such as going to the doctor (action) at 4pm (cue). Event-based prospective memories are intentions triggered by cues, such as remembering to post a letter (action) after seeing a mailbox (cue). Cues do not need to be related to the action (as the mailbox/letter) however, people use lists, sticky-notes, knotted handkerchiefs or string around the finger as cues that enhance prospective memory.

Neurophysiology of memory:

Although there is little direct evidence how brain remembers and discriminates objects, most neurophysiological studies on memory suggests that multiple items may be held in memory by oscillatory activity across neuronal populations. Warden and Miller[32] reported that prefrontal cortex (PFC) in brain is an important area involved in attention and action recognition-dependent behavior which is also vital for maintenance of short term memory. PFC promotes attention mechanism, allows learning and memory. Buschman and Miller[33] and Fries et al.[34] recorded neuronal activity from the prefrontal cortices of primate remembering two visual objects over a brief interval and reported that oscillatory neuronal synchronization mediates a phase-dependent coding of memorized objects in the prefrontal cortex. Moreover, neuronal information about two objects held in short-term memory is enhanced at specific phases of underlying oscillatory population activity in hippocampus. The neural system, responsible for working memory, involves a large number of brain regions, but abundant neurophysiological evidence and lesion studies in nonhuman primates indicate that prefrontal cortex is a critical component[35]. Ranganath et al.[36] suggesting a strong relationship between working memory and long-term memory when they reported working memory signals in both medial temporal lobe (a brain area strongly associated with long-term memory) and prefrontal cortex with functional magnetic resonance imaging (fMRI) . However, the substantially more working memory signals seen in the prefrontal lobe suggest that this area play a more important role in working memory than medial temporal lobe[37].

Broca's area (the pars triangularis and pars opercularis of the left inferior frontal gyrus) and Wernicke's area (the posterior part of the left superior/middle temporal gyrus) were involved in language production and comprehension, respectively[38]. However, these two important regions are also activated for working memory-related processes, at least, including executive functions and short term memory processes and the processes of storage and access to long term memory of linguistic information. This memory system could be assumed essential for language comprehension. For example, for sentence comprehension, we have to tentatively memorize several words comprising the sentence to compute the syntactic and semantic structure of the sentence and comprehend the sentence. Hence, in order to understand a language expression, we need the involvement of both the short and long term memory systems.

There is a wealth of evidence that auditory and visual word processing have at least partly independent neural bases, particularly in the early stages of stimulus processing. Chee et al.[39] reported that the left inferior frontal and middle temporal gyri were commonly activated for both auditory and visual word processing. While visual word processing activated visual-related areas including the occipital lobe, auditory word processing engaged the ventral part of inferior temporal gyrus and the fusiform gyrus. It is assumed that the anterior part of the left inferior frontal gyrus (the pars triangularis of the inferior frontal gyrus/ Brodomann area 45) and the left inferior parietal region (the supramarginal gyrus) comprise the verbal working memory circuit[40]. The former area is thought to be involved in articulatory rehearsal and the latter in phonological storage[41]. The left inferior frontal region, the left lateral and ventral middle/inferior temporal regions, and the left inferior parietal region are activated during semantic processing tasks[42]. Demb et al.[8] reported that brain activity in left inferior frontal region is greater for more difficult semantic processing tasks than for corresponding less difficult semantic processing tasks. The inferior temporal region is commonly known to be involved in the storage or long term memory of word information.

Brain-imaging studies, using PET (positron emission tomography) and fMRI(functional magnetic resonance imaging), have also demonstrated that the human prefrontal cortex is implicated in working memory[43,44]. fMRI, demonstrated neuronal activity during a face recognition memory in prefrontal area. In human studies, event-related potentials (ERPs) have been taken for understanding the neural basis of object recognition and an early ERP component, the N170 wave, was observed significantly larger when subjects view image with face than when they view other objects[45,46]. On the contrary, patients with prosopagnosia, (inability to recognize faces) fail to demonstrate an enhanced N170 wave[47]. Although brain imaging has given important functional information about brain learning and memory, it cannot reveal how the brain works at level of individual neurons. There is increasing evidence that information encoding may depend on the temporal dynamics between neurons; e.g, from relative spikes to rhythmic activity across the neural population, generating local field potential (LFP)[32, 48].

Hippocampus is another brain area important for learning and memory. It is important for explicit memory, spatial learning and memory consolidation. Without the hippocampus, new memories are unable to be stored into long-term memory. Furthermore, it may be involved in changing neural connections for a period of three months or more after the initial learning. The hippocampus receives input from different parts of the cortex and sends its output to different parts of the brain also. The input comes from secondary and tertiary sensory areas that have already processed the information. Hippocampal damage may also cause memory loss and problems with memory storage. It exhibits relevant theta (4-7 Hz) frequency oscillations in vivo during behavioural activity. Lee et al.[49] demonstrated that brain hippocampal theta rhythmicity could contribute to learning and memory. In rat, spatial memory is supported by interaction between hippocampus and cortical areas, mainly frontal cortex which is critically involved in attention and learning[50]. König et al.[51] showed that the important electrophysiological mechanism, by which hippocampus learns and discriminates objects in novelty detection, is the hippocampal theta activity. However there still remains difference of opinion within the researchers, with some reporting drop in the frequency of theta in novelty detection experiments [52] and others reporting no change in theta frequency[53]. Podol'skii et al.[54] reported that new experience and novel environment induces increase in cholinergic input to the hippocampus and increase in ACh release which affects hippocampal theta activity. Nevertheless, taken together both findings suggest that theta oscillations in hippocampus are affected by novelty and that this probably gives reasons for hippocampal learning.

It is well documented that central cholinergic system plays a crucial role in cognitive functions; therefore, from an electrophysiological and neuro-chemical point of view, the integrity of the frontal cortex and hippocampus circuitry is essential for brain cognitive processes. Research has shown that direct injections of cortisol or epinephrine help the storage of recent experiences. This is also true for stimulation of the amygdala which is thought to be involved in emotional memory. This proves that excitement enhances memory by the stimulation of hormones that affect the amygdala. Excessive or prolonged stress (with prolonged cortisol) may hurt memory storage. Patients with amygdalar damage are no more likely to remember emotionally charged words than non-emotionally charged ones.

Scientists have gained much knowledge about the neuronal codes from the studies of plasticity, but most of such research has been focused on simple learning in simple neuronal circuits; it is considerably less clear about the neuronal changes involved in more complex examples of memory, particularly declarative memory that requires the storage of facts and events.

Encoding of working memory involves the spiking of individual neurons induced by sensory input, which persists even after the sensory input disappears[55]. Encoding of episodic memory involves persistent changes in molecular structures that alter synaptic transmission between neurons. Examples of such structural changes include long-term potentiation (LTP) or spike-timing-dependent plasticity (STDP). The persistent spiking in working memory can enhance the synaptic and cellular changes in the encoding of episodic memory.

Consolidation of short term memory into long term memory at the molecular level probably involves two processes; synaptic consolidation and system consolidation. Synoptic consolidation involves a protein synthesis process in the medial temporal lobe (MTL), whereas the systemic consolidation transforms the MTL-dependent memory into an MTL-independent memory over months to years. Recent studies have shown that post-retrieval treatment with protein synthesis inhibitors and many other compounds can lead to an amnestic state[56,57]. These findings on reconsolidation fit with the behavioral evidence that retrieved memory is not a carbon copy of the initial experiences, rather updated during retrieval. Sleep is thought to be improving consolidation of information, as several studies have demonstrated that memory depends on getting sufficient sleep between training and test. Further neuroimaging studies have shown activation patterns in the sleeping brain which imitate those recorded during the learning of tasks from the previous day, suggesting that new memories may be solidified through such rehearsal.

Processing of information affects memory:

Craik and Lockhart[58] proposed that it is the method and depth of processing that affects how an experience is stored in memory, rather than rehearsal. Processing of the information included organization, distinctiveness, efforts and elaboration. Mandler[59] suggested that the organization of memory is one of its central aspects. He demonstrated that when participants were given a pack of word cards and asked to sort them into any number of piles using any system of categorization they liked. Thereafter when they were asked to recall as many of the words as they could, those who used more categories remembered more words. Eysenck and Eysenck[60] demonstrated that distinctiveness of information potentiated its recall. He asked participants to say words in a distinctive way, e.g. spell out the words loud and such participants recalled the words better than those who simply read them off a list. Tyler *et al.*[61] showed that the information which involved efforts while encoding were recalled better than the information which was easy and effortless. It was illustrated that elaborative information was better recalled.

Memory in infants and elders:

Substantial advancement in memory research now indicates that infants as young as 6-months can recall information after a 24-hour delay and as the infants grow older they can store information for longer periods of time. 9-month-olds can recollect information after up to five weeks and 20-month-olds after as long as twelve months. As the age increases the infants can store information faster, whereas 14-month-olds can recall a three-step sequence after being exposed to it once, 6-month-olds need approximately six exposures in order to remember it. Although 6-month-olds can recall information over the short-term, they have difficulty recalling the temporal order of information. It is only by 9 months of age that infants can recall the actions in the correct temporal order which is not true in 6 month olds. Nine month-olds tend to imitate the actions of the sequence in the correct order (step 1 and then step 2) whereas 6-month-olds can only recall one step of a two-step sequence. It is suggested that these age differences are probably due to under development of dentate gyrus of the hippocampus and the frontal components of the neural network at the age of 6-months.

One of the key concerns of older adults is the experience of memory loss. Research has revealed that individuals' performance on memory tasks that rely on frontal regions declines with age. Older adults tend to exhibit deficits on tasks that involve knowing the temporal order in which they learned information. Memory tasks that require either to remember the specific circumstances or context in which they learned information or involve remembering to perform an act at a future time are referred as source and prospective memory tasks respectively. Older adults can deal with prospective memory deficits by using appointment books.

Memory Construction:

Although we like to think that our memory operates like recording equipment that is not actually the case. The molecular mechanisms underlying the induction and maintenance of memory are very dynamic and comprise distinct phases covering a time window from seconds to even a lifetime. In fact research has revealed that our memories are constructed. People can construct their memories when they encode them and/or when they recall them. Loftus and Palmer[62] conducted experiments in which people were instructed to watch a film of a traffic accident and then asked about what they saw. They found that, those people who were asked, "How fast were the cars going when they smashed into each other?" gave higher estimates than those who were asked, "How fast were the cars going when they hit each other?" Furthermore, when asked a week later whether they have seen broken glass in the film, those who had been asked the question with smashed were twice more likely to report that they have seen broken glass than those who had been asked the question with hit. There was no broken glass depicted in the film. Thus, the wording of the questions distorted viewers' memories of the event. Importantly, the wording of the question led people to construct different memories of the event – those who were asked the question with smashed recalled a more serious car accident than they had actually seen. The findings of this experiment were replicated around the world and researchers consistently demonstrated that when people were provided with misleading information they tended to misremember, a phenomenon known as the misinformation effect.

Interestingly, research has revealed that asking individuals to repeatedly imagine actions that they have never performed could result in false memories. Goff and Roediger[63] asked participants to imagine that they performed an act (e.g., break a toothpick) and then later asked them whether they had done such a thing. Findings revealed that those participants who repeatedly imagined performing such an act were more likely to think that they had actually performed that act during the first session of the experiment. Similarly, Garry et al.[64] asked college students to report how certain they were that they experienced a number of events as children (e.g., broke a window with their hand). They found that one-fourth of the students asked to imagine the four events, reported that they had actually experienced such events as children.

REFERENCES:

1. Mohs RC (2007): How Human Memory Works. < http://health.howstuffworks.com/ human-memory.htm>
2. Harrison C., and Semin A, (2009): Psychology. New York Press, pp 222.
3. Baddeley A., Eysenck M.W., and Anderson M.C, (2009): Memory. London: Psychology Press, pp. 44-59.
4. Belova M.A., Morrison S.E., Paton J.J., and Salzman C.D, (2006): The primate amygdala represents the positive and negative value of visual stimuli during learning. Nature 439: 865-870.
5. Brown S.C., and Craik F.I.M, (2000): Encoding and retrieval of information. In E Tulving & FIM Craik Eds. The Oxford handbook of memory. New York: Oxford University Press, pp. 93–107.
6. Carlson N.R., and Heath, (2010): Psychology the Science of Behaviour. Canada: Pearson Education Inc, pp. 233.
7. Acheson D.J., MacDonald M.C., and Postle B.R, (2010): The interaction of concreteness and phonological similarity in verbal working memory. Journal of Experimental Psychogy: Learning, Memory and Cognitio 36: 17-36.
8. Demb J.B., Desmond J.E., Gabrieli J.D., Glover G.H., Vaidya C.J., and Wagner A.D, (1995): Semantic encoding and retrieval in the left inferior prefrontal cortex: a functional MRI study of task difficulty and process specificity. The Journal of Neuroscience 15: 5870-5878.
9. Lepage M., Habib R., and Tulving E, (1998): Hippocampal PET activations of memory encodingand retrival. The HIPER model. Hippocampus 8: 313-322
10. Grady C.L., Horwitz B., Haxby J.V., Maisog J.M., McIntosh A.R., Mentis M.J., Pietrini P., Schapiro M.B., and Underleider L.G, (1995): Age-related reductions in human recognition memory due to impaired encoding. Science 269:218-221.
11. Birmes P., Escande M., Schmitt L., and Senard J.M, (2002): Biological Factors of PTSD: neurotransmitters and neuromodulators. Encephale 28: 241-247.
12. Wagner M (2008): The His452Tyr variant of the gene encoding the 5-HT (2a) receptor is specifically associated with consolidation of episodic memory in humans. International Journal of Neuropsychopharmacology 11: 1163-1167.
13. Carlson NR (2010): Psychology the science of behavior. Canada: Pearson Education Inc, pp. 232.
14. Coltheart M (1980): Iconic memory and visible persistence. Perception and Psychophysics 27:183–228.
15. Winkler I., and Nelson C, (2005): From sensory to long-term memory evidence from auditor, memory reactivation studies. Experimental Psychology 52: 3–20.
16. Sperling G (1963): A model for visual memory tasks. Human Factors 5: 19-31.
17. Claude A., David L.W., and Robert T.K, (1998): A distributed cortical network for auditory sensory memory in humans. Brain Research 812: 23–37.
18. Dubrowski CS (2009): "Evidence for Haptic Memory", Third Joint Euro Haptics conference and Symposium on Haptic Interfaces for Virtual Environment and Teleoperator Systems, retrieved 2011-03-08
19. George MA (1956): "The magical number seven, plus or minus two: some limits on our capacity for processing information". Psychological Review 63 (2): 81–97.
20. Conrad R (1964): Acoustic Confusions in Immediate Memory. British Journal of Psychology 55: 75–84.
21. Atkinson R.C., Shiffrin R.M, (1968) Human memory: A proposed system and its control Processes. In KW Spence and JT Spence (Eds): The psychology of learning and motivation. New York: Academic Press, pp 89–195.
22. Davelaar E.J., Goshen-Gottstein Y., Haarmann H.J., Usher M., and Usher M, (2005): The demise of short-term memory revisited: empirical and computational investigation of recency effects. Psychological Review 112: 3–42.

23. Brown G.D.A., Neath I., and Chater N, (2007): A ratio model of scale-invariant memory and identification. *Psychological Review*, 114: 539–576.
24. Lewandowsky S., Duncan M., and Brown G.D.A, (2004): Time does not cause forgetting in short-term serial recall. Psychonomic Bulletin and Review 11: 771–790.
25. Oberauer K., and Kliegl R, (2006): A formal model of capacity limits in working memory. Journal of Memory and Language 55: 601–626.
26. Mongillo G., Barak O., and Tsodyks M, (2008): Synaptic theory of working memory. Science 319: 1543–6.
27. Baddeley A.D., and Hitch G, (1974): Working memory. In GH Bower (Ed.): *The psychology of learning and motivation: Advances in research and theory*. New York: Academic Press, pp. 47–58.
28. Alloway T (2010): Improving Working Memory: Supporting Students' Learning. London: Sage Publications, pp 99-112.
29. Alloway T (2009): The cognitive and behavioral characteristics of children with low working memory. *Child Development* 80: 606-621.
30. Marra R., Rotirot D., and Rispoli V, (2012): Neural basis of object recognition In Advances in Object Recognition Systems. Intech Janeza Trdine, Rijeka.
31. Anderson JR (1976): Language, memory, and thought. Hillsdale, New Jersey: L. Erlbaum Associates Inc Publishers.
32. Warden M.R., and Miller E.K, (2010): Task-dependent changes in short-term memory in the Prefrontalcortex. J. Neurosci 30: 15801-10.
33. Buschman T.J., and Miller E.K, (2009) Serial, covert shifts of attention during visual search are reflected by the frontal eye fields and correlated with population oscillations. Neuron 63: 386–396.
34. Fries P., Nikolic D., and Singer W, (2007): The gamma cycle. Trends Neurosci 30: 309–316.
35. Fuster JM (1990): Behavioral electrophysiology of the prefrontal cortex of the primate. In & MGP.Feenstra), Elsevier Amsterdam. pp. 313-323.
36. Ranganath, C.C., Michael B.X., and Craig J.B, (2005): Working Memory Maintenance Contributes to Long-term Memory Formation: Neural and Behavioral Evidence. Journal of Cognitive Neuroscience 17(7): 994–1010.
37. Suzuki WA (2007): Integrating associative learning signals across the brain. Hippocampus 17: 842-50.
38. Geschwind N (1970): The organization of language and the brain. Science 170: 940–944.
39. Chee M.W., Caplan D., Soon C.S., Sriram N., Tan E.W., Thiel T., and Weekes B, (1999): Processing of visually presented sentences in Mandarin and English studied with fMRI. Neuron 23 (1): 127-37.
40. Vigneau M., Beaucousin V., Herve P.Y., Duffau H., Crivello F., Houde O., Mazoyer B., and Tzourio M.N, (2006): Meta-analyzing left hemisphere language areas: phonology, semantics, and sentence processing. Neuroimage 30: 1414-1432.
41. Paulesu E., McCrory E., Fazio F., Menoncello L., Brunswick N., Cappa S.F., Cotelli M., Cossu G., Corte F., Lorusso M., Pesenti S., Gallagher A., Perani D., Price C.J., and Frith C.D, (2000): A cultural effect on brain function. Nature Neuroscience 3:.91-96.
42. Baddeley AD (2003): Working memory: Looking back and looking forward. NatureReviews: Neuroscience 4: 829-839
43. D'Esposito M., Detre, J.A., Alsop D.C., Shin R.K., Atlas S., and Grossman M, (1995): The neural basis of the central executive system of working memory. Nature, 378: 279-281.
44. Courtney S.M., Ungerleider L.G., Maisog J.M., and Haxby J.V, (1997): Differences in transient fMRI responses during face encoding and recognition in a working memory task. Soc. Neurosci 23: 1679.
45. Allison T., Puce A., Spencer D.D., McCarthy G, (1999): Electrophysiological studies of human face perception. I: Potentials generated in occipito-temporal cortex by face and non-facestimuli. Cereb.Cortex 9: 415-30.
46. Eimer M (2000): The face-specific N170 component reflects late stages in the structural encoding of faces. Neuroreport 11: 2319-24.
47. Eimer M., and McCarthy R.A, (1999): Prosopagnosia and structural encoding of faces: evidence from event-related potentials. Neuroreport 10: 255-9.
48. Siegel M., Warden M.R., and Miller E.K, (2009): Phase-dependent neuronal coding of objects in Short-Term memory. Proc. Natl. Acad. Sci. USA 106: 21341-6.
49. Lee H., Simpson G.V., Logothetis N.K., and Rainer G, (2005): Phase locking of single neuron activity to theta oscillations during working memory in monkey extra striate visual cortex. Neuron 45: 147–156.
50. Monosov I.E., Sheinberg D.L., and Thompson K.G, (2010): Paired neuron recordings in the prefrontal and inferotemporal cortices reveal that spatial selection precedes object identification during visual search. Proc. Natl. Acad. Sci. USA 107: 13105-10.

51. König P., Engel A.K., Roelfsema P.R., and Singer W, (1995): How precise is neuronal synchronization? Neural Comput 7: 469–485.
52. Jeewajee A., Lever C., Burton S., O'Keefe J., and Burgess N, (2008): Environmental novelty is signaled by reduction of the hippocampal theta frequency. Hippocampus 18: 340–348.
53. Sambeth A., Meeter M., and Blokland A, (2009): Hippocampal Theta Frequency and Novelty. Hippocampus 19: 407–408.
54. Podol'skii I.Y., Vorob'ev V.V., and Belova N.A, (2001): Long-term changes in hippocampus and neocortex. EEG spectra in response to pharmacological treatments affecting the cholinergic system. Neurosci. Behav. Physiol 31: 589–595.
55. Fransen E., Alonso A.A., and Hasselmo M.E, (2002): Simulations of the role of the muscarinic activated calcium-sensitive nonspecific cation current INCM in entorhinal neuronal activity during delayed matching tasks. J. Neurosci 22: 1081–1097
56. Alberini MC (2011): The role of reconsolidation and the dynamic process of long-term memory formation and storage. Front Behav. Neurosci 5: 12.
57. Dudai Y (2006): Reconsolidation: the advantage of being refocused. Current Opinions in Neurobiology 16(2): 174-178.
58. Craik F.I.M., and Lockhart R.S, (1972): Levels of processing: A framework for memory research. Journal of Verbal Learning and Verbal Behavior 11: 671–684.
59. Mandler G (2011): From association to organization. Current Directions in Psychological Science 20 (4), 232-235.
60. Eysenck M.W., and Eysenck M.C, (1980): Effects of processing depth, distinctiveness, and word frequency on retention. British Journal of Psychology 71 (2): 263–274.
61. Loftus and Palmer (1974): Retrieved from www.simplypsychology.org/loftus-palmer.html
62. Tyler S.W., Hertel P.T., McCallum M.C., and Ellis H.C, (1979): Human Learning and Memory. Journal of Experimental Psychology 5(6): 607-617.
63. Goff L.M., and Roediger H.L, (1998): Imagination inflation for action events: Repeated imaginings lead to illusory recollections. Memory and Cognition 26: 20–33.
64. Garry M., Manning C.G., Loftus E.F., and Sherman S.J, (1996): Imagination inflation: Imagining a childhood event inflates confidence that it occurred. Psychonomic Bulletin and Review 3: 208–214.

Figure - 1

Figure - 2