Lecture 12 - Memory
The Physiology of the Senses

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Objectives

1) Define memory, learning and remembering.
2) Compare the characteristics of the different types of memory.
3) Detail the processes that result in an augmented blink response to particular sensations.
4) Consider the factor or factors that make memory fragile or resistant to interference.
5) Assess the role of the hippocampus in memory by comparing the effects of hippocampal lesions on memory in patient H.M.
6) Assess the role of the amygdala in memory by examining the effects of its lesion.

Introduction

Why have a chapter in memory in a course on the senses? This is because everything we sense is more a product of our memories than what is perceived by your senses. When you hear someone talk to you, what you hear is the product of years of learning, forming memories of the sounds of phonemes, words, their meanings etc. View TED talk by Anil Seth, cognitive neuroscientist.

Your brain does not contain memories. It is memories. The word **memory** has two meanings. It can refer to *information* that is stored (e.g. the memory of grandmother) and also the *structure* that stores this information (e.g. the strength of synapses in a particular part of the brain).**Learning** refers to the storage process, the creation of memories (e.g. what mediates a change in synaptic strength). **Remembering** refers to the retrieval of stored information.

In this chapter we will examine the various types of memory and learn how memory plays an important sensory function. For example, a loss of one type of memory can result in our not being able to recognise ourselves in the mirror.

Types of Memory

Memory is first subdivided into **short and long term**.
Then long term is in turn subdivided into **procedural and declarative**.
And finally, declarative is subdivided into **semantic and episodic**.
Let us exam each of these in more detail.

Short term / Working memory

We have seen in previous chapters that working memory acts like a scratchpad, which allows for the temporary storage of information. Working memory involves the frontal lobe and has a very limited capacity (Figure 12.1)(Fukuda et al 2010).

Example 1: storing numbers during mental addition.

Example 2: storing words that one reads, one at a time, to form a meaningful sentence.

Example 3: storing the spatial location of objects so that after you close your eyes you can point to their remembered positions.

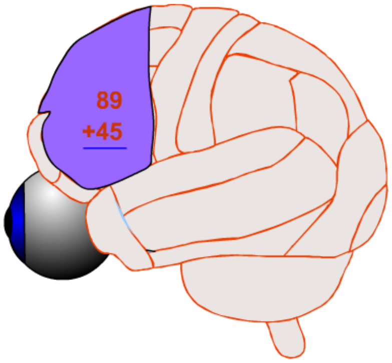


Figure 12. 1 Short Term Working Memory in the Frontal Lobe

Long Term

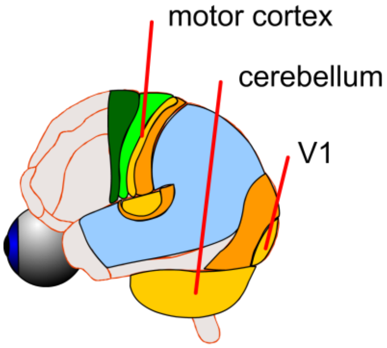
Two types of long term memory are procedural and declarative.

Procedural (implicit/knowing how)

Characteristics:

- remembering motor skills such as skiing
- remembering a particular sequence of finger movements on piano keys
- established slowly by practice
- one is not conscious of the skill's details (e.g. standing)
- starts to develop at birth (e.g. the ability to crawl)
- is not affected in amnesia
- is coded and stored in much of the cortex, for example, the tuning of binocular cells for stereopsis during the critical period in area V1, and the storing of motor skills in the cerebellum and motor cortex (Figure 12.3).

Figure 12. 2 Procedural Long Term Memory This is coded in much of the cortex and cerebellum.

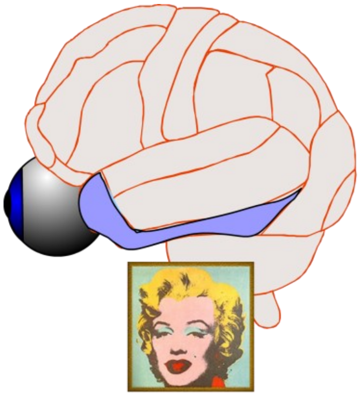


Declarative (explicit/knowing that)

Characteristics:

- representations of objects and events e.g. the face of a friend
- involves associations e.g. matching the name to a face
- often established in one trial
- one is conscious of remembering
- starts only after the age of 2 yrs.
- is affected by amnesia
- learning requires the hippocampus in the medial temporal lobe
- memories are stored in most of the association areas but in particular in the inferior part of the temporal lobe (Figure 12.3).

Figure 12. 3 Declarative Long Term Memory These require the hippocampus to form and most association areas to store memories.



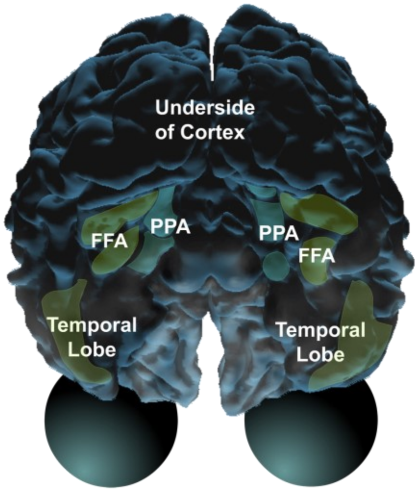
Two types of declarative memory are semantic and episodic.

Semantic

Characteristics:

- remembering faces and places.
- remembering facts and concepts.
- the visual aspects of places are recognized and stored in the parahippocampal place area (PPA) near the midline of inferior temporal lobe (Figure 12.4).
- those of faces, in the fusiform face area (FFA) in the more lateral side of the inferior temporal lobe.

Figure 12. 4 Some semantic memories are stored in the inferior temporal lobe. Parahippocampal place area (PPA). Fusiform face area (FFA).



Episodic

Characteristics:

- remembering objects and places in one's personal past.
- associating who and what with where and when.
- episodic are composed of several semantic memories.
- in episodic memory one not only recognizes the person in the picture but also when the picture was taken. "I visited Paris with the kids when they were young" (Figure 12.5).
- these can also be the sequence of places one passes while walking home. The synthesis of such representations provides us with a map of the spatial layout of the city.
- the areas activated by recalling these memories are the same as those activated during their perception.
- different areas are specialized for different categories of objects. We saw that the FFA is activated during face perception. After a lesion in FFA, patients develop prosopagnosia.

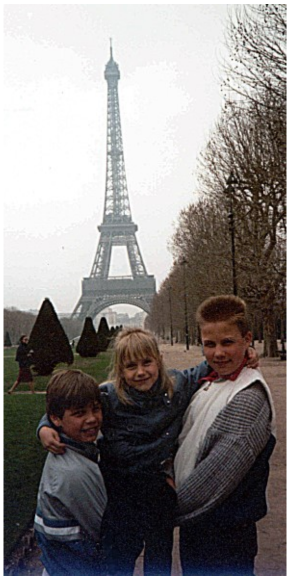


Figure 12. 5

An Example of Episodic Memory "My kids in Paris when they were young"

Working Memory

Working memory has several compartments. Three compartments are (Figure 12.6):

- Spatial Locations
- Words
- Visual Objects

Each has its own separate limited capacity (Fukuda et al 2010, MILLER 1956). One compartment can be full while the others are empty.

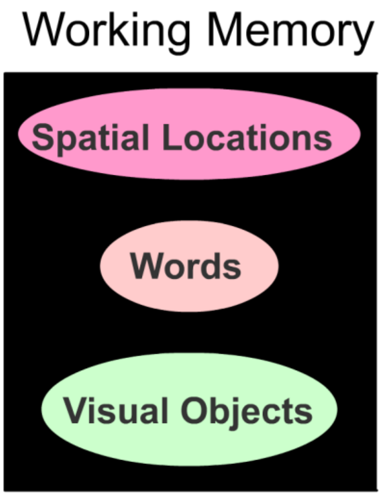


Figure 12. 6

Three Compartments of Working Memory

Visual working memory of objects is thought not to be stored in the eye’s view (retinal coordinates) because this is continuously changing. Rather objects appear to be stored in a more invariant and abstract form in object centered coordinates.

Working memory may involve reverberating networks (Figure 12.7A). In such a feedback circuit, the output neuron reactivates itself and activity continues long after input/sensation ends. In the frontal lobe, this circuit is dependent on dopamine. Recently this transmitter was found to be more abundant in humans than other primates (Sousa et al 2017).

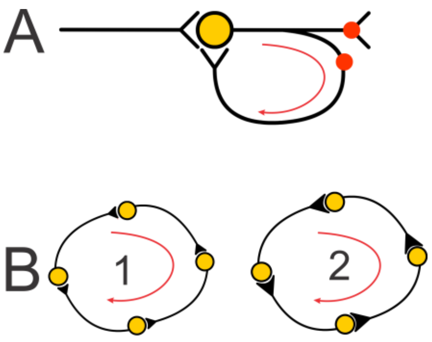


Figure 12. 7 **A: Working memory may involve reverberating networks.** The neuron (yellow) outputs an action potential and also, through feedback, reactivates itself. That leads to another action potential as output as well as feedback, and so on. **B: Long term memory involves a physical change in the synaptic strength.** The synapses in 2 are stronger than in 1.

Long Term Memory

Long term memory involves semi-permanent changes in synaptic strength between assemblies of neurons (Figure 12.7B). For example, rats raised in a rich environment have a thicker cortex with larger and more synapses. In the case of long term procedural memory, such as the ability to skate on ice, the changes are produced gradually by repeated exposure to the stimulus.

Molecular Basis of Long Term Memory

As we have seen in previous chapters, the key in long term learning is the NMDA receptor which opens only when the neuron is strongly depolarised. If two synapses fire at the same time (synchronously) they produce a larger depolarization than if they fire at different times (asynchronously). Cells that fire together wire together (Figure 12.8). Signals from cells that arrive at different times are weak and their connections become weaker. This is the basis for plasticity or learning throughout the cortex.

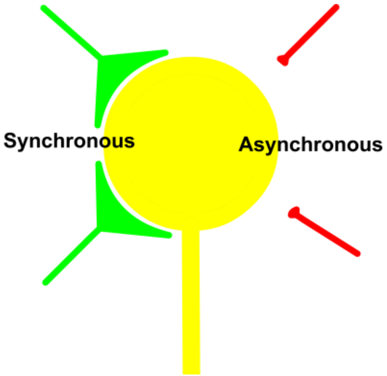


Figure 12. 8 **Inputs that arrive together (green) strengthen each other, whereas those that arrive at different times (red) develop weak connection.**

Mechanisms of Learning Procedural Memories

Classical conditioning is an example of learning a procedural task using long-term memory. Here a person is trained to produce blinks in response to a sound. One begins with a naive subject; one who does not blink in response to a flash of light or some other stimulus, such as a sound (Figure 12.9).

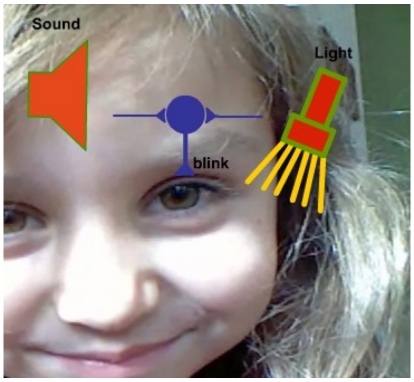


Figure 12. 9 **A neuron that causes a blink receives a very weak input from a sound (left) or a light (right).**

The next thing needed is a good teacher: in this case a stimulus that will always produce a blink. A puff of air is a good teacher. A puff of air, through a strong synapse, always produces a blink on its own (Figure 12.10). The puff depolarises the blink neuron and this strengthens the synapse from any paired (simultaneous) stimulus, in this case the sound's synapse (on the left). Thus the puff of air teaches sound's synapse to become stronger (Fig 12.10). At the same time the synapse from the light becomes weaker. This is called classical conditioning. A similar strengthening and pruning of synapses is the basis of all forms of long term memories. Trillions of such connections are changed in a similar way throughout one's life. And your trillions are unique.

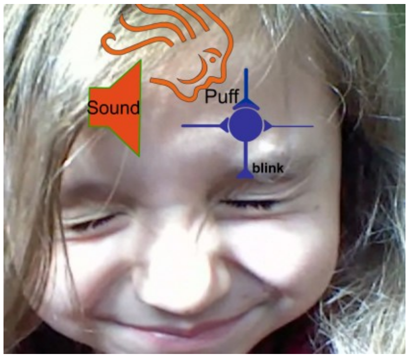


Figure 12. 10 **When the strong input from a puff of air is paired with a sound, the sound's synapse becomes stronger.**

After conditioning, the synapse from the sound is strong and can produce a blink on its own (Figure 12.11). Thus the blink becomes associated to sound, but not to some other stimulus such as a light. While connections from sounds are strengthened, those from a light are weakened.

This particular type of long term procedural memory involves the cerebellum. A lesion of the cerebellum eliminates the learnt blink to a sound. A cerebellar lesion would also disrupt many other procedural memories such as those of skiing and bike-riding.

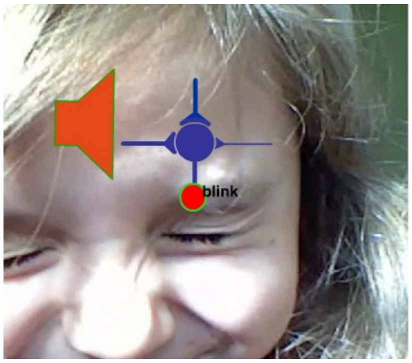


Figure 12. 11 **After conditioning the sound always produces a blink.**

Procedural memory is consolidated with practice.

New long-term memories, both procedural and declarative, are **fragile**. If one learns, by repetitive practice, a particular sequence of finger taps, such as the notes in a simple tune, and soon after learns a second sequence, the skills (speed and accuracy) learned in the first practice are disrupted (Figure 12.12).

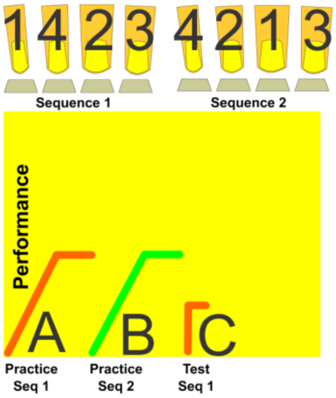


Figure 12. 12 With practice, performance improves. Top: the keys are pressed with the four fingers in two sequences. After practicing sequence 1(A), then sequence 2 (B), performance in sequence 1 becomes poorer (C).

Over a period of several hours the memory of these skills undergoes consolidation, making it **resistant to interference**. Now learning a second sequence does not disrupt the skills learned in the first practice (Figure 12.13).

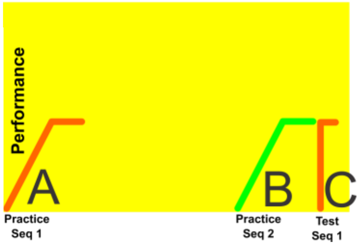


Figure 12. 13 Leaving time between learning sequence 1 (A) and sequence 2 (C) allows the memory of sequence 1 to consolidate and become resistant to interference (B).

Surprisingly, after a memory has been consolidated, a **brief rehearsal** of the sequence returns its memory to an **unstable** state (Walker et al 2003). This unstable state is normally good because practice can now improve and refine the sequence and its memory.

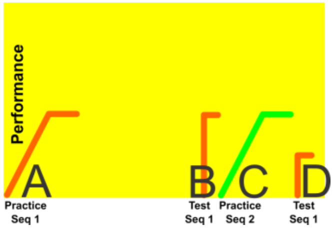


Figure 12. 14 After learning sequence 1 (A), a brief rehearsal of sequence 1 (B) makes its memory fragile. Now practicing sequence 2 (C) impairs the memory of sequence 1 (D).

However, this unstable state can also have negative consequences. In Figure 12.14, a brief rehearsal of sequence 1(B) makes it unstable and now a practice of sequence 2 (C) disrupts one's skill in sequence 1 (D).

The observation that practice makes old memories unstable again, applies not only to procedural memories. Remembering episodes in our past makes them suggestive to change. Sometimes these suggestions can be incorrect and result in a **false memory**. But making old memories unstable through practice can be beneficial because it also allows for refining what we have learned. Presumably this also holds for all semantic and episodic declarative memories.

Memories also improve during sleep. The performance of a learned motor skill is enhanced after a night's sleep that includes periods of slow wave sleep (Tamaki et al 2013).

Where are these modifiable synapses located?

Motor Cortex

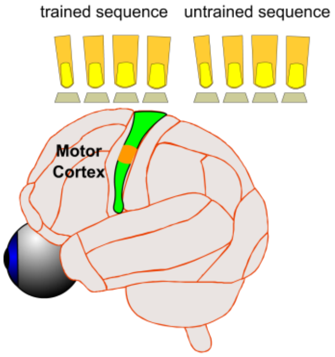


Figure 12. 15 The hand area (orange) of motor cortex (green) expands when a practiced sequence of finger movements is performed.

For motor skills, like a sequence of finger taps, the synapses undergoing plastic changes are distributed in various motor areas.

One key area is primary motor cortex. After training, a larger area is activated in the hand area of motor cortex when the trained sequence is performed than for a naive sequence (Figure 12.15).

In violinists, who use their left hand for fingering, the left hand’s area in the right motor cortex, becomes larger than the right hand’s. No doubt the thumb’s area has expanded in the last ten years with the advent of texting.

Auditory Cortex

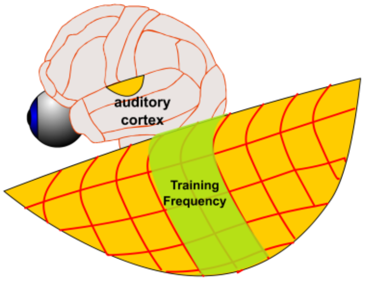


Figure 12. 16 Practice in discriminating frequencies expands the cortical representation of these frequencies.

When trained to discriminate between slightly different frequencies of sound, around a mean frequency, one's ability to discriminate these frequencies improves. This improvement is specific for frequencies near the mean training frequency (Figure 12.16). Training causes expansion of the region representing this frequency in the primary auditory cortex (A1).

Visual Cortex

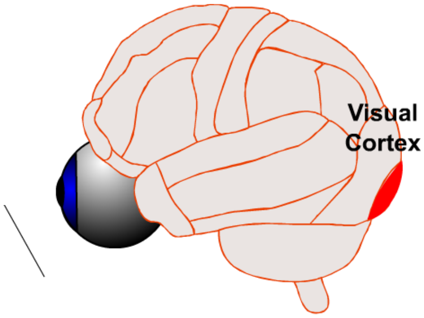


Figure 12. 17 Practice in detecting a break in a line of a particular orientation expands the representation of that orientation in primary visual cortex.

You can also improve your vision by training. Your ability to detect a break in a line improves with practice (Figure 12.17). This improvement is specific for the orientation that you trained for and involves plasticity in the primary visual cortex. Presumably, the pinwheel segment, containing the simple cells with this trained orientation, has expanded.

Take Home Message:

Memories continue to be consolidated in the primary sensory and motor regions. Not all plasticity is lost after the critical period (there is hope for elderly profs).

Declarative Memories

Brenda Milner's Famous Patient H.M.

Because of head trauma in his teens, H.M. developed recurring epilepsy. At 27 years of age, to relieve worsening epilepsy, H. M.'s medial temporal lobe and hippocampus were removed bilaterally (Figure 12.18).

This had an unexpected effect on one type of memory.

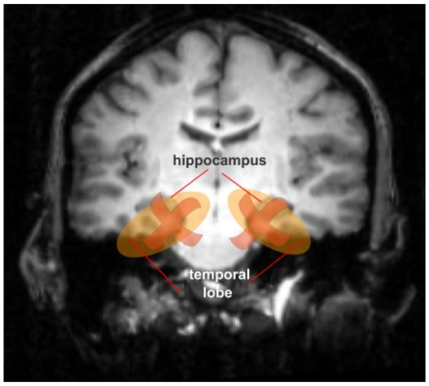


Figure 12. 18 H.M.'s lesion included the hippocampus and the medial part of the temporal lobe.

What was not affected?

Working: H.M. remembered new names for as long as he was not distracted.

Old Procedural: H.M.'s language abilities remained normal.

New Procedural: H.M. learnt to golf late in life.

Old Declarative: H.M. could recognise pictures of his mother.

What was affected?

New Declarative: H.M. could not remember new acquaintances.

What is it like to be H.M.? Some examples:

"Right now, I'm wondering, 'Have I done or said anything amiss?' You see, at this moment everything looks clear to me, but what happened just before? That's what worries me. It's like waking from a dream." -- H.M., 1965

"Every day is alone in itself, whatever enjoyment I've had, and whatever sorrow I've had." -- H.M., 1968

H. M. would eat multiple meals if not reminded that he had already eaten. He was good at mowing the family lawn because he could see what had been cut, but he had to be reminded each time of where the lawn mower was stored.

The lesion of the hippocampus produced anterograde amnesia (Figure 12.19). The hippocampus is critical in the formation of new long-term declarative memories. But the hippocampus is not where these new memories reside.

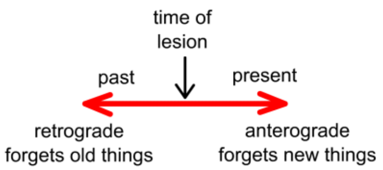


Figure 12. 19 Two Types of Amnesias

H.M. had anterograde amnesia because he could not form long-term declarative memories since the time of his lesion. Retrograde amnesia occurs when the old declarative memoirs formed prior to the lesions are lost.

H.M. died in 2008 at the age of 82. Remarkably, late in life, he had trouble recognising himself in a mirror. His memory of himself was as he was at the time of surgery when he was 27 (Figure 12.20). He was also unable to remember the contribution he made to our understanding of memory.

Figure 12. 20 The Young H.M.

Encoding Declarative Memories

The ventral stream, 1) extracts the visual features which form an object, 2) encodes these features into an object centered reference frame, 3) stores them temporarily in working memory in the frontal lobe (Figure 12.21).

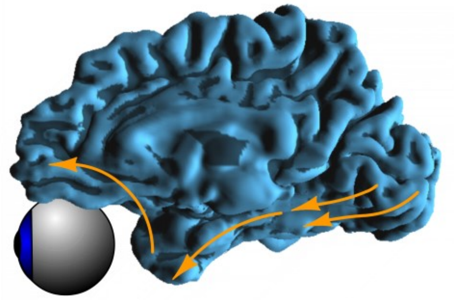


Figure 12. 21 Visual perception of objects travels through the ventral stream to the frontal lobe and is first stored in short term memory.

Consolidation of short term working memory into long-term declarative memory involves the hippocampus. Unlike procedural long-term memory which requires repetitive practice, declarative memory often requires only a single exposure. This is because the hippocampus is an excellent teacher (Figure 12.22).

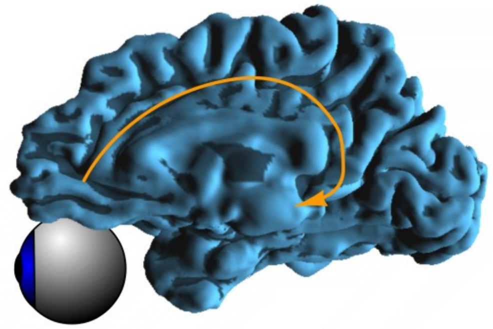


Figure 12. 22 Then this memory is transformed by the hippocampus into long term memory.

The hippocampus is located in the medial part of the inferior temporal lobe (Figure 12.23). This is a unique part of the cortex. Unlike other cortical areas, it continuously generates new neurons, more than 1000/day in adults (Spalding et al 2013). A much higher rate of neuron formation in young infants interferes with the formation of long term memories (Akers et al 2014) and may explain why few of us can remember our first couple of years of life. On the other hand, new neurons are formed well into old age but their number is reduced significantly with Alzheimer's (Moreno-Jimenez et al 2019).

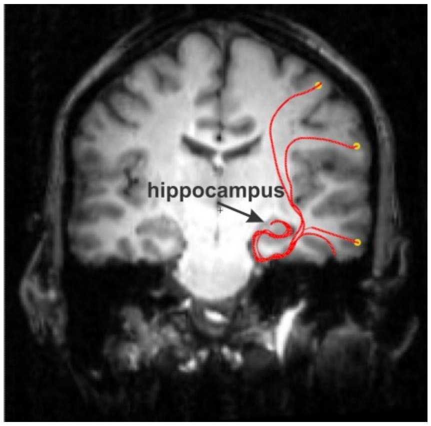


Figure 12. 24 The hippocampus associates this memory with others in the past.

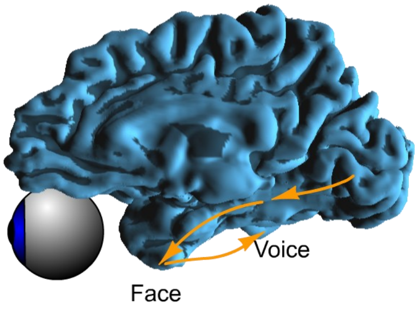


Figure 12. 23 Once formed, this memory and its associations can be triggered without the hippocampus.

New neurons also appear in the olfactory bulb (the cortical area important for smell). This is not a coincidence. The hippocampus evolved from the olfactory bulb. The hippocampus is well connected, an important attribute of a good teacher. It receives input from all the association areas and sends signals back to them, as well as others, thus creating new associations. The hippocampus associates the current features of the perceived object with other older memories related to the same object. The activation somehow binds together/associates various features into a rich, multi-modal memory. The memory of your grandmother's face is associated with the sound of her voice and a multitude of related memories. The hippocampus is like an amazing secretary that files our short term memories into long term memories. What make this secretary unique is that the files are placed so that they are also connected to related long term memories that were previously filed. This is important because, should the secretary vanish, all these memories can still be retrieved.

This memory is long term and requires the changes in the structure of synapses. These structural changes are accompanied by activity dependent expressions of gene patterns inside the neurons (Tyssowski et al 2018). Patients like H.M. suggest that once this long-term memory is formed, seeing the same object, e.g. grandmother's face, will activate the same associations directly, without the need of activating the hippocampus (Figure 12.24). Thus, the hippocampus is not where the memory of your grandmother is stored. Rather these memories are stored in those areas of the ventral stream that were first activated by the visual or auditory stimuli related to your grandmother. These same areas are now also activated when you remember your grandmother (Cichy et al 2012). In fact, when we remember and imagine objects, the primary visual cortex is activated (Kosslyn et al 1995).

An fMRI study of taxi drivers in London showed a larger posterior hippocampus than controls (Maguire et al 2000). One interpretation is that a larger number of locations was stored in the hippocampus either through an increase in neurons or in connections. Another interpretation, consistent with the studies of HM, is that the hippocampus becomes larger in taxi drivers to encode more locations in other cortical areas.

Hippocampal Place Cells

A good example of associations formed by the hippocampus is those used to navigate to particular locations, such as finding our way home.

For example, in the rat, hippocampal cells, called Place Cells, fire when the rat senses that it is in a particular place. The place is associated by a particular combination of visual, auditory, somatosensory, and olfactory cues.

A useful tool used to examine spatial memories in the rat is the water maze (Figure 12.25). One takes a small pool and fills it with milky water. One then hides a platform just below the surface of the milky water. Then one puts visual landmarks around the pool. Finally, one drops a rat into the pool.

Rats are good swimmers but don't seem to enjoy it. Because of this, they hunt for the platform and tend to quickly find it.

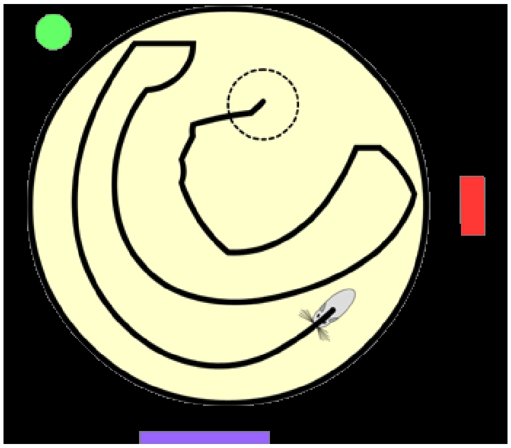


Figure 12. 25 The Rat Swimming in a Water Maze The water maze is surrounded by visual cues (green circle and red and purple rectangles). Because the water is milky the rat cannot see the hidden platform (dashed circle) and swims in circles until it finds the platform.

Rats are also very good at remembering the location of the platform. Presumably they remember the platform location with respect to landmarks around the pool. When placed in the same maze on the next day, the rat will swim directly for the platform.

Place cells code the allocentric location of the platform. The firing rates of several place cells, each denoting the location of a visual landmark, is used to locate the hidden platform (Figure 12.25) (e.g. the platform is between the red block and the green sphere, and far from the purple block).

A key step is that once the platform is reached, the hippocampus associates elsewhere in the brain, this visual landmark configuration with the tactile sense of the platform. On subsequent days the rat can find the platform without the help of the hippocampus.

However, if a rat with a lesioned hippocampus is placed in a new water maze, it will not learn the new location of the landmark. Like patient HM, the rat will remember locations learned some time before the hippocampal lesion. This suggests that the hippocampus is critical in forming long term memories of the associative spatial landmarks in brain areas that are outside the hippocampus.

Working memory in the frontal lobe is critical in decision making.

Suppose the phone rings while you are **at home**.

The sound triggers one's long term memory of a phone. Visual inputs locate you in your house. The frontal lobe, with these working memories, decides that the appropriate action in this context is to **pick up the phone** (Figure 12.26).

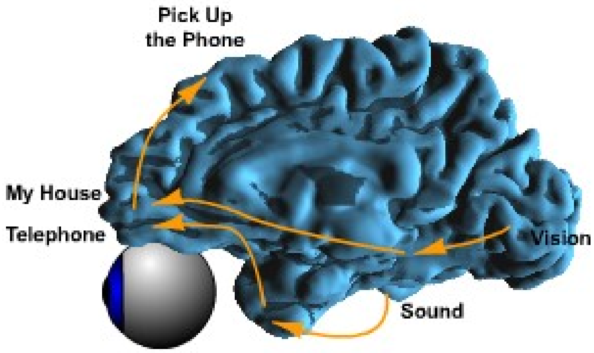


Figure 12. 26 The memory of your house is combined with that of your telephone in the frontal lobe in order to decide to pick up the phone.

Suppose the phone rings while you are **at your friend's house**.

Again, the sound triggers one's long term memory of a phone. Visual inputs locate you in your friend's house. The frontal lobe with these working memories decides that the appropriate action in this context is **not** to pick up the phone (Figure 12.27)(Mante et al 2013).

Working memory allows us to assess our perceptions in the context of our memories. This process is critical in decision making.

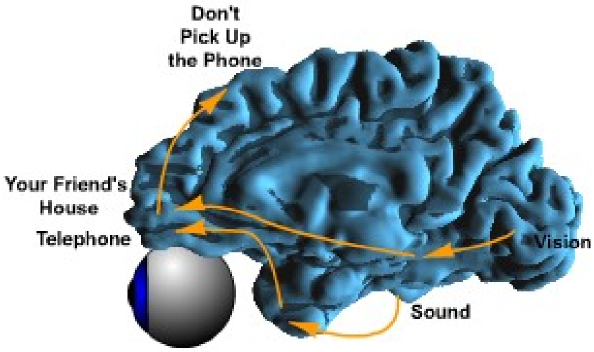


Figure 12. 27 The memory of your friend’s house is combined that of his telephone in the frontal lobe in order to decide to not pick up the phone.

The Amygdala

The Amygdala and Learning Emotional Responses

The amygdala (Figure 12.28) is essential for the acquisition and expression of conditioned emotional responses, such as a fear response to the sight of a lion. In the laboratory you can be conditioned to sweat to the sound of a horn. One needs a horn that is loud enough to elicit a startle response and the accompanying sweat response. Next, one pairs this sound to a sight of a blue square. Squares of other colors are shown as well, but without accompanying sounds. This pairing selectively strengthens the connections between the neurons detecting blue and those producing sweat (a bit more complicated than the one shown in Figure 12.29).

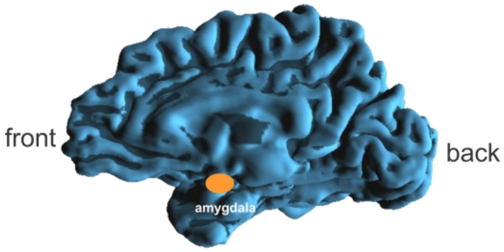


Figure 12. 28 The Location of the Amygdala in the Medial Cortex

In normal subjects, after this conditioning, a blue square will elicit a sweat response on its own and the subject will remember which stimulus was associated with the sound of the horn. Such associations are established by the hippocampus (Kim & Cho 2020). Patients with a lesion of the amygdala will not learn to produce a sweat response to the blue square. Patients with a lesion of the hippocampus will not remember which color was associated with the horn but will sweat to the blue color without remembering why.

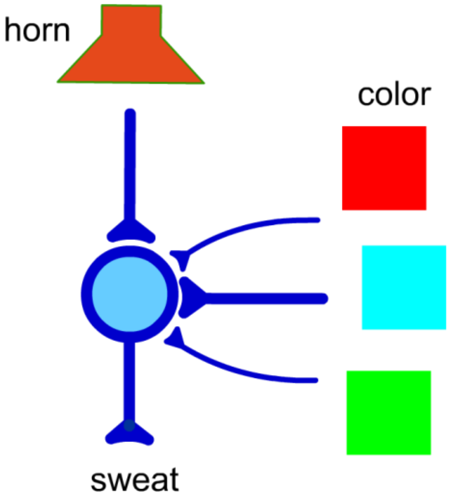


Figure 12. 29 After conditioning with a loud sound combined with the sight of a blue square, the sight of the square on its own may cause a sweat response.

Summary: The amygdala is required to consolidate the autonomic responses to a stimulus. It also adds an emotional tone (e.g. fear or pleasure) to the memory of past events. The amygdala is also involved (via the adrenal gland) with the release of stress related hormones (e.g. epinephrine).

The Amygdala and Face Recognition

The amygdala is also involved in face recognition. The path to the amygdala is fast (Freeman et al 2014). This is the path responsible for the “glow” of familiarity that often precedes conscious recognition. Depending on whether the person one saw was a friend or foe, this path could also elicit a sense of trust or fear. In some cases, the fear response may be accompanied by autonomic responses such as sweating. These responses can be entirely unconscious. It is these autonomic responses that are the basis of lie detector tests, which measure the changes in skin conductance.

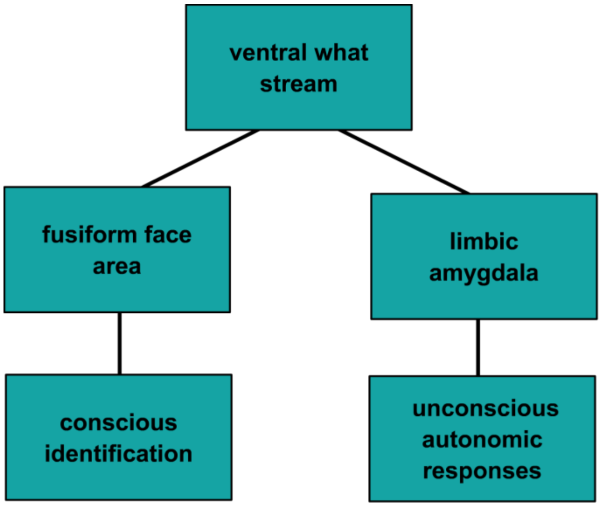


Figure 12. 30 Two Paths for Face Recognition

The fusiform face area distinguishes the details between faces while the amygdala responds quickly to the general aspects such as familiarity**.**

These two aspects of face recognition are mediated by two parallel pathways (Figure 12.30) from the visual “what” stream:

1) to the right inferior temporal cortex (fusiform face area) for the conscious identification of the face.

2) to the limbic amygdala for the rapid but unconscious autonomic responses (Gschwind et al 2012).

A lesion of the fusiform face area produces a sense of familiarity without being able to identify who that person is (prosopagnosia).

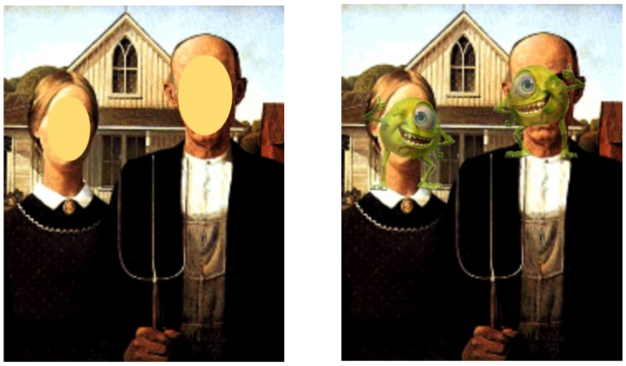


Figure 12. 31

Left: A lesion of the fusiform face region results in prosopagnosia.

Right: A lesion of the amygdala results in loss of familiarity and other emotional responses.

A lesion of the connection from the ventral what stream to the amygdala produces the converse. The patient can identify who the person is, but the person elicits no sense of familiarity. One such young man, after a car accident which lesioned the amygdala pathway could

1) recognize his parents

2) however, because their faces elicited no sense of familiarity, he felt that they had been replaced by aliens (Figure 12.31, Right). Also, he had no sense of familiarity when looking at a photograph of himself. He did, however, sense familiarity when talking to his parents on the telephone (Hirstein & Ramachandran 1997).

In Summary

It is remarkable that we can recognize a multitude of objects, including faces, in a fraction of a second and with no apparent effort (Besson et al 2017).

Each image of a face activates millions of retinal ganglion cells. Although we typically see a face many times, we never see the same exact image on our retina twice.

Somehow these neurons activate a unique group of neurons in FFA each time and this activation triggers recognition, presumably in the frontal lobes.

How? It is also remarkable that that is still a mystery!

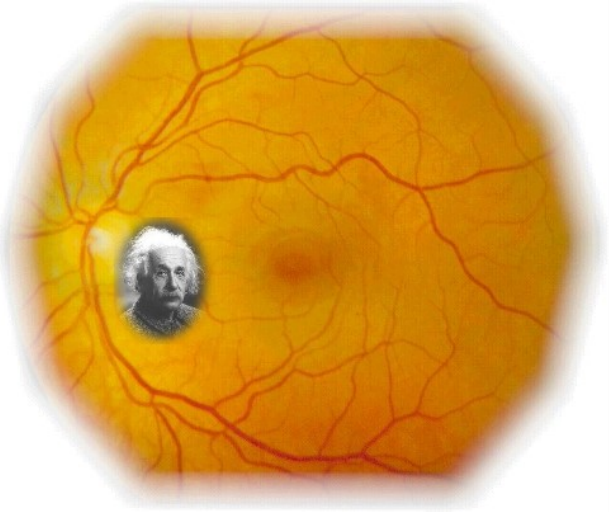


Figure 12. 32 Einstein on the Retina

See Problems and Answers Posted On

http://www.tutis.ca/Senses/L12Memory/L12MemoryProb.swf

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