Brain regions activated in different types of Context-Dependent Memory: a Review Abigail Bogdanovsky

Abstract

Encoding refers to the initial learning of information and storing it and retrieval is the recovery of the information from the storage. Oftentimes the memory or recall of an individual's experience is improved when that experience is encoded and then retrieved within the same context. This phenomenon is referred to as context-dependent memory (CDM; Hupbach et al., 2008). The four commonly referenced types of CDM are environmental context, state-dependent learning, mood-dependence/congruence, and cognitive context, which are outlined below. These four refer to different shared contexts between encoding and retrieval; more specifically, an environmental context could be a shared location (ex: learning and being tested in the same classroom), a state-dependent context would be a shared physical or emotional space (ex: learning and recalling information while being intoxicated), congruence would be a shared mood (ex: learning and being tested in a good mood), and a cognitive context would be a shared cognitive state (ex: recalling information in a certain language that were incurred in that language). Neurally, the hippocampus, prefrontal cortex and the specific regions of the parietal lobe have been implicated in CDM more broadly. However, the majority of experiments testing different types of CDM on different tasks are often experimented behaviorally rather than looking deeper into the physical brain regions the different types of CDM activate and rely on. To address how the different brain regions are involved between the four types of context, we will review studies of the subtypes of CDM and will consolidate them in this review. Our goal is to discern if all subtypes of CDM rely on the same brain regions or if there are variations across subtypes.

Introduction

Events that make up our memories often have a shared time, setting or internal state (emotion) - in other words, a shared context. Thus, context situates events that occur in one's daily life and plays a crucial role in the formation and recollection of memories by categorizing information for encoding (the process of forming memories) and cues for retrieval (the process of recovering memories).

For instance, imagine you have just graduated from high school and are thinking about your years from elementary school until now- are you able to remember the specific days of the 13 different years of school that you have attended? Do you have distinct memories for each of these days? Likely, no. As you speak to a friend, you recall moments from one of the classes that you shared - freshmen year biology class.



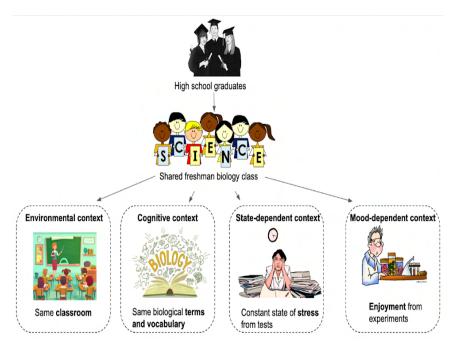


Fig 1: Example of Contexts + subevents.

Though you may recall the entertaining and fun classes and time-consuming projects more easily, the other hundreds of days spent in the class have a shared context — the same people sitting around you, the same teacher, the same classroom setting, and probably the same mood— and thus, are harder to remember (Fig 1).

All of these schooldays ("subevents") are likely grouped together based on the fact that they have a shared context and thus are retrieved from our memories as one singular event, which is why it is hard for us to dissociate them. At the same time, a particularly exciting day would come with its own unique emotional state or location or activity (like a fun field trip), thus breaking away from the shared context, and existing as a new, dissociable "event" in our memories.

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Learned	Tested	Memory		Initial Mood	Recall Mood	Word Recalled
A COM						positive
-						negative
****	-	8		$\overline{\mathbf{C}}$		negative
initive			Sta	ite		
Encoding Language	Recall Language	Memory		Encoding State	Recall State	Memory
english	english	S		intoxicated	intoxicated	S
russian	russian	S		sober	sober	S
english	russian	8		intoxicated	sober	8
russian	english	8		sober	intoxicated	8
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1	Vinney, C. (n.d.)	. How Context-De	pendent M			Very

Fig 2: Types of Context-Dependent Memories and Summary of an Experiment Conducted Testing It.



Context can come from many aspects of an event. This paper specifically focuses on the environmental, state, cognitive, and mood contexts (Fig 2). These four are the most commonly studied contexts when researching the topic of context-dependent memory (CDM). To see all articles included in this review, see the section titled Supplementary Materials. CDM is the phenomenon that refers to the recollection of an individual's experience that can be improved when the experience is encoded and later retrieved within the same context. Such improved recollection is a part of one's everyday life.

Environmental dependent memory is when a memory can be enhanced when the setting of the period for encoding and retrieval are the same. For example, in the research of Godden & Baddeley, environmental context was studied by comparing memories on dry-land versus underwater (Godden & Baddeley 325 - 331). The experiment consisted of divers in several test groups that experimented with learning lists of words in different environments (underwater or dry land). They were then asked to recall the word lists in either the same setting as they had learned it in, or a different setting. The results of the experiment showed that subjects recalled the lists better if they had been asked to recall the lists in the same environment in which they learned them, confirming the presence of environmental context. A meta-analysis conducted by Smith and Vela (203 - 220) looked across many investigations testing environment CDM and confirmed that this form of context has clear effects on memory.

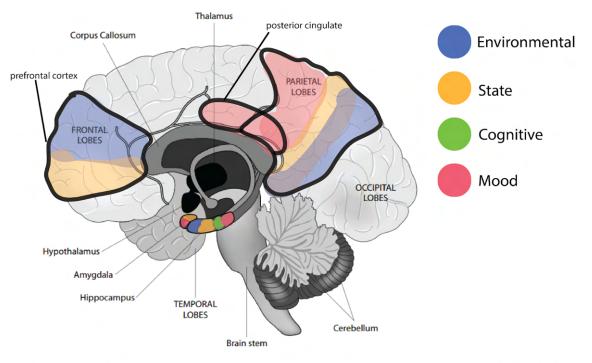
Cognitive dependent memory has been primarily studied in literature in relation to recall in different languages. Marian and Neisser conducted an experiment testing whether recall is improved when the language the recall was in was the same as encoding (Marian & Neisser 361 - 368). Subjects in the study were Russian immigrants and bilingual Russian and English speakers and were prompted to think of certain life events in response to prompted words. They found that the subjects were able to recall and remember more of their past if their past experiences were prompted in the same language that the experiences had occurred in. For example, the participants were able to better recall events that occurred in their old home in Russia if they were prompted to recall in Russian. A similar experiment was conducted with Japanese-Americans Matsumoto & Stanny. The results from this study demonstrated that cue words written in Japanese led to easier recollection of events from their past residence in Japan compared to cued words written in English (Matsumoto & Stanny 378 - 390). Ultimately, many studies exploring cognitive CDM corroborate the effect of language in memory function, but the majority of this work has been limited to language-based designs (see Conclusion).

State-dependent memory (SDM) correlates one's different physiological states during encoding and retrieval to the efficiency and accuracy of their memory. SDM is commonly tested with different types of substances such as alcohol, or other drugs to induce a certain state in the subject. A study conducted by Eich and colleagues had a group of subjects either smoke marajiuana or a placebo (Eich J. E. et al. 408 - 417). The study found that the words learned during the intoxicated state were better remembered by the subjects if they were asked to recall them again in an intoxicated state. Goodwin and colleagues (191 - 198) found commensurate results when investigating drunk and sober subjects. The subjects were medical students tasked with memorizing a list while they were either in their assigned sober or drunk state. Twenty-four hours later the students were asked to recall the words in either the same state as they were in during the list memorization period, or in the opposite state. Similar to the results from the previous study, this study found that participants who were in the same state during encoding and recall performed better.



Mood dependent memory emphasizes the significance of emotion during the process of encoding and recalling memories. When studying mood-dependent memory (MDM), experimenters attempted to stimulate a certain mood in different participants. In the study, Eich ad Metcalfe (443-455), participants had to generate 16 target items based on certain criteria and given the first letter of a word, and read 16 of the target items while either feeling pleasant or unpleasant. Two days after the encoding of the generated by criteria target items, and the read target items, they tested the subjects retention through free-recall and several other methods. The subjects were either in the same pleasant or unpleasant mood as they had encoded in, or the opposite mood. The results showed an impact of mood on the efficiency of memory with participants retesting in the same mood as in encoding outperforming the participants retesting in a different mood. In another study, researchers Eich and Macaulay (244–248) had similar goals. The study had several experimental groups. The participants were either set in a happy or sad mood for encoding and were instructed to generate autobiographical moments. Two days later they were either recalling the memories from the same mood as they had been in previously, or the opposite mood. The results of the research support MDM, as memories were more likely to be recalled if the subject was in the same mood as during encoding.

The four types of CDM, environmental, cognitive, state, and mood, have all been extensively studied to determine their impact on memory. Years of research has shown that all types have the potential to be extremely impactful in their ability to improve recall. Overall, encoding a certain task in a specific context and recalling that task in the same context proved to aid in recall, therefore improving memory. While CDM is one example of how context can enhance memory, many other factors also contribute to context.



Edited Version of major brain structures from Schunk, Dale H. (2012). Learning theories. An educational perspective. 6th edition.

Fig 3: Neural basis of different types of CDM.



A typical view of context is that it sets up expectations or contingencies that can serve as ways of organizing information or as cues for retrieval. Context provides a rich set of retrieval cues, which can range from an emotional state to a physical space. The research investigating the four main types of CDM all use different tests, stimuli, and are generally conducted in very different ways. Despite these differences, the neural mechanisms responsible for the phenomena are mostly shared between the types. This paper will now address some of the shared anatomical structures that execute CDM (Fig 3).

Hippocampus

The hippocampus has been shown to play a role in the four types of CDM discussed. The hippocampus is a brain structure that is most recognized for its role in memory. The hippocampus is responsible for processing events and then helping retrieve the memory of the event. Given its relevance to the foundation of memories, it plays a key role in CDM.

The significance of the hippocampus to the function of memory was shown in a case report. An epilepsy patient had a bilateral medial temporal lobectomy which removed $\frac{2}{3}$ of his hippocampus, and other brain structures, with the intent to abrogate seizure activity. After surgery, it was discovered that the patient had developed severe memory impairment. Recent events up to events from minutes ago were forgotten. It was the hippocampal lesions in this patient that clarified the involvement of the hippocampus in memory formation and retention.

The hippocampus is not necessarily needed for all types of memory, such as in dealing with old memories that have been semanticized (not an episodic memory anymore, such as memorizing a word meaning) or memories that are non-declarative (ex: riding a bike, brushing your teeth). But, in general the hippocampus is still crucial to the development of declarative memories (ex: recall of an event, including the processing of and formation of new memories from the event).

Parietal Cortices

Parts of the parietal cortices, particularly the somatosensory cortex, play a huge role in sensory understanding. This brain region utilizes and processes input from systems all around the body. Although involvement of the parietal cortices in episodic memory was previously unclear, it does have a role in memory. My review found evidence of the parietal cortices involvement in environmental, state, and mood CDM, but not cognitive CDM. Recent research has shown that certain parts of the parietal cortices are, in fact, heavily utilized during CDM. Studies were conducted on patients with parietal cortices lesions to examine the specific complications (Cabeza 613 - 625). One patient endured lesions in her left and right ventral parietal cortex (VPC) and noticed that she was still capable of remembering events in her life, but was unsure of where her memories came from. Other patients with VPC lesions reported feeling as though their recollection was not functioning properly, as their memories were not vivid or familiar to them. Another part of the study examined the differences between the VPC and dorsal parietal cortex (DPC) using neuroimaging and evidence from the lesions. There were significant differences noted, such as functional differences regarding attention during encoding. Their functional differences help emphasize how parts of the parietal cortices are relevant to CDM. The research conducted with parietal cortex lesions has helped demonstrate how the parietal cortex may be activated during episodic memory and also contribute to encoding and retrieval during the CDM phenomena.



Prefrontal Cortex (PFC)

The prefrontal cortex is heavily involved in two out of the four types of CDM: environmental and state. The PFC is known for its role in carrying out executive functions such as goal setting, self control, staying focused, dealing with behavior, understanding consequences, and regulating personality. Its underlying functions are critical to storing memories as the PFC helps focus attention to encoding, and retrieval of memories.

A study conducted by, Zhang and colleagues found that the PFC, more specifically the left inferior frontal gyrus (IFG) was involved in CDM (Zhang, W et al. 579 - 593). The study utilized different pictures of faces overlaid on different backgrounds. The goal was to see if altering the picture background would affect memory in some way. The IFG showed stronger coupling, or a stronger feedback relationship, with regions involved selectively with face processing, when those faces were, in fact, remembered. The IFG helped generate and synthesize information from different areas of the brain that function in recognition and processing contexts. This study suggests that the PFC plays a significant role in CDM. Given the PFC's broad functions in working memory and emotion processing, further research is needed to determine the possible involvement of the PFC in mood and cognitive CDM.

Other Minorly Involved Neural Mechanisms

Memory is a complicated task that requires many different bodily systems to collaborate. Some brain regions are more heavily involved in the processes than others. Other brain regions involved in CDM are the midbrain, basal ganglia, posterior part of the cingulate gyrus, and the amygdala. They are relevant in at least one of the types of CDM, and could be relevant in more research that my review has not yet found. Below, I will highlight several relevant subfields of research, their corresponding neural underpinnings, and how they may relate to CDM.

Memory retrieval system

CDMs are forms of episodic memories, or memories of events. The posterior medial system (including countless parts of the brain such as the retrosplenial cortex, the mamillary bodies, anterior thalamic nuclei, presubiculum, parasubiculum, posterior cingulate, precuneus, angular gyrus, and ventromedial PFC) is a network of brain regions thought to support the encoding and retrieval of episodic memories and specifically, the retrieval of autobiographical memories (the memories of personal events) (Robinson 578 - 595). This system is also broadly attributed to functioning in attention, spatial navigation, memory, emotion, and understanding rewards. Although I've only found specific evidence for a subset of these regions, I would suggest that *all* of them are crucial to the generalized process of CDM due to their heavy attribution to processing memories.

Emotion/ mood

One type of CDM, mood CDM, heavily relies on one's personal emotions during the encoding and retrieval of memories. Two brain regions important for processing emotion include the amygdala and the basal ganglia. The amygdala is known for its relation in regulating emotions and processing stimuli that triggers certain emotions. Its prevalence in the process of emotional learning suggests that it may play an important and complex role in mood CDM.

Similarly, the basal ganglia is attributed to several different functions, such as motor control, executive functioning, behavior, emotion, and reward processing. The latter three play a

huge role in the types of experimental tasks used in CDM studies, and in the formation of memories in general. The relation of the basal ganglia to the formation of memories means that it could be relevant to all of the types of CDM.

Movement

A key part of memory retrieval as seen with the CDM phenomena is having a repeated cue during encoding to aid the process of retrieval. Many different types of cues have been discussed in this paper, but an important cue that is part of everyday life is movement. Three relevant structures are involved in movement, including the basal ganglia, the midbrain, and the cerebellum.

While the basal ganglia is recognized for its significance in emotion and mood, it is also necessary for motor control. The basal ganglia is partially composed of three pathways that communicate with other brain areas to enact movement and prevent competing movements from interfering with the intended movement.

The midbrain is mostly commonly associated with the movement of the body and head; but when the hippocampus and midbrain interact, movements and choices are encoded into the hippocampus. This encoded moment is then essentially put into "storage" and can be later used to help guide any future decision making that is relevant to the past encoded moment.

The cerebellum is often associated with the phenomena of muscle memory, a type of procedural memory in which muscles are able to essentially remember a movement or are able to easily return to a certain strength due to repetitive actions or muscle stimulation. This procedural memory is more involved in environmental CDM experiments such as the Godden and Baddeley (325 - 331) which involved the exercise of scuba diving , but it could be applicable to other CDM experiments where movement is involved.

Conclusion

Context-dependent memory is a complex phenomena that utilizes many brain regions in order to make memory retrieval more efficient. There are 4 different subtypes of CDM, environmental CDM, cognitive CDM, state CDM, and mood CDM. They all are differentiated by certain factors affecting the context of encoding and retrieval. The distinction in context (environmental, cognitive, state, and mood) leads to the involvement of different brain regions to enact the different types of CDM. This review was able to discover several variations in the involvement of different brain regions in different types of CDM (i.e., several brain regions that are "uniquely" involved in a subtype). Some of these variations were important to note with the parietal cortices and the prefrontal cortex. Though my review found many differential brain regions involved, it is expected that future work will uncover that there is more overlap than previously expected. For instance, the prefrontal cortex has not yet been reported to be involved in mood or cognitive CDM, which is surprising due to the PFC's involvement in cognitive functioning. The restriction of specific subtypes to certain brain regions may stem from the inclination of neuroscience research to adopt a region-of-interest approach. While this approach allows researchers to focus on the role of specific sub-regions, it poses challenges in identifying broader functions. By combining across multiple studies with this review, we can start to take a whole-brain approach.

CDM has been studied for several decades, but environmental CDM has been studied more in depth compared to the other types of CDM. Environmental is the easiest CDM to explore due to the flexibility of testing in different settings; meanwhile cognitive, state, and mood



CDM are not able to be manipulated as easily as the environment. Finding different environments to investigate is an easy feat, meanwhile manipulating a person's mood, or cognitive, or mental state is a lot more difficult to achieve experimentally. Currently, research regarding state CDM has only been able to manipulate a person's state by intoxicating them, while cognitive CDM has only been experimented with using different languages for the memory tests. In order for our understanding of CDM to progress, we need to find more complex and diverse ways to study these types of CDM.



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Supplementary Material

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