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The Neuroscience of Motivated Memory

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ABSTRACT

Motivation is essential to memory because it ensures important memories are prioritized for future behavior. Recent studies have looked into the multi-faceted relationship between motivation and memory; other biological evidence which links motivation and memory has given rise to an examination of the underlying neurobiological basis that facilitates this connection. The neurotransmitter dopamine is strongly associated with motivation. Particularly, midbrain dopamine neurons in the reward-regulating ventral tegmental area which project to the hippocampus are well-positioned to enable a motivational influence on memory formation. This prompts an examination of the differing effects of extrinsic and intrinsic motivation on memory encoding and consolidation, as well evidence supporting the crucial role of coordinated activity between the mesolimbic pathway and the hippocampus. In this review, we first look into hypotheses about the biological processes through which dopamine is associated with reward motivation and memory. We then examine and summarize the neurobiologic hypotheses and recent evidence on the interplay between motivation and declarative memory with a focus on dopamine as the linking mechanism.

Introduction

We often encounter situations where we are motivated to remember things. For instance, rewards such as grades, or intrinsic curiosity can motivate the learning of information (such as when studying). Often, we remember this information more easily than when we are not strongly motivated to learn it. Students who are motivated to learn experience improved memory and academic performance (Pascoe et al., 2018). How do different types of motivation affect memory, and how do the neural circuits in the brain support this process?

Memory is crucial to guiding behavior through past experience with adaptive behavior–behavior and choices which can be improved by utilizing motivationally important past experiences. Motivation is a key factor in what experiences are most important and remembered; a crucial aspect of this connection between memory and motivation is the mechanism by which it occurs. Dopamine, a neurotransmitter, has long been associated with motivation and reward (Wise, 2004). Recent evidence indicates that dopamine also plays a vital role in memory formation and consolidation in the hippocampus. In this paper, we explore the interaction between dopamine, motivation, and memory, which is key to understanding why specifically motivation can affect memory, and how this effect is exerted: dopamine not only drives motivated behavior but importantly, affects the memory of events that are motivationally significant. This provides insights into how memory can lead to adaptive behavior.

Motivation may have different effects on different types of memory. Memory can be divided at the highest level into two types: declarative and nondeclarative. The type that we will focus on in relation to motivation is declarative memory, which consists of consciously remembered facts, experiences, and concepts. Declarative memory is dependent on the medial temporal lobe system (MTL), which includes the hippocampus, amygdala, parahippocampal cortex, and perirhinal cortex. In particular, episodic memory, a type of declarative memory dependent on the MTL, contains “spatial, temporal, or associative relations between multiple stimuli” (e.g. what you read in a textbook, where you read it, and when). The MTL is also crucial to a memory’s “representational flexibility” (Delgado et al., 2011), which is its ability to apply these previously learned associations to new contexts (for instance, applying a pattern of events in European history to American history). These two characteristics allow the MTL to create a “generalizable and flexible representation of the environment” (Delgado et al., 2011) which can be applied to guide future behavior.

Increasing evidence shows that the MTL may coordinate such memory representations with motivation to guide behavior (Delgado et al., 2011).The concept of motivation is vague, with many overlapping theories, so it is difficult to create a comprehensive definition or theory that integrates these unique perspectives (Kim, 2013). Motivation is generally defined as the energizing of behavior (activation of an action) that pursues a goal (Braver et al., 2014). The definition of motivation depends on each field; different perspectives address different aspects of motivation. In particular, neuroscience focuses on simple, goal directed behaviors, such as a rat pressing a lever to receive a reward, and often overlooks higher level cognition (Braver et al., 2014). In social and personality psychology, the definition of motivation is a description of why one response is made over another, as well as the “how” (e.g. frequency or intensity) of responses. For instance, a motivator such as a scholarship might explain why one chooses to study over doing something else, as well as how often and how long one studies. This definition examines motivation on a higher level and focuses on how the needs and expectations of an individual gives rise to the motivation to create desired outcomes or states (Braver et al., 2014). When examining motivated memory, it is important to consider multiple perspectives on motivation and remember that there are multiple aspects of motivation.

Motivation and reward is regulated by the mesolimbic pathway, a dopaminergic pathway which connects the ventral tegmental area (VTA) and the ventral striatum, including the nucleus accumbens (NAcc); mesolimbic activation indicates a state of motivation (Adcock et al., 2006). Midbrain dopamine neurons in the VTA project to the MTL and modulate learning in the MTL that is specifically activated by novelty and reward (Tsetsenis et al., 2023). This link between the motivation-regulating VTA and the MTL creates a high possibility of a motivational influence on memory. This paper will examine recent studies and evidence indicating the relationship between motivation and memory, as well as the neurological underpinnings of these connections. It will first delve into the multi-faceted role dopamine plays in enabling motivation; it will then examine evidence indicating how dopamine in the MTL and the VTA facilitate motivation’s influence on memory formation and consolidation.

Dopamine and Motivation

Dopamine is well known to be important to motivation. The first associations between dopamine and motivation were found when dopamine antagonists, as well as damage to dopamine fibers were found to inhibit motivation (such as rats’ responses to rewards such as food or drink) (Wise, 2004). There are multiple hypotheses about dopamine’s role in motivation; many of these hypotheses overlap and address different aspects of motivation.

Dopamine Hypothesis of Reinforcement and Incentive Motivation

In the dopamine hypothesis of reinforcement, dopamine “stamps in” associations between stimuli and responses, and stimuli and rewards in reinforcement learning; dopamine is necessary to maintain those associations (Wise, 2004). When dopamine antagonists are administered, animals cannot learn these associations, and if they are already learned, the associations are lost; rewarding stimuli becomes ineffective as a reinforcer. Dopamine is crucial to these reward association memories. For instance, dopamine-inhibited rats cannot learn to press a lever for food, and already-trained rats will no longer exhibit this learned behavior (Wise, 2004). According to the dopamine hypothesis of incentive motivation, dopamine enables the association of stimuli that precede and predict rewards and thus allows those stimuli to gain motivational value, which encourages behavior in order to gain that reward. If dopamine is blocked, the stimuli no longer has any incentive value and will not motivate responses or the energizing of behavior (Wise, 2004). Midbrain dopamine neuron projections to the striatum specifically drive these stimulus-response associations and are essential to reward feedback learning. Similarly, midbrain dopamine neurons also project to the hippocampus, suggesting that reward may play a similar role in modulating hippocampal episodic memory (Tsetsenis et al., 2023).

Value, Salience, and Alerting Dopamine

In contrast to theories which attempt to define dopamine's role in motivation as a singular signal or mechanism, evidence supports the idea that the role dopamine neurons play in motivation is multifaceted and more complex than a single signal which serves a single purpose in motivation. Accordingly, Bromberg-Martin et al. (2010) proposed a new hypothesis to address the existence of multiple types of motivational dopamine signals and explain dopamine's role in signaling not only rewarding events, but also non-rewarding events that are still important to motivational processing. In this hypothesis, dopamine neurons and signals come in multiple types with distinct functions. Motivational dopamine signals can be categorized into salience signals, value signals, or alerting signals. Dopamine neurons are either salience coding neurons, which receive salience and alerting signals, or value coding neurons, which receive value and alerting signals.

Dopamine salience signals indicate motivational relevance and importance. These signals can be induced by both rewarding or aversive (desirable or undesirable) events. Salience signals are responsible for directing attention to the detection of and response to important events, no matter rewarding or aversive. They also stimulate cognitive processing, engaging memory to energize actions in response to cues and remember the outcome of the actions. This allows the most important events to be prioritized in both response and memory.

Dopamine value signals are excited by rewarding events and inhibited by aversive events. This type of motivational signal directs the seeking of rewards, evaluation of outcomes, and learning of actions. They affect behavior when seeking out stimuli and then evaluating whether something should be avoided or sought in the future based on whether value signals inhibit or excite dopamine neurons.

Alerting signals signify potentially important events that capture attention based on multiple factors such as sensory input, novelty, etc. They are correlated with immediate reactions and trigger behavior to further examine the stimulus. They motivate fast reactions to important events. Because alerting signals are sent to both value and salience coding neurons, they have similar effects to value and salience signals when sent to the respective neurons. Alerting signals to salience coding neurons support attention to stimuli and the motivation to act on them quickly, which could occur through immediate effects on processing. This fits with the role of salience signals, which enhance cognitive processing such as in the enhancement of memory. On the other hand, alerting signals which are sent to value coding neurons could assign positive value to important sensory stimuli and regulate behavior to seek after environments where these important stimuli can be anticipated; this function of alerting signals would allow better prediction of and response to these events.

Dopamine in Synaptic Plasticity

Dopamine is additionally hypothesized to enable learning by affecting synaptic plasticity (the strength of synaptic connections). One form of synaptic plasticity is long-term potentiation (LTP), which forms the cellular basis of memory. The release of dopamine in the hippocampus, which subsequently facilitates LTP, is one potential mechanism by which motivation can exert its effect on memory (Adcock et al., 2006). When neurons fire together and a reward is gained as a result of the behavior this firing causes, dopamine is released, which reinforces the strength of the connection between these neurons. Midbrain dopamine neurons target the MTL

(Shohamy & Adcock, 2010) and dopamine stimulates protein production in the hippocampus, which is necessary for late-phase LTP. If D1 dopamine receptors are blocked, synaptic plasticity in the hippocampus is inhibited. Many have then subsequently proposed that dopamine modulates LTP and hippocampal synaptic plasticity, which is induced during memory formation and storage (i.e. dopamine plays a key role in LTP, which is vital to memory and learning) (Martin et al., 2000).

Motivation and Memory

Motivation affects what is encoded and remembered. An essential function of memory is to guide behavior by improving choices; motivational relevance can affect the prioritization of information in memory to enable this adaptive behavior. Things that are more important or motivating are prioritized to be retained in memory. To support this idea, evidence which biologically ties motivation to memory, such as through dopamine, has given rise to a subdiscipline which examines this relationship (Dickerson & Adcock, 2018).

The effects of motivation on memory are most easily measured in memory encoding. Since encoding, which is the process by which information is stored in memory, is the foremost step of memory formation, it is the easiest to influence and measure through immediate memory tests. Thus, most studies which test the effects of motivation on memory have manipulated memory encoding; memory is then tested with immediate retrieval or 24-hour delayed retrieval tests (Dickerson & Adcock, 2018). Motivation is manipulated through motivation incentives, which can be broadly categorized into either extrinsic motivation and intrinsic motivation.

Effects of Extrinsic Motivation On Memory Encoding

Extrinsic motivation is driven by external, tangible stimuli or outcomes. For example, an action performed in exchange for a reward such as food or money is extrinsically motivated (Morris et al., 2022). Many studies have used reward incentives, most commonly monetary incentives, to examine the effects of extrinsic motivation on memory, and evidence shows improved memory recall. In a key study, (Adcock et al., 2006) presented a cue for a monetary reward of $5 or 10¢ followed by an image of a scene for 2 seconds. Participants were given a memory test the next day and paid the monetary reward for correct recognition of the pictures. Crucially, participants were significantly more likely to remember pictures preceded by high-value reward cues than pictures preceded by low-value reward cues, meaning reward motivation enhanced memory performance.

Furthermore, the VTA, NAcc, and hippocampus were selectively activated prior to high-value stimuli that were later remembered (Adcock et al., 2006). This selectivity was with respect to both memory and value (activation only occurred for scenes that were both high-value and remembered). Activation for remembered stimuli in the VTA and NAcc only occurred prior to encoding, while MTL memory regions showed activation both before and during encoding. Because activation in the VTA was associated with memory formation only before a stimulus is presented, this correlation is not due to properties of the stimulus, but a distinct neural system that potentiates memory formation preceding a stimulus. In line with previous research, the NAcc and the VTA were activated by anticipation of monetary reward (circuitry localized through a rewarded reaction time task). Recruitment of these regions was correlated with successful memorization; higher activation during the anticipatory state predicted superior memory performance. Additionally, individuals with greater correlation between activation of the hippocampus and activation of the VTA showed better memory performance on high-value scenes in comparison to low-value scenes. This suggests that reward anticipation for motivationally significant events enhances memory through mesolimbic recruitment (including the VTA, NAcc, and hippocampus) prior to memory formation.

In a similar study, Wolosin et al. (2012) used a variation of the encoding task in Adcock et al. (2006); in this variation, participants were presented with and encoded photographs of common objects in pairs instead of photographs of scenes. Here, the parahippocampus also showed greater activity for successfully remembered, high-value object pairs, suggesting that the parahippocampal encoding processes are similarly enhanced by reward motivation (Wolosin et al., 2012). The parahippocampus has previously been shown to bind associations of information, including contextual information; taken together, this suggests that motivational significance could be enhancing either the associative binding processes of the objects in the object pairs to each other, or the binding of the pairs to the presented reward context. In contrast to the study by Adcock et al. (2006), however, Wolosin et al. (2012) did not observe a correlation between the magnitude of reward modulation of memory (i.e. the difference in successful remembering of high-value pairs versus low-value pairs) and the effect of reward on activation in any region.

There are several potential mechanisms by which reward motivation enhances memory formation. Correlated activation of the VTA and hippocampus could indicate that activation of the VTA modulates memory encoding mechanisms in the hippocampus, since the VTA is activated prior to encoding, while the hippocampus is activated during encoding (Adcock et al., 2006). One such possible mechanism which explains the correlated activity of the VTA and hippocampus is increased firing of VTA dopamine neurons, which leads to release of dopamine in the hippocampus: "The BOLD signal appears to be closely correlated with firing rates in active regions (Mukamel et al., 2005). When VTA dopamine neurons increase their firing rates, extracellular dopamine concentrations in VTA targets such as the MTL increase (Garris and Wightman, 1994)." (Adcock et al., 2006) This is consistent with the role of dopamine in LTP; according to previous studies, dopamine release prior to neural activity facilitates LTP. Wolosin et al. (2012), which used object pairs instead of pictures, obtained similar results in that participants were more likely to remember high-value object pairs, and the VTA was selectively activated for high-value, remembered object pairs.

Similar results were seen in several other studies (see Miendlarzewska et al. (2016) for a review). Overall, these results suggest that extrinsic reward motivation enhances memory performance through mesolimbic recruitment.

Effects of Intrinsic Motivation On Memory Encoding

Instead of using extrinsic reward as a motivator, other studies have used intrinsic motivational incentives, which may differ in their effects on memory compared to extrinsic motivators. Intrinsic motivation is internal; an intrinsically motivating action is inherently rewarding (done for its own sake and not as a result of external stimuli). One common example of an intrinsic motivator is curiosity, which motivates the seeking of information even without any external reward. The effect of intrinsic motivation on memory has most commonly been studied through manipulating curiosity, an intrinsic motivator which stems from the need to reduce the unpleasant state of a gap in knowledge (Duan et al., 2020). In a common task, study participants rate their curiosity for the answers to a set of trivia questions, learn the answers to those questions, and are tested on these answers later. Trivia questions which participants rate as higher-curiosity enhance memory of the answers to those questions (Duan et al., 2020, Kang et al., 2009), (Padulo et al., 2022, McGillivray et al., 2015, Gruber et al., 2014). Memory for unrelated, incidental information (e.g. images of unrelated faces) which is presented during states of curiosity has also been shown to be enhanced (Gruber et al., 2014, Padulo et al., 2022, Murphy et al., 2021). This implies that the effect of motivation on memory extends beyond an increased, motivated effort to remember information; motivation also induces an unconscious, biological strengthening of memory.

Intrinsic motivation appears to influence memory through similar mechanisms to extrinsic motivation. In the curiosity trivia task by Gruber et al. (2014), the VTA, NAcc, and other midbrain regions which show increased activity during reward anticipation also showed increased activity when anticipating interesting information (the answers to trivia questions) but not while the information was being presented. Activity during the anticipatory state for interesting information also predicted increased memory performance, consistent with the results from (Adcock et al., 2006) which used reward as a motivator; this suggests similarities between the effects and mechanisms by which extrinsic and intrinsic motivation modulate memory formation. Resulting

BOLD fMRI signals in the NAcc and midbrain, which have been shown to be correlated with dopamine release in the striatum, may support the explanation that dopamine plays a large role in enhanced memory of motivationally important events. Additionally, regions which are believed to be targets of midbrain dopamine neurons were also associated with states of curiosity in this study, which provides further support for the idea that dopamine facilitates the enhancing effect of intrinsic reward motivation on memory. The correlation between activity in the VTA and hippocampus and improved memory on both trivia answers and incidentally encoded faces is consistent with the mechanism of dopaminergic modulation of LTP in the hippocampus enhancing learning and memory. The retention timescale of this curiosity-enhanced memory is also in line with the timescale of late LTP, further supporting this idea. Taken together, this evidence indicates that intrinsic motivation enhances memory formation in a similar way to extrinsic motivation.

The effects of the interaction between intrinsic and extrinsic motivation on memory performance has also been examined. Xue et al. (2023) found that external rewards reduce the impact of internal motivators in delayed memory in an extension of the traditional undermining effect (the effect where extrinsic motivation reduces intrinsic motivation and leads to overall worse performance). However, memory was still enhanced overall. Murayama & Kuhbandner (2011) found that extrinsic motivators only enhanced memory in the absence of intrinsic motivation. Duan et al. (2020), on the other hand, found a significant increase in memory performance with both intrinsic and extrinsic motivators, but a non-significant interaction between intrinsic and extrinsic motivation. Overall, studies on the interaction between intrinsic and extrinsic motivation on memory have led to conflicting results.

Effects of Motivation On Consolidation

Though most studies have focused on encoding in memory, some studies have begun to investigate the impact of motivation on consolidation. Consolidation refers to the processes after encoding which stabilize memory representations. Manipulations which affect only delayed tests and not immediate tests can indicate that consolidation in particular is affected; therefore, the effects of motivation on consolidation are usually studied with manipulations after encoding or can be seen in delayed memory tests (Dickerson & Adcock, 2018, Murty & Dickerson, 2016). Results from some studies have found that rewarding events enhance performance on delayed tests but not immediate tests (Salvetti et al., 2014, Murayama & Kuhbandner, 2011, Murayama & Kitagami, 2014, Patil et al., 2017 (see Cowan et al., (2021) for more). A few other studies have used post-encoding reward motivation to manipulate consolidation; in particular, Salvetti et al. (2014) found that memory performance on a spatial navigation task was improved when reward was presented following the task. Taken together, these results suggest that motivation has an effect on the consolidation and the storage of memory in addition to memory encoding.

Conclusion

To summarize, evidence indicates that motivation can significantly influence the formation and consolidation of episodic memories. Hippocampal memories guide future behavior through adaptable and generalizable representations of the environment. Dopamine regulates reward and motivation through the mesolimbic pathway and crucially projects to the MTL; this positioning suggests that motivation may play a role in modulating these hippocampal memories and subsequent behavior. Key studies show both intrinsic and extrinsic motivation enhance memory encoding and consolidation; furthermore, higher activation of hippocampus, VTA, and NAcc predicted higher memory performance, highlighting the importance of the connections between these regions in motivation-enhanced memory. Greater correlation between activation of the hippocampus and the VTA suggests that this effect may be exerted through increased firing of dopaminergic neurons in the VTA which project to the hippocampus. Regardless of the mechanism, the interaction between motivation and memory is significant and crucial in order for adaptive behavior to utilize motivationally significant past experiences.

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