CHAPTER 7

Motivation and Memory

KATHRYN C. DICKERSON AND R. ALISON ADCOCK

INTRODUCTION

What makes humans curious and motivated to learn about the world around us? What makes us want to interact and play in our environments? Why do we remember some events or places in great detail, others only vaguely, and forget others entirely? How can we better retain the information that is important to achieving our goals? Humans have been asking these and related questions for centuries (Bloom, 1991; James, 1950). It has long been theorized that motivational incentives modulate learning systems in the brain (Berridge, 2004; Niv, Joel, & Dayan, 2006; Salamone & Correa, 2012), and incentives for desirable outcomes or performance are usually necessary to demonstrate learning in animals. Recent work moves beyond simple associative learning to enrich our understanding of the complexity of motivation and elucidate its neural underpinnings. Although many exciting challenges remain, this emerging literature shows that motivation is an essential factor in laying down the multisensory representations we think of as "memories."

For decades, the potential influence of motivational incentives on memory formation was not explored. In fact there was a strong assumption that motivation would have no impact on memory formation (Craik, 2002; Craik & Lockhart, 1972; Craik & Tulving, 1975). Only recently have scientists challenged this assumption by directly manipulating motivational incentives relevant to memory formation. Here we discuss the recent compelling evidence that motivation does indeed modulate memory encoding and consolidation. These emerging findings lead to exciting questions regarding what kinds of motivation exist and the very purpose of memory itself.

In this chapter we specifically explore the intersection between motivation and memory, focusing primarily on how motivation affects what we learn and subsequently remember. We first review extant literatures on motivation, discussing the operationalization and dimensions of the construct of motivation. Motivation has been of interest for centuries to philosophers and was an early focus of experimental psychology (see Braver et al., 2014). We provide an overview of the ways people have studied motivation as well as discuss how motivation is defined and

---

This publication was supported by the National Center for Advancing Translational Sciences of the National Institutes of Health under Award Number 5KL2TR001115. The content is solely the responsibility of the authors and does not necessarily represent the official views of the National Institutes of Health. The authors would like to thank Dr. Vishnu Murty, Dr. Kimberly Chiew, and Laura Lerebours for their helpful comments and suggestions.

Stevens' Handbook of Experimental Psychology and Cognitive Neuroscience, Fourth Edition, edited by John T. Wixted.

DOI: 10.1002/9781119170174.epcn107

conceptualized in the literature. We then discuss learning, specifically outlining multiple types of learning and describing how motivation affects learning. From there we follow scientific progress to the exciting new discoveries made in the past decade illustrating how motivation modulates memory encoding and consolidation.

Here, we also describe a novel framework suggesting how motivation provides an adaptive context for memory encoding (Murty & Adcock, 2017; Shohamy & Adcock, 2010). This framework synthesizes decades of basic research using animal models and human participants and posits three main tenets about motivation's impact on memory: (1) Motivational state is critically important to determining the brain structures engaged during memory formation, (2) the neural structures that support memory formation dictate the form and content of memory, and (3) motivational incentives do not have a uniform influence on individuals; consequently, how an individual reacts to an incentive can change which brain structures are engaged to support memory formation.

We conclude by outlining open questions and future directions for the next generation of scientists to explore. We also discuss the impact of this novel framework and the research supporting it on models of memory, models of motivation, and translation to clinical treatments.

BACKGROUND ISSUES

Operationalizing Motivation

You may be asking yourself, "What is motivation?" The answer depends in part on whom you ask. Motivation is not a unitary construct, and there are multiple definitions and conceptualizations of motivation that vary widely based on the field of study. Motivation has been most commonly examined by researchers in personality and social psychology, as well as cognitive and systems neuroscience (see Braver et al., 2014). All of these disciplines bring their unique perspectives to bear on the topic, making the study of motivation complex and multifaceted. Personality and social psychologists conceptualize motivation as the efficacy, needs, and expectations of an individual (Bargh, Gollwitzer, & Oettingen, 2010). Using this framework, they try to understand why individuals choose one option over another: for example, why someone may choose health care option A, which includes dental insurance, and why someone else chooses health care option B, with no dental insurance.

Systems neuroscientists often use animal models to examine motivation and typically define motivation in terms of activation and direction (Salamone & Correa, 2012). Activation in this context means invigoration of an action. For example, scientists may measure the response rate of a rat pushing on a lever in order to receive a reward, such as juice. Direction refers to response biases. For example, an animal may move from one environment to another in order to receive a reward or escape a punishment. This perspective of motivation from systems neuroscience is somewhat related to the characterization of motivation in the field of cognitive neuroscience. Here motivation is thought of in terms of how expectations predict decisions (see Braver et al., 2014). Cognitive scientists are interested in understanding how the expected value of a future event (e.g., eating your favorite cupcake) dictates the amount of effort you are willing to expend to achieve the desired outcome (e.g., driving across town and waiting in line for 20 minutes to get the best cupcake in town). The perspective presented here focuses on motivation to seek information so that successful memory encoding is a behavioral readout of motivational state. As can be surmised, there is no single or correct way to study motivation. Valuable information has been gained from all these perspectives, and research in all of these domains will continue to inform our understanding of motivation and its profound impact on our daily lives.

Dimensions of Motivation

In addition to the multiple methods used to define and examine motivation across disciplines there is also variability in the way that motivation is described in terms of its dimensionality. The main dimensions used in the literature are (1) conscious versus nonconscious, (2) extrinsic versus intrinsic, (3) approach versus avoidance (4) positive versus negative feedback, (5) transient versus sustained, (6) goal setting versus goal striving, and (7) goal-directed versus habit (see Braver et al., 2014). In the following we discuss how each of these approaches has aided in our understanding of motivation and suggest an additional important dimension that has been absent from the prior literature.

Most studies have manipulated motivation consciously, as we discuss in detail in the following sections. However, it should also be noted that work conducted since the new millennium suggests that nonconscious or implicit motivation can also affect human behavior (Bijleveld, Custers, & Aarts, 2010; Capa, Bustin, Cleeremans, & Hansenne, 2011; Custers & Aarts, 2010; Custers, Eitam, & Bargh, 2012; Pessiglione et al., 2007). For example, reward cues, such as an image of money or food, presented to a participant subliminally engage brain regions classically involved in conscious reward processing and motivated behavior (e.g., the basal ganglia) (Schmidt et al., 2008; Pessiglione et al., 2007). Furthermore, participants who are implicitly primed in an experiment will expend more cognitive effort for cues paired with a high reward ($5) compared to cues paired with a low reward ($1) (Pessiglione et al., 2007). These findings suggest that the implicit primes, although not consciously processed, do indeed influence overt behavior. Aside from implicit priming, nearly all other experimental manipulations of motivation are overt and are processed consciously. The discussion throughout the remainder of the chapter, therefore, focuses on the influence of such conscious motivational manipulations.

The majority of research on motivation has manipulated extrinsic motivation, such as varying the amount of food or monetary reward given for achieving a set goal. Intrinsic motivation, however, refers to when an individual engages in something for the inherent pleasure of the activity with no extrinsic rewards promised (Braver et al., 2014; Deci, 1971; Deci, Koestner, & Ryan, 1999; Deci & Ryan, 1985; Murayama, Matsumoto, Izuma, & Matsumoto, 2010). For example, imagine a man named Tom who loves to write for pleasure. He may write daily entries in his journal, which will never be published or perhaps ever read by another individual. Nevertheless, Tom loves to write and finds inherent pleasure in this process. Extrinsic and intrinsic motivation can also interact: Somewhat paradoxically, extrinsic incentives have been shown to undermine the value and pleasure associated with intrinsic reasons for doing something (Deci et al., 1999). This is known as the *undermining effect* and has been shown to reduce activation in reward regions in the brain (Murayama et al., 2010). Recently scientists examined the undermining effect in a beautiful study (Murayama et al., 2010) that reveals much about the neural basis and interactions between these forms of motivation. Participants learned to play a simple game in which they viewed a stopwatch and were asked to try to press a button as soon as possible after the stopwatch read 5 seconds. Two groups of participants played the game in two consecutive sessions. One group was provided with money rewards for accurate performance in the game (reward group). A second group was given the same amount of money; however, their payment was unrelated to their task performance (control group). After all participants finished this first phase, they were left alone in a quiet room for a few minutes. During this time, they could choose what to do: play the same stopwatch game, read a book, or do something else. Then, participants in both groups played the same stopwatch game again, but this time neither group was given performance-based rewards. Murayama et al. (2010) reported two interesting findings: First, people in the reward group chose to play the stopwatch game during the free-choice period significantly less than people in the control group. Second, using functional magnetic resonance imaging (fMRI) the authors observed that although people in the control group showed equivalent levels of brain activation in regions commonly associated with reward in the two sessions, people in the reward group showed a dramatic decrease in responses to success in the second, unrewarded session. This study powerfully demonstrates that giving extrinsic rewards for an activity can dramatically decrease the inherent interest in doing it and the neural responses to task success. This is consistent with the canonical effect that participants who receive extrinsic rewards to do something spend significantly less time than those who receive no rewards engaging in the task (Deci et al., 1999; Tang & Hall, 1995; Wiersma, 1992).

Another widely useful framework for studying motivation distinguishes approach from avoidance motivation (see Braver et al., 2014). Experimentalists may classify a subject's behavior as approaching something rewarding (e.g., spending time with friends) or avoiding something threatening (e.g., avoiding a bully). This is sometimes conflated with affect (commonly described as feeling positive or negative; see Chiew & Braver, 2011, for discussion on the distinction between reward and positive affect). It is often assumed that positive affect is associated with approach motivation (e.g., moving toward a cute puppy) and negative affect is associated with avoidance motivation (e.g., walking away from an alligator); however, there is not a direct mapping between affect and approach-avoidance motivated behavior. Take, for example, the emotion anger. Anger is thought of as producing negative affect. Rather than producing avoidance behavior (e.g., sulking on the couch), however, it often drives approach behavior (e.g., telling your friend that you're upset with her) (Carver & Harmon-Jones, 2009; Harmon-Jones, 2003; see Chapter 17 in Volume 4). The approach-avoidance framework may also be important to understanding the effects of feedback valence on goal pursuit: Research has shown that positive feedback is more effective than negative feedback when goal commitment is low (encouraging goal approach), but negative feedback is more effective than positive feedback when goal commitment is high (indicating closing the remaining gap in order to achieve one's goal) (Carver & Scheier, 2001; Higgins, 1987).

Motivation has also been examined and categorized across multiple timescales, including transient versus sustained effects. Transient effects are often induced by the presence of a motivating cue, such as a reward cue, whereas sustained effects occur at a longer, slower timescale. Some experimental paradigms have reward or punishment cues that vary at the level of an individual trial ($1 for every correct trial), allowing for the manipulation of motivation at a more transient timescale (Adcock et al., 2006;

Chiew & Braver, 2013; Jimura, Locke, & Braver, 2010; Mather & Schoeke, 2011; Murty, LaBar, & Adcock, 2012; Wittmann et al., 2005; Wolosin, Zeithamova, & Preston, 2012). Other tasks may have manipulations at the block level ($5 for all cues in the block), inducing a motivational state that must be sustained over multiple trials (Chiew & Braver, 2013; Loh, Deacon, de Boer, Dolan, & Düzel, 2015; Loh et al., 2016; Murty & Adcock, 2014; Murty, LaBar, & Adcock, 2016). Interestingly, evidence suggests that transient and sustained motivational states may be supported by differential signaling by a single neurotransmitter: dopamine (Niv, 2007; Salamone & Correa, 2012; Shohamy & Adcock, 2010).

Multiple Types of Learning and Memory

Similar to motivation, learning is also not a unitary construct. At the broadest level, learning and memory are divided into two types: declarative and non-declarative (Squire, 1992a, 1992b; Squire & Wixted, 2011). Declarative learning and memory refer to memories that can be readily "declared" aloud. This includes facts and events, for instance, remembering where you went on family vacation last year. Non-declarative memory is broader and encompasses essentially all other types of learning that are not declarative. This includes procedural learning, priming and perceptual learning, classical conditioning, as well as nonassociative learning (Squire, 1992a, 1992b; Squire & Wixted, 2011).

Research over the past century has revealed that these distinct types of learning engage and depend on discrete neural architecture in the brain. Declarative memory is dependent on the function of the medial temporal lobes (MTL). The main function of the MTL is to bind associations across context, space, and time, into rich, flexible associations (Davachi 2006; Paller & Wagner, 2002; Squire, 1992b). When people talk about memory, they almost always mean this type of memory. The MTL consists of multiple substructures including the hippocampus, amygdala, parahippocampal cortex, and perirhinal cortex (Davachi, 2006; Shohamy & Adcock 2010; Squire, Stark, & Clark, 2004). Interestingly, research suggests that these independent components of the MTL contribute to memory formation in unique ways (Davachi, 2006). The perirhinal cortex, for example, has been shown to encode the features and identity of items, such as the art pieces you viewed at a new art gallery. The nearby parahippocampal cortex encodes the spatial location of the item or event, including which room each piece was in and what art pieces were located in the same room. The hippocampus then integrates this item and context information into one rich, detailed, flexible representation: You having a lovely afternoon walking around the gallery with your friends (Davachi, 2006).

Non-declarative memory, however, comprises multiple diverse kinds of memory and therefore engages a host of brain structures including the basal ganglia, neocortex, amygdala, and cerebellum (Eichenbaum & Cohen, 2004; Squire, 2004). Procedural learning, including trial-and-error learning, engages the basal ganglia system (Delgado, 2007; Squire, 2004). A classic example of procedural learning is learning a motor skill, such as how to tie your shoes or ride a bicycle. These processes take a long time, are filled with trial and error, and involve development of motor skills and memories. This type of learning is very robust against decay—"like riding a bike," as the old saying goes. The architecture of the basal ganglia system is optimized for this type of learning, and experiments have shown that the basal ganglia (in particular the striatum) is critical for procedural learning (for a review, see Delgado, 2007). To test trial-and-error learning in experimental settings, participants usually learn the associations between one or more cues and different outcomes slowly over time. They do so by initially guessing an association (e.g., "Maybe Sally likes pepperoni pizza.") and subsequently correcting their responses based on informative feedback (e.g., "Sally does not like pepperoni pizza; she likes mushroom pizza instead.").

Priming and perceptual learning are functions associated with the neocortex (Squire, 2004). In a typical priming experiment, participants are primed with words or pictures of a certain category (e.g., *medicine*) and then are asked to fill in the following word (e.g., *doc*___) with any ending they like. Once primed, participants are more likely to write *doctor* than another word beginning with *doc,* such as *documentary,* even if they cannot produce the word *medicine* when asked directly what word they viewed (Tulving & Schacter, 1990; Tulving, Schacter, & Stark, 1982). Perceptual learning includes learning about categories such as speech sounds and related forms of artificial grammars (Squire, 2004).

Another highly studied type of non-declarative learning is called *classical conditioning*. Classical conditioning consists of pairing an unconditioned stimulus (e.g., air puff to the eye) with a conditioned stimulus (e.g., auditory tone). Over time, subjects will display an unconditioned response (e.g., blinking) to the conditioned stimulus, indicating learning between the association of the tone and air puff (Clark, Manns, & Squire, 2002; Clark & Squire, 1998). This type of associative learning has been extensively studied in animals. The neural mechanisms of classical conditioning vary depending on the conditioned response and the delay between events. Important neural substrates include the cerebellum and, when a delay is interposed, the hippocampus (Clark et al., 2002). Last, fear conditioning, a type of classical conditioning (e.g., pairing a foot shock with an auditory tone) has been shown to be dependent on an intact amygdala (Johansen, Cain, Ostroff, & LeDoux, 2011; see also Chapter 2 in this volume).

Motivation's Impact on Learning

A rich history of research has established that motivation is essential to non-declarative learning. In animal and human research it has been documented that animals will work to receive rewards (e.g., food, money) and to avoid punishments (e.g., shock) (Daw & Doya, 2006; Schultz, 2016; Wise, 2004). Historically the literature examined motivation's impact on conditioning and trial-and-error learning, both of which consist of associations between stimuli acquired over time. Pavlovian conditioning is a form of passive stimulus-stimulus learning (e.g., pairing a light with a tone to predict food delivery). Trial and error learning is a form of active stimulus–outcome learning during which the subject must act to induce an outcome, facilitating learning (Corbit & Balleine, 2015), for example, pairing a stimulus (light) with an action (press lever) to produce a learnable outcome (receive food reward). Substantial research has investigated motivation's impact on these types of learning, which modulate many aspects of behavior including choice, vigor, and frequency (Delgado, 2007; Wise, 2004). For example, a rat will work harder for his favorite food reward (e.g., chocolate) than for his typical dinner (e.g., chow). In this manner, incentives have profound ability to modulate future behavior based on past experience.

Although the role of motivation was a dominant focus in the study of non-declarative learning for decades, it has only recently begun to be investigated in declarative memory. Scientists studying declarative learning and memory were long focused on cognition, that is, information processing. For decades, declarative memory research was driven forward by an important theory, the levels of processing theory (Craik & Tulving, 1975). This theory suggested that what determined how effectively something was encoded into long-term memory was dependent on the type of encoding: shallow or deep. When encoding under shallow conditions, for example, participants might be asked to attend to whether or not words to be remembered are presented in lowercase or capital letters. Under conditions of deep encoding, participants might be asked to determine the meaning of a word in a sentence. Deep encoding requires participants to process memoranda (to-be-remembered content) more thoroughly. This deeper processing provided more cues for later retrieval. As a result, words encoded under deep conditions are better remembered than those encoded under shallow conditions. A crucial finding was that if encoding strategies were experimentally matched for levels of processing, intentional memorization did not yield any better memory performance than "incidental" encoding tested by a surprise memory test (Craik & Tulving, 1975). These compelling findings and theory were highly consistent with the cognitive perspective that dominated declarative memory research for decades. Therefore, researchers focused, productively, on studying and understanding encoding strategies. Scientists turned to exploring motivation effects on declarative memory only since about the new millennium. Similar to the study of memory for emotional events, in which modulation of memory traces during consolidation implied a noncognitive phenomenon, the more recent focus on motivation in declarative memory was prompted in large part by neurobiological evidence: Neuromodulators such as dopamine and norepinephrine, centrally important to motivation, are known to be essential for lasting brain plasticity. The implications of these biological findings stimulated the emergence of a subdiscipline focused on motivated memory. We will turn now to discuss the behavioral and neural findings in animals and humans in this nascent field.

EMERGING TRENDS: CHARACTERIZING MOTIVATION AND ITS EFFECTS ON MEMORY

Extrinsic Motivation: Reward Influences on Memory Encoding

A powerful way to examine motivation's impact on memory is to explicitly manipulate memory encoding (see Figures 7.1 and 7.2). One of the first studies to do so rewarded research participants $5 or $0.10 for remembering a picture to be tested the following day (Adcock et al., 2006). Rather than rewarding immediate learning via feedback, akin to trial-and-error learning, the key design manipulation here was to motivate only encoding. Participants were rewarded only for each correctly remembered picture during the memory test, which occurred the next day. In this and similar studies (Wolosin et al., 2012) reward improved memory: Participants remembered more images paired with large rather than small rewards. Importantly, because the reward cues preceded the memoranda, the influence of motivation on behavior and neural systems could be examined independent of the properties of the stimuli to be-remembered. In regions closely associated with dopamine neurotransmission, including the ventral tegmental area (VTA) of the dopaminergic midbrain, fMRI activation following a high-reward cue predicted memory for an upcoming scene image. In addition, correlated activity

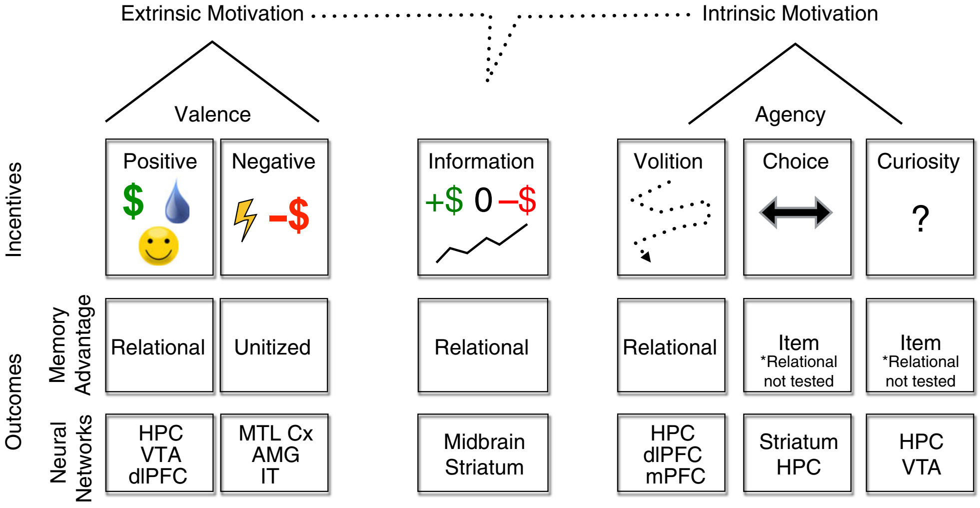

Figure 7.1 Experimental approaches to engaging motivated memory. This taxonomy summarizes the main experimental manipulations used to examine motivational influences on memory, organized by conventional taxonomies of incentive. The majority of research has examined how extrinsic incentives, such as rewards and punishments, influence memory and its neural substrates.

between the midbrain and hippocampus predicted successful memory formation.

Similar effects of reward boosting memory encoding have been observed during incidental learning. Incidental learning refers to learning in which individuals are not explicitly told during encoding that there will be a memory test later. This is in contrast to intentional learning paradigms in which participants are explicitly told that their memory will be tested (such as in the study by Adcock et al., 2006, described previously). In incidental learning tasks, each item to be remembered can be paired with anticipation of reward (e.g., living but not nonliving items predict an opportunity to earn reward; Wittmann et al., 2005) or items can be embedded in a rewarding context (e.g., participants view many pictures associated with high or low reward; Loh et al. 2015, 2016; Murty & Adcock, 2014). Similar to during intentional learning tasks, reward improved memory accuracy during incidental memory tests. The differences between motivation's impact on incidental and intentional memory remain unknown and will be an interesting direction for future research.

In addition to examining the impact of motivation on encoding alone, some researchers have combined feedback and encoding manipulations within the same task. In one such study, Wittman and colleagues (2005) observed better memory for images that predicted reward, compared with non-reward predictive stimuli. However, in this experiment participants were also given feedback about task performance in addition to being promised a reward. To address the question of the relative importance of the feedback and the reward cue on memory, Mather and colleagues conducted a study with intermingled reward anticipation and reward receipt (Mather & Schoeke, 2011). In this paradigm, outcome feedback had a larger impact on memory than reward-incentive cues. Specifically, regardless of signaling potential gains or losses, stimuli associated

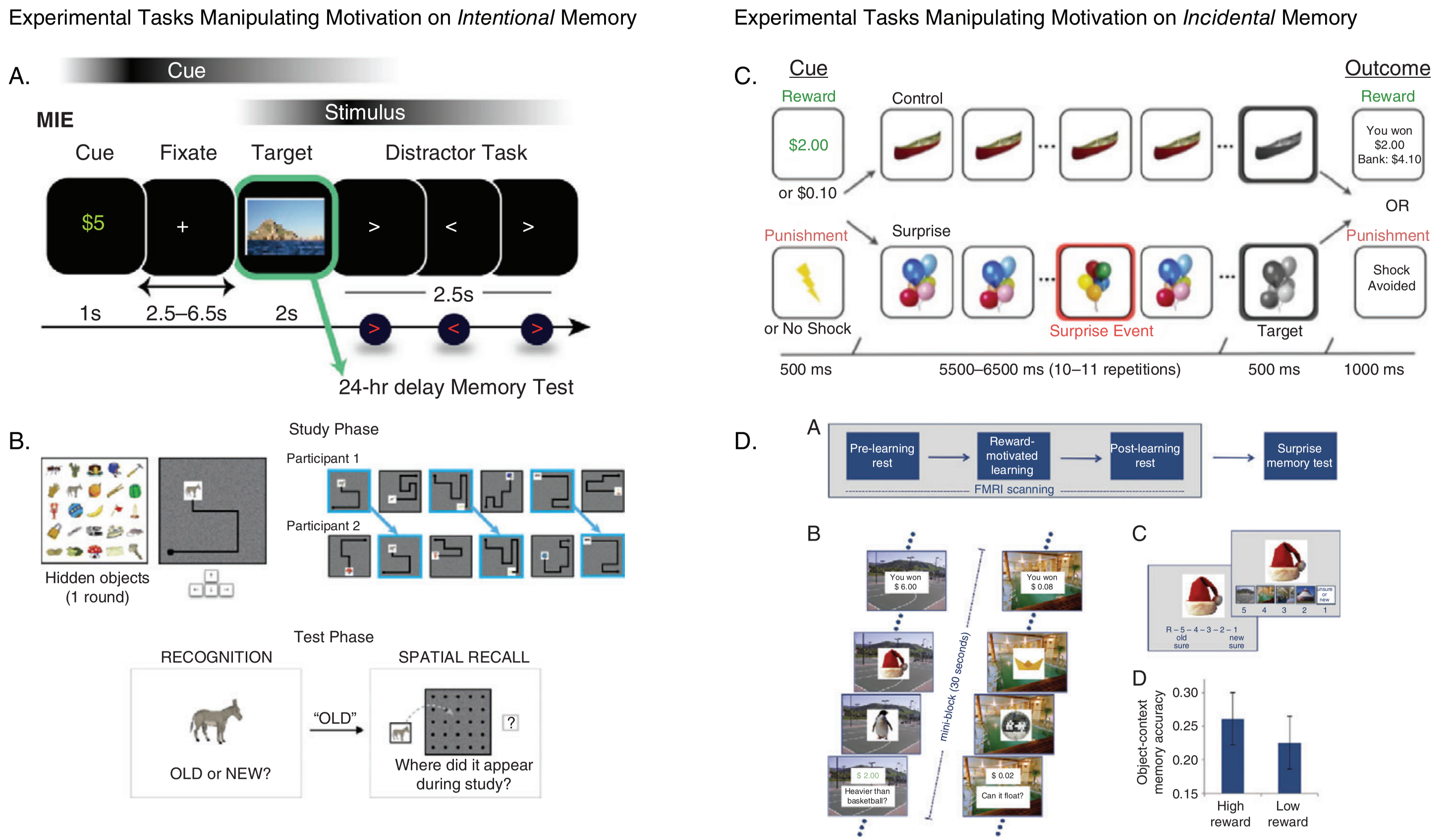

Figure 7.2 Example experimental tasks used to study motivated memory. A. The Motivated Incentive Encoding (MIE) task developed by Adcock et al. (2006). Participants are incentivized to remember upcoming images by the promise of reward receipt if they remember the images during a memory test given the next day. This task used extrinsic incentives to manipulate intentional memory encoding. B. In the task designed by Markant, DuBrow, Davachi, and Gureckis (2014) the authors asked participants to navigate through a grid in order to reveal "hidden" objects. On some trials participants controlled their movement through the space; in others, their movement was yoked to another participant's movement. In this manner, the researchers examined how self-guided learning influences memory. During the test, they were asked to identify if the objects were old and if so, what was their location on the grid. C. The task developed by Murty et al. (2016) incentivized memory by asked participants to press a button as soon as a color image turned gray scale. Participants were incentivized to do so in order to earn money or avoid future shock. This task used extrinsic incentives to manipulate incidental memory encoding. D. The task developed by Gruber, Ritchey, Wang, Doss, and Ranganath (2016) examined post-encoding effects on memory. Participants incidentally encoded a series of objects in a high- or low-rewarding context. The experimenters then examined whether changes in brain activity from pre-encoding to post-encoding rest periods predicts memory performance. This task used extrinsic incentives to examine memory consolidation.

with positive feedback outcomes (either receiving money or avoiding losing money) were better remembered.

Last, motivated memory has been investigated with non-monetary extrinsic incentives. Some scientists have used natural reinforcers (such as juice) or emotional stimuli (such as smiling faces) to manipulate motivation. In all of these scenarios, motivation has improved memory. For example, in participants who were thirst deprived, memory was better for images paired with liquid reward compared with no reward (Rainey, Dickerson, & Adcock, 2014). In the domain of emotional stimuli, memory for names paired with smiling faces was greater than memory for names paired with neutral faces (Tsukiura & Cabeza, 2008; for a review of emotion and memory, see Chapter 1 of this volume). Taken as a whole, results from the described studies, which used diverse reward incentives including money, natural reinforcers, and emotional stimuli, converge to suggest that reward motivation boosts memory performance.

Extrinsic Motivation: Punishment Influences on Memory Encoding

Humans learn things under many different contexts. We are not always rewarded for the things we need to remember. In fact, sometimes we learn things under states of anxiety or potential punishment. Recently researchers have begun to directly examine memory performance in the context of punishment to examine how negative states affect learning. In one such study, participants viewed a series of pictures and were told that they would receive a mildly irritating shock on the wrist the next day during a memory test for any images they failed to remember (Murty et al., 2012). Importantly, participants were not shocked during encoding. Rather participants encoded the images under the threat of shock, presumably in a mildly fearful or anxious state. Interestingly, the authors observed that the threat of shock did boost memory performance. Related studies have replicated this finding and observed that punishment may enhance memory for simple information but impair memory for more complex information (Bauch, Rausch, & Bunzeck, 2014; Murty, LaBar, Hamilton, & Adcock, 2011). For example, Bauch and colleagues used the threat of a mildly painful thermal probe during memory encoding. They observed improved familiarity memory (meaning a simple memory for the item, with no further memory for contextual details) but worse recollection memory (which is a richer memory for the entire episode).

Intrinsic Motivation: Categories and Experimental Manipulations

Not all studies have used extrinsic manipulations as motivational incentives. Intrinsic motivation, as discussed in the section “Dimensions of Motivation,” refers to engaging in an activity for the inherent enjoyment and pleasure of the activity (Deci & Ryan, 1985). Multiple types of intrinsic motivation are important to learning. Only recently researchers have started exploring the behavioral and neural components of these non-extrinsic categories of motivation as well as constructs related to these types of motivation, including curiosity, the value of information, agency, and even volition. The study of intrinsic motivation is highly relevant to learning in daily life, which is often self-motivated, and not directly reinforced by extrinsic incentives (Ryan & Deci, 2000). Studying intrinsic motivation is more challenging, however, particularly when using animal models. This is in part why the study of extrinsic motivation has dominated the field for so long: It is usually necessary to incentivize an animal to motivate it to complete a task that is interesting to an experimenter. A rat will run a maze in order to receive a Fruit Loop treat, but it may not run the maze otherwise. Human participants are also typically readily motivated by extrinsic reward, including food and money, as previously discussed. Fortunately, we can also query humans regarding their subjective feelings, thoughts, and motivations. In addition, we can observe their choices when they participate in free-choice paradigms. In this and other manners described in the following sections, researchers are beginning to investigate the behavioral and neural correlates of intrinsic motivation.

Only in recent years have scientists begun to examine the neural basis of intrinsic motivation. For example, Lee and Reeve (2013) asked participants to read example phrases of activities that could be done for intrinsic reasons, extrinsic reasons, or neither (neutral). For instance, one could write a document for fun (intrinsic), for extra credit (extrinsic), or because it is required (neutral). The authors found that when participants chose to engage in something for intrinsic reasons there was increased activation in the insula, whereas extrinsic reasons engaged the posterior cingulate cortex. The insula is involved in emotional processing (among other things including agency, discussed in the following section), whereas the cingulate is engaged in many processes, including decision making. The authors hypothesized that people chose to do something based on intrinsic reasons because it was self-satisfying and for extrinsic reasons because of socially acquired values (such as extra credit).

Volitional Motivation

Extrinsic and intrinsic incentives are often thought of as eliciting behavior (including learning) in a relatively automatic way. However, humans often work toward abstract goals with remote, and at times highly uncertain, outcomes via behaviors with low perceived intrinsic reward. For example, you might not enjoy brushing your teeth every day, but you do so because you know it's good for the health of your teeth. Achieving such goals may require deliberate cognitive strategies. One such strategy is to recall long-term goals to make them more salient in the moment ("I don't want all of my teeth to fall out!"). Another strategy is to essentially self-generate or simulate motivation: such as by mentally regenerating prior motivational states that arose under effective proximal incentives (e.g., "I'll pretend I'm at a dance party while brushing my teeth to make it more fun."). Strategic, internal motivational states are challenging to study, but recent work has begun to examine the strategic regulation of the brain circuits implicated as an index of volitional self-motivation (MacInnes, Dickerson, Chen, & Adcock, 2016). This work revealed that healthy young adults can learn to increase activation within the dopaminergic midbrain, specifically the VTA, on demand using self-generated motivational thoughts. Critically, learning in this task was dependent on participants receiving accurate, anatomically specific feedback regarding the level of activation within their own VTA. VTA activation during and after neurofeedback training was also correlated with increased activity within other regions implicated in motivated memory, including the hippocampus. Further research is under way to tie these biological signatures to effects on learning and memory.

Intrinsic Motivation: Influences on Memory Curiosity

When we think of engaging in an activity for intrinsic reasons, one common reason that comes to mind for doing so is because we are curious. Recent work has experimentally examined behavioral and neural markers of curiosity and their effects on successful memory formation. In an innovative study, Gruber and colleagues (2014) asked participants to view many trivia questions and to rate two things: how likely they were to know the answer and how interested they were in knowing the answer. Then participants were scanned using fMRI and viewed a series of the trivia questions and answers. Between the question and answer periods, the authors displayed novel face images. The authors then tested memory for the trivia questions and for the faces. Importantly, they sorted memory according to how curious participants were to know the answer. Not surprisingly, participants' memory was better for the information they were more curious about (additionally demonstrated by Kang et al., 2009; Stanek, 2016). Surprisingly, however, incidental memory for the face images was also enhanced when associated with high curiosity information. Similar to the Adcock and colleagues (2006) study that used extrinsic monetary incentives, Gruber et al. (2014) observed brain activation following the cue (here, a question) in regions closely associated with dopamine neurotransmission, including the nucleus accumbens and midbrain. These activations closely tracked curiosity rather than monetary reward. Similarly, correlated activity between the midbrain and hippocampus was important for memory formation.

Value of Information

The construct of curiosity implies that information itself is valuable (Blanchard, Hayden, & Bromberg-Martin, 2015). This is evident not just in overt information-seeking behavior but also in the impact of feedback on learning. In a fascinating set of studies, Bromberg-Martin and colleagues have shown that animals value information about an upcoming reward and will even sacrifice reward receipt in order to gain information (Blanchard et al., 2015; Bromberg-Martin & Hikosaka, 2009). The evidence that people seek even negative feedback when it is informative for improving performance is another example of this idea that information is valuable (DePasque & Tricomi, 2015; DePasque Swanson & Tricomi, 2014; Lempert & Tricomi, 2016; Tricomi & Fiez, 2008, 2012). In a pioneering study, DePasque and Tricomi (2015) examined the effect of a motivational intervention on an associative learning task. Participants learned pairs of words over time via feedback. The authors introduced a motivation manipulation in which they asked participants to rate how important it was for them to do well on the task. The authors found that memory performance scaled with self-reported motivation so that memory for the word pairs was better when motivation was higher (though in this study the authors were unable to dissociate pure motivation ratings from participants' post-hoc assessment of their own performance). This task beautifully combines what is traditionally thought of as feedback learning with declarative learning. Although there is a growing literature examining the boundaries between feedback-based and declarative learning (Davidow, Foerde, Galván, & Shohamy, 2016; Delgado & Dickerson, 2012; Dickerson & Delgado, 2015; Dickerson, Li, & Delgado, 2011; Dobryakova & Tricomi, 2013; Foerde, Race, Verfaellie, & Shohamy, 2013; Foerde & Shohamy, 2011; Mattfeld & Stark, 2011, 2015; Murty, DuBrow, & Davachi 2015; Shohamy & Turk-Browne 2013; Wimmer, Braun, Daw, & Shohamy, 2014; Wimmer & Shohamy, 2012), for the purposes of this chapter, we limit our discussion to how this interaction affects memory formation (declarative learning). In short, the findings point to a view of information value in tuning behavior, rather than a simple reward-punishment dichotomy. This pattern of behavior is consistent with the idea that even in feedback-based "instrumental" paradigms, intrinsic motivation to understand the world is a primary driver of learning.

Interrelationships Between Motivated Declarative Memory and Feedback Learning

Historically, feedback learning and declarative memory have been studied independently. However, these two types of learning likely interact to promote successful learning and memory. In the past few years, scientists have designed experiments combining declarative memory encoding and retrieval with feedback learning and decision making (Dickerson & Delgado, 2015; Murty et al., 2015; Murty, Hall, Hunter, Phelps, & Davachi, 2016; Wimmer et al., 2014). In one example study, Wimmer et al. (2014) examined how declarative memory encoding interacts with feedback learning. Participants were asked to learn which colored square (blue or green) predicted reward. Overlaid on the colored squares were objects (e.g., cat) associated with reward probabilities. The authors asked participants to remember the objects in a surprise memory test given the next day. Wimmer and colleagues found an inverse relationship between reward learning and memory in that greater memory was associated with decreased influence of reward on choice. In addition, when memory was strong, the classic reward prediction error signal (indicating a difference between an expected and actual outcome) in the basal ganglia (specifically the striatum) was weak. The authors concluded from their results that these distinct learning systems may interact in an opposing way to support declarative memory.

Not all studies support negative interactions between feedback learning and declarative memory systems. A study by Dickerson and Delgado (2015) used declarative memory retrieval concurrent with feedback learning to examine how the neural systems supporting these types of learning interact and specifically how the hippocampus may contribute to feedback learning. Here the authors found the greatest amount of activation in the striatum, midbrain, and hippocampus during feedback learning concurrent with memory retrieval compared to control conditions (no memory interference). In addition, hippocampal activity predicted feedback learning. Furthermore, feedback learning accuracy decreased when there were competing memory demands, suggesting the hippocampus may support the ventral striatum in feedback learning. We direct the reader to the following sources for additional discussion beyond the scope of this chapter on feedback learning and how multiple memory systems interact (Davidow et al., 2016; Delgado & Dickerson, 2012; Dickerson et al., 2011; Dickerson & Delgado, 2015; Dobryakova & Tricomi, 2013; Foerde & Shohamy, 2011; Foerde et al., 2013; Mattfeld & Stark, 2011, 2015; Murty et al., 2015; Shohamy & Turk-Browne, 2013; Wimmer & Shohamy, 2012; Wimmer et al., 2014).

Agency, Action, and Choice

Feedback learning is sometimes associated with agency, because individuals typically choose between two or more stimuli and receive feedback based on their choice. They are therefore actively (rather than passively) engaged in learning. Research since the mid-1990s has begun to examine the behavioral and neural correlates of agency within and beyond the domain of feedback learning. A recent review paper revealed that activation in the insula is related to self-agency, whereas activation in other regions including the precuneus, dorsomedial prefrontal cortex, pre-supplementary motor area, and temporoparietal junction was more associated with external agency (Sperduti, Delaveau, Fossati, & Nadel, 2011). Indeed, others have observed insula activation related to self-agency (Farrer & Frith, 2002; Lee & Reeve, 2013) and activation in the parietal cortex, including the angular gyrus, in response to non-self-determined behavior (Farrer & Frith, 2002; Lee & Reeve, 2013).

The construct of agency is highly related to that of choice. In a very simple and elegant study, Leotti and Delgado (2011) examined the subjective and neural correlates of free choice. The authors designed a simple choice paradigm in which on some trial participants pressed one of two buttons in order to try to receive a monetary reward ($0, $50, $100; choice condition). On other trials, participants simply made a response indicating which key the computer had selected, which lead to similar monetary outcomes (no-choice condition). Thus the manipulation regarded choice, not monetary outcome. The authors found that participants self-reported liking the cues associated with choice more than the no-choice cues. Furthermore, regions in the dopamine system (including the ventral striatum and midbrain) showed greater activation in anticipation of choice trials than no choice trials. In a follow-up experiment, Leotti and Delgado (2014) examined how the experience of choice was modified by the value of outcomes (positive, negative). To test this, in addition to the original gain trials, the authors included a new condition in which participants could choose between cues to try to avoid a loss (−$0, −$50, −$100). Results replicated their first study (participants liked choice cues more than no-choice cues when they were playing to gain money; this was associated with ventral striatal activation). Interestingly, when gain and loss trials were intermixed, participants did not prefer choice over no-choice trials. However, if participants were given only loss trials, they did prefer choice over no-choice trials. Individual differences in loss-choice preference corresponded with ventral striatal activation. Taken together, these results suggest that anticipating making a choice engages reward circuitry of the brain, but that this activity depends on context (gain only, loss only, gain and loss) and individual differences.

These fundamental studies in choice spurred related studies examining how choice affects memory performance. Emerging findings suggest choosing what and how to study in a self-guided manner improves memory (Clement, 2016; Harman, Humphrey, & Goodale, 1999; Koster, Guitart-Masip, Dolan, & Düzel, 2015; Liu, Ward, & Markall, 2007; Markant et al., 2014; Meijer & Van der Lubbe, 2011; Murty et al., 2015; Plancher, Barra, Orriols, & Piolino, 2013; Voss, Galvan, & Gonsalves, 2011; Voss, Gonsalves, Federmeier, Tranel, & Cohen, 2011; Voss, Warren, et al., 2011). In two example seminal studies, scientists explored how the act of choosing improves memory. Voss and colleagues designed an experiment in which participants explored an environment in two conditions: one in which they could control their movement through a virtual environment and a second in which they had no control over their movement through the space (Voss, Gonsalves, et al., 2011). As people explored the environment, objects were revealed (e.g., a bike); participants were later tested on their memory for the objects they encountered as well as the location of each object. Results revealed a fascinating finding: Participants' memory for the objects and their location was better when they had volitional control through the environment. Furthermore, activation in the hippocampus was correlated with a brain network of regions important for memory formation. This seminal study highlights that memory is an active process and links hippocampal activity to active learning. Further work has confirmed that the activate nature of learning is critical for memory success (Markant et al., 2014)

Murty and colleagues performed a conceptually related study examining the impact of choice on memory (Murty et al., 2015). Here participants completed the task in two conditions: choice and fixed. In the choice condition, participants chose between two occluder screens in order to remove the occluder and reveal an object. In the fixed condition, participants were told which button to press in order to reveal the object. In both conditions they were instructed to remember the object for a memory test to occur the following day. The authors observed that participants' memory was better for objects they chose versus those they did not. Interestingly, activation within the striatum was greater for choice than fixed cues. Furthermore, activation within the striatum, as well as correlated activity between the striatum and hippocampus, correlated with memory for choice (but not fixed) cues.

The mechanisms underlying these effects are still unknown. However, these combined results put forth a compelling case that the hippocampus plays a critical role in driving exploration and optimizing learning. As Voss, Gonsalves, et al. (2011) postulate, this may occur through interactions between cortical areas and the hippocampus during learning: The hippocampus may be ideally positioned to modulate attention, goal states, and strategic control thereby affecting learning and memory. Murty and colleagues suggest that the mesolimbic dopamine system may be involved in active learning, a hypothesis consistent with prior data demonstrating the dopamine system's role in volitional behavior (MacInnes et al., 2016; Niv, 2007; Salamone & Correa, 2012; Salamone et al., 2016; Stuber, Roitman, Phillips, Carelli, & Wightman, 2005; Tricomi, Delgado, & Fiez, 2004). Together, this emergent work provides compelling evidence that volitional action (choice, movement) improves memory (Clement 2016; Harman et al., 1999; Koster et al., 2015; Liu et al., 2007; Markant et al., 2014; Meijer & Van der Lubbe, 2011; Murty et al., 2015; Plancher et al., 2013; Voss, Galvan, et al., 2011; Voss, Gonsalves, et al., 2011; Voss, Warren, et al., 2011), which has profound implications for theories of learning, memory, and education.

Motivation as a Neural Context for Memory Formation

Applying traditional taxonomies developed to characterize motivation toward understanding its effects on memory reveals important dilemmas, with implications not only for understanding memory but also for motivation itself. Examples of traditional taxonomies include (1) goal orientation—approach versus avoidance, (2) valence—positive versus negative, and (3) motivational drive—extrinsic versus intrinsic (see Braver et al., 2014). These dimensions, developed outside the context of learning and memory, introduce several ambiguities. In the following sections we demonstrate that incorporating motivation to learn as a critical dimension may offer a more parsimonious account of motivated behavior.

Recently work from our laboratory has proposed distinct information-based motivational states to better characterize motivation's impact on memory (Murty & Adcock, 2017), namely, interrogative and imperative motivation (Figure 7.3). *Interrogative* refers to information processing relevant not only to an individual's current goal but also future goals and resolving goal conflict. *Imperative* refers to information processing that is relevant to resolving an immediate, highly

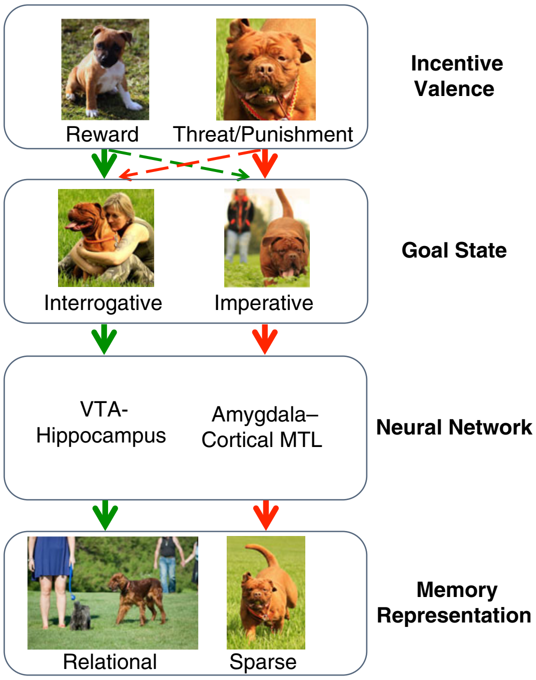

Figure 7.3 Goal states impact memory formation. Imagine you are at a dog park and encounter an adorable puppy. The puppy acts as a reward, putting you in an interrogative goal state: You want to interact with him and other dogs. This state engages VTA-hippocampal circuitry promoting relational memory of you having a great time at the dog park. Alternatively, you could experience a large dog running directly toward you, which may put you in an imperative goal state: You try to stay away from the dog. This state engages amygdala-cortical-MTL circuitry promoting a sparse memory for the salient event of escaping the dog, without the contextual information of being at a dog park. Importantly, what is perceived as rewarding or punishing varies across individuals, changing our goal states (interrogative or imperative) and, subsequently, the very nature of our memories (relational or sparse).

compelling goal. For example, if Christopher is exploring a new city late at night and has encountered an unknown individual walking toward him on a dark side street, he may act in an imperative state, quickly avoiding interacting with the individual approaching him and simplifying his information seeking to identify escape routes. Similarly, if Christopher has just finished a 10-mile race and is very thirsty, satisfying his thirst is an imperative goal that will strongly shape learning about his environment. However, if Christopher is exploring the same city on a beautiful day and considering multiple moderately attractive (or repulsive) options, he may interact with his environment in an interrogative manner, chatting with the people he meets on the street and discovering new favorite spots in the city. In these divergent scenarios, his information processing and brain states are fundamentally different, notably, even if the physical environment is identical.

This novel framework using information-based motivational states to characterize motivation's impact on memory is particularly compelling because it maps onto distinct neuromodulatory systems engaged during motivated learning; these circuits are centered on either the VTA or the amygdala. Substantial prior empirical work from the animal and human literature suggests that the dopaminergic midbrain, in particular the VTA, is important for reward motivation and hippocampally dependent memory encoding (for reviews see Miendlarzewska, Bavelier, & Schwartz, 2016; Shohamy & Adcock, 2010). The amygdala, however, is most reliably engaged during punishment learning and has been associated with cortical MTL-dependent encoding (Bauch et al., 2014; Murty et al., 2012; Schwarze, Bingel, & Sommer, 2012). In the following sections we will review the literature supporting engagement of these distinct brain networks during different types of learning and memory encoding. Based on this evidence, we argue that an interrogative-imperative account solves some dilemmas posed by the valence account (using positive-negative as the framework) that might emerge from isolated consideration of the task incentives.

Interrogative Motivational States

In the recent model proposed by Murty and Adcock (2017), interrogative goal states reflect two primary things: pursuit of an immediate goal and exploration of the environment with the aim of supporting adaptive behavior. As we discuss further, reward motivated behavior is typically associated with (1) interrogative goal states, (2) the dopamine system, and (3) activation within the VTA. Although there is much research supporting this (as described), it is important to note that there is a not a direct, singular relationship among value (reward), motivational state (interrogative), and brain architecture (VTA). There are scenarios in which anticipated punishment, rather than reward, is associated with interrogative goal states; such avoidance states also engage the VTA (Bromberg-Martin, Matsumoto, & Hikosaka, 2010; Salamone, 1994). Although the mapping among value, motivational state, and brain architecture is not unitary, the majority of evidence supports reward engaging the VTA and supporting interrogative motivational states. In the next section we discuss the literature supporting the brain circuitry underlying interrogative motivated behavior.

VTA Activation Supports Motivated Behavior

Seminal research using animal models beginning in the 1950s documented engagement of the VTA in motivated behavior. Rats implanted with electrodes within the VTA will directly self-stimulate this region, shockingly completely ignoring natural reinforcers in their environments (such as food or sex; Olds & Milner, 1954). This compelling result suggests that activation of the VTA is highly motivating and rewarding. Indeed VTA activation produces behavioral activation and exploratory behavior, including orientation to novel stimuli (Düzel, Bunzeck, Guitart-Masip, & Düzel, 2010; Ikemoto & Panksepp, 1999; Kakade & Dayan, 2002). Importantly, work using human subjects and functional neuroimaging has supported these classic findings in the animal literature. Activation in the VTA has been observed in reward-motivated behavior as well as during other salient events including surprise, novelty, and loss avoidance (Boll, Gamer, Gluth, Finsterbusch, & Büchel, 2013; Bunzeck & Düzel, 2006; Carter, Mckell, Macinnes, Huettel, & Adcock, 2009; Krebs, Heipertz, Schuetze, & Düzel, 2011; Krebs, Schott, & Düzel, 2009; Wittmann, Bunzeck, Dolan, & Düzel, 2007). These findings are consistent across species and suggest that the VTA tracks current and future events relevant to motivated behavior.

VTA-Hippocampal Connectivity

Substantial evidence across species documents that the VTA is structurally and functionally connected with the hippocampus. Monosynaptic dopamine projections travel from the VTA to the hippocampus (Amaral & Cowan, 1980; Samson, Wu, Friedman, & Davis, 1990). Dopamine receptors (specifically D1/D5) are present in the hippocampus in rodents and nonhuman primates (as well as the basal ganglia) and generally have an excitatory effect when activated by dopamine (see Shohamy & Adcock, 2010, for a review).

Neuroimaging studies in humans converge with the evidence from animal work. Functional connectivity, which measures correlated activity between two or more regions of the brain, has been observed between the VTA and hippocampus when participants are resting (not engaged in any explicit task). Connectivity during rest may be a signature for intrinsic connectivity between these areas in the brain (Kahn & Shohamy, 2013; Murty et al., 2014; Tomasi & Volkow, 2014). Furthermore, diffusion tensor imaging (DTI) results have shown white matter projections (i.e., the neuron axons) extending from the midbrain to the hippocampus (Kwon & Jang, 2014). Lastly, positron imaging tomography (PET) studies on human cadavers have found dopamine receptor expression in the human hippocampus, providing direct evidence of dopamine in the hippocampus (Camps, Kelly, & Palacios, 1990; Khan et al., 2000; Little, Carroll, & Cassin, 1995; Mukherjee et al., 2002).

VTA Activation Promotes Hippocampal-Dependent Memory Encoding

Work from the animal and human literature shows that dopamine and VTA activation modulate hippocampal-dependent memories. Dopamine release prior to and following memory encoding improves hippocampal memory, whereas dopamine antagonists disrupt memory (O'Carroll, Martin, Sandin, Frenguelli, & Morris, 2006; Salvetti, Morris, & Wang, 2014; Wang & Morris, 2010). Furthermore, novel environments, which capture VTA activation, result in improved spatial learning dependent on the hippocampus. Importantly, this novelty-driven boost in memory is abolished by dopamine antagonists, suggesting that this effect is dopamine dependent (Li, Cullen, Anwyl, & Rowan, 2003).

In addition to the compelling evidence from the animal literature, work from human studies also supports the idea that dopamine and VTA activation improve hippocampal-dependent memory performance. It is impossible to measure neurotransmitter activity directly using fMRI. To directly examine dopamine neurotransmitter effects in humans, researchers may manipulate dopamine through dopamine agonists or dopamine depletion protocols and then examine the effects on behavior and brain activation. For example, one study gave participants L-dopa (the precursor to dopamine) prior to a motivated memory encoding task. Interestingly, the authors observed that participants with the worst memory performance in the task also had personality and genetic scores indicative of low dopamine; these individuals benefited the most from L-dopa (Sumner, Duffy, Chen, & Adcock, 2013). Regarding the neural circuitry, in paradigms in which reward cues precede memoranda (information to be remembered; see Adcock et al., 2006; Callan & Schweighofer, 2008; Cohen, Rissman, Suthana, Castel, & Knowlton, 2014; Rainey et al., 2014; Wolosin et al., 2012) and in which the memorandum itself predicts reward (Bunzeck, Doeller, Dolan, & Düzel, 2012; Wittmann et al. 2005), activation within the VTA and hippocampus predict declarative memory performance. Indeed some studies have demonstrated that correlated activation between the VTA and hippocampus, not just activation within each region alone, predicts memory performance (Adcock et al., 2006; Callan & Schweighofer, 2008; Cohen et al., 2014;Wolosin et al., 2012).

Building on this fundamental work, recent research has investigated the behavioral and neural benefits of embedding neutral memoranda within rewarding contexts. Rather than directly incentivizing individual items, some studies have embedded neutral items within rewarding contexts. Loh and colleagues (2015) found that neutral items within a rewarding context received a memory boost and engaged the VTA to promote hippocampal-dependent memory. Murty and Adcock (2014) also observed VTA activation that predicted hippocampal responses to neutral, but unexpected, information.

To summarize, cross-species evidence suggests that activation of the VTA promotes hippocampal-dependent encoding, resulting in encoding of rich, flexible, relational memories. This is typically achieved via reward-related motivation, which drives an interrogative motivational state. This reward motivation can be achieved via directly incentivizing the memoranda as well as placing neutral items within a rewarding context.

Imperative Motivational States

We now turn to imperative motivational states and discuss the neural structures supporting this state, most centrally, the amygdala. We define imperative goal states as those focused on obtaining one immediate, compulsory goal. For the purpose of this chapter, we will highlight threat- and punishment-related behaviors. In general, research conducted in animals and humans alike suggests the amygdala is involved in threat and startle behaviors, which promote the animal achieving its immediate goal as opposed to promoting exploratory, interrogative behaviors.

Amygdala Activation Supports Motivated Behavior

Seminal work from the 1960s demonstrated that animals with amygdala lesions fail to demonstrate classic fear responses to threats (Davis, 1992; Xue, Steketee, & Sun, 2012). For example, they will no longer exhibit fear behavior in response to a predator. Beyond fear response deficits, animals with amygdala lesions also fail to effectively learn new fear associations, such as a light predicting a foot shock (LaBar & Cabeza, 2006; LeDoux 1992, 2003). Humans with amygdala lesions display characteristic behavioral deficits in perceiving and responding to threats as well (Adolphs et al., 2005; Broks et al., 1998; Scott et al., 1997). Supporting the animal and human patient work, human neuroimaging studies have found that the amygdala is active during punishment-motivated reinforcement learning (Büchel, Morris, Dolan, & Friston, 1998; LaBar, Gatenby, Gore, LeDoux, & Phelps 1998; LaBar, LeDoux, Spencer, & Phelps, 1995; Prévost, Liljeholm, Tyszka, & O'Doherty, 2012; Prévost, McCabe, Jessup, Bossaerts, & O'Doherty, 2011) as well as during the anticipation (Hahn et al., 2010) and avoidance of punishments (Mobbs et al., 2007; Mobbs, Marchant, et al., 2009; Schlund & Cataldo, 2010).

Amygdala-Cortical-MTL Connectivity

The amygdala directly projects to the hippocampus as well as the adjacent cortical MTL (McGaugh, 2004). This connectivity has been shown to support memory formation because amygdala stimulation increases long-term potentiation, the cellular marker of memory, in the hippocampus and cortical MTL (Akirav & Richter-Levin, 1999; Frey, Bergado-Rosado, Seidenbecher, Pape, & Frey, 2001; Ikegaya, Abe, Saito, & Nishiyama, 1995). Of note for this chapter is that early research examining connectivity with the amygdala did not discriminate strength of connectivity between the amygdala and cortical MTL compared to the amygdala and hippocampus. However, there is emerging evidence suggesting the amygdala may bias encoding of information in the cortical MTL over the hippocampus, as described next.

Amygdala Activation Supports Cortical-MTL-Dependent Encoding

Accumulating evidence forms a compelling story that (1) punishment motivation and threat processing engage the amygdala and (2) amygdala activation in these negative contexts facilitates cortical-MTL-dependent memory encoding (rather than hippocampal-based encoding). Here and in the following sections we discuss the meaning of the distinct engagement of these discrete memory networks. Research indicates that the form and content of memory differs depending on the neural networks engaged during encoding. Specifically cortical-MTL-dependent memories are sparse, inflexible, and decontextualized. Their purpose is to extract salient features from a motivationally relevant event. For example, if you see an unfamiliar, large dog running directly toward you while you are at a dog park with a friend, you may have heightened encoding of the dog and your interaction with it but not really remember anything else about your surroundings. Hippocampal-dependent memories, however, are rich, flexible, and contextualized. In the dog example, if you love dogs and you see an adorable, very friendly puppy in a park, you might remember the entire experience, including the park environment, the weather, and friends you were in the park with, rather than encoding just the sparse event (i.e., the interaction with the dog; Figure 7.3).

Although the amygdala has anatomical connections to the hippocampus and cortical MTL, there is evidence to suggest that the amygdala preferentially supports memory reliant on the cortical MTL. For example, lesions in the amygdala selectively disrupt memory processing dependent on the cortical MTL but not the hippocampus (Farovik, Place, Miller, & Eichenbaum, 2011). Stimulation of the amygdala has also been shown to decrease hippocampal-dependent memories (Kim, Lee, Han, & Packard, 2001; McDonald & White, 1993; Roozendaal, Griffith, Buranday, De Quervain, & McGaugh, 2003). In human research, it has been observed that threat-related stimuli disrupt more flexible, relational memory (such as source memory) (Dougal, Phelps, & Davachi, 2007; Rimmele, Davachi, Petrov, Dougal, & Phelps, 2011; Rimmele, Davachi, & Phelps, 2012). Neuroimaging research also supports a strong relationship between amygdala activation and cortical-MTL-dependent memories. A common manner of dissociating the neural architecture supporting these types of memories is whether memory for items is enhanced, suggesting cortical-MTL engagement, or if relational, spatial, or contextual information is enhanced, suggesting hippocampal engagement. Studies have found that amygdala activation during encoding predicts memory for threatening items but not memory for items in their surrounding context (Dougal et al., 2007; Kensinger & Schacter, 2006). Related work has shown that successful encoding of emotional stimuli depends on interactions between the amygdala and cortical MTL but not the amygdala and hippocampus (Dolcos, LaBar, & Cabeza, 2004; Ritchey, Dolcos, & Cabeza, 2008).

Punishment-Motivated Behavior Supports Cortical-MTL-Dependent Encoding

As introduced in the section “Extrinsic Motivation: Punishment Influences on Memory

Encoding," researchers have recently begun to study how punishment modulates memory and how it may or may not differ from motivation by reward incentives. Work in our laboratory, among others, has used punishment incentives in humans, complementing the large body of research in animals using shocks as incentives. In one study, from our laboratory we used monetary rewards and punishment (shocks) as incentives in a spatial navigation task (Murty et al., 2011). This task was a virtual version of the Morris water maze, a classic task used in the animal literature in which rats must swim around an opaque pool to find an escape platform they can rest on. Rats complete this many times, and learning is assessed based on time and path length to the platform (D'Hooge & De Deyn, 2001; Vorhees & Williams, 2006). In the human variation, participants navigated the virtual space in order to find a reward or to escape a shock. Navigating to find rewards improved memory and navigating to avoid shocks impaired memory. This behavioral paradigm supports prior research suggesting that reward (Murty et al., 2011, 2016; Wolosin et al., 2012), but not punishment (Dougal et al., 2007; Kensinger & Schacter, 2006; Murty et al., 2011, 2016; Qin, Hermans, van Marle, & Fernández, 2012; Schwarze et al., 2012), contributes to relational memory.

In order to investigate whether engagement of the amygdala-cortical-MTL circuitry supports punishment-motivated encoding, our group (and others) has begun to use punishment as an incentive in neuroimaging studies (Bauch et al., 2014; Murty et al., 2012, 2016; Qin et al., 2012; Schwarze et al., 2012). In the Murty et al. (2012) study (using punishment rather than monetary incentives to influence encoding) the threat of shock improved memory for the scenes. However, unlike reward incentives, which engage the VTA-hippocampal network, the threat of shock engaged the amygdala-cortical-MTL network to predict memory enhancements.

In addition to punishment effects on intentional encoding paradigms, we have also investigated the impact of the threat of punishment on incidental learning. In a paradigm adapted from Murty and Adcock (2014), we embedded neutral but unexpected items within a string of items viewed in either a high- or low-motivational state (Murty et al., 2016). Two groups completed the task: one under reward incentives ($2 or $0.10) and a second group under punishment incentives (shock, no shock). In support of our predictions, results revealed that items viewed in a high reward state received a motivated memory boost, and items viewed in the high punishment state did not. Consistent with our prior work, reward engaged the hippocampus, but not cortical MTL, whereas punishment engaged cortical MTL, but not hippocampus. This work revealed a double dissociation between motivational state and MTL-dependent encoding. Related work from other labs confirms engagement of the amygdala and cortical MTL during punishment motivated encoding (Bauch et al., 2014; Qin et al., 2012; Schwarze et al., 2012).

Working Model: Motivational State Engages MTL Networks to Differentially Shape the Form and Content of Memory

Recently, Murty and Adcock (2017) formulated a comprehensive model outlining how motivational states engage discrete MTL regions to influence what we remember and how it is encoded in the brain. The model suggests three main tenets: (1) the motivational state of a person during encoding predicts which brain regions are engaged during memory formation, (2) brain areas recruited during learning determine the representations

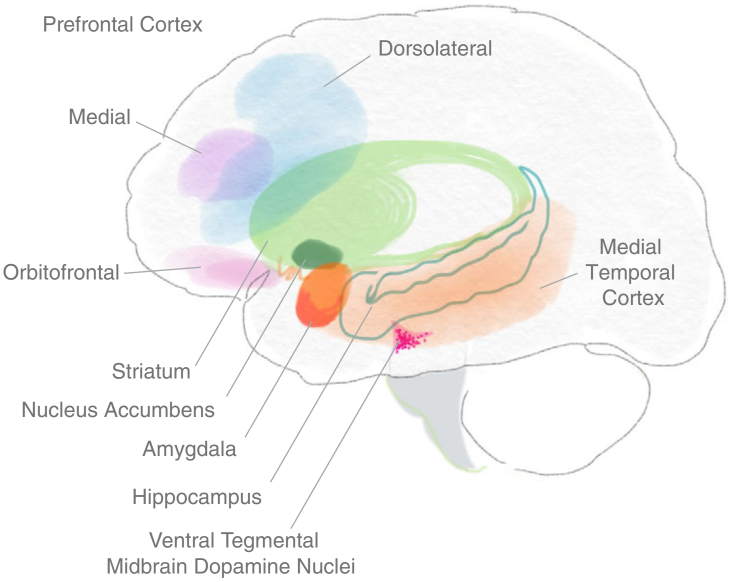

Figure 7.4 Brain structures implicated in motivated memory. Interrogative motivational states, most often elicited experimentally using motivation to obtain rewards, are associated with activation of the VTA and nearby nuclei regions (fuchsia dots). VTA activation is typically accompanied by enhanced encoding activation in the hippocampus proper (teal outline) and increased connectivity with the nucleus accumbens (green oval) and lateral and dorsomedial prefrontal cortex (blue and violet wash). Imperative motivational states, most often elicited experimentally by avoidance of punishments, are associated with activation of the amygdala (orange oval). Amygdala activation is typically accompanied by enhanced encoding activation in the medial temporal lobe cortex (peach wash) and increased connectivity with orbitofrontal cortex (pink wash).

of memory, and (3) across individuals, motivational incentives show varying modulation of memory formation predicted by individual functional architecture (Figures 7.3 and 7.4).

This model uses the framework of imperative and interrogative motivational states. Reward incentives typically prime people for interrogative motivational states, and punishment typically primes people for imperative states. As already described in detail, imperative motivational states are associated with amygdala neuromodulation. Interrogative motivational states, however, typically recruit the VTA and dopamine neuromodulation to support memory. Moreover, the distinct MTL regions recruited to support memory formation differ based on motivational state: Imperative motivation reliably engages the cortical MTL, and interrogative motivation typically recruits the hippocampus proper. Via this differential encoding architecture, motivational state also influences the form of memory. Imperative states are associated with improved item memory but not relational memory. Therefore, environmental representations are reduced, and item-specific memory is enhanced. Interrogative memory, however, is associated with improved item, contextual, and relational memory. This model aims to integrate information about the valence of the incentive (reward-punishment), with motivational state (interrogative-imperative) to describe how the neural substrates supporting memory are engaged (VTA-hippocampus–amygdala-cortical-MTL) to modulate different types of memory (relational-sparse).

Valence, Motivational States, and Neural Network

As described throughout this chapter, typically interrogative motivational states have been elicited via use of reward incentives, whereas imperative motivational states have been elicited via punishment incentives. However, the mapping between valence and motivational state is not one-to-one. For example a high-salience reward can engage an imperative motivational state (Ariely, Gneezy, Loewenstein, & Mazar, 2009; Callan & Schweighofer, 2008; Lesscher & Vanderschuren, 2012; Mobbs, Hassabis, et al., 2009; Murty et al., 2011; Robinson, Warlow, & Berridge, 2014; Yu, 2015), and a low-salience punishment can engage an interrogative motivational state (Carter et al., 2009; Delgado, Jou, & Phelps, 2011). Likewise, the mapping between valence and the neural substrates engaged by reward and punishment is not categorical (see Murty & Adcock, 2017, for a review). The theoretical framework proposed by Murty and Adcock (2017) and described here argues that rather than using valence as a method of framing motivation's impact on memory, it may be more parsimonious to use the motivational state of the individual (regardless of incentive valence) and the neural regions engaged to characterize how motivation affects memory.

Two common scenarios in which reward does not correspond with an interrogative motivational state are addiction and choking under pressure. Some individuals exhibit an aversive arousal response to opportunities for reward, displaying increased measures of subjective (self-report) and objective anxiety (galvanic skin response) as well as poor hippocampal-dependent memory and reduced VTA and hippocampal activation (Callan & Schweighofer, 2008; Murty et al., 2011).

In the context of addiction, drugs cues (once well learned) activate the central amygdala and result in devaluation of other motivational goals that are not drug related (Lesscher & Vanderschuren, 2012). Furthermore, in addicted individuals, hippocampal learning has been shown to be impaired relative to striatal learning, which is more rigid and supports the development of habits (Packard, 2009; Wingard & Packard, 2008). As a result, inflexible associations are established between drugs and the actions needed to obtain them. These associations are insensitive to contextual information (Yin & Knowlton, 2006). In this manner, reward motivation can produce imperative motivational states that actually disrupt, rather than promote, hippocampal encoding.

Likewise, there are circumstances in which punishment recruits interrogative motivational states and VTA rather than amygdala activation. In circumstances in which a punishment is distal and avoidable, the hippocampus rather than the amygdala is engaged (Mobbs, Marchant, et al., 2009). Similarly, in cases in which monetary loss, rather than aversive shock, is used as a punishment, the VTA and hippocampus are recruited during learning (Carter et al., 2009; Delgado et al., 2011). These more minor punishments or losses appear to be less salient and less imperative, resulting in interrogative states, supporting elaborated learning about the environment so that the individual can avoid future loss.

FUTURE DIRECTIONS

Mechanisms and Timescales: Memory Encoding Versus Consolidation

Thus far, we have described motivation's influence on memory encoding. By far the majority of research on motivation and memory has focused on the encoding phase. These encoding manipulations have been tested using immediate retrieval (e.g., Wolosin et al., 2012) and delayed retrieval (typically 24 hours; e.g., Adcock et al., 2006). Interestingly, motivation effects on immediate and delayed retrieval are not always consistent. Work from our laboratory suggests this may have to do with reward predictability, stimulus timing, and presumed engagement of the dopamine system (Stanek, 2016). Future work is needed, however, to fully elucidate any differences between the impact motivation has on immediate versus delayed memory retrieval.

Recent research is beginning to examine how motivation influences memory consolidation directly. Consolidation describes the processes that occur after memory encoding to stabilize memory representations. These include cellular-level processes as well as systems-level processes that serve to stabilize memory (Dudai, Karni, & Born, 2015; Mednick, Cai, Shuman, Anagnostaras, & Wixted, 2011). The most common manner of studying memory consolidation is to manipulate delayed, rather than immediate, memory. In this way, scientists are able to probe memories that have been consolidated into long-term storage. Work from the animal literature demonstrated that administering dopamine agonists facilitates markers of late long-term potentiation (LTP), a cellular signature of memory (Huang & Kandel, 1995). Furthermore, administration of dopaminergic drugs (e.g., dopamine antagonists) influenced delayed, but not immediate, memory tests (Wang & Morris 2010).

Additional work has linked post-encoding effects on memory with motivation and the VTA-hippocampal network. Interestingly, as an additional way of testing motivation effects on consolidation, researchers are now performing explicit behavioral manipulations following encoding in order to test post-encoding dynamics. In one exemplary study, Salvetti and colleagues (2014) had rodents perform a spatial navigation task, which was followed by either neutral or rewarding events. Note that unlike the majority of work we have described thus far, the manipulation here occurred after the encoding period. The authors observed improved task performance on the spatial navigation task during a delayed memory test following rewarding events, compared with neutral events. Furthermore, post-encoding manipulations using reward are impaired by blocking dopamine, suggesting that post-encoding enhancement of memory depends on the dopamine system (Feld, Besedovsky, Kaida, Münte, & Born, 2014).

Similar work using human participants replicates the effects observed in the animal literature (Braun, Vail, Wimmer, & Shohamy, 2014; Murayama & Kitagami, 2014; Murayama & Kuhbandner, 2011; Murty, Tompary, Adcock, & Davachi, 2017; Patil, Murty, Dunsmoor, Phelps, & Davachi, 2017). Indeed work by Murayama and Kuhbander (2011) showed that rewarding individuals for learning trivia facts improved delayed, but not immediate, tests of memory. This post-encoding reward boost to delayed, but not immediate, memory has been replicated by other groups as well (Braun et al., 2014; Murayama & Kitagami, 2014; Patil et al., 2017). Similar to the animal literature, when human participants are given dopamine antagonists post-encoding, the reward benefits to delayed memory are abolished (Feld et al., 2014).

Although the neural mechanism underlying post-encoding boosts to memory remains to be fully elucidated, there is recent work suggesting that replay of memory traces occurs following encoding to strengthen memories. Research using animal models and human participants has shown replay of memory traces following encoding during periods of rest. In rodent models, events paired with reward are replayed more frequently than those associated with no reward (Gomperts, Kloosterman, & Wilson, 2015; Singer & Frank, 2009; Valdes, McNaughton, & Fellous, 2011). In humans, changes in connectivity in the reward circuitry (including the VTA, MTL, and sensory cortex) predict reward's benefit on memory. To date, no work has examined the post-encoding effects of punishment on memory formation. This will be an interesting future direction for scientists to pursue.

Individual Differences Modulate Motivation's Impact on Memory

Generally speaking, much research investigating motivation's impact on memory formation suggests that reward engages an interrogative goal state, promotes co-activation between the VTA and hippocampus, and produces rich, flexible, and highly contextualized memories. However, not all individuals have the same reaction to reward incentives. Indeed, research examining individual differences in reward responsivity has found that some individuals respond to reward in a manner similar to punishment (Ariely et al., 2009; Mobbs, Hassabis, et al., 2009; Yu, 2015). For example, high-anxiety individuals (characterized via either self-report (Callan & Schweighofer, 2008) or increased galvanic skin responses (Murty et al., 2011) engage the amygdala and cortical MTL during reward-motivated learning, producing memories that are item-specific, inflexible, and devoid of contextual information (Murty & Adcock, 2017; Murty & Dickerson, 2016). Thus, the neural networks engaged and resultant memory representations resemble stereotypical learning under threat rather than reward. This work illustrates the importance of examining individual differences in interpreting the effects of motivational incentives and the subsequent impact on memory.

Taken as a whole, the findings regarding individual differences in interpreting motivational incentives have profound implications for how different individuals engage and learn from their environments. Continued work in this area is needed to help us fully understand how individuals react to different motivational states in order to learn from their environments.

CONCLUSION

The goal of this chapter is to discuss the exciting research that has occurred since the new millennium uniting the fields of motivation and memory. Newly emerging work has described how motivation affects the form and content of declarative memory. Motivational incentives (i.e., reward, punishment) elicit motivational states (i.e., interrogative, imperative), which recruit distinct neural networks (i.e., VTA-hippocampus, amygdala-cortical-MTL) to promote different types of memory (relational, sparse). This new work has exciting implications for extant models of memory and models of motivation. In addition, it has implications for translation to everyday life for healthy humans and clinical populations alike.

Implications for Models of Memory

The evidence described in this chapter revises a long prevailing view of memory: that the primary determining factor predicting variations in memory success is cognitive, that is, encoding strategy. This traditional model of memory can now be updated based on the research showing how motivation affects declarative memory formation, shaping memories to support future behavior.

Implications for Models of Motivation

The newly emerging work discussed here also updates former models of motivation.

Motivation has historically been examined piecemeal. As described at the beginning of the chapter, many different subfields within neuroscience and psychology have studied motivation and operationalized it in very different ways (see Braver et al., 2014). It is important to try to unify current approaches to and definitions of motivation into a cohesive model for the field to progress further. The work reviewed here highlights how multiple dimensions of motivation, including approach-avoidance, extrinsic-intrinsic, and positive-negative can be integrated by considering how motivation affects learning and memory. Here we combined valence (positive-negative) and goal orientation (approach-avoidance) to reconceptualize these combined states as interrogative or imperative goal states. This framework is advantageous because it predicts how an individual may interact and respond to an incentive as well as how an individual's goal state affects brain activity, plasticity, and, ultimately, subsequent behavior.

Implications for Translation

Finally, the work described here has the potential for translation to understanding motivation in daily life in healthy and clinical populations. One important finding from the body of research described here is that individual differences strongly modulate motivational state and, subsequently, the degree to which people engage with their environments in an interrogative or imperative manner. Experimental evidence supports that motivational state determines the neural networks engaged during learning (VTA-hippocampus or amygdala—cortical-MTL), which subsequently affects the content and form of memory (relational versus sparse). Knowledge of how different individuals respond to incentives and engage with their environments has profound implications for the fields of education, parenting, and business. In these circumstances, people are often learning under contexts of punishment. Even under contexts of reward, some individuals may interpret reward opportunities as threats. If so, they are likely to encode sparse item information rather than rich, contextual information. This dictates how they are later able to recall and interact with the information, which can affect performance and future behavior.

How motivation affects declarative memory is also important for translation to clinical domains. As we understand more about how the brain learns and remembers and how motivation affects this process, we can try to develop better learning-based therapies to improve treatment in a variety of clinical disorders. The majority of neurological and psychological disorders are not completely treated by medication or therapy. This situation demands new treatments that are safe and effective. As our understanding of the biology and psychology of how motivation modulates learning and memory improves, we are hopeful that this knowledge can be applied to improve treatments and ultimately patient outcomes.

Future Directions and Open Questions

Opportunities for building on the foundational work and exciting new findings described here include more basic research on topics such as intrinsic motivation, punishment, and individual differences as well as translation to clinical populations and investigation in applied contexts, such as education and business. Although the work described in this chapter has generated substantial new knowledge, many open questions remain. In general, our understanding of how intrinsic motivation modulates memory is not as complete as our knowledge of how extrinsic reinforcers influence behavior. Exciting new directions examining how volitional motivation affects memory performance will surely improve our knowledge of memory and motivation. Further work examining individual differences in perceiving motivational incentives will also help us understand brain function and behavior. Indeed, there are many open research questions that remain available for the next generation of eager scientists exploring the fascinating topic of human-motivated behavior.

REFERENCES

Adcock, R. A., Thangavel, A., Whitfield-Gabrieli, S., Knutson, B., & Gabrieli, J.D.E. (2006). Reward-motivated learning: Mesolimbic activation precedes memory formation. *Neuron*, *50*(3), 507–517.

Adolphs, R., Gosselin, F., Buchanan, T. W., Tranel, D., Schyns, P., & Damasio. A. R. (2005). A mechanism for impaired fear recognition after amygdala damage. *Nature*, *433*(7021), 68–72.

Akirav, I., & Richter-Levin, G. (1999). Priming stimulation in the basolateral amygdala modulates synaptic plasticity in the rat dentate gyrus. *Neuroscience Letters*, *270*(2), 83–86.

Amaral, D. G., & Cowan, W. M. (1980). Subcortical afferents to the hippocampal formation in the monkey. *The Journal of Comparative Neurology*, *189*(4), 573–591.

Ariely, D., Gneezy, U., Loewenstein, G., & Mazar, N. (2009). Large stakes and big mistakes. *The Review of Economic Studies*, *76*(2), 451–469.

Bargh, J. A., Gollwitzer, P. M., & Oettingen, G. (2010). Motivation. In S. Fiske, D. Gilbert, & G. Lindzey (Eds.), *Handbook of social psychology* (Vol. 5, pp. 268–316). New York, NY: Wiley.

Bauch, E. M., Rausch, V. H., & Bunzeck, N. (2014). Pain anticipation recruits the mesolimbic system and differentially modulates subsequent recognition memory. *Human Brain Mapping*, *35*(9), 4594–4606.

Berridge, K. C. (2004). Motivation concepts in behavioral neuroscience. *Physiology & Behavior*, *81*(2), 179–209.

Bijleveld, E., Custers, R., & Aarts, H. (2010). Unconscious reward cues increase invested effort, but do not change speed-accuracy tradeoffs. *Cognition*, *115*(2), 330–335.

Blanchard, T. C., Hayden, B. Y., & Bromberg-Martin, E. S. (2015). Orbitofrontal cortex uses distinct codes for different choice attributes in decisions motivated by curiosity. *Neuron*, *85*(3), 602–614.

Bloom, A. D. (1991). *The republic of Plato: Philosophy, political theory*. New York, NY: Basic Books.

Boll, S., Gamer, M., Gluth, S., Finsterbusch, J., & Büchel, C. (2013). Separate amygdala subregions signal surprise and predictiveness during associative fear learning in humans. *The European Journal of Neuroscience*, *37*(5), 758–767.

Braun, E., Vail, B., Wimmer, G., & Shohamy, D. (2014). *Both rewards and losses retroactively enhance memory for preceding neutral events*. Presented at the annual meeting for the Society for Neuroscience, November, Washington, DC.

Braver, T. S., Krug, M. K., Chiew, K. S., Kool, W., Westbrook, J. A., Clement, N. J., Adcock, R. A., et al. (2014). Mechanisms of motivation-cognition interaction: Challenges and opportunities. *Cognitive, Affective & Behavioral Neuroscience*, *14*(2), 443–472.

Broks, P., Young, A. W., Maratos, E. J., Coffey, P. J., Calder, A. J., Isaac, C. L., Mayes, A. R., et al. (1998). Face processing impairments after encephalitis: Amygdala damage and recognition of fear. *Neuropsychologia*, *36*(1), 59–70.

Bromberg-Martin, E. S., & Hikosaka, O. (2009). Midbrain dopamine neurons signal preference for advance information about upcoming rewards. *Neuron*, *63*(1), 119–126.

Bromberg-Martin, E. S., Matsumoto, M., & Hikosaka, O. (2010). Dopamine in motivational control: Rewarding, aversive, and alerting. *Neuron*, *68*(5), 815–834.

Büchel, C., Morris, J., Dolan, R. J., & Friston, K. J. (1998). Brain systems mediating aversive conditioning: An event-related fMRI study. *Neuron*, *20*(5), 947–957.

Bunzeck, N., Doeller, C. F., Dolan, R. J., & Düzel, E. (2012). Contextual interaction between novelty and reward processing within the mesolimbic system. *Human Brain Mapping*, *33*(6), 1309–1324.

Bunzeck, N. N., & Düzel, E. (2006). Absolute coding of stimulus novelty in the human substantia nigra/VTA. *Neuron*, *51*(3), 369–379.

Callan, D. E., & Schweighofer, N. (2008). Positive and negative modulation of word learning by reward anticipation. *Human Brain Mapping*, *29*(2), 237–249.

Camps, M., Kelly, P. H., & Palacios, J. M. (1990). Autoradiographic localization of dopamine D1 and D2 receptors in the brain of several mammalian species. *Journal of Neural Transmission*, *80*(2), 105–127.

Capa, R. L., Bustin, G. M., Cleeremans, A., & Hansenne, M. (2011). Conscious and unconscious reward cues can affect a critical component of executive control. *Experimental Psychology*, *58*(5), 370–375.

Carter, R. M., Macinnes, J., Huettel, S. A., & Adcock, R. A. (2009). Activation in the VTA and nucleus accumbens increases in anticipation of both gains and losses. *Frontiers in Behavioral Neuroscience*, *3*(August), 21.

Carver, C. S., & Harmon-Jones, E. (2009). Anger is an approach-related affect: Evidence and implications. *Psychological Bulletin*, *135*(2), 183–204.

Carver, C. S., & Scheier, M. F. (2001). *On the self-regulation of behavior*. New York, NY: Cambridge University Press.

Chiew, K. S., & Braver, T. S. (2011). Positive affect versus reward: Emotional and motivational influences on cognitive control. *Frontiers in Psychology*, *2*(October), 279.

Chiew, K. S., & Braver, T. S. (2013). Temporal dynamics of motivation-cognitive control interactions revealed by high-resolution pupillometry. *Frontiers in Psychology*, *4*(January), 15.

Clark, R. E., Manns, J. R., & Squire, L. R. (2002). Classical conditioning, awareness, and brain systems. *Trends in Cognitive Sciences*, *6*(12), 524–531.

Clark, R. E., & Squire, L. R. (1998). Classical conditioning and brain systems: The role of awareness. *Science*, *280*(5360), 77–81.

Clement, N. (2016). *Modulation of active exploratory processes in humans*. PhD thesis, Duke University.

Cohen, M. S., Rissman, J., Suthana, N. A., Castel, N. A., & Knowlton, B. J. (2014). Value-based modulation of memory encoding involves strategic engagement of fronto-temporal semantic processing regions. *Cognitive, Affective & Behavioral Neuroscience*, *14*(2), 578–592.

Corbit, L. H., & Balleine, B. W. (2015). Learning and motivational processes contributing to Pavlovian-instrumental transfer and their neural bases: Dopamine and beyond. *Current Topics in Behavioral Neuroscience*, *27*, 259–289.

Craik, F.I.M. (2002). Levels of processing: Past, present, and future? *Memory*, *10*(5–6), 305–318.

Craik, F.I.M., & Lockhart, R. S. (1972). Levels of processing: A framework for memory research. *Journal of Verbal Learning and Verbal Behavior*, *11*(6), 671–684.

Craik, F.I.M., & Tulving, E. (1975). Depth of processing and the retention of words in episodic memory. *Journal of Experimental Psychology*. Retrieved from http://psycnet.apa.org/journals/xge/104/3/268/

Custers, R., & Aarts, H. (2010). The unconscious will: How the pursuit of goals operates outside of conscious awareness. *Science*, *329*(5987), 47–50.

Custers, R., Eitam, B., & Bargh, J. A. (2012). Conscious and unconscious processes in goal pursuit. In H. Aarts & A. J. Elliot (Eds.), *Goal-directed behavior*. New York, NY: Psychology Press.

Davachi, L. (2006). Item, context and relational episodic encoding in humans. *Current Opinion in Neurobiology*, *16*(6), 693–700.

Davidow, J. Y., Foerde, K., Galván, A., & Shohamy, D. (2016). An upside to reward sensitivity: The hippocampus supports enhanced reinforcement learning in adolescence. *Neuron*, *92*(1), 93–99.

Davis, M. (1992). The role of the amygdala in fear and anxiety. *Annual Review of Neuroscience*, *15*(1), 353–375.

Daw, N. D., & Doya, K. (2006). The computational neurobiology of learning and reward. *Current Opinion in Neurobiology*, *16*(2), 199–204.

Deci, E. L. (1971). Effects of externally mediated rewards on intrinsic motivation. *Journal of Personality and Social Psychology*, *18*(1), 105.

Deci, E. L., & Ryan, R. M. (1985). *Intrinsic motivation and self-determination in human behavior: Perspectives in social psychology*. New York, NY: Springer US.

Deci, E. L., Koestner, R., & Ryan, R. M. (1999). A meta-analytic review of experiments examining the effects of extrinsic rewards on intrinsic motivation. *Psychological Bulletin*, *125*(6), 627–668; discussion 692–700.

Delgado, M. R. (2007). Reward-related responses in the human striatum. *Annals of the New York Academy of Sciences*, *1104*(May), 70–88.

Delgado, M. R., & Dickerson, K. C. (2012). Reward-related learning via multiple memory systems. *Biological Psychiatry*, *72*(2), 134–41.

Delgado, M. R., Jou, R. L., & Phelps, E. A. (2011). Neural systems underlying aversive conditioning in humans with primary and secondary reinforcers. *Frontiers in Neuroscience*, *5*(May), 71.

DePasque, S., & Tricomi, E. (2015). Effects of intrinsic motivation on feedback processing during learning. *NeuroImage*, *119*(October), 175–186.

DePasque Swanson, S., & Tricomi, E. (2014). Goals and task difficulty expectations modulate striatal responses to feedback. *Cognitive, Affective & Behavioral Neuroscience*, *14*(2), 610–620.

D'Hooge, R., & De Deyn, P. P. (2001). Applications of the Morris water maze in the study of learning and memory. *Brain Research. Brain Research Reviews*, *36*(1), 60–90.

Dickerson, K. C., Li, J., & Delgado, M. R. (2011). Parallel contributions of distinct human memory systems during probabilistic learning. *NeuroImage*, *55*(1), 266–276.

Dickerson, K. C., & Delgado, M. R. (2015). Contributions of the hippocampus to feedback learning. *Cognitive, Affective & Behavioral Neuroscience*, *15*(4), 861–877.

Dobryakova, E., & Tricomi, E. (2013). Basal ganglia engagement during feedback processing after a substantial delay. *Cognitive, Affective & Behavioral Neuroscience*, *13*(4), 725–736.

Dolcos, F., LaBar, K. S., & Cabeza, R. (2004). Interaction between the amygdala and the medial temporal lobe memory system predicts better memory for emotional events. *Neuron*, *42*(5), 855–863.

Dougal, S., Phelps, E. A., & Davachi, L. (2007). The role of medial temporal lobe in item recognition and source recollection of emotional stimuli. *Cognitive, Affective & Behavioral Neuroscience*, *7*(3), 233–242.

Dudai, Y., Karni, A., & Born, J. (2015). The consolidation and transformation of memory. *Neuron*, *88*(1), 20–32.

Düzel, E., Bunzeck, N., Guitart-Masip, M., & Düzel, S. (2010). Novelty-related motivation of anticipation and exploration by dopamine (NOMAD): Implications for healthy aging. *Neuroscience and Biobehavioral Reviews*, *34*(5), 660–669.

Eichenbaum, H., & Cohen, N. J. (2004). *From conditioning to conscious recollection: Memory systems of the brain*. New York, NY: Oxford University Press.

Farovik, A., Place, R. J., Miller, D. R., & Eichenbaum, H. (2011). Amygdala lesions selectively impair familiarity in recognition memory. *Nature Neuroscience*, *14*(11), 1416–1417.

Farrer, C., & Frith, C. D. (2002). Experiencing oneself vs. another person as being the cause of an action: The neural correlates of the experience of agency. *NeuroImage*, *15*(3), 596–603.

Feld, G. B., Besedovsky, L., Kaida, K., Münte, T. F., & Born, J. (2014). Dopamine D2-like receptor activation wipes out preferential consolidation of high over low reward memories during human sleep. *Journal of Cognitive Neuroscience*, *26*(10), 2310–2320.

Foerde, K., Race, E., Verfaellie, M., & Shohamy, D. (2013). A role for the medial temporal lobe in feedback-driven learning: Evidence from amnesia. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *33*(13), 5698–5704.

Foerde, K., & Shohamy, D. (2011). Feedback timing modulates brain systems for learning in humans. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *31*(37), 13157–13167.

Frey, S., Bergado-Rosado, J., Seidenbecher, T., Pape, H. C., & Frey, J. U. (2001). Reinforcement of early long-term potentiation (early-LTP) in dentate gyrus by stimulation of the basolateral amygdala: Heterosynaptic induction mechanisms of late-LTP. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *21*(10), 3697–3703.

Gomperts, S. N., Kloosterman, F., & Wilson, M. A. (2015). VTA neurons coordinate with the hippocampal reactivation of spatial experience. *eLife*, *4*(October). doi:10.7554/eLife.05360.

Gruber, M. J., Gelman, B. D., & Ranganath, C. (2014). States of curiosity modulate hippocampus-dependent learning via the dopaminergic circuit. *Neuron*, *84*(2), 486–496.

Gruber, M. J., Ritchey, M., Wang, S. F., Doss, M. K., & Ranganath, C. (2016). Post-learning hippocampal dynamics promote preferential retention of rewarding events. *Neuron*, *89*(5), 1110–1120.

Hahn, T., Dresler, T., Plichta, M. M., Ehlis, A.-C., Ernst, L. H., Markulin, F., Polak, T., et al. (2010). Functional amygdala-hippocampus connectivity during anticipation of aversive events is associated with Gray's trait "sensitivity to punishment." *Biological Psychiatry*, *68*(5), 459–464.

Harman, K. L., Humphrey, G. K., & Goodale, M. A. (1999). Active manual control of object views facilitates visual recognition. *Current Biology*, *9*(22), 1315–1318.

Harmon-Jones, E. 2003). Anger and the behavioral approach system. *Personality and Individual Differences*, *35*(5), 995–1005.

Higgins, E. T. (1987). Self-discrepancy: A theory relating self and affect. *Psychological Review*, *94*(3), 319–340.

Huang, Y. Y., & Kandel, E. R. (1995). D1/D5 receptor agonists induce a protein synthesis-dependent late potentiation in the CA1 region of the hippocampus. *Proceedings of the National Academy of Sciences of the United States of America*, *92*(7), 2446–2450.

Ikegaya, Y., Abe, K., Saito, H., & Nishiyama, N. (1995). Medial amygdala enhances synaptic transmission and synaptic plasticity in the dentate gyrus of rats in vivo. *Journal of Neurophysiology*, *74*(5), 2201–2203.

Ikemoto, S., & Panksepp, J. (1999). The role of nucleus accumbens dopamine in motivated behavior: A unifying interpretation with special reference to reward-seeking. *Brain Research Reviews*, *31*(1), 6–41.

James, W. (1950). *The principles of psychology*. Mineola, NY: Dover. (Originally published in 1890)

Jimura, K., Locke, H. S., & Braver, T. S. (2010). Prefrontal cortex mediation of cognitive enhancement in rewarding motivational contexts. *Proceedings of the National Academy of Sciences of the United States of America*, *107*(19), 8871–8876.

Johansen, J. P., Cain, C. K., Ostroff, L. E., & LeDoux, J. E. (2011). Molecular mechanisms of fear learning and memory. *Cell*, *147*(3), 509–524.

Kahn, I., & Shohamy, D. (2013). Intrinsic connectivity between the hippocampus, nucleus accumbens, and ventral tegmental area in humans. *Hippocampus*, *23*(3), 187–192.

Kakade, S., & Dayan, P. (2002). Dopamine: Generalization and bonuses. *Neural Networks: The Official Journal of the International Neural Network Society*, *15*(4–6), 549–559.

Kang, M. J., Hsu, M., Krajbich, I. M., Loewenstein, G., McClure, S. M., Wang, J. T.-Y., & Camerer, C. F. (2009). The wick in the candle of learning: Epistemic curiosity activates reward circuitry and enhances memory. *Psychological Science*, *20*(8), 963–973.

Kensinger, E. A., & Schacter, D. L. (2006). Amygdala activity is associated with the successful encoding of item, but not source, information for positive and negative stimuli. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *26*(9), 2564–2670.

Khan, Z. U., Gutiérrez, A., Martín, R., Peñafiel, A., Rivera, A., & de la Calle, A. (2000). Dopamine D5 receptors of rat and human brain. *Neuroscience*, *100*(4), 689–699.

Kim, J. J., Lee, H. J., Han, J. S., & Packard, M. G. (2001). Amygdala is critical for stress-induced modulation of hippocampal long-term potentiation and learning. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *21*(14), 5222–5228.

Koster, R., Guitart-Masip, M., Dolan, R. J., & Düzel, E. (2015). Basal ganglia activity mirrors a benefit of action and reward on long-lasting event memory. *Cerebral Cortex*, *25*(12), 4908–4917.

Krebs, R. M., Schott, B. H., & Düzel, E. (2009). Personality traits are differentially associated with patterns of reward and novelty processing in the human substantia nigra/ventral tegmental area. *Biological Psychiatry*, *65*(2), 103–110.

Krebs, R. M., Heipertz, D., Schuetze, H., & Düzel, E. (2011). Novelty increases the mesolimbic functional connectivity of the substantia nigra/ventral tegmental area (SN/VTA) during reward anticipation: Evidence from high-resolution fMRI. *NeuroImage*, *58*(2), 647–655.

Kwon, H. G., & Jang, S. H. (2014). Differences in neural connectivity between the substantia nigra and ventral tegmental area in the human brain. *Frontiers in Human Neuroscience*, *8*(February), 41.

LaBar, K. S., & Cabeza, R. (2006). Cognitive neuroscience of emotional memory. *Nature Reviews Neuroscience*, *7*(1), 54–64.

LaBar, K. S., Gatenby, J. C., Gore, J. C., LeDoux, J. E., & Phelps E. A. (1998). Human amygdala activation during conditioned fear acquisition and extinction: A mixed-trial fMRI study. *Neuron*, *20*(5), 937–945.

LaBar, K. S., LeDoux, J. E., Spencer, D. D., & Phelps, E. A. (1995). Impaired fear conditioning following unilateral temporal lobectomy in humans. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *15*(10), 6846–6855.

LeDoux, J. E. (1992). Brain mechanisms of emotion and emotional learning. *Current Opinion in Neurobiology*, *2*(2), 191–197.

LeDoux, J. (2003). The emotional brain, fear, and the amygdala. *Cellular and Molecular Neurobiology*, *23*(4–5), 727–738.

Lee, W., & Reeve, J. (2013). Self-determined, but not non-self-determined, motivation predicts activations in the anterior insular cortex: An fMRI study of personal agency. *Social Cognitive and Affective Neuroscience*, *8*(5), 538–545.

Lempert, K. M., & Tricomi, E. (2016). The value of being wrong: Intermittent feedback delivery alters the striatal response to negative feedback. *Journal of Cognitive Neuroscience*, *28*(2), 261–274.

Leotti, L. A., & Delgado, M. R. (2011). The inherent reward of choice. *Psychological Science*, *22*(10), 1310–1318.

Leotti, L. A., & Delgado, M. R. (2014). The value of exercising control over monetary gains and losses. *Psychological Science*, *25*(2), 596–604.

Lesscher, H.M.B., & Vanderschuren, L.J.M. J. (2012). Compulsive drug use and its neural substrates. *Reviews in the Neurosciences*, *23*(5–6), 731–745.

Li, S., Cullen, W. K., Anwyl, R., & Rowan, M. J. (2003). Dopamine-dependent facilitation of LTP induction in hippocampal CA1 by exposure to spatial novelty. *Nature Neuroscience*, *6*(5), 526–31.

Little, K. Y., Carroll, F. I, & Cassin, B. J. (1995). Characterization and localization of [125I] RTI-121 binding sites in human striatum and medial temporal lobe. *The Journal of Pharmacology and Experimental Therapeutics*, *274*(3), 1473–1483.

Liu, C. H., Ward, J., & Markall, H. (2007). The role of active exploration of 3D face stimuli on recognition memory of facial information.

Journal of Experimental Psychology: Human Perception and Performance, *33*(4), 895–904.

Loh, E., Deacon, M., de Boer, L., Dolan, R. J., & Düzel, E. (2015). Sharing a context with other rewarding events increases the probability that neutral events will be recollected. *Frontiers in Human Neuroscience*, *9*, 683.

Loh, E., Kumaran, D., Koster, R., Berron, D., Dolan, R., & Düzel, E. (2016). Context-specific activation of hippocampus and SN/VTA by reward is related to enhanced long-term memory for embedded objects. *Neurobiology of Learning and Memory*, *134 Pt A*(October), 65–77.

MacInnes, J. J., Dickerson, K. C., Chen, N.-K., & Adcock, R. A. (2016). Cognitive neurostimulation: Learning to volitionally sustain ventral tegmental area activation. *Neuron*, *89*(6), 1331–1342.

Markant, D., DuBrow, S., Davachi, L., & Gureckis, T. M. (2014). Deconstructing the effect of self-directed study on episodic memory. *Memory & Cognition*, *42*(8), 1211–1224.

Mather, M., & Schoeke, A. (2011). Positive outcomes enhance incidental learning for both younger and older adults. *Frontiers in Neuroscience*, *5*(November), 129.

Mattfeld, A. T., & Stark, C.E.L. (2011). Striatal and medial temporal lobe functional interactions during visuomotor associative learning. *Cerebral Cortex*, *21*(3), 647–658.

Mattfeld, A. T., & Stark, C.E.L. (2015). Functional contributions and interactions between the human hippocampus and subregions of the striatum during arbitrary associative learning and memory. *Hippocampus*, *25*(8), 900–911.

McDonald, R. J., & White, N. M. (1993). A triple dissociation of memory systems: Hippocampus, amygdala, and dorsal striatum. *Behavioral Neuroscience*, *107*(1), 3–22.

McGaugh, J. L. (2004). The amygdala modulates the consolidation of memories of emotionally arousing experiences. *Annual Review of Neuroscience*, *27*, 1–28.

Mednick, S. C., Cai, D. J., Shuman, T., Anagnostaras, S., & Wixted, J. T. (2011). An opportunistic theory of cellular and systems consolidation. *Trends in Neurosciences*, *34*(10), 504–514.

Meijer, F., & Van der Lubbe, R.H.J. (2011). Active exploration improves perceptual sensitivity for virtual 3D objects in visual recognition tasks. *Vision Research*, *51*(23–24), 2431–2439.

Miendlarzewska, E. A., Bavelier, D., & Schwartz, S. (2016). Influence of reward motivation on human declarative memory. *Neuroscience and Biobehavioral Reviews*, *61*(February), 156–176.

Mobbs, D., Hassabis, D., Seymour, B., Marchant, J. L., Weiskopf, N., Dolan, R. J., & Frith, C. D. (2009). Choking on the money: Reward-based performance decrements are associated with midbrain activity. *Psychological Science*, *20*(8), 955–962.

Mobbs, D., Marchant, J. L., Hassabis, D., Seymour, B., Tan, F., Gray, M., Petrovic, P., Dolan, R. J., & Frith, C. D. (2009). From threat to fear: The neural organization of defensive fear systems in humans. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *29*(39), 12236–12243.

Mobbs, D., Petrovic, P., Marchant, J. L., Hassabis, D., Weiskopf, N., Seymour, B., Dolan, R. J., & Frith, C. D. (2007). When fear is near: Threat imminence elicits prefrontal-periaqueductal gray shifts in humans. *Science*, *317*(5841), 1079–1083.

Mukherjee, J., Christian, B. T., Dunigan, K. A., Shi, B., Narayanan, T. K., Satter, M., & Mantil, J. (2002). Brain imaging of 18F-fallypride in normal volunteers: Blood analysis, distribution, test-retest studies, and preliminary assessment of sensitivity to aging effects on dopamine D-2/D-3 receptors. *Synapse*, *46*(3), 170–188.

Murayama, K., & Kitagami, S. (2014). Consolidation power of extrinsic rewards: Reward cues enhance long-term memory for irrelevant past events. *Journal of Experimental Psychology. General*, *143*(1), 15–20.

Murayama, K., & Kuhbandner, C. (2011). Money enhances memory consolidation—but only for boring material. *Cognition*, *119*(1), 120–124.

Murayama, K., Matsumoto, M., Izuma, K., & Matsumoto, K. (2010). Neural basis of the undermining effect of monetary reward on intrinsic motivation. *Proceedings of the National Academy of Sciences of the United States of America*, *107*(49), 20911–20916.

Murty, V. P., & Adcock, R. A. (2014). Enriched encoding: Reward motivation organizes cortical networks for hippocampal detection of unexpected events. *Cerebral Cortex*, *24*(8), 2160–2168.

Murty, V. P., & Adcock, R. A. (2017). Distinct medial temporal lobe network states as neural contexts for motivated memory formation. In D. E. Hannula & M. C. Duff, *The hippocampus from cells to systems: Structure, connectivity, and functional contributions to memory and flexible cognition*. New York, NY: Springer International.

Murty, V. P., & Dickerson, K. C. (2016). Motivational influences on memory. In S.-I. Kim, J. Reeve, & M. Bong (Eds.), *Recent developments in neuroscience research on human motivation: Advances in motivation and achievement* (Vol. *19*, pp. 203–27). Bingley, UK: Emerald Group Publishing Limited.

Murty, V. P., DuBrow, S., & Davachi, L. (2015). The simple act of choosing influences declarative memory. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *35*(16), 6255–6264.

Murty, V. P., Hall, O. F., Hunter, L. E., Phelps, E. A., & Davachi, L. (2016). Episodic memories predict adaptive value-based decision-making. *Journal of Experimental Psychology: General*, *145*(5), 548–558.

Murty, V. P., LaBar, K. S., & Adcock, R. A. (2012). Threat of punishment motivates memory encoding via amygdala, not midbrain, interactions with the medial temporal lobe. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *32*(26), 8969–8976.

Murty, V. P., LaBar, K. S., & Adcock, R. A. (2016). Distinct medial temporal networks encode surprise during motivation by reward versus punishment. *Neurobiology of Learning and Memory (February)*. doi:10.1016/j.nlm.2016.01.018

Murty, V. P., LaBar, K. S., Hamilton, D. A., & Adcock, R. A. (2011). Is all motivation good for learning? Dissociable influences of approach and avoidance motivation in declarative memory. *Learning & Memory*, *18*(11), 712–717.

Murty, V. P., Shermohammed, M., Smith, D. V., Carter, R. M., Huettel, S. A., & Adcock, R. A. (2014). Resting state networks distinguish human ventral tegmental area from substantia nigra. *NeuroImage*, *100*(October), 580–589.

Murty, V. P., Tompary, A. R., Adcock, R. A., & Davachi, L. (2017). Selectivity in post-encoding connectivity with high-level visual cortex is associated with reward-motivated memory. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *37*(3), 537–545.

Niv, Y. (2007). Cost, benefit, tonic, phasic: What do response rates tell us about dopamine and motivation? *Annals of the New York Academy of Sciences*, *1104*(May), 357–376.

Niv, Y., Joel, D., & Dayan, P. (2006). A normative perspective on motivation. *Trends in Cognitive Sciences*, *10*(8), 375–381.

O'Carroll, C. M., Martin, S. J., Sandin, J., Frenguelli, B., & Morris, R.G.M. (2006). Dopaminergic modulation of the persistence of one-trial hippocampus-dependent memory. *Learning & Memory*, *13*(6), 760–769.

Olds, J., & Milner, P. (1954). Positive reinforcement produced by electrical stimulation of septal area and other regions of rat brain. *Journal of Comparative and Physiological Psychology*, *47*(6), 419–427.

Packard, M. G. (2009). Anxiety, cognition, and habit: A multiple memory systems perspective. *Brain Research*, *1293*(October), 121–128.

Paller, K. A., & Wagner, A. D. (2002). Observing the transformation of experience into memory. *Trends in Cognitive Sciences*, *6*(2), 93–102.

Patil, A., Murty, V. P., Dunsmoor, J. E., Phelps, E. A., & Davachi, L. (2017). Reward retroactively enhances memory consolidation for related items. *Learning & Memory*, *24*, 65–69.

Pessiglione, M., Schmidt, L., Draganski, B., Kalisch, R., Lau, H., Dolan, R. J., & Frith, C. D. (2007). How the brain translates money into force: A neuroimaging study of subliminal motivation. *Science*, *316*(5826), 904–906.

Plancher, G., Barra, J., Orriols, E., & Piolino, P. (2013). The influence of action on episodic memory: A virtual reality study. *Quarterly Journal of Experimental Psychology*, *66*(5), 895–909.

Prévost, C., Liljeholm, M., Tyszka, J. M., & O'Doherty, J. P. (2012). Neural correlates of specific and general Pavlovian-to-instrumental transfer within human amygdalar subregions: A high-resolution fMRI study. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *32*(24), 8383–8390.

Prévost, C., McCabe, J. A., Jessup, R. K., Bossaerts, P., & O'Doherty, J. P. (2011). Differentiable contributions of human amygdalar subregions in the computations underlying reward and avoidance learning. *The European Journal of Neuroscience*, *34*(1), 134–145.

Qin, S., Hermans, E. J., van Marle, H.J.F., & Fernández, G. (2012). Understanding low reliability of memories for neutral information encoded under stress: Alterations in memory-related activation in the hippocampus and midbrain. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *32*(12), 4032–4041.

Rainey, C., Dickerson, K. C., & Adcock, R. A. (2014). *Interoceptive signals for encoding*. Presented at the annual meeting for the Society of Neuroscience, November, Washington, DC.

Rimmele, U., Davachi, L., Petrov, R., Dougal, S., & Phelps, E. A. (2011). Emotion enhances the subjective feeling of remembering, despite lower accuracy for contextual details. *Emotion*, *11*(3), 553–562.

Rimmele, U., Davachi, L., & Phelps, E. A. (2012). Memory for time and place contributes to enhanced confidence in memories for emotional events. *Emotion*, *12*(4), 834–846.

Ritchey, M., Dolcos, F., & Cabeza, R. (2008). Role of amygdala connectivity in the persistence of emotional memories over time: An event-related FMRI investigation. *Cerebral Cortex*, *18*(11), 2494–2504.

Robinson, M.J.F., Warlow, S. M., & Berridge, K. C. (2014). Optogenetic excitation of central amygdala amplifies and narrows incentive motivation to pursue one reward above another. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *34*(50), 16567–16580.

Roozendaal, B., Griffith, Q. K., Buranday, J., De Quervain, D.J.F., & McGaugh, J. L. (2003). The hippocampus mediates glucocorticoid-induced impairment of spatial memory retrieval: Dependence on the basolateral amygdala. *Proceedings of the National Academy of Sciences of the United States of America*, *100*(3), 1328–1233.

Ryan, R. M., & Deci, E. L. (2000). Self-determination theory and the facilitation of intrinsic motivation, social development, and well-being. *The American Psychologist*, *55*(1), 68–78.

Salamone, J. D. (1994). The involvement of nucleus accumbens dopamine in appetitive and aversive motivation. *Behavioural Brain Research*, *61*(2), 117–133.

Salamone, J. D., & Correa, M. (2012). The mysterious motivational functions of mesolimbic dopamine. *Neuron*, *76*(3), 470–485.

Salamone, J. D., Pardo, M., Yohn, S. E., López-Cruz, L., SanMiguel, N., & Correa, M. (2016). Mesolimbic dopamine and the regulation of motivated behavior. *Current Topics in Behavioral Neurosciences*, *27*, 231–257.

Salvetti, B., Morris, R.G.M., & Wang, S.-H. (2014). The role of rewarding and novel events in facilitating memory persistence in a separate spatial memory task. *Learning & Memory*, *21*(2), 61–72.

Samson, Y., Wu, J. J., Friedman, A. H., & Davis, J. N. (1990). Catecholaminergic innervation of the hippocampus in the cynomolgus monkey. *The Journal of Comparative Neurology*, *298*(2), 250–263.

Schlund, M. W., & Cataldo, M. F. (2010). Amygdala involvement in human avoidance, escape and approach behavior. *NeuroImage*, *53*(2), 769–776.

Schmidt, L., Forgeot d'Arc, B., Lafargue, G., Galanaud, D., Czernecki, V., Grabli, D., Schüpbach, M., et al. (2008). Disconnecting force from money: Effects of basal ganglia damage on incentive motivation. *Brain: A Journal of Neurology*, *131*(Pt 5), 1303–1310.

Schultz, W. (2016). Reward functions of the basal ganglia. *Journal of Neural Transmission*, *23*(7), 679–693.

Schwarze, U., Bingel, U., & Sommer, T. (2012). Event-related nociceptive arousal enhances memory consolidation for neutral scenes.

The Journal of Neuroscience: The Official Journal of the Society for Neuroscience, *32*(4), 1481–1487.

Scott, S. K., Young, A. W., Calder, A. J., Hellawell, D. J., Aggleton, J. P., & Johnson, M. (1997). Impaired auditory recognition of fear and anger following bilateral amygdala lesions. *Nature*, *385*(6613), 254–257.

Shohamy, D., & Adcock, R. A. (2010). Dopamine and adaptive memory. *Trends in Cognitive Sciences*, *14*(10), 464–472.

Shohamy, D., & Turk-Browne, N. B. (2013). Mechanisms for widespread hippocampal involvement in cognition. *Journal of Experimental Psychology: General 142*(4), 1159–1170.

Singer, A. C., & Frank, L. M. (2009). Rewarded outcomes enhance reactivation of experience in the hippocampus. *Neuron*, *64*(6), 910–921.

Sperduti, M., Delaveau, P., Fossati, P., & Nadel, J. (2011). Different brain structures related to self- and external-agency attribution: A brief review and meta-analysis. *Brain Structure and Function*, *216*(2), 151–157.

Squire, L. R. (1992a). Declarative and nondeclarative memory: Multiple brain systems supporting learning and memory. *Journal of Cognitive Neuroscience*, *4*(3), 232–243.

Squire, L. R. (1992b). Memory and the hippocampus: A synthesis from findings with rats, monkeys, and humans. *Psychological Review*, *99*(2), 195–231.

Squire, L. R. (2004). Memory systems of the brain: A brief history and current perspective. *Neurobiology of Learning and Memory*, *82*(3), 171–177.

Squire, L. R., Stark, C.E.L., & Clark, R. E. (2004). The medial temporal lobe. *Annual Review of Neuroscience*, *27*, 279–306.

Squire, L. R., & Wixted, J. T. (2011). The cognitive neuroscience of human memory since H. *M. Annual Review of Neuroscience*, *34*, 259–288.

Stanek, J. K. (2016). *Expectation modulates episodic memory formation via dopaminergic circuitry*. PhD thesis, Duke University.

Stuber, G. D., Roitman, M. F., Phillips, P.E.M., Carelli, R. M., & Wightman, R. M. (2005). Rapid dopamine signaling in the nucleus accumbens during contingent and noncontingent cocaine administration. *Neuropsychopharmacology: Official Publication of the American College of Neuropsychopharmacology*, *30*(5), 853–863.

Sumner, E. J., Duffy, K. B., Chen, J. J., & Adcock, R. A. (2013). *Dopaminergic modulation of reward-motivated memory*. Presented at the annual meeting of the Cognitive Neuroscience Society, April 16, San Francisco, CA.

Tang, S.-H., & Hall, V. C. (1995). The overjustification effect: A meta-analysis. *Applied Cognitive Psychology*, *9*(5), 365–404.

Tomasi, D., & Volkow, N. D. (2014). Functional connectivity of substantia nigra and ventral tegmental area: Maturation during adolescence and effects of ADHD. *Cerebral Cortex*, *24*(4), 935–944.

Tricomi, E. M., Delgado, M. R., & Fiez, J. A. (2004). Modulation of caudate activity by action contingency. *Neuron*, *41*(2), 281–292.

Tricomi, E., & Fiez, J. A. (2008). Feedback signals in the caudate reflect goal achievement on a declarative memory task. *NeuroImage*, *41*(3), 1154–1167.

Tricomi, E., & Fiez, J. A. (2012). Information content and reward processing in the human striatum during performance of a declarative memory task. *Cognitive, Affective & Behavioral Neuroscience*, *12*(2), 361–372.

Tsukiura, T., & Cabeza, R. (2008). Orbitofrontal and hippocampal contributions to memory for face-name associations: The rewarding power of a smile. *Neuropsychologia*, *46*(9), 2310–2319.

Tulving, E., & Schacter, D. L. (1990). Priming and human memory systems. *Science*, *247*(4940), 301–306.

Tulving, E., Schacter, D. L., & Stark, H. A. (1982). Priming effects in word-fragment completion are independent of recognition memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *8*(4), 336–342.

Valdes, J., McNaughton, B., & Fellous, J.-M. (2011). Experience-dependent reactivations of ventral tegmental area neurons in the rat. *BMC Neuroscience*. doi:10.1186/1471–2202–12-S1-P107.

Vorhees, C. V., & Williams, M. T. (2006). Morris water maze: Procedures for assessing spatial and related forms of learning and memory. *Nature Protocols*, *1*(2), 848–858.

Voss, J. L., Galvan, A., & Gonsalves, B. D. (2011). Cortical regions recruited for complex active-learning strategies and action planning exhibit rapid reactivation during memory retrieval. *Neuropsychologia*, *49*(14), 3956–3966.

Voss, J. L., Gonsalves, B. D., Federmeier, K. D., Tranel, D., & Cohen, N. J. (2011). Hippocampal brain-network coordination during volitional exploratory behavior enhances learning. *Nature Neuroscience*, *14*(1), 115–120.

Voss, J. L., Warren, D. E., Gonsalves, B. D., Federmeier, K. D., Tranel, T., & Cohen, N. J. (2011). Spontaneous revisitation during visual exploration as a link among strategic behavior, learning, and the hippocampus. *Proceedings of the National Academy of Sciences of the United States of America*, *108*(31), E402–E409.

Wang, S.-H., & Morris, R.G.M. (2010). Hippocampal-neocortical interactions in memory formation, consolidation, and reconsolidation. *Annual Review of Psychology*, *61*, 49–79, C1–C4.

Wiersma, U. J. (1992). The effects of extrinsic rewards in intrinsic motivation: A meta-analysis. *Journal of Occupational and Organizational Psychology*, *65*(2), 101–114.

Wimmer, G. E., Braun, E. K., Daw, N. D., & Shohamy, D. (2014). Episodic memory encoding interferes with reward learning and decreases striatal prediction errors. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *34*(45), 14901–14912.

Wimmer, G. E., & Shohamy, D. (2012). Preference by association: How memory mechanisms in the hippocampus bias decisions. *Science*, *338*(6104), 270–273.

Wingard, J. C., & Packard, M. G. (2008). The amygdala and emotional modulation of competition between cognitive and habit memory. *Behavioural Brain Research*, *193*(1), 126–131.

Wise, R. A. (2004). Dopamine, learning and motivation. *Nature Reviews Neuroscience*, *5*(6), 483–494.

Wittmann, B. C., Bunzeck, N., Dolan, R. J., & Düzel, E. (2007). Anticipation of novelty recruits reward system and hippocampus while promoting recollection. *NeuroImage*, *38*(1), 194–202.

Wittmann, B. C., Schott, B. H., Guderian, S., Frey, J. U., Heinze, H.-J., & Düzel, E. (2005). Reward-related FMRI activation of dopaminergic midbrain is associated with enhanced hippocampus-dependent long-term memory formation. *Neuron*, *45*(3), 459–467.

Wolosin, S. M., Zeithamova, D., & Preston, A. R. (2012). Reward modulation of hippocampal subfield activation during successful associative encoding and retrieval. *Journal of Cognitive Neuroscience*, *24*(7), 1532–1547.

Xue, Y., Steketee, J. D., & Sun, W. (2012). Inactivation of the central nucleus of the amygdala reduces the effect of punishment on cocaine self-administration in rats. *The European Journal of Neuroscience*, *35*(5), 775–783.

Yin, H. H., & Knowlton, B. J. (2006). The role of the basal ganglia in habit formation. *Nature Reviews Neuroscience*, *7*(6), 464–476.

Yu, R. (2015). Choking under pressure: The neuropsychological mechanisms of incentive-induced performance decrements. *Frontiers in Behavioral Neuroscience*, *9*(February), 19.