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Integrating Cognitive and Affective Neuroscience

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Abstract: A growing body of literature indicates that motivation can critically shape long-term memory formation in the service of adaptive behavior. In the present chapter, we review recent cognitive neuroscience evidence of motivational influences on memory, with a focus on anatomical pathways by which neuromodulatory networks support encoding-related activity in distinct subregions of the medial temporal lobe. We argue that engagement of distinct neural circuits as a function of motivational context at encoding leads to formation of different memory representations, supporting different patterns of adaptive behavior. We present a novel neurocognitive model, the *Interrogative/Imperative model of information-seeking*, to account for pursuit of learning goals. Interrogative or imperative modes of information-seeking are often, but not necessarily, associated with approach or avoidance motivation, respectively. We also discuss additional influences on motivated memory encoding, including intrinsic motivation, curiosity, choice and cognitive control processes. Taken together, this body of research suggests that the nature of memory representations depends on an individual's neurophysiological response to, rather than extrinsic qualities of, a given motivational manipulation or context at the time of encoding. Finally, we discuss potential applications of these research findings to real-life educational settings and directions for future research.

Motivated Memory: Integrating Cognitive and Affective Neuroscience

Motivation is critical to learning and memory, and there is widespread use of strategies to motivate learning in the classroom, many of which rely on intuition. However, empirical neuroscience research has only recently begun to examine the large repertoire of motivated behaviors and memory processes

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central to education, positioning itself to provide evidence-based solutions. Early work in neuroscience focused on relatively simple forms of associative learning. These included Pavlovian stimulus-stimulus learning (where a motivationally significant stimulus is associated with a previously neutral stimulus; for example, the sound of a bell with a food reward) and instrumental stimulus-response learning (where the strength of a behavior is modified by rewarding or punishing consequences; for example, learning to press a button to receive a food reward). Using such models has yielded rich psychology and neuroscience literature on motivation in associative learning. More recently, these investigations have been augmented by new lines of cognitive neuroscience research that address a common intuition among educators: motivation plays a critical role in the way information is learned and encoded into long-term memory.

The recognition that motivational influences can act on long-term memory processing by the medial temporal lobe (MTL) represents an important advance in memory research. Learning and memory over extended timescales (i.e., multiple days or years) is essential to adaptive behavior and cannot be accounted for by the Pavlovian or instrumental associative learning mechanisms historically studied in the context of motivation. In the present chapter, we review emerging cognitive neuroscience evidence regarding motivational effects on learning and memory formation. We discuss several factors important to motivational contexts and their impact on neural activity and cognition, including incentive salience, expectation, extrinsic versus intrinsic motivation, curiosity, and choice. Although this new research area opens many questions, based on present evidence we argue that distinct motivational states serve as adaptive contexts for learning, engaging distinct neural circuitry to support memory encoding and, thus, leading to distinct forms of memory representation. Importantly, present evidence suggests that an individual's neurophysiological response to a motivational manipulation is critical in determining the nature of the encoded memory representation, rather than extrinsic qualities of the incentive. Finally, we discuss the implications of these basic scientific findings regarding motivation and learning in applied settings, such as educational or managerial environments.

Motivation and Memory Encoding: Core Neural and Psychological Substrates

The MTL areas of the brain have long been recognized as critical to the encoding and retrieval of declarative long-term memory (Squire, Zola-Morgan, & Stuart, 1991; Tulving & Markowitsch, 1998). The MTL comprises substructures that play complementary, yet distinct, roles in these processes; these structures include the hippocampus (and surrounding cortical regions: the perirhinal, parahippocampal, and entorhinal cortices; reviewed in Davachi,

2006). Decades of research in both animal and human models suggest that the hippocampus plays an essential role in binding elements of an episode into an interrelated, multimodal long-term memory (Eichenbaum, 2000; Tulving & Murray, 1985, Tulving, 2002). More recent evidence has refined this account, suggesting that overlying cortical regions represent distinct aspects or features of an episode to be bound together: the perirhinal cortex selectively supports memory for items previously encountered, and the parahippocampal cortex supports memory for the environmental context in which the items were encountered. The hippocampus thus binds item and context memory together to produce a coherent memory episode (Davachi, 2006; Konkel & Cohen, 2009; Ranganath, 2010).

Largely distinct from the research literature investigating the MTL and long-term memory, a separate body of affective neuroscientific research has sought to characterize the modulatory neurotransmitter dopamine and its effects on motivated behavior. Widespread evidence suggests that the mesolimbic and mesocortical dopamine pathways, which primarily originate in the *ventral tegmental area* (VTA) and associated nuclei in the midbrain and project widely to regions in the limbic system and cerebral cortex, critically support motivated pursuit of a broad range of rewards, such as food and sex (Olds & Milner, 1954; Willner & Scheel-Krüger, 1991). Given the opportunity to directly self-stimulate the VTA (i.e., through a button press), rodents forego other biologically relevant rewards to continue self-stimulation, providing direct evidence for a critical role of the VTA in motivation and reinforcement (Olds & Milner, 1954). Neuroimaging studies in humans, using functional magnetic resonance imaging (fMRI), have likewise observed increased mesolimbic activity during anticipation and pursuit of reward relative to non-reward outcomes, typically using secondary rewards such as money (Carter, MacInnes, Huettel, & Adcock, 2009; Knutson, Taylor, Kaufman, Peterson, & Glover, 2005).

Functional relationships between the mesolimbic dopamine system and the MTL are well positioned to support motivated learning. Animal studies have long demonstrated anatomical connectivity between the VTA and hippocampus (Amaral & Cowan, 1980; Samson, Wu, Friedman, & Davis, 1990). Novel stimuli can elicit midbrain dopamine neuron activity, and dopamine released in the hippocampus stabilizes long-term potentiation,[1] supporting learning of new information (reviewed in Lisman & Grace, 2005), including single-trial learning (Neugebauer, Korz, & Frey, 2009; O'Carroll et al., 2006; reviewed further in Shohamy and Adcock, 2010).

Despite these findings in learning and memory and the robust link between dopamine and motivation, the potential effects of motivational manipulations on encoding into long-term memory and their supporting neural circuitry have only recently begun to be investigated. Wittmann et al. (2005) examined

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1 Long-term potentiation refers to a persistent increase in synaptic strength based on recent patterns of neuronal firing at that synapse.

incidental memory (with a three-week delay between encoding and retrieval) for reward predictive and non-reward predictive picture stimuli, and observed a subsequent memory benefit for stimuli that predicted reward over those that did not. The researchers found that this memory benefit was associated with enhanced activity, both in the dopaminergic midbrain and in the hippocampus, at the time of encoding. Likewise, a seminal experiment from our laboratory (Adcock, Thangavel, Whitfield-Gabrieli, Knutson, & Gabrieli, 2006) examined neural activity during memory encoding as a function of a reward incentive manipulation. In contrast to incidental memory encoding in the study by Wittmann and colleagues (2005), participants intentionally encoded picture stimuli in anticipation of receiving monetary incentive (signaled prior to each picture stimulus with a high versus low value reward cue) for successfully remembering each in a recognition test 24 hours later. Recognition memory was superior for stimuli associated with high versus low value cues. Additionally, encoding of high (versus low) value stimuli was associated with enhanced anticipatory activity in the VTA as well as the hippocampus. Importantly, on a trial-by-trial basis, functional connectivity between the VTA and hippocampus at the time of encoding predicted subsequent memory success.

In addition to mesolimbic and MTL regions, research has indicated a role for higher cortical regions in motivated memory encoding. The lateral prefrontal cortex (PFC) is robustly innervated by dopamine (Goldman-Rakic & Friedman, 1991; Sawaguchi & Goldman-Rakic, 1991), may provide informational input to the dopaminergic midbrain to support adaptive behavior (Ballard et al., 2011), and plays a fundamental role in supporting cognitive control processes (Miller & Cohen, 2001); accordingly, recognition of the contributions of such PFC-based control processes to memory encoding is steadily growing (Blumenfeld & Ranganath, 2007; Wang & Morris, 2010). In a recent study from our laboratory, lateral PFC activity and hippocampal connectivity were associated with the encoding of surprising information under reward anticipation (Murty, LaBar, & Adcock, 2016); similarly, PFC and VTA co-activation has been observed during reward-motivated memory encoding (Cohen, Rissman, Suthana, Castel, & Knowlton, 2014). Together, these findings indicate a role for PFC-based control processes, potentially as mediators of interactions between neuromodulatory and MTL memory systems, in supporting motivated memory encoding. Neuroanatomical circuitry associated with motivated memory encoding is shown in Figure 21.1.

Taken together, these studies suggest that manipulating motivation through reward anticipation can lead to enhanced encoding and long-term memory via dopaminergic input from the VTA to the hippocampus, with potential modulation via the PFC. Wittmann and colleagues (2005) characterized enhanced memory for reward-signaling stimuli as a function of VTA and hippocampal activity. Adcock and colleagues (2006) observed that anticipatory activity in mesolimbic dopamine system regions – that is, activity elicited prior to the presentation of stimuli to be remembered – predicted enhanced memory. This
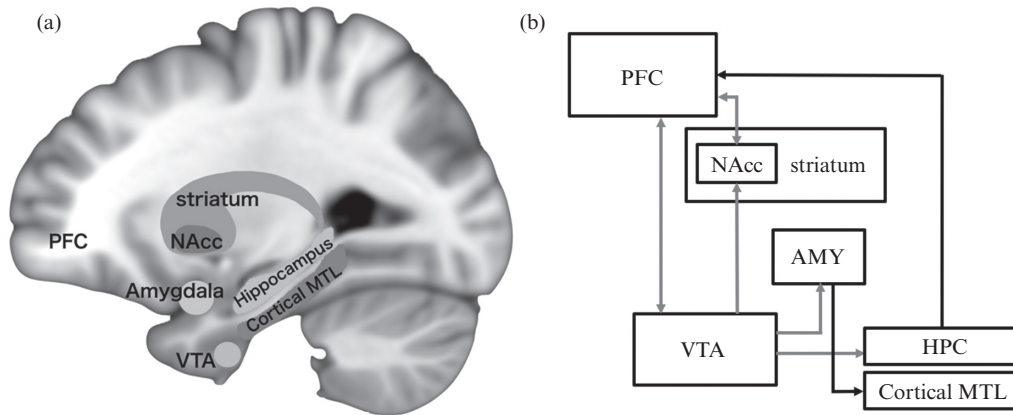
Figure 21.1. *Key neuroanatomical circuitry associated with reward-motivated memory encoding shown in terms of (A) an anatomical schematic and (B) proposed connections between regions. Note that these diagrams are not intended to be comprehensive, but instead highlight key regions and connections for clarity. Mesolimbic dopamine neurons primarily originating in the VTA project widely to limbic and cortical targets (indicated by red arrow pathways). Under reward incentive, the hippocampus (HPC) receives dopaminergic input from the VTA and critically supports long-term memory formation. In contrast, under punishment motivation, the amygdala (AMY) is engaged and connects to cortical MTL regions. The VTA also projects to the nucleus accumbens (NAcc), a region within the ventral striatum associated with encoding reward value, and to the PFC, involved in the maintenance of information and control processes critical to memory encoding*

time course of activity parallels psychological conceptualizations of motivation as a sustained state that might enhance learning (Dweck, 1986; Schunk, Meece, & Pintrich, 2014; Utman, 1997), in contrast to prior observations of memory enhancement in response to transient signals of reward, novelty, surprise, or distinctiveness (Parkin, 1997; Tulving & Kroll, 1995). This observation further suggests that a motivational state can serve as an encoding context for memory independent of stimulus features, optimizing memory for different aspects of information depending on the goals that are active at the time of encoding.

Effects of Incentive Valence on Motivated Memory Encoding

Although early studies examining motivational effects on declarative long-term memory primarily manipulated motivation using rewards, the associative learning literature also has a rich history of characterizing the effects of punishments or threats on behavior using both classical (Pavlovian) and instrumental conditioning (Colwill & Rescorla, 1986; Mackintosh, 1983; Rescorla & Wagner, 1972). By emphasizing avoidance of undesired outcomes instead of

approach to desired outcomes, threat- or punishment-oriented motivational contexts might differ from reward-oriented motivational contexts in terms of relevant information and adaptive behavior, leading to different learning and memory outcomes. A recent study from our laboratory sought to clarify this issue, investigating episodic memory encoding following the encoding paradigm used in Adcock et al. (2006), but under threat of punishment via electric shock instead of reward incentives (Murty, LaBar, & Adcock, 2012). Recognition memory was enhanced under high versus low threat of punishment, but encoding under these conditions was associated with activity in neural regions distinct from those observed under reward-motivated encoding (e.g., in Adcock et al., 2006). Specifically, Murty and colleagues observed that successful memory encoding under threat of punishment was associated with enhanced anticipatory activity in the amygdala and enhanced connectivity between the amygdala and the parahippocampal and orbitofrontal cortices. This finding contrasts with successful reward-motivated memory encoding, which was instead associated with enhanced VTA activation and VTA-hippocampal connectivity (Adcock et al., 2006; Wittmann et al., 2005). Observed patterns of differential neural engagement associated with reward- versus punishment-motivated encoding are summarized in Figure 21.2.

Given that, as noted above, different substructures within the MTL may support distinct aspects of declarative memory (Davachi, 2006; Eichenbaum,
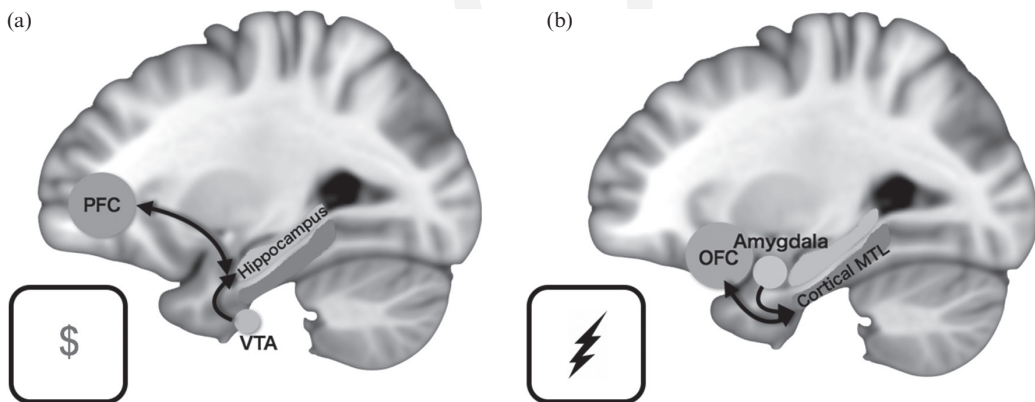

Figure 21.2. *Reward- versus punishment-motivated memory encoding is characterized by differential connections between neuromodulatory centers, MTL regions, and the neocortex. (A) Reward-motivated memory encoding (using money) is associated with enhanced VTA activity and connectivity to the hippocampus (Adcock et al., 2006), as well as enhanced hippocampus–PFC connectivity (Murty, LaBar, & Adcock, 2016). (B) In contrast, under threat of punishment (electric shock), memory encoding is associated with enhanced amygdala activity and connectivity to cortical MTL regions (specifically, parahippocampal cortex; Murty, LaBar, & Adcock, 2012) and cortical MTL–OFC connectivity (Murty, LaBar, & Adcock, 2016).*

Yonelinas, & Ranganath, 2007), the dissociable patterns of MTL activity observed in association with encoding success under reward- versus punishment-motivated encoding have important downstream implications for the potential nature of the memory representations encoded. The perirhinal and parahippocampal MTL cortices are linked to the encoding of item and context memory, respectively, but are thought to support relatively isolated, unitized representations of this information; in contrast, the hippocampus is thought to critically bind item and context information together into a coherent declarative memory episode. Thus, under punishment-motivated encoding, the absence of enhanced hippocampal engagement (as observed by Murty, LaBar, & Adcock, 2012) means that, although simple recognition may still be enhanced, benefits to relational memory (i.e., dependent on item-context binding) would not be predicted.

Behavioral evidence consistent with this prediction was observed in another recent study from our laboratory (Murty, LaBar, Hamilton, & Adcock, 2011), in which we investigated spatial memory performance under approach versus avoidance motivation using a virtual reality version of the Morris water task, requiring participants to navigate to correct platforms while avoiding incorrect platforms. Participant performance was assessed under reward (monetary incentives) or punishment (threat of electric shock) motivation, relative to a no-incentive baseline condition. We observed that, relative to the baseline, in the reward incentive condition performance improved, but under punishment incentives performance was impaired. Given that Morris task performance depends on relational memory for the platforms and their spatial locations relative to one another – processes that have been robustly linked to hippocampal function (Burgess, Maguire, & O'Keefe, 2002) – this pattern of performance is consistent with the hypothesis that reward (or approach) motivation might specifically promote hippocampally dependent memory, while punishment (or avoidance) motivation might not.

Beyond Reward and Punishment: Interrogative and Imperative Goal States

Limitations of the Valence Account of Motivated Encoding

Although differences have been observed in neural circuitry and behavioral outcome as a function of motivational valence, it is important to note that objective descriptors of external incentives (i.e., rewards or punishments) alone cannot determine motivational states (Higgins, 1998; Strauman & Wilson, 2010). Beyond goal valence (i.e., approach versus avoidance), factors such as situational context, other characteristics of the extrinsic incentives (i.e., salience) or individual differences may influence the nature of the motivational state evoked, the neural circuitry engaged, and the behavioral outcome

elicited. Despite growing recognition of the complex relationships between the valence of external incentives, the motivational states they may elicit, and the corresponding influence on behavior, these complexities have only recently begun to be systematically explored.

One well-characterized example of a putative disconnect between extrinsic incentive, anticipated motivational state, and behavioral outcomes is the phenomenon of "choking under pressure" (Baumeister, 1984; Beilock & Carr, 2001). In contrast to enhanced task performance under incentives, choking is characterized by performing more poorly than expected, given an anxious desire to perform well in a high-reward situation (Beilock & Carr, 2001). Arguably, this pattern of performance might reflect a situation where failing to obtain a high-stakes reward is interpreted as a threat or punishment, leading to a motivational state and behavioral outcome more typically associated with a punishment orientation. This situation and the choking outcome might in turn depend on aspects of the reward (i.e., salience or stakes) and individual variability (i.e., in tendencies toward stress or anxiety).

An important finding from different literature – Murty et al.'s (2011) investigation of reward versus punishment motivation on spatial memory encoding – supports the idea that individual variability may play a critical role in determining motivational outcome. In addition to the main effects of incentive valence previously described, individual variability in physiological arousal during the task, characterized using measures of skin conductance level (SCL), appeared to modulate the effect of motivational incentives on spatial memory performance. Specifically, increased SCL arousal in response to reward incentives was associated with decreased performance, both within and across subjects. In contrast, under punishment incentives, SCL arousal was globally elevated and did not correlate with memory performance. These observations were interpreted as evidence that high arousal could negate or reverse the benefits of reward incentives on spatial memory, and further suggest that any opportunity to gain reward that elicits a high state of physiological arousal might result in paradoxical encoding of memory representations similar to those encoded under threat of punishment.

The Interrogative/Imperative Model of Information-Seeking

Our laboratory proposed the *interrogative/imperative model of information-seeking* to account for the complexities observed in the research reviewed in this chapter's previous section. This model is summarized in Figure 21.3. It goes beyond valenced incentives to consider motivational contexts as adaptive modes of information-seeking; this model thus permits more specific predictions regarding the effects of different motivational contexts on learning and memory (Murty & Adcock, 2017). In part, this model was proposed to address observations that extrinsic incentive structures do not sufficiently characterize motivational states (Higgins, 1998). It asserts that goals can be primarily
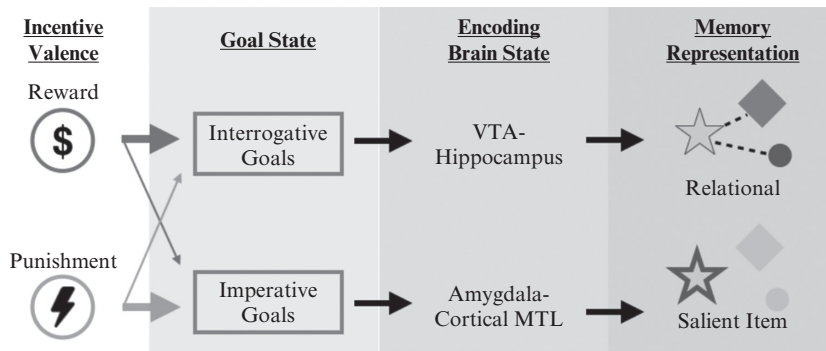
Figure 21.3. *The interrogative/imperative model of information-seeking and its predictions regarding the effects of motivation on MTL-dependent memory. This model predicts that reward- and punishment-valenced incentives generally (but not exclusively) drive interrogative versus imperative information-seeking goal states, respectively. These goal states in turn are associated with the engagement of discrete neural circuits during encoding, including different subregions of the MTL, ultimately leading to the formation of different memory representations. Memories encoded in an interrogative state are predicted to be richly detailed and highly relational, while memories encoded in an imperative state are predicted to be relatively sparse and centered on salient items. From "Distinct medial temporal lobe network states as neural contexts for motivated memory formation," by V. P. Murty and R. A. Adcock, 2017, in D. E. Hannula and M. C. Duff (eds.),* The Hippocampus from Cells to Systems*, pp. 467–501.*

associated with interrogative or imperative modes of information-seeking. Within this framework, an imperative mode is thought to be elicited when goal states are highly salient, urgent, and unambiguous; information-seeking in this model is thought to be relatively restricted and in the service of immediate goal outcomes, with additional information being of limited utility. In contrast, the interrogative mode is thought to be elicited when goal states are diffuse, low-urgency, or conflicting; this context elicits expansive information-seeking, supporting both immediate and more remote adaptive behavior. As such, the interrogative/imperative model of information-seeking predicts that learning in a high-threat or, more generally, a high-urgency situation tends to be limited, while learning in a low-threat or low-urgency situation might lead to greater exploration and thus improved retention of contextual information. By this account, valence is incompletely predictive, so that the anticipation of reward more often leads to an interrogative state, whereas the threat of punishment typically leads to an imperative state. However, other factors, including incentive salience (discussed in more detail later in the chapter) and individual differences (such as trait anxiety and stress reactivity) may also contribute to the goal state evoked. Ultimately, Murty and Adcock (2017) argue

that interrogative and imperative modes of information-seeking reflect the brain systems recruited during a motivational state, and that these modes and networks, rather than incentive valence, are the primary determinants of the nature of the memory representations encoded.

The model has the ability to account for experimental findings that reward-motivated learning is typically associated with enhanced activity in the VTA-hippocampal circuit and may be characterized by the encoding of more relational information, whereas punishment-motivated learning is typically associated with enhanced activity in an amygdala–cortical MTL circuit and is characterized by sparser, more item-based encoding. The model's predictions are also consistent with broader experimental evidence relating differential neural substrates to distinct patterns of motivated, adaptive behavior. In addition to being linked with enhanced declarative memory, activity in the mesolimbic dopamine system has been associated with both motor and cognitive exploratory behaviors (Düzel, Bunzeck, Guitart-Masip, & Düzel, 2010). This is consistent with the conception of this system as supporting information-seeking in an interrogative mode. In contrast, the central amygdala is thought to play a critical role in mediating physiological arousal and responses to threat, including freezing and inhibitory behaviors (Choi, Cain, & LeDoux, 2010; Davis, 1992) and fear conditioning behaviors (LaBar, Gatenby, Gore, LeDoux, & Phelps, 1998; LeDoux, 2003). This profile of behavior under threat is associated with restricted information-seeking, consistent with the decreased utility of additional information-seeking in an imperative state.

Open Questions Facing the Interrogative/Imperative Model

Although the interrogative/imperative model of information-seeking can potentially account for a range of empirical observations regarding adaptive memory under different motivational contexts, open questions remain. One currently unresolved aspect of this model concerns *incentive salience*, the extent to which a person perceives a stimulus to be rewarding. Attribution of incentive salience is related to both the sensory representation and the learned significance of a stimulus: making it, for example, an object of desire or "wanting," and associating it with specific behaviors as motivated responses (Berridge, 2007; Berridge & Robinson, 1998). A stimulus must, by definition, have incentive salience to elicit any motivated behavior. High levels of incentive salience would be expected to engender an imperative goal state irrespective of the valence of the incentive. Such high-saliency, imperative goal states have typically been associated with compulsive, inflexible behaviors: for example, those that characterize drug addiction (Everitt, Dickinson, & Robbins, 2001; Flagel, Akil, & Robinson, 2009) and often result in impaired performance, such as "choking under pressure" (Beilock & Carr, 2001; Mobbs et al., 2009). These patterns of behavior in response to highly salient stimuli are consistent with our model's conceptualization of imperative information-seeking.

Neuroanatomical evidence suggests that brain regions assumed to be associated with *both* interrogative and imperative modes are implicated in supporting incentive salience. In rodent models, processing of incentive salience has been associated both with activity in the central amygdala (Mahler & Berridge, 2009, 2012), a critical node of the proposed imperative network, and the mesolimbic dopamine system (Berridge, 2007), which is thought to underlie interrogative information-seeking. Further, these brain regions have been argued to operate synergistically, with the amygdala increasing gain in mesolimbic dopaminergic regions and amplifying incentive salience (Mahler & Berridge, 2012; Phillips, Vacca, & Ahn, 2008). It should be noted that amygdala nuclei are selectively implicated in learning or acquisition of salience. For example, a human neuroimaging study of a high-stakes reward task with over-learned cues showed that "choking" behavior during active avoidance was associated with activation in ventral, dopamine-rich midbrain regions, but not activation in the amygdala (Mobbs et al., 2009). Similarly, during a punishment-motivated memory encoding task (Murty, LaBar, & Adcock, 2012), significant amygdala activity was observed during subsequently remembered versus forgotten trials, but was not observed in analyses collapsing across memory success and failure. This finding suggests that amygdala activation might specifically be associated with successful (but not unsuccessful) motivated memory formation.

An additional open question is the extent to which different modes of information-seeking might be characterized by the interplay of activity in different neuromodulator systems. The midbrain-hippocampal circuit associated with the interrogative mode of information-seeking is primarily innervated by dopamine, but dopaminergic modulation is also associated with punishment processing and avoidance behavior more consistent with an imperative information-seeking mode (Carter et al., 2009; Maia & Frank, 2011; Oleson, Gentry, Chioma, & Cheer, 2012). It has been proposed that distinct populations of dopamine neurons play different modulatory roles in the adaptive control of behavior (Bromberg-Martin, Matsumoto, & Hikosaka, 2010), and such cell-level differences may account for the observed behavioral outcomes. Meanwhile, norepinephrine is a candidate neuromodulator supporting imperative processing, due to its role in arousal and stress response (Aston-Jones & Bloom, 1981; Morilak et al., 2005) and its innervation of the amygdala (Berridge & Waterhouse, 2003). The complex role of the norepinephrine system in higher cognitive processes beyond threat and arousal is increasingly recognized, and norepinephrine may mediate the balance between exploratory and exploitative behaviors (Aston-Jones & Cohen, 2005). Moreover, this system may work in concert with other neuromodulatory systems, including the dopaminergic system, to support adaptive behavior (Briand, Gritton, Howe, Young, & Sarter, 2007; Cools, 2008; Verguts & Notebaert, 2009). Thus, it may be proposed that dopamine and norepinephrine interact to regulate interrogative and imperative modes of information-seeking via distinct pathways engaging different MTL subcomponents, leading to differential memory representations. In this conception, the neuromodulatory systems are synergistic;

however, to the degree that memory representations emphasize some aspects of experience, the effects of interrogative versus imperative motivational states on memory may be competitive. Research specifically testing this hypothesis is ongoing, but preliminary data suggest that neural substrates and behavioral elements play overlapping roles in both information-seeking modes.

Having a new framework that relates motives specific to information-seeking to memory formation introduces many questions for future research, and may help account for a broad range of existing empirical observations of motivated behavior and learning in both animal and human models. Importantly, the interrogative/imperative framework clarifies the adaptive value of information under different motivational contexts and makes specific predictions about the nature of the memory representations encoded. For example, it predicts that variation in the urgency or salience of a reward anticipation state (induced via experimental manipulation or considered through examination of trait differences) will lead to increased engagement of the amygdala–cortical MTL circuitry and memory outcomes previously associated with punishment motivation. Further, it is currently unknown whether reward-enhanced versus punishment-impaired relational (spatial) memory performance (as behaviorally observed in Murty, 2011) is associated with activity in VTA-hippocampal and amygdala–cortical MTL circuits, respectively, as has been observed in our other studies of declarative memory encoding under reward and punishment motivation (Adcock et al., 2006; Murty, LaBar, & Adcock, 2012). These issues and others remain to be addressed by ongoing research.

Beyond Extrinsic Incentives: Intrinsic Influences on Motivated Learning

Thus far, our review of motivational influences on declarative learning and memory has primarily focused on experimental work manipulating motivation via the use of extrinsic incentives such as money. In addition to such extrinsic motivators, intrinsic motivation – that is, motivation to volitionally engage in a task for its own sake or satisfaction (Ryan & Deci, 2000) – also serves as an important influence on learning and behavior. While intrinsic motivation is an important construct in the social psychology literature, it has been relatively underexplored in the cognitive neuroscience literature, given the challenges of experimentally manipulating and characterizing intrinsic motivation. Recent studies have begun to address this gap, delineating the cognitive and neural mechanisms supporting intrinsic motivation and its effects on performance, as well as potential interactions between intrinsic and extrinsic motivation.

Neural Characterizations of Intrinsic Motivation

While there are methodological challenges in investigating the neural basis of intrinsic motivation, a number of recent studies have elegantly addressed this

question with psychological paradigms amenable to functional neuroimaging. Murayama and colleagues (Murayama, Matsumoto, Izuma, & Matsumoto, 2010) investigated neural activity associated with the *undermining effect*, a well-characterized interaction between intrinsic and extrinsic motivation, and provided hints regarding the neural basis of intrinsic motivation. The undermining effect is a phenomenon whereby intrinsic motivation tends to decrease after extrinsic rewards have been given and then withdrawn (Deci, 1971; Deci, Koestner, & Ryan, 1999). Murayama and colleagues developed an fMRI-compatible, intrinsically interesting "stopwatch" task (requiring participants to stop within 50 milliseconds of a five-second time limit) and examined the effects of a reward incentive manipulation on task engagement and neural activity, both during the first session (with the incentive manipulation) and in a subsequent, no-incentive session. Individuals who had received reward incentives showed decreased task engagement in the subsequent session, consistent with an undermining effect; this change in behavior was accompanied by reduced neural activity in regions associated with value representation and task maintenance (i.e., anterior striatum, PFC). Together, this pattern of findings suggests that both extrinsic and intrinsic motivators can engage reward- and task performance-related brain circuitry, but when extrinsic rewards are introduced and then taken away, the intrinsic value associated with task performance (and related neural activation) decreases, undermining behavioral engagement.

A recent study from our laboratory demonstrated a more direct characterization and enhancement of the neural activity associated with internally derived motivation of a different sort (MacInnes, Dickerson, Chen, & Adcock, 2016). Using an innovative technique – *cognitive neurostimulation*,[2] or volitional activation of neuromodulatory source nuclei using self-generated thoughts and imagery – together with real-time fMRI feedback from the VTA, we demonstrated that participants were able to learn to volitionally sustain VTA activation via self-generated motivational strategies over the course of an experimental session (shown in Figure 21.4). Importantly, learned VTA activation was not observed in a visual control condition, in a false feedback condition, or in response to feedback from a different dopamine-rich region, the nucleus accumbens. Further, the learned enhancement in VTA activation was accompanied by increased functional connectivity with the hippocampus, identified previously as a downstream target of mesolimbic dopamine and implicated in motivated memory using studies of extrinsic reward incentive (Adcock et al., 2006; Murty & Adcock, 2014; Wolosin, Zeithamova, & Preston, 2012). Taken together, these findings suggest that participants who learn to volitionally sustain VTA activity via self-generated motivational strategies could intentionally promote memory encoding via the hippocampus. This neuroanatomical characterization of internally generated motivation is

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2 "Cognitive neurostimulation," a term developed by our laboratory and first introduced in MacInnes et al. (2016), refers to the activation of neuromodulatory source nuclei using only thoughts and imagery, without external aids.
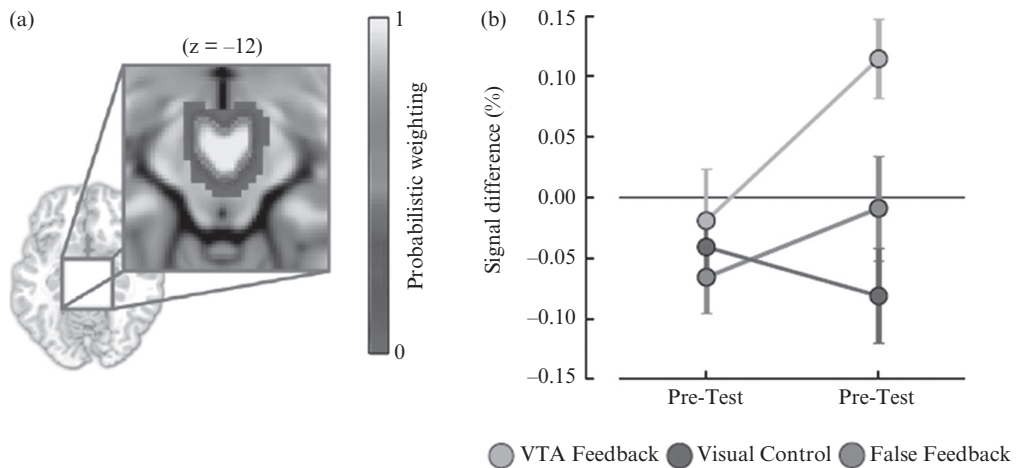
Figure 21.4. *MacInnes, Dickerson, Chen, & Adcock (2016) demonstrated that participants can learn to volitionally enhance and sustain VTA activation using intrinsic, self-generated motivational strategies and fMRI feedback. (A) Participants up-regulated and received feedback from the VTA, anatomically defined using a probabilistic region of interest (ROI). (B) Following training (pre- to post-test), participants who received VTA feedback were more successful in enhancing VTA activity (in activation versus control trials) than participants who received a visual control, false feedback manipulation or feedback from the nucleus accumbens (for full results, refer to MacInnes et al., 2016). From "Cognitive neurostimulation: Learning to volitionally sustain ventral tegmental area activation," by J. J. MacInnes, K. C. Dickerson, N. Chen, and R. A. Adcock, 2016,* Neuron *89(6), pp. 1331–42.*

highly analogous to the circuitry identified during reward anticipation under external motivators (Adcock et al., 2006; Wittmann et al., 2005) and holds much promise as a safe, efficient method of enhancing dopaminergic function without the side effects associated with external interventions. Whether the effects of cognitive neurostimulation can enhance learning and memory outcomes similarly to reward-enhanced declarative learning remains to be tested.

Curiosity and Information Search: Intrinsic Motivation to Learn?

Intrinsic motivation to learn can act as a powerful driver of human behavior. Arguably, the most important behaviors supported by intrinsic motivation are learning behaviors dedicated to seeking new information. Although information-seeking behaviors can be deployed in the service of a larger goal, information-seeking can also be experienced as an end in itself – this process has been conceptualized as characteristic of both *curiosity* (Gottlieb, Oudeyer, Lopes, & Baranes, 2013) and *interest* (Hidi & Renninger, 2006), constructs that are often referred to interchangeably, but are beginning to be understood

as separable[3] (Grossnickle, 2016). Recent work has begun to characterize the concept of information search – the desire to learn what is unknown – in terms of fundamental cognitive and neural mechanisms. These investigations have suggested overlap in the neurocognitive mechanisms supporting extrinsic and intrinsic motivation to learn.

Neuronal recordings in primates indicate that advance informative cueing about upcoming rewards has been associated with phasic activity in the dopaminergic midbrain, including the VTA (Bromberg-Martin & Hikosaka, 2009); this has been interpreted as evidence for the intrinsic motivational value of information. Complementary findings have been observed in the human cognitive neuroscience literature, where neuroimaging studies have identified enhanced mesolimbic dopamine system activity in association with increasing levels of curiosity. In one of the first investigations of curiosity within a neurocognitive perspective (Kang et al., 2009), participants were scanned using fMRI as they read trivia questions and silently guessed the answers. Neural activity associated with questions eliciting high versus low levels of curiosity was contrasted, which revealed that higher levels of curiosity were associated with increased activity within the caudate, a brain region associated with reward anticipation (Delgado, Locke, Stenger, & Fiez, 2003; Delgado, Nystrom, Fissell, Noll, & Fiez, 2000). Additionally, high versus low curiosity during incorrect guesses was associated with enhanced activity in frontal and MTL regions associated with memory encoding. Along with these neural findings, in a separate behavioral study, Kang and colleagues observed enhanced memory for incorrect answers soliciting high versus low curiosity (Kang et al., 2009). Taken together, these findings were interpreted as evidence that curiosity enhances memory for surprising new information via a midbrain-MTL-frontal circuit similar to the dopaminergic circuit previously associated with memory enhancement via external reward incentives.

Additional evidence that curiosity enhances memory via neural circuitry previously associated with the processing of extrinsic rewards was illustrated in a study by Gruber and colleagues (Gruber, Gelman, & Ranganath, 2014). This study expanded on findings by Kang and colleagues (Kang et al., 2009) in that it investigated neural activity associated with curiosity-related anticipatory states and subsequent memory benefits, both for target stimuli (answers to trivia questions that participants were curious about) and incidental stimuli (faces presented during an anticipatory period between trivia question and

3 The distinction between curiosity and interest has yet to be clearly delineated in the cognitive neuroscience literature, but has been of growing interest in other literature, such as that of educational psychology (as discussed at length in Grossnickle, 2016). Comprehensive discussion of the distinction between curiosity and interest is beyond the scope of the present chapter. Instead, it should be noted that information-seeking as discussed here can be considered characteristic of both curiosity and interest, and that the neuroscience studies described here as investigating curiosity or information-seeking do not explicitly attempt to disentangle these constructs from interest; in neuroscience literature, this empirical distinction has yet to be made.

answer). Gruber et al. observed that high versus low curiosity during the antic-ipation period between question and answer was associated with enhanced activity in the midbrain and nucleus accumbens, regions previously character-ized as part of the mesolimbic dopamine system. Notably, memory for inci-dentally encoded face stimuli was enhanced under high versus low curiosity states; individual variability in curiosity-enhanced memory was associated with anticipatory activity in the midbrain and hippocampus, as well as func-tional connectivity between these regions (Gruber, Gelman, & Ranganath, 2014). This finding parallels a key finding from our laboratory: enhanced memory for stimuli encoded under extrinsic reward incentive is associated with enhanced anticipatory activity in the midbrain and hippocampus, as well as enhanced connectivity between these regions (Adcock et al., 2006). Similar memory benefits and engagement of common neural circuitry in association with encoding under reward anticipation and curiosity anticipation further suggest that extrinsic and intrinsic motivation support learning via common neural mechanisms.

New research from our laboratory (Stanek et al., in preparation) has built upon these observations to develop a more nuanced characterization of brain activity and potential memory enhancement during a state of curiosity. Given findings suggesting that curiosity may benefit memory via similar neural cir-cuitry to reward anticipation, we sought to examine whether curiosity-related benefits to memory could likewise be characterized by sustained, anticipatory neural signal. We developed a curiosity-eliciting trivia-question paradigm similar to that used by Gruber, Gelman, and Ranganath (2014), but different in that it permitted the separation of neural activity during distinct tempo-ral phases of the curiosity signal: cue (i.e., curiosity-eliciting trivia question), anticipation, and outcome (receipt of the answer to the trivia question). Our paradigm also included an action response manipulation to systematically characterize how action might impact motivated learning, given prior research findings that action contingency might enhance striatal activation specifically associated with reward reinforcement processes (Tricomi, Delgado, & Fiez, 2004). This paradigm contrasts with Gruber, Gelman, and Ranganath (2014), whose paradigm required an incidental button-press on each trial to receive the trivia question response.

Using this paradigm, robustly enhanced memory was observed for high versus low curiosity-eliciting information. Memory benefit was also observed for information requiring a response action (versus no response action). Interestingly, the action-related memory benefit was more pronounced for low- versus high-curiosity information, paralleling findings that motivational manipulations such as monetary incentive might benefit memory more for uninteresting versus interesting information (Murayama & Kuhbandner, 2011). In terms of neural findings, high versus low curiosity-eliciting cues led to enhanced activity in mesolimbic reward processing regions and memory-related MTL regions, as well as in the PFC; activity in many of these regions
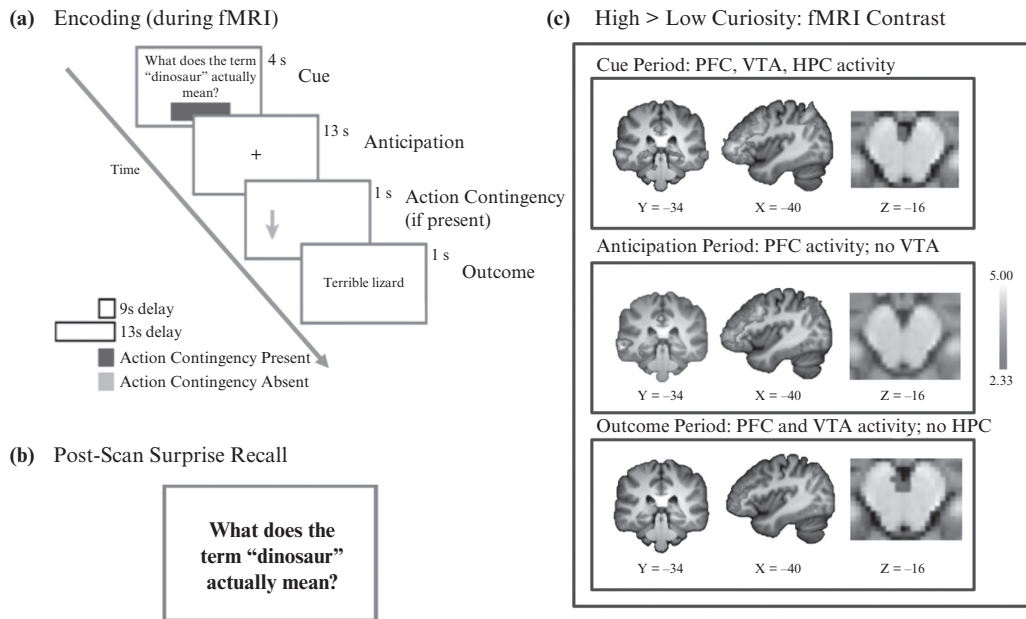
(a) Encoding (during fMRI)

What does the term "dinosaur" actually mean? 4 s Cue

13 s Anticipation +

1 s Action Contingency (if present)

1 s Outcome Terrible lizard

Time

☐ 9s delay
☐ 13s delay
■ Action Contingency Present
■ Action Contingency Absent

(b) Post-Scan Surprise Recall

What does the term "dinosaur" actually mean?

(c) High > Low Curiosity: fMRI Contrast

Cue Period: PFC, VTA, HPC activity

Y = –34   X = –40   Z = –16

Anticipation Period: PFC activity; no VTA

Y = –34   X = –40   Z = –16

5.00

2.33

Outcome Period: PFC and VTA activity; no HPC

Y = –34   X = –40   Z = –16

Figure 21.5. *Stanek et al. (in preparation) characterized brain regions supporting curiosity-enhanced memory encoding using fMRI. (A) A trivia-question paradigm with cue, variable anticipation, and outcome phases and an action-contingency manipulation was used to elicit curiosity for subsequent answers at encoding. (B) Following the encoding phase, participants recalled as many answers as possible to the trivia questions seen during the encoding phase. (C) A robust memory benefit was observed for high versus low curiosity answers. This was accompanied by enhanced PFC, VTA, and HPC engagement at cue: PFC activity was maintained through anticipation and outcome, VTA activity decreased during the anticipation period and returned during the outcome phase, and HPC engagement decreased at the outcome stage*

was also associated with enhanced subsequent memory. These findings are summarized in Figure 21.5. Stanek and colleagues' design also dissociated activity at the cue, anticipation, and outcome phases of curiosity: at the time of a curiosity-eliciting cue, the midbrain and hippocampus showed activation related to memory enhancement, but a sustained curiosity signal during the anticipation period prior to outcome was seen primarily in the PFC instead of in the mesolimbic regions. Interestingly, curiosity effects in the PFC were greater for no-action than action trials, paralleling our behavioral results where the enhancement of memory by curiosity was greater in no-action trials.

These studies are just beginning to characterize the neural mechanisms by which intrinsic motivation to learn can lead to enhanced memory, but already suggest an important takeaway point: the neural circuitry engaged during curious anticipation is highly consistent with the neural circuitry elicited during reward anticipation or the interrogative mode of information-seeking.

Additionally, Stanek and colleagues demonstrated that action contingency is associated with memory benefit, and that this benefit might be particularly pronounced for information that is not intrinsically motivating to learn (i.e., low-curiosity information). This result complements prior work suggesting that extrinsic motivational manipulations might benefit memory specifically when information itself is not of intrinsic value (Murayama & Kuhbandner, 2011). These findings converge on action-related recruitment of the dopaminergic and striatal circuits associated with reinforcement (Tricomi, Delgado, & Fiez, 2004) and suggest that the additional utility of action-based approaches to learning, in real-life settings such as the classroom or workplace, is greatest for intrinsically uninteresting information. These findings also raise interesting questions about whether action requirements could have undercutting effects on curiosity, similar to extrinsic rewards. Finally, as noted at the beginning of this section, information-seeking may be driven by both curiosity and interest. These constructs have not been clearly distinguished in the neuroscience literature, despite separation in the educational psychology literature (Grossnickle, 2016); examining whether curiosity and interest are separable in terms of neurobiological substrates also remains to be addressed by future research.

Choice and Control Processes Influence Motivated Memory Encoding

The research described earlier considers motivated action mainly in terms of its interactions with other forms of motivation in shaping learning and memory. However, compared to the passive intake of information, self-driven or active processes are theorized to provide an increasingly wide range of benefits to learning and memory. Much research investigating active learning has been conducted from an educational psychology perspective in classroom settings, as opposed to a fundamental neurocognitive perspective (e.g., Freeman et al., 2014; Hake, 1998). However, the emergence of new research on the cognitive and neural mechanisms of decision processes, including volitional choice and cognitive control, supports the growing recognition that action and memory processes must interact to support the learning and implementation of adaptive, goal-directed behavior.

Effects of Volition and Choice on Memory Encoding

One line of research has investigated the online control of behavior and related brain activity during exploratory learning (Voss, Gonsalves, Federmeier, Tranel, & Cohen, 2011a; Voss et al., 2011b) and has shown that the ability to implement volitional control has important effects on subsequent memory. Voss and colleagues developed a novel paradigm that manipulated the extent to which participants could volitionally control object viewing within a stimulus array (i.e., via a "moving window," controlled with a computer mouse, through which stimuli were viewed) presented for a predetermined time period.

Volitional control was associated with subsequent memory benefit, as well as with enhanced functional connectivity between the hippocampus (associated with memory encoding) and the PFC and parietal regions (associated with executive control; Voss et al., 2011a). Additionally, Voss and colleagues observed spontaneous adjustments in behavior during exploratory learning, which were associated with hippocampal activity and connectivity with frontocerebellar circuits. Specifically, when exploring a visual array, "spontaneous revisitation" of previously visited objects (i.e., using the moving window, which was participant-controlled with a computer mouse) was associated with enhanced hippocampal activity and subsequent memory for those objects (Voss et al., 2011b). Importantly, amnesic patients with hippocampal damage failed to display volition-related memory benefits (Voss et al., 2011a) and displayed fewer revisitation behaviors than the controls (Voss et al., 2011b). Taken together, these observations in healthy and lesioned participants indicate not only that the hippocampus is essential for learning, but also that the hippocampus communicates with regions associated with executive control to support specific, adaptive behaviors leading to optimal learning under volitional control.

Voss and colleagues' studies elegantly illustrate that agency over learning may offer memory benefits supported by MTL memory systems. However, these studies employed a volitional exploration paradigm that combined multiple potential benefits to memory, including control of study content, order, and timing. In a follow-up study, Markant, DuBrow, Davachi, and Gureckis (2014) systematically manipulated each of these factors using a series of behavioral experiments to pinpoint the specific cognitive mechanisms by which self-directed study leads to enhanced memory. Markant and colleagues observed that the advantage of self-directed over passive learning was present even when volitional control determined only the timing, but not the order or content, of study material. The authors argue that the memory advantage for self-directed study might be related to the ability to match stimulus presentation to the current attentional or preparatory state to optimize learning.

Research investigating the neurobiological basis of this memory advantage suggests that a sense of agency or choice might enhance memory through the same mesolimbic dopamine pathways implicated in reward processing and motivated behavior. Perception of agency or choice has been behaviorally characterized as subjectively rewarding and associated with activity in mesolimbic dopamine regions associated with reward processing, including the caudate and ventral striatum (Leotti & Delgado, 2011; Tricomi, Delgado, & Fiez, 2004). A recent study directly investigated whether the perception of choice was associated with enhanced declarative memory and characterized the neurobiological mechanisms associated with this effect using fMRI (Murty, DuBrow, & Davachi, 2015). Participants were presented with two occluded stimuli on each trial and either freely chose to reveal, or were directed to reveal, one of the two stimuli. Importantly, participant choice had no influence on the stimulus content revealed, leading Murty and colleagues to contrast memory behavior

and neural activity as a function of perceived choice, in addition to controlling for actual stimulus content. Free choice was associated with robust benefits in memory performance, enhanced anticipatory activity in the striatum, and subsequent connectivity between the striatum and hippocampus during stimulus encoding. These findings were interpreted as a novel observation of the neural mechanisms supporting active learning, but are also consistent with prior observations indicating that engagement of the mesolimbic dopamine system (whether elicited via action contingency or motivational context) and mesolimbic input to the hippocampus can support memory encoding.

Control Processes Influence Task Performance and Memory Encoding

In addition to choice, the implementation of cognitive control itself might impact how information is encoded and represented in memory. As previously noted, PFC-based control processes are recognized to play a contributing role in memory encoding (Blumenfeld & Ranganath, 2007), particularly during self-directed exploration (Voss et al., 2011a). However, direct interactions between controlled task performance and memory encoding are just beginning to be characterized in the research literature. A hallmark of increased cognitive control is increased attention to task-relevant information, which might lead to a benefit for such information in long-term memory (Chun & Turk-Browne, 2007). Consistent with this prediction, a recent study demonstrated enhanced incidental memory for stimuli in a task-switching paradigm that were presented under conditions – including advance preparation time, volitional task switching, and reward incentives – eliciting enhanced top-down control (Richter & Yeung, 2015). Similarly, incidental memory for task-relevant stimuli in a Stroop paradigm was superior for stimuli presented during incongruent versus congruent trials (eliciting higher versus lower control, respectively; Krebs, Boehler, De Belder, & Egner, 2015). Functional neuroimaging in the latter study identified a conflict-triggered lateral PFC region predictive of subsequent retrieval success. Further, this PFC region displayed connectivity with hippocampal and parahippocampal MTL regions associated with memory encoding; PFC–MTL functional coupling was stronger during high versus low control (incongruent versus congruent) trials, providing evidence that top-down control might influence subsequent memory via PFC input to MTL regions supporting memory encoding.

As we have argued elsewhere, characterizing the role of motivation in adaptive behavior will require the integration of observations across multiple cognitive domains (Chiew, Stanek, & Adcock, 2016). Recent work has extended the investigation of motivational influences on memory to examine cognitive control-memory interactions as a potential mechanism for these effects. Both control and memory processes are necessary for motivated, adaptive behavior and, although an extensive body of work has characterized the effects of motivational influences on cognitive control and task performance (Botvinick & Braver, 2015; Chiew & Braver, 2013; Cools, 2008), for the most part, this

literature has developed separately from research examining the effects of motivation on declarative memory. In an early investigation integrating these questions, Richter and Yeung (2015) used reward incentives to elicit increased top-down control in a task-switching paradigm and examined the effects on subsequent memory for task stimuli. The authors observed that reward-enhanced task performance was associated with enhanced memory for task-relevant stimuli. Although these findings offer exciting preliminary evidence that motivation exerts effects on both controlled task performance and subsequent memory, further work is needed to clarify whether motivational contexts produce these shifts coherently and synergistically in multiple domains. It also remains to be determined whether changes in control-memory interactions differ under rewarding versus punishing motivational contexts, as has been observed separately in both the memory domain (i.e., Murty, LaBar, & Adcock, 2012, 2016; and reviewed here) and the control domain (Braver, Paxton, Locke, & Barch, 2009; Stürmer, Nigbur, Schacht, & Sommer, 2011). In particular, to our knowledge, no existing investigations of the effects of cognitive control on subsequent memory have separately characterized item and relational memory measures. Finally, the effects of punishment or high salience reward incentives on controlled task performance and subsequent memory will inform an integrated account of how motivational context influences these diverse cognitive processes to shape memory.

Developing a coherent account of the role of motivation and cognition across both control and memory domains has important implications for our understanding of goal-directed, adaptive behavior. Cognitive control and learning processes are intimately intertwined: goal pursuit is not only dependent on online performance in the present moment, but also requires that we learn from past situations to inform and refine our adaptive behavior in future. At present, the mechanistic basis of these processes is not well-characterized; thus, considering the role of cognitive control in motivated memory is an exciting new research direction that holds much promise in advancing our understanding of the multiple timescales of adaptive behavior.

Motivated Memory Research: Potential Applications to Real-Life Educational Settings

Taken together, the research findings reviewed in this chapter provide evidence that motivational influences can profoundly affect the nature of memory representations, and that these effects are supported by neuromodulatory input, particularly from the mesolimbic dopaminergic system, to MTL structures involved in memory encoding. Additionally, empirical evidence indicates that motivated learning and memory outcomes depend on a number of factors, including valence, salience, extrinsic incentives, intrinsic curiosity, motor demands, choice, and cognitive control processes. Each of these factors represents a source of variance that can be potentially manipulated to optimize

learning and memory in real-life settings such as educational and workplace environments.

The first conclusion we wish to highlight from this research is that different motivational contexts (i.e., rewarding versus punishing) are associated with the encoding of distinct memory representations. Specifically, motivational states that are characterized by high urgency or salience, perception of threat, or anxiety (even if not actually associated with extrinsic punishment incentives) are predicted to promote an imperative mode of information-seeking. This mode of information-seeking may not be optimal for learning in the educational setting: while an imperative mode may lead to enhanced item memory, experimental evidence suggests that this kind of processing may result in suboptimal or even impaired relational memory encoding. Interrogative processing, on the other hand, may enhance relational memory (Murty et al., 2011). Hallmarks of relational memory include its richness of detail and high levels of contextualization; these characteristics support the role of relational memory in conceptual knowledge (Kumaran, Summerfield, Hassabis, & Maguire, 2009; Shohamy & Turk-Browne, 2013) and might be critical to both the advancement of knowledge and development of the critical thinking skills that education seeks to foster. Accordingly, educators might consider teaching strategies that encourage an interrogative learning mode while discouraging an imperative learning mode (i.e., minimizing the use of threats or punishments to motivate students, especially with those already tending toward anxiety or those facing high-urgency problems in other domains of their lives).

A second finding emerging from the reviewed research literature with potentially important implications for applied settings is that motivational processes enhancing memory can be anticipatory – in other words, they can be induced ahead of the information to be learned. Benefits of anticipatory motivation have been observed both with extrinsic and intrinsic motivators, such as curiosity, as well as with both intentionally and incidentally encoded stimuli (Adcock et al., 2006; Gruber, Gelman, & Ranganath, 2014). Although states of curiosity offer robust benefits to learning (Gruber, Gelman, & Ranganath, 2014; Kang et al., 2009; Stanek et al., in preparation), extrinsic motivators can also improve memory when used judiciously, as they may benefit memory for uninteresting material (Murayama & Kuhbandner, 2011). However, extrinsic motivators also have the potential to undermine intrinsic motivation (Murayama et al., 2010); thus, it appears that their use should be aimed at reinforcing beneficial processes like control and attention rather than outcomes. Assessing the application of these findings in naturally occurring educational settings – for example, exploring the potential impact of putting students in a motivated, anticipatory state (using gentle incentives or prizes, sparking curiosity, or using information-incidental manipulations like upbeat music) before presenting new information – should be explored.

A third finding emerging from the reviewed literature is that action and volition might play important roles in enhancing learning and subsequent

memory. Volitional control over a learning context leads to enhanced memory compared to passive intake of information (Markant et al., 2014; Murty, DuBrow, & Davachi, 2015), even if the learner does not control information content or order. When considered together with Murayama et al.'s observation that external incentives might boost memory for uninteresting material (Murayama & Kuhbandner, 2011), this observation suggests the potential availability of multiple strategies to help encourage learning when the material itself does not intrinsically appeal. Additionally, evidence from Stanek and colleagues (in preparation) suggests that action might be particularly beneficial to learning for information that is not interesting. Such a strategy would avoid the potential problem, presented by extrinsic rewards, of undermining future learning in the same context, an outcome that remains to be tested experimentally.

Concluding Thoughts

Advances in cognitive neuroscience have allowed us to move beyond intuition and toward a more mechanistic account of how motivation might be beneficial to declarative, long-term learning and memory. A growing body of evidence has characterized the memory representations and neural circuitry associated with encoding under different motivational contexts, with a particular focus on interactions between mesolimbic pathways associated with reward motivational processing and MTL regions supporting memory function. This work has supported the development of theoretical frameworks positing different adaptive learning modes and has generated specific predictions for future research. Additionally, neuroimaging studies have indicated that information search, choice, and volitional action might promote activity in mesolimbic pathways historically associated with reward anticipation and processing, leading to benefits in declarative memory similar to those observed under the influences of extrinsic reward incentives. Finally, given recent evidence suggesting that controlled task performance can influence downstream memory, we point to a need for future research to investigate the effect of motivation on such control-memory interactions. Such work would advance an understanding of goal pursuit, in terms of both present performance and adaptive learning to support future behavior. Although many open questions remain, extant research is rapidly laying a foundation for understanding the biological mechanisms underlying adaptive cognition and behavior, and stands available to inform evidence-based strategies for enhancing learning in educational settings.

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