

RUNNING HEAD: Motivated Memory: Neurobiological Mechanisms of Selectivity

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Neurobiological Mechanisms of Selectivity in Motivated Memory

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Memory is a way of telling you what's important to you. – Salman Rushdie

Introduction

Our memory systems are capable of storing massive amounts of information over extended periods of time – in some cases, as long as a lifetime. The information stored in our memories informs our sense of identity, our understanding of the world around us, and our future actions. However, our memories are not a comprehensive record of every piece of information encountered over a lifetime – while some milestone moments are recalled vividly, many other events are forgotten over time. The recognition that our memory systems have evolved to selectively prioritize some information for encoding and storage, while other information is forgotten, represents a major advance in our understanding of human memory. A growing literature indicates that the motivational relevance of information is a major determinant of its selectivity in memory, with a growing literature now focused on the cognitive and neurological mechanisms supporting prioritization for reward associated information.

Given the survival importance of motivationally-relevant information, its prioritization in memory can be understood as an evolved tendency supporting adaptive behavior. However, the modulation of memory by reward and motivation is complex and may operate via various mechanisms leading to multiple possible outcomes. A key question in this literature concerns the role of strategic control in motivational modulation of memory. Along with the growing literature indicating that memory outcomes are influenced by motivation, evidence has demonstrated motivational effects on cognitive processes in other domains, particularly cognitive control (Botvinick & Braver, 2015; Chiew & Braver, 2013, 2016; Kouneiher, Charron, & Koechlin, 2009;

Shenhav, Botvinick, & Cohen, 2013; Westbrook & Frank, 2018); and separately, an extensive body of literature has indicated the importance of control processes in supporting memory performance (Badre & Wagner, 2007; Benjamin, 2007; Jacoby, Shimizu, Daniels, & Rhodes, 2005; Kuhl & Wagner, 2009; McGillivray & Castel, 2017). In spite of this prior work, it is still unclear to what extent the prioritization of motivationally relevant information in memory is the product of strategic control. While some studies of motivated memory have suggested contributions of control mechanisms, other studies suggest that motivation may enhance memory through mechanisms independent of control. We suggest that motivation can modulate memory via both control-dependent and control-independent mechanisms, but the extent to which different mechanisms are engaged may depend on task parameters, many of which have yet to be systematically evaluated and disentangled. In the present article, we review key experimental paradigms used in the study of motivated memory and discuss how aspects of task design may have guided the mechanisms engaged and memory outcomes observed as a function of reward. We also discuss new work aiming to help disentangle the contributions of these multiple mechanisms to motivated memory as well as highlight where ambiguities remain. The goal of this manuscript is to advance a more comprehensive understanding of the multiple and complex mechanisms by which motivational relevance may modulate memory performance, clarify the role of strategic control in motivated memory, and identify unanswered questions for future research.

The Monetary Incentive Encoding (MIE) vs. Value Directed Remembering (VDR)Paradigms

Two experimental designs have been commonly used in the study of motivated memory: the Monetary Incentive Encoding (MIE) paradigm (Adcock, Thangavel, Whitfield-Gabrieli, Knutson, & Gabrieli, 2006) and the Value Directed Remembering (VDR) paradigm (Castel, Benjamin, Craik, & Watkins, 2002; Cohen, Rissman, Suthana, Castel, & Knowlton, 2014; see Figure 1). The MIE paradigm typically manipulates reward motivation at the encoding stage, with a cue at the beginning of each trial of the encoding task indicating the amount an upcoming stimulus (usually, an image) is worth if successfully remembered on a subsequent memory task. The value of the reward cues may vary, but often is manipulated to compare between the effect of a high- and low-value reward (e.g., \$5.00 versus \$0.10; Adcock et al., 2006) on a trial-by-trial basis. Subsequent memory in the MIE paradigm has usually been assessed using a recognition test after a 24-hour interval. This test may, to prevent liberal responding and endorsement of all test items as “old”, employ a financial penalty for false-alarm responses with a value intermediate to the high and low values assigned to reward cues (e.g., for high and low value rewards of \$5.00 and \$0.10, a false-alarm penalty of \$2.55 may be used). In the VDR paradigm, participants are typically presented with several study-test blocks. During study (encoding), stimuli (usually words) are paired with a point value that ranges from low to high (e.g., ranging from 1-12 points). Participants are instructed that successfully remembering the word stimuli will earn them the associated amount of points, and that they should try to maximize their earned points by prioritizing encoding of high over low point value items for a subsequent memory test. Immediate,

free recall tests are often used after each study block to assess memory. Generally, observations using both of these paradigms indicate better memory, or greater selectivity, for high compared to low value items, but evidence has been inconsistent regarding the stage at which reward may influence memory, as well as the extent to which such modulation depends on controlled processes, across the two paradigms.

Investigating Motivated Memory with the MIE Paradigm

Observations using fMRI indicate that reward-related enhancement of memory in the MIE paradigm is associated with enhanced anticipatory activity (i.e., at the time of reward cue) in the ventral tegmental area (VTA) of the midbrain as well as nucleus accumbens in the ventral striatum, key brain structures of the mesolimbic dopaminergic reward system, as well as in the hippocampus, long recognized as critical to encoding and retrieval of long-term episodic memory (Adcock et al., 2006). Additionally, Adcock and colleagues (2006) reported that on a trial-by-trial basis, VTA-hippocampus connectivity during reward anticipation was also associated with memory success for the subsequently presented stimulus, an observation interpreted as suggesting that dopaminergic input from the VTA may enhance hippocampally-based encoding of new information, consistent with animal studies indicating anatomical connectivity between the VTA and hippocampus (Lisman & Grace, 2005; Samson, Wu, Friedman, & Davis, 1990; further reviewed in Shohamy & Adcock, 2010). The involvement of VTA-hippocampal activity and connectivity as key neural mechanisms supporting reward-enhanced memory in the MIE paradigm was originally observed using a 24-hour retention interval between encoding and retrieval tasks. Without manipulating the

encoding-retrieval interval, it remains unclear whether such a 24-hour interval period, allowing consolidation processes to unfold, is necessary or not for such motivational effects to emerge. Additionally, most early MIE studies were not designed to explicitly test the potential importance of strategic control processes in the prioritization of motivationally-relevant information in memory, and fMRI analyses did not target motivational modulation of PFC activity during the MIE task, which if identified, might suggest that reward enhancement of memory is related to changes in strategic control. Follow-up work using adaptations of the MIE paradigm have begun to test the importance of consolidation period and the role of strategic control in observed effects of reward within the context of this task.

During consolidation, largely transpiring during sleep, a set of time-dependent processes unfold where initially fragile memories are reactivated and replayed, strengthening the memory trace via interaction between the hippocampus and distributed cortical regions (Schapiro, McDevitt, Rogers, Mednick, & Norman, 2018; Walker & Stickgold, 2004). To investigate the importance of consolidation to reward-related modulation of memory, Spaniol, Schain, and Bowen (Spaniol, Schain, & Bowen, 2014) carried out two experiments employing the MIE with younger and older adults, and compared recognition memory performance when memory was immediately assessed after encoding, versus after a 24-hour interval. They observed that for both age groups, reward-related enhancement of memory was observed with a 24-hour interval between encoding and retrieval, but such enhancements were not observed with an immediate memory test. These observations were interpreted as suggesting that a consolidation period may be necessary for reward-related memory modulation

where high reward-associated memories are prioritized and strengthened during consolidation, over low reward-associated memories. In further support of the idea that reward motivation can enhance memory via post-encoding effects, Murayama and Kitagami (Murayama & Kitagami, 2014) observed that reward cues were associated with enhanced memory for associated stimuli after a 1 week delay, but not on an immediate memory test; and using fMRI both during a motivated encoding task as well as during resting-state pre/post-encoding, Gruber and colleagues (Gruber, Ritchey, Wang, Doss, & Ranganath, 2016) identified reward-related hippocampal activity post-encoding, associated with subsequent memory success (but note that both the post-encoding period and subsequent memory test in this study occurred on the same day as encoding, without a 24-hour interval between encoding and retrieval). Notably, both Murayama and Kitagami (2014) and Gruber et al. (2016) used incidental encoding paradigms (where reward outcomes are not contingent on memory success) instead of intentional encoding, as in the original MIE paradigm (Adcock et al., 2006); we discuss the potential effect of reward contingency further in the *Intentional versus Incidental Motivated Memory* section of this article.

The potential role of strategic control within the context of the MIE paradigm is not well understood. However, reward modulation of memory using a directed forgetting paradigm similar in structure to the MIE (Bowen, Gallant, & Moon, 2020) provided evidence that reward anticipation may not engage cognitive control processes or strategic encoding. On each trial of the typical item-method directed forgetting paradigm, participants are presented with a stimulus, followed by instructions to either remember or forget that item for a subsequent memory test (manipulated on a trial-by-

trial item basis; MacLeod, 1998). The ability to intentionally forget in this paradigm is thought to rely on successful inhibitory control over memory encoding processes. By beginning each trial of a directed forgetting task with a high- or low-value reward cue, Bowen et al. found memory benefits for stimuli associated with high versus low reward cues regardless of the instruction to remember or forget, and no increase in successful directed forgetting for stimuli associated with high versus low value rewards. This observation was interpreted as indicating that cue-induced reward anticipation does not necessarily lead to increased cognitive control over encoding processes, but instead may lead to dopaminergic up-regulation of hippocampus-related memory encoding. Interestingly, Bowen et al. observed these effects with an immediate, not delayed, memory test, prompting questions about the extent to which reward processes modulating memory are time-dependent.

Given findings that dopamine activity may operate on multiple timescales (i.e., rapid, phasic activity versus sustained, tonic activity; Niv, 2007) that may reflect distinct neural mechanisms supporting motivated memory, additional recent work (Gholston & Chiew, in preparation) considered the extent to which sustained and transient reward (putatively associated with tonic and phasic dopamine activity respectively) might be associated with enhanced memory and processing speed during encoding in an adapted MIE paradigm. The encoding-retrieval interval was manipulated (from immediate to 24 hours) across experiments. Following prior work (Chiew & Braver, 2013, 2014, 2016), this study used a mixed block/event design to manipulate both sustained reward context (comparing between a baseline block with no reward prospect, and a reward block where 50% of presented stimuli would be associated with

a reward upon subsequent memory success) and transient reward (within the reward block, reward status was manipulated trial-by-trial and indicated with an anticipatory cue prior to the to-be-remembered target stimulus). Additionally, following presentation of a target stimulus on each trial, participants completed a reaction-time task (identifying the direction of three sequentially-presented arrow stimuli, originally intended to limit elaboration of the target stimulus, following Adcock et al., 2006). This study revealed that transient, but not sustained, reward was associated with enhanced recognition memory in both an immediate and a delayed (24-hour) recognition test; additionally, performance on the reaction-time task also improved with transient reward, and this improvement significantly correlated with transient reward-related memory enhancement. These observations suggest that reward-enhanced memory in the MIE paradigm might specifically depend on transient reward, and that these memory benefits might be linked to processing at encoding instead of being consolidation-dependent. This is in contrast to other observations suggesting the importance of consolidation-dependent mechanisms to motivated memory in the MIE paradigm; additional research will be needed to address these inconsistencies.

Investigating Motivated Memory with the VDR Paradigm

In contrast to many studies using the MIE paradigm and variants that suggest a role for post-encoding mechanisms in motivated memory, a large literature using the VDR paradigm has demonstrated robust reward effects on immediate recall. Both younger and older adults demonstrate high *selectivity* on this task: successfully recalling relatively more high-point value items, compared to low-point value items. This

selectivity effect has been interpreted as evidence of successful cognitive control over encoding processes, suggesting that reward-enhanced memory in the VDR paradigm may require strategic control to a greater extent than in the MIE paradigm. The VDR paradigm typically involves verbal (word) stimuli and a small number of trials in each study block, with immediate, intermittent feedback that may encourage metacognitive monitoring. These aspects of task design differ from the classic MIE paradigm (which has typically used pictorial stimuli, longer task blocks, and no feedback about memory performance during the encoding period) and may encourage differential semantic processing of high versus low value items at encoding, a mechanism thought to depend on strategic control (Cohen, Cheng, Paller, & Reber, 2019; Cohen et al., 2014; Cohen, Rissman, Suthana, Castel, & Knowlton, 2016; Hennessee, Patterson, Castel, & Knowlton, 2019). Consistent with this assertion, value effects on memory in the VDR have been observed to increase over the course of the task (e.g., Castel, 2007); given that memory performance is typically assessed and feedback is provided after each task block, this improvement over time may be thought of as reflecting controlled adjustment of performance in response to feedback. The potential importance of strategic control in supporting reward-enhanced memory in the VDR paradigm is suggested not only by behavioral findings (Hennessee et al., 2019), but also fMRI evidence indicating greater activity in left frontotemporal regions linked to semantic processing and control, in association with greater memory selectivity for high-value items (Cohen et al., 2019, 2014).

Taken together, behavioral and neuroimaging evidence from the MIE and VDR paradigms suggests that multiple mechanisms, both control-dependent and control-

independent, may contribute to reward-related enhancement of memory. Specifically, dopaminergic input from midbrain areas (e.g., VTA) to the hippocampus may be a consolidation-dependent mechanism supporting reward-enhanced memory relatively independently of strategic control; the use of PFC-based metacognitive strategies to guide motivated encoding may be a second, control-dependent, mechanism enhancing reward-related memory with effects primarily at encoding. In the following sections, we discuss specific aspects of task design, across the two paradigms, that might contribute to the mechanisms engaged, but have yet to be disentangled. We also discuss potential contributions of motivation and strategic control at retrieval, which have been studied less than these influences at encoding and consolidation stages of memory.

Intentional versus Incidental Motivated Memory

The distinction between intentional and incidental memory is potentially important to consider when clarifying the mechanisms by which reward motivation may modulate memory outcomes. Generally speaking, this distinction refers to whether participants are aware that their memory for presented stimuli is or will be tested. This may be manipulated at the encoding stage, where participants may be aware or unaware of a subsequent memory test when presented with stimuli, or the retrieval stage, where participants may be aware that they are being tested on previously-encountered stimuli with a declarative memory test; or unaware of being tested (i.e., with a sentence-completion or processing speed test). In the motivated memory literature, task designs have varied in intentional/incidental encoding, but have typically used intentional memory tests at retrieval. The status of motivational manipulations as intentional versus

incidental has also varied across studies: in some, rewards are performance-contingent on memory success; in others, they are not. Despite this variability in task designs, it is not well-understood whether intentional versus incidental motivated encoding may engage differing mechanisms supporting memory performance.

In the classic versions of both the MIE and VDR paradigm (Adcock et al., 2006; Castel et al., 2002), reward cues and information at encoding explicitly indicate that reward receipt is performance-contingent on subsequent memory success; thus, these task designs may be considered to include both intentional reward and intentional memory encoding. In contrast, paradigms have also been used where reward information is encountered at encoding, but not yoked to subsequent memory success – such a paradigm can be thought to elicit incidental encoding, given that the memory test is typically a surprise, as well as enabling examination of incidental reward effects on memory success (Bowen & Spaniol, 2017; Cheng et al., 2020; Mather & Schoeke, 2011; Stanek, Dickerson, Chiew, Clement, & Adcock, 2019; Wittmann, Schiltz, Boehler, & Düzel, 2008; Yan, Li, Zhang, & Cui, 2018). Note that in such a paradigm where reward is incidental to memory, it may be contingent on subject performance in a separate task (i.e., a semantic or perceptual judgment of presented stimuli at encoding). Additionally, while intentional encoding and incidental reward could theoretically be combined in a single paradigm (i.e., participants know that they will complete a subsequent memory task, but reward is incidental to memory performance), to our knowledge, such a design has not been used.

For the most part, both performance-contingent and incidental rewards have been linked to enhanced memory performance. For example, an early fMRI study

probing the neural correlates of reward-related memory enhancement identified that increased dopaminergic midbrain and hippocampal activity predicted subsequent memory recognition of reward-predicting cues (Wittmann et al., 2005). Notably, in this paradigm, reward cues indicated whether an immediately upcoming number comparison task would be incentivized or not; reward receipt was not contingent on memory performance, and can be considered to be incidental to encoding. Wittmann et al.'s paradigm thus differs in some important ways from the MIE paradigm previously introduced (Adcock et al., 2006): unlike in the MIE, reward receipt is not contingent on memory success; additionally, Wittmann et al. used unique objects on each trial as reward-predicting cues (where object category predicted reward or not) and then tested memory for these object cues, while Adcock et al. used one cue to signal reward prospect or not, prior to presentation of a to-be-remembered, unique target image, with reward receipt contingent on successful recognition of these images. However, both Wittmann et al. (2005) and Adcock et al. (2006) reported superior memory for reward-associated stimuli, compared to non-reward-associated stimuli, and identified enhanced activity in both dopaminergic midbrain and hippocampal regions in association with memory success. It is thus unclear whether the differing status of reward across these two paradigms – i.e., incidental to or contingent on memory success – may have led to differing mechanisms supporting reward-related memory enhancement.

Potential differences in the neural mechanisms supporting intentional and incidental motivated memory have not been delineated. Neuroimaging studies comparing intentional versus incidental retrieval (i.e., with a declarative memory task versus a separate processing task, such as stimulus categorization, that indirectly

measures memory via processing speed) in the absence of motivational manipulations have suggested greater prefrontal cortex activity during intentional versus incidental retrieval, potentially reflecting greater use of control (Kompus, Eichele, Hugdahl, & Nyberg, 2011; Rugg, Fletcher, Frith, Frackowiak, & Dolan, 1997). However, to our knowledge, neural activity during intentional and incidental memory encoding has not been directly compared, and neither has intentional and incidental motivated memory (at either the encoding or retrieval stage). This may be important to pursue, given preliminary evidence that intentional memory might be associated with greater use of strategic control and arguably, rewards contingent on memory success (as opposed to incidental rewards) might be anticipated to increase cognitive effort. The role of reward prospect in enhancing cognitive effort has become an important topic in the motivation-cognition literature (Inzlicht, Shenhav, & Olivola, 2018; Shenhav et al., 2013; Vassena et al., 2014; Westbrook & Braver, 2015), with dopaminergic systems identified as playing a role in biasing the potential benefits versus costs of cognitive effort (Westbrook et al., 2020). However, the potential contributions of cognitive effort to motivated memory success have not been systematically investigated. To date, many studies characterizing motivational influences on cognitive effort have probed performance in terms of overt action (i.e., performance on an N-back working memory task; Westbrook et al., 2020). In contrast, most studies of motivated memory have manipulated reward during the encoding stage, where overt action responses may not necessarily be required or examined as a function of motivation or effort. This is in spite of the fact that dopaminergic systems support movement and action, as well as reward processing (A. D. Crocker, 1997; Joshua, Adler, & Bergman, 2009; Joshua et al., 2014;

Marshall & Berrios, 1979; Panigrahi et al., 2015) and motivation-related dopamine has been identified as enhancing response vigor of goal-directed actions (Niv, Daw, & Dayan, 2005). Additionally, reward-related activity in the caudate (a key region in the dopaminergic reward system) has been shown to be dependent on action contingency (Tricomi et al., 2004) and memory success is enhanced when action and agency are possible versus when they are not (Vishnu P. Murty, DuBrow, & Davachi, 2015; Voss, Gonsalves, Federmeier, Tranel, & Cohen, 2011). Taken together, these findings suggest that intentional versus incidental motivated memory might differ in terms of strategic control and cognitive effort expended, and that motivated encoding might benefit specifically from action outcomes, or such motor-based outcomes might correlate with subsequent memory success. However, these possibilities remain open questions for future research.

Effects of Reward Anticipation Versus Outcome on Motivated Memory

In addition to the distinction between performance-contingent and incidental reward discussed in the previous section, reward effects on motivated memory may potentially differ between anticipation and outcome. Processing of reward anticipation and outcome have been associated with both overlapping and distinct brain regions, with activity in ventral striatal regions such as the nucleus accumbens observed at both reward anticipation and outcome, while activity in ventromedial prefrontal cortex (VMPFC) and orbitofrontal cortex has been observed specifically at reward outcome (Knutson, Fong, Adams, Varner, & Hommer, 2001; Oldham et al., 2018). In studies investigating effects of incidental reward on memory, both reward anticipation and

outcome (which may either be feedback-contingent on a secondary task incidental to memory, or non-contingent) have been employed. Using hierarchical linear modeling to disentangle the effects of reward anticipation and feedback outcome (incentives on a secondary, speeded-response task) on subsequent memory performance, Mather and Schoeke (Mather & Schoeke, 2011) reported that reward feedback enhanced subsequent memory to a greater extent than reward anticipation. Bowen and Spaniol (Bowen & Spaniol, 2017) also observed greater effects of reward feedback compared to reward anticipation on incidental memory, particularly for information presented after performance-contingent feedback from a speeded-response task compared to non-contingent feedback. However, unlike Mather and Schoeke's (2011) findings, this was more pronounced for loss than for gain feedback.

A growing number of studies have begun to characterize, in more fine-grained detail, the psychological and neural mechanisms by which reward events such as anticipation and outcome might influence memory encoding, with evidence for temporally-specific, context-sensitive effects. The results of these studies may eventually help clarify the relative contributions of reward anticipation versus outcome to memory. For example, building on observations from the animal literature that dopaminergic cells might exhibit temporally distinct patterns of activity (rapid, phasic firing vs. slower, ramping activity), respectively sensitive to expected reward value and uncertainty during reward anticipation (Fiorillo, Tobler, & Schultz, 2003), a recent study demonstrated enhanced memory for stimuli incidentally presented at one of two separate timepoints during a reward anticipation period as a function of expected reward value and uncertainty (Stanek et al., 2019). These behavioral results are

consistent with the idea that dopaminergic activity during reward anticipation may operate on multiple timescales sensitive to differing contextual factors, and that these dopaminergic dynamics might make separable contributions to reward-enhanced memory encoding. Additional work has sought to understand reward anticipation and feedback effects on cognitive performance in terms of reward-related prediction errors, or discrepancies between anticipated and actual reward outcome, indexed by activity in the mesolimbic dopamine system. While reward prediction errors have long been associated with trial-and-error, or reinforcement learning (e.g., Glimcher, 2011) a growing body of new work has suggested that reward prediction errors may also influence episodic memory encoding (Greve, Cooper, Kaula, Anderson, & Henson, 2017; Jang, Nassar, Dillon, & Frank, 2019; Rouhani, Norman, Niv, & Bornstein, 2020; Sinclair & Barense, 2018), likely via dopaminergic input to the hippocampus (Ergo et al., 2020). Interestingly, a recent study (Aberg, Kramer, & Schwartz, 2020) suggests that reward feedback signals presented during memory encoding may elicit phasic dopamine responses, as well as accumulate over the course of a task, with tonic dopamine tracking average reward; and that both reward feedback signals on each trial as well as accumulated average reward might predict subsequent memory performance.

Taken together, these results indicate that the cognitive and neural mechanisms operating during reward anticipation and outcome are complex and may have contextually and temporally specific effects on memory formation. Despite the advancements in our understanding of reward anticipation, outcome, and memory that this recent literature has provided, the greater impact of feedback than anticipation

observed by Mather and Schoeke (2011) and Bowen and Spaniol (2017) still remains an outstanding issue. One possibility that has yet to be addressed in the motivated memory literature is whether reward outcome events (whether or not they are performance-contingent feedback) are treated as environmental signals indicating that alterations in strategic control may be needed. This concept has been extensively explored in the cognitive control literature, where rewarding or punishing outcomes have been robustly associated with adjustments in online performance (Braem, Verguts, Roggeman, & Notebaert, 2012; Hajcak, Moser, Holroyd, & Simons, 2006; Stürmer, Nigbur, Schacht, & Sommer, 2011). While the motivated memory literature suggests that strategic control can be deployed to enhance reward-related memory at least some of the time (i.e., as suggested by evidence using the VDR paradigm and related tasks; Cohen et al., 2014), to our knowledge, the role of reward feedback as a potential signal leading to adjustments in control, with downstream influences on memory outcomes, remains to be explored in future research.

Effects of Reward Motivation on Memory versus Decision Processes

Many investigations of motivated memory have focused on the effects of reward and motivation manipulations on memory formation, in terms of both reward-enhanced dopaminergic input to hippocampus during and following encoding and reward-enhanced strategic control at encoding as putative mechanisms (as previously described in *The MIE vs. VDR Paradigms* section). Memory performance using these paradigms has typically been measured in terms of hit rates (i.e., number of successfully remembered items at retrieval) as a function of motivation condition at

encoding. However, the MIE and related paradigms typically employ a recognition memory task where participants must indicate, for each presented stimulus, whether that stimulus is old (i.e., presented at encoding) or new. This judgment may not only depend on memory sensitivity, but also on decision processes (i.e., at what threshold an individual may choose one memory decision versus the other), which may also be modulated by motivation. In recognition memory-based paradigms such as the MIE, false alarm penalties are often used to prevent liberal responding at retrieval, such as the loss of money or points for incorrect responses to lures. It is common to employ a single false alarm penalty that falls between the values of the high and low rewards offered for correct recognition of target items, but whether the magnitude of the penalty matters and effectively prevents response bias has been inferred, rather than empirically tested. One reason for this is that, in a typical MIE paradigm, target items are randomly assigned a reward value at the time of encoding (i.e., high or low value; this may be either incidentally or intentionally), but lures are typically not associated with varying reward values in the same manner; thus, only a single false alarm rate can be calculated from recognition memory performance. Response bias as a function of differing motivation conditions cannot be properly calculated from a single false alarm value; thus it is largely unclear the extent to which motivation manipulations, such as varying reward values, might affect memory sensitivity versus decision biases contributing to recognition memory performance. To systematically assess the effects of reward on memory discriminability as well as response bias, Bowen, Marchesi, and Kensinger (Bowen, Marchesi, & Kensinger, 2020) employed an adapted MIE paradigm in three experiments where stimulus category (indoor versus outdoor scenes) was

associated with high- versus low-value rewards, enabling calculation of separate false alarm rates (and thus, separate response biases) as a function of stimulus category and therefore associated reward value. In Experiment 1, when a single false alarm penalty was employed with a value intermediate to the high and low reward values awarded for successful recognition of target stimuli, response bias (calculated as signal detection parameter *criterion*) was generally conservative, indicating that the false alarm served its purpose in preventing liberal responding, but depended on the value of the stimulus category. Participants were more liberal (responding “old” more often) to high-reward category items. In Experiment 2, when false alarm penalties were matched to rewarded values for hits, response bias was reduced; and in Experiment 3, when false alarm penalties were matched to rewarded values for hits, and a metacognitive judgment was introduced, response bias as a function of associated reward was eliminated. These results suggest that when false alarm penalties are held equal across stimulus categories, decision thresholds may be more liberal for stimuli associated with high- versus low-value rewards; however, when potential rewards for hits and penalties for false alarms are matched within-category, response bias is reduced. These shifting decision thresholds may reflect changing strategies at recognition to maximize rewards for hits and avoid penalties for false alarms, but the potential control mechanisms underlying such strategy changes have not yet been delineated. Importantly, in their data, Bowen et al. (2020) observed larger effects of reward on response bias than memory discriminability, suggesting that understanding motivational modulation of decision processes may be critical to understanding their effects on recognition memory performance overall.

Retrieval-Based and Retroactive Effects of Motivation on Memory

Many studies examining the effects of motivational manipulations on memory have introduced them at memory encoding (as in both the MIE paradigm, where target stimuli are presented in close proximity to reward cues and/or outcome feedback at encoding, as well as in the VDR paradigm, where target stimuli are presented at encoding in task blocks along with varying reward values). However, it is not always clear at the time of encoding what information will be motivationally meaningful later. A small but growing number of studies has begun to demonstrate that motivational information introduced *after* encoding may also modulate memory performance. Here, we discuss observations from two types of task designs that have utilized post-encoding motivational manipulations: paradigms that have manipulated motivation at memory retrieval, and paradigms that have manipulated motivation following encoding, during the retention interval between encoding and retrieval. We will refer to these two types of designs as investigating retrieval-based and retroactive effects of motivation, respectively.

Retrieval-Based Effects of Motivation on Memory

The processes engaged and the kinds of details successfully remembered during memory retrieval have often been characterized in terms of top-down goals – for example, a student retrieving studied information in order to succeed on a test, or an eyewitness who is asked to report their memory for a crime. Despite this, the role of motivation at the time of memory retrieval is not well-understood, and current evidence has been inconsistent across studies. One such study (Marini, Marzi, & Viggiano, 2011)

used a modified MIE paradigm that manipulated reward incentives both during encoding and during retrieval (in a recognition memory test), and observed that memory performance was strongest and response times at recognition were fastest for target stimuli presented with reward cues at both encoding and retrieval. Two additional studies have examined the effect of reward manipulations at the time of retrieval only. Han et al. (Han, Huettel, Raposo, Adcock, & Dobbins, 2010) examined the effects of high value incentives, low value incentives, or no incentives for correct responses on a recognition memory test. During recognition, incentives were, on a blocked basis, tied to either “Old” responses (hits rewarded, false alarms penalized, and no incentives for “new” responses) or “New” responses (correct rejections rewarded, false alarms penalized, and no incentives for “old” responses). While incentives did not modulate memory discriminability or response bias, reaction times were faster and memory confidence was higher when making the response associated with incentive (i.e., either Old/New) on that given task block. A second study by Yan and colleagues (Yan et al., 2018) manipulated incentives on a recognition memory test at retrieval on a trial-by-trial basis, with either correct responses (either old or new) rewarded and incorrect responses penalized on incentivized trials, or no incentives at stake. In contrast to Han et al. (2010), Yan and colleagues observed that incentives at retrieval were associated with enhanced memory accuracy, but no significant changes in reaction times (and memory confidence was not evaluated). Taken together, these observations suggest that motivational manipulations at retrieval may influence recognition memory performance, but given inconsistent results (where memory accuracy is affected by reward in some, but not other studies; likewise for response times and memory

confidence), the specific mechanisms by which motivation may modulate retrieval are not yet clear. In particular, while a long tradition of research has indicated an important role for strategic control in memory retrieval (Jacoby et al., 2005; Reder, 1988), the potential role of motivation in modulating strategic control at retrieval remains unknown. This is in contrast to extensive evidence demonstrating that motivation can modulate strategic control at encoding and optimize memory for high-value information (for example, using the VDR paradigm discussed above). Clarifying the contributions of strategic control and other candidate mechanisms potentially influenced by motivation at retrieval remains an important issue for future work.

Retroactive Effects of Motivation on Memory

In addition to observations that motivational effects introduced at retrieval can modulate memory performance, a number of recent studies have also suggested that introducing motivational manipulations post-encoding (i.e., retroactively) but pre-retrieval may also affect memory outcomes. Drawing on neurobiological evidence from the animal literature that memory traces for weakly encoded events can be strengthened by salient events occurring post-encoding (the “tag-and-capture” hypothesis), Dunsmoor and colleagues (Dunsmoor, Murty, Davachi, & Phelps, 2015) demonstrated that fear conditioning could retroactively enhance memory for conceptually related, previously encountered information that was weakly encoded. In this study, participants incidentally encoded objects from two categories (by completing a semantic judgment task); then, after a brief delay, novel objects from one of the two categories became associated with electric shock through a Pavlovian conditioning

paradigm. Following a 24-hour interval, a surprise recognition memory test revealed enhanced memory for objects from the category associated with shock, even though the recognized objects had been encountered prior to the association between the object category and shock. Patil et al. (Patil, Murty, Dunsmoor, Phelps, & Davachi, 2017) used a similar paradigm to examine retroactive effects of reward: incidental encoding of objects from two categories was followed by an incentivized delay match-to-sample task where objects from one of the two categories were associated with reward, which was then followed by a recognition memory test. At recognition, a retroactive benefit of reward to memory for previously encountered, related information was observed. Relatedly, a third study demonstrated that retroactive benefits of reward to object memory could be characterized along a gradient in terms of distance from reward, with objects closest to reward receiving the strongest retroactive memory benefit (Braun, Wimmer, & Shohamy, 2018). In all three of these studies, retroactive effects of the motivation manipulation on memory were observed with a 24-hour interval between encoding and retrieval, but not with immediate retrieval, suggesting that retroactive benefits of motivationally-relevant information to memory might require processes that occur at consolidation. Given this, the mechanisms supporting the retroactive benefits of motivators to memory observed in these studies might be similar to those supporting consolidation-dependent motivated memory with reward information presented at the encoding stage, as previously described (e.g., Murayama & Kitagami, 2014; Spaniol et al., 2014). Generally, strategic control has been considered independent of such consolidation-dependent mechanisms of motivated memory, but whether this also holds for retroactive effects of motivational information on memory remains an open question.

Effects of Varying Motivational Incentive Manipulations

As previously discussed, different experimental task designs have been used to test the effects of motivation on memory performance. Additionally, within such designs, the nature of the motivational incentives used may also vary, leading to potential differences in task performance. Despite this, the potential effects of differing incentives on motivated memory outcomes have yet to be delineated. In this section, we discuss important distinctions that have been made between different types of motivational incentives and their potential impact on memory performance. We focus on primary versus secondary incentives, magnitude of reward value and adaptive scaling, and interactions between motivator types. Note that these are not an exhaustive list; additional potential distinctions between motivators have been proposed, such as the distinction between intrinsic and extrinsic motivators (discussed elsewhere in Chiew & Adcock, 2019), and comparing money versus points (not yet investigated).

Primary vs. Secondary Incentives and the Role of Valence

The majority of studies experimentally characterizing effects of motivational incentives on cognition have employed monetary rewards or points, whereby participants may aim to maximize monetary rewards or number of points earned and receive a corresponding payout upon completion of the task. Use of money as a reward incentive has been commonplace in the literature on motivation-cognition interactions, given the assumed universality of its value, ease of implementation, and extensive prior observations of monetary incentive effects on performance. However, in addition to

monetary rewards, a range of other incentives have been employed to investigate motivated cognitive performance: these include monetary losses, threat of electric shock, food and liquid rewards and punishments, and social incentives (Beck, Locke, Savine, Jimura, & Braver, 2010; Carsten, Hoofs, Boehler, & Krebs, 2019; Chiew & Braver, 2016; Crawford et al., 2020; Vishnu P. Murty, LaBar, & Adcock, 2012). Such incentives may vary in terms of valence (i.e., rewards and punishments) as well as in whether they represent a primary versus secondary incentive (i.e., an incentive with immediate motivational value, such as a pleasurable food/liquid or an unpleasant electric shock; versus an incentive such as money, where reward value must be learned through association with directly rewarding stimuli).

In terms of valence, many studies characterizing motivation-cognition interactions have relied on the use of rewards; as a result, the potential effects of punishment or threat motivators on cognition are less understood, despite a long tradition of literature suggesting that negative reinforcers may be learned and used to guide behavior (Iwata, 1987). While a full discussion of valence is beyond the scope of the present manuscript (and has been discussed in more depth elsewhere; e.g., Bowen, Kark, & Kensinger, 2018; Chiew & Adcock, 2019; Murty & Adcock, 2017), a growing body of literature suggests that rewards and punishments may lead to differing effects on motivated memory, potentially by engaging distinct neural circuits supporting formation of differing memory representations (Adcock et al., 2006; Murty et al., 2012; Shigemune, Tsukiura, Kambara, & Kawashima, 2014; Wittmann et al., 2005). In particular, while reward-motivated memory has been observed to engage regions in the mesolimbic dopamine system such as the VTA, as well as the hippocampus (Adcock et al., 2006; Wittmann et

al., 2005), punishment-motivated memory has been observed to engage the amygdala and the parahippocampal cortex, but not hippocampus, in the medial temporal lobe (Murty, LaBar, & Adcock, 2016; Murty et al., 2012). Given the role of hippocampus in binding item and context information together into a coherent memory episode (Davachi, 2006; Staresina & Davachi, 2009; Yonelinas, 2013), it has been proposed that the lack of hippocampal engagement in punishment-motivated memory may be associated with vivid, but less coherent, memories encoded under threatening contexts (Murty & Adcock, 2017). While it has been debated whether such memory differences should be attributable specifically to valence or more so to arousal (Clewett & Murty, 2019), these observations suggest that reward and punishment motivators may be associated with differing memory outcomes and should be explored further.

While primary incentives (e.g., food, liquid, electric shock) have been used on a more limited basis than secondary incentives (e.g., money) to examine effects of motivation on human cognition, it has been suggested that the use of primary incentives might provide important insight into core motivational mechanisms guiding cognition and behavior (Krug & Braver, 2014). When studying motivational processes in animal models, primary incentives are typically employed (Berridge, 2004); thus, using primary incentives when examining effects of motivation on human performance may enable a closer bridging between animal and human literatures. Additionally, given that primary rewards and punishments are usually directly consumed or experienced, it has been argued that this enables more precise control over the timing and manipulation of incentive delivery than secondary incentives (Krug & Braver, 2014). While an fMRI meta-analysis (Sescousse, Caldú, Segura, & Dreher, 2013) suggests that processing

both primary and secondary rewards engages a network of common regions including bilateral striatum, anterior insula, and ventromedial PFC, additional fMRI evidence (Beck et al., 2010) suggests that primary versus secondary reward incentives during a working memory task can lead to comparable enhancements in behavioral performance, but differential temporal dynamics of activity in cognitive control-related PFC regions, with primary liquid rewards related to increased transient activity and secondary monetary rewards related to increased sustained activity. Further investigations have demonstrated that monetary and liquid incentives can be combined and integrated in terms of motivational value and impact on cognitive performance (Crawford et al., 2020; Yee, Adams, Beck, & Braver, 2019; Yee, Krug, Allen, & Braver, 2016). In contrast to these findings suggesting that primary and secondary rewards may engage overlapping neural substrates, leading to similar behavioral effects, an fMRI study comparing neural responses associated with aversive conditioning via primary reinforcers (shock) to secondary reinforcers (monetary losses) observed greater skin conductance (a marker of emotional arousal) to shock, and amygdala engagement only during shock, not monetary loss (Delgado, Jou, & Phelps, 2011). While participants showed evidence of learning from both types of reinforcers, as well as learning-related striatal activity, Delgado et al. suggested that the differential patterns of neural activity observed for shock versus monetary loss indicated that shock-based learning might more heavily depend on biologically-based fear systems than learning under monetary loss. On the basis of these findings, we may speculate that the use of primary incentives such as shock may potentially induce a motivational state denoted by avoidance of a punishing outcome to a greater extent than secondary incentives.

Additional studies characterizing differences in motivation induced by avoidance of an undesirable outcome (i.e., shock threat) versus potential loss of a desirable outcome (i.e., monetary loss) should explore this distinction further.

An important point in this literature is that experimental designs that utilize primary incentives have typically also employed immediate feedback (i.e., receipt of a consumable reward or punishment immediately after response, on a trial-by-trial basis). As such, a number of the studies using primary incentives have examined their effects on cognitive control performance, where task success on a given trial may be evaluated immediately; studies of primary incentives on memory encoding, when reward or punishment receipt may not be evaluated until the retrieval stage, are rarer (although see Murty et al., 2012, 2016 for examples of study designs using threat of shock at encoding). In such a design where rewards and punishments for performance cannot be administered immediately as feedback, as is the case in a memory paradigm (where performance cannot be evaluated until retrieval), primary incentives may be processed as more abstract and distant, which has been speculated to lead to effects on cognitive performance more similar to secondary incentives (Krug & Braver, 2014). To our knowledge, use of primary and secondary incentives on memory performance has yet to be compared; additionally, while effects of reward outcome during memory encoding have been considered (as discussed previously in *Effects of Reward Anticipation versus Outcome on Motivated Memory*), these studies have all employed secondary incentives such as monetary rewards. Thus, the potential effects of primary incentive receipt during memory encoding remain unknown.

Adaptive Scaling of Rewards in Motivated Memory

One important aspect of task design in motivated memory that has received very little empirical attention is the precise values or magnitude of rewards that will effectively evoke differing levels of motivation for task performance. In the MIE paradigm, two or three levels of potential reward value are typically included: i.e., high, low, and/or no reward, but the quantitative difference between these reward levels is usually quite small (e.g., \$1.00, \$0.50, \$0) and overall performance rewards accumulate to small payouts. It is currently unclear whether reward might influence intentional memory in a linear fashion, and what the upper and lower boundaries on this relationship might be. Studies examining the effects of rewards on performance have suggested the possibility of an inverted-U relationship between reward and performance enhancement, whereby rewards of too high a magnitude may actually lead to a decrement in performance – this phenomenon has been termed “choking under pressure” (Beilock & Carr, 2001; Yu, 2015) and has been observed across a range of cognitive domains, including mathematical processing (Beilock & Carr, 2005; Beilock, Kulp, Holt, & Carr, 2004), learning tasks (Markman, Maddox, & Worthy, 2006), motor control (Lee & Grafton, 2015), as well as incidental memory performance when participants are unaware their memory for the reward-predicting stimuli would be tested (Cheng et al., 2020). However, the upper boundary of reward magnitude at which point cognitive performance may no longer be enhanced has been difficult to quantify. Reward magnitude may be neurally coded in a relative, rather than absolute fashion. For example, studies of dopamine neuron activity in animal models indicate that prediction errors are sensitive to the extent to which outcomes deviate from an expected value,

instead of being sensitive to reward magnitude *per se* (Schultz, 1998; Tobler, Fiorillo, & Schultz, 2005). In an fMRI study with human participants, Bunzeck, Dayan, Dolan & Duzel (Bunzeck, Dayan, Dolan, & Duzel, 2010) observed evidence of *adaptive scaling* within regions of the brain associated with reward processing. Specifically, they observed that reward-related brain activity was not sensitive to the absolute magnitude of the reward in a linear fashion; instead, activation scaled with the relative value of the reward within an expected context. For example, reward-related brain regions responded differently to a reward of \$0.50, depending on whether that reward was the higher or lower value within the present task context. Additionally, adaptive scaling was linked to successful memory encoding, such that subsequent item memory was modulated by associated rewards of high versus low value, but this memory effect was also context-dependent. Thus, memory for items associated with a reward of \$0.50 was observed to be enhanced in contexts where this reward constituted a high-value reward, but not in contexts where this reward constituted a low-value reward. Notably, however, a pre-registered behavioral replication of Bunzeck et al.'s study (Mason, Ludwig, & Farrell, 2017) did not reproduce these memory findings: while a marginal effect of context was observed, the memory benefit was associated with *lower* reward outcomes relative to higher, a result interpreted as potentially consistent with observed benefits of punishment-based, as well as reward-based, motivators to memory success.

Additionally, Madan and Spetch (Madan & Spetch, 2012) identified an U-shaped relationship between reward magnitude and memory performance in an incidental memory paradigm, whereby memory success was enhanced for items associated with the highest- and lowest-value rewards, and items associated with intermediate rewards

were more likely to be forgotten. This pattern of findings was interpreted as indicating a significant role of reward *saliency* in motivated memory, above and beyond reward magnitude. This is consistent with additional accounts that the relationship between reward and memory may depend on multiple parameters, including reward saliency, arousal, and relative contributions of top-down versus bottom-up processing (Clewett & Mather, 2014). Taken together, the present literature suggests that relative, rather than absolute, reward value may guide motivational effects on memory performance, but additionally that these effects may be non-linear and observations have been inconsistent, potentially due to modulation by additional influences that may not yet be identified.

Participant Compensation in Experimental Studies of Motivated Memory

In addition to considering types of incentives and their magnitude within an experimental study, it may also be important to consider interactions between motivation for research participants to take part in the study and task-based rewards. In many experimental psychology studies, participants are recruited via two basic methods: participants may be undergraduate students who receive partial or bonus course credit for participation in research studies, or participants are paid (e.g., \$10/hour) to participate. Findings by Bowen and Kensinger (Bowen & Kensinger, 2017) suggest that the motivation to participate in research studies (as indirectly indexed via the form of experiment compensation) may impact reward-related modulation of memory performance. In a study employing a typical MIE paradigm, Bowen and Kensinger observed that those who participated in the study for monetary compensation

(at a flat rate that was provided regardless of task performance) demonstrated typical reward-related enhancements in memory performance: i.e., greater memory for items associated with high- vs. low-value rewards. In contrast, they observed that participants who completed the study for course credit did not demonstrate this reward-related memory benefit in the task, despite comparable memory performance overall. Neither group was aware of task-based rewards until they attended the experimental session. Additionally, those who were offered bonus course credit (instead of monetary rewards) as an incentive contingent on task performance, in addition to course credit for experiment participation, did not show increased memory selectivity for high-value items, ruling out the possibility of a congruency effect between motivation to participate and task-based rewards. While the potential differences in motivational context or encoding strategy that may have been induced by these two different compensation structures was not directly evaluated, increased memory selectivity for high-value items relative to low-value items has typically been considered the product of strategic control in paradigms such as the VDR (Castel et al., 2002), raising the intriguing possibility that aspects of experimental design that are usually considered inconsequential to studied outcomes (i.e., compensation offered for research participation) may interact with the motivational value of incentives offered or strategies used in the task.

These studies indicate that incentives of varying type, valence, and magnitude have been used in the motivated memory literature; while a few investigations have sought to elucidate potential differences in the psychological mechanisms engaged as a result of these differing incentives, many aspects of their potential effects are not well-understood. Additionally, the use of incentives may interact with other aspects of

experiment structure that are usually considered inconsequential to behavioral outcomes, such as standard participant compensation. We argue that motivational incentives, like other aspects of task design discussed in the present manuscript, may potentially vary on multiple parameters with important implications for behavioral outcomes. This remains an important area for future research.

Conclusion

Given the limitations of human memory, mechanisms that select and prioritize some pieces of information over others may be understood as adaptive and necessary for human survival. Motivational relevance is a major determinant of such prioritization in memory and, while important strides have been made in understanding the psychological and neural mechanisms underlying motivation-modulated memory, there are still many unanswered questions (see Figure 2). One theme that emerges from the existing literature is that there are multiple neurobiological and cognitive mechanisms that support prioritization of motivationally-relevant information in memory, and that these mechanisms vary in the extent to which they engage strategic control. In the present article, we reviewed evidence suggesting that the use of control dependent and control independent mechanisms may be contributing to the various behavioral findings that high value information is prioritized in memory. Further, we contend that whether control dependent vs. independent mechanisms are employed may depend on a number of different task parameters that have not been fully disentangled, such as: task demands (MIE vs. VDR paradigms), intentional versus incidental encoding, the presence or absence of a consolidation period, the use of reward anticipation versus

outcome, the stage of memory formation that performance-based reward motivation is introduced (e.g., encoding vs. retrieval), and characteristics of the motivational incentives used, such as type, valence, and magnitude. There are still many unanswered questions (noted in Figure 2) regarding the effects of varying these different task parameters as well as their potential interactions with one another. Given the selective quality of human memory, answering these questions will be important for gaining a full understanding of motivational significance as a determinant of general memory function. Additionally, understanding how motivation can modulate memory has important implications for education, where this may be leveraged to optimize learning and academic performance (Linnenbrink, 2006), as well as in psychopathology, where both motivational and cognitive processes are often disrupted (L. D. Crocker et al., 2013). Taken together, a more comprehensive characterization of motivated memory will critically inform our understanding of adaptive human behavior.

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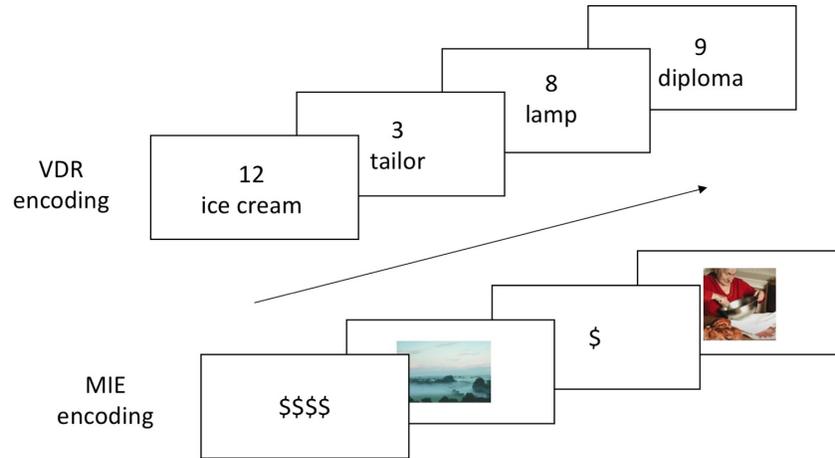


Figure 1. Depiction of encoding trials for the Value Directed Remembering (VDR) and Monetary Incentive Encoding (MIE) paradigms. The VDR task typically involves verbal stimuli paired with a point value (e.g., ranging from 1-12). The MIE task typically involves pictorial stimuli cued with a high (\$\$\$\$) or low (\$) reward value.

Unanswered Questions and Future Directions

Elucidating under what circumstances reward-motivated memory requires a period of consolidation, particularly when motivation is induced at encoding versus retrieval

If consolidation processes are necessary, investigating the role of strategic control in encoding, retrieval, and retroactive effects of motivational information on memory

Untangle whether motivated memory benefits from action outcomes and/or increases expended cognitive effort in incidental and intentional paradigms

Compare reward anticipation and feedback effects on memory to uncover why reward and punishment outcomes have such strong effects on memory

Examine motivational influences on memory sensitivity and/or decisional biases at retrieval, and what task parameters, like false alarm penalties, modulate this relationship

Characterize motivators and their various effects on memory including positive (approach) versus negative (avoidance) valence, magnitude of reward and punishment values, and interactions between rewards and other aspects of task design

Figure 2. Based on the literature reviewed in this article, there many unanswered questions and directions that should be addressed in future research posed here.