SOCIAL COGNITION (J BEADLE, SECTION EDITOR)



Examining Memory in the Context of Emotion and Motivation

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Abstract

Purpose of the Review In this review, I summarize the limited literature that includes manipulations of both emotion and motivation within the same experiment to examine their interactive and distinct effects on episodic memory. I position this work within the context of theories according to which emotion and motivation are inseparable, as well as other theories that view these constructs as dissociable.

Recent Findings Memory studies that manipulate emotion and motivation within the same trial provide support for theories that view them as separate constructs. Although separate constructs, studies that compare emotion and motivation, indicate they have similar effects on memory, but the extent of this similarity may depend on affective valence, task-relevance, and retention interval

Summary Investigating the behavioral effects of emotion and motivation on memory can inform our theoretical understanding of these constructs, with value for practical and clinical applications ranging from academic performance to psychopathology.

Keywords Memory · Emotion · Motivation · Reward · Valence

Introduction

A quote attributed to novelist Salman Rushdie states, "memory is a way of telling you what's important to you" [1]. From a scientific perspective, Rushdie has it backwards. Rather than memory telling you what's important, researchers have discovered that what is important, and carries affective and motivational significance, is more likely to be encoded and stored in memory. Emotion and motivation are the two most studied types of affective significance in the memory literature, but these lines of research rarely inform each other (see Fig. 1, top panel). A recent review paper [2...] has considered the effects of reward and emotion as related constructs within the broader context of motivated cognition. The goal of this review is to focus on the limited literature intentionally manipulating both emotion and motivation, within the same paradigm, to connect and compare their effects on episodic memory-defined as memory for events that can be recollected within a temporal and spatial context. In this paper, I conceive of emotion as positive or negative affect that is induced by an external stimulus in the environment, and motivation as the urge to engage in goal-directed behavior to obtain a reward or avoid punishment. Both emotion-modulated and motivation-modulated memories are considered to be adaptive. For example, stimuli that evoke feelings of fear like a dangerous animal, or information that must be studied to achieve a certain grade, will be better remembered than neutral or unimportant information because these memories contribute to survival, current and future goals, and well-being. I will discuss general theories of emotion and motivation to argue that studying their separate and combined effects on memory may advance our general understanding of these constructs. I will also discuss some future directions and applications of this research.

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Emotion- and Motivation-Modulated Memory

Several reviews have outlined emotion-modulated memory [3–8] and motivation-modulated memory [9–11], with one recent review detailing these literatures in parallel [12•]. Decades of memory research indicate that valence [6, 8]—the affective quality of the emotion, ranging from negative to positive—and arousal [4, 7]—the intensity of



the emotion, ranging from low to high—play an important role. This modulation occurs at multiple stages: emotional information is prioritized at encoding [13], focused on postencoding [4], consolidated [14], recapitulated [6, 15–18], and remembered with enhanced recollection and richness [19–21], even if remembered details are not accurate [22]. Emotion processing involves a large network of brain regions, including the limbic system [23, 24] and the prefrontal cortex [25]. The amygdala, one of the most frequently studied brain regions, is thought to mediate aspects of emotional learning and facilitate memory operations in other memory-related regions including the hippocampus and prefrontal cortex [26–29].

Investigations into motivation¹-modulated memory have characterized how reward (and punishment) anticipation [30-40], and reward feedback [41, 42••] influence memory formation. Research on reward processing has implicated regions in the dopaminergic midbrain, including the ventral tegmental area and substantia nigra (often dubbed the "reward network") [43], as well as medial frontal cortex [44]. Specifically, reward anticipation is associated with increased activation in the orbitofrontal cortex, amygdala, dorsal and ventral striatum [31, 37, 45–49], and insula [50]. Reward feedback has been shown to activate the ventromedial prefrontal cortex [44, 51], but there have been mixed findings on the role of the nucleus accumbens [44, 52]. Dopaminergic neurons also become active during reward predicting cues, novel stimuli, and punishment [53]. Interactions between regions in the midbrain and hippocampus are thought to modulate memory encoding of stimuli proximal to reward cues [31, 53, 54]. Figure 2 depicts neuroimaging evidence signifying that emotion and reward processing have both overlapping and distinct neural correlates.

Are Emotion and Motivation the Same Construct?

The literatures reviewed above indicate emotion and reward motivation can modulate memory processes and have overlapping neural correlates, but does this indicate that they are the same construct? There has been debate about whether emotion and motivation are in fact separable. Many experimental paradigms conflate the two constructs, making it difficult to separate their influences on cognition and behavior [55]. Some researchers take the stance that the two constructs are one and the same and thus can never be separated

¹ The terms motivation, reward motivation, and reward are used interchangeably in the current review. Most studies in the human literature have used monetary rewards to evoke a motivational response.



[56] making it impossible to study their unique and interactive effects on cognition [57]. The authors of a recent review argue that emotion and motivation are integrated and eventually merge into a single process with overlapping neural correlates [58•]. Indeed, there can be activation in reward circuitry during an "emotional" experience: for example, when participants are in a positive mood [59] or recalling positive autobiographical memories [60]. As pointed out by Goschke and Bolte [61], it may not be particularly surprising that positive emotions, like those elicited by recalling positive memories, would be rewarding, and that earning rewards, such as winning money at a slot machine, would evoke positive emotions. It may also seem reasonable that given this overlap, emotion and motivation would have similar effects on memory. If emotion and motivation are one construct that cannot be separated because they engage the same cognitive and neural mechanisms, it would follow that experimental combinations of emotional and motivational manipulations should produce no interactive effects on memory performance.

Few studies have examined this issue directly to date. Wittmann et al. [62] used a paradigm in which reward motivation and emotion were manipulated orthogonally (see Fig. 1, middle panel). Reward was not explicitly tied to successful memory for emotional pictorial stimuli, but was presented in close temporal and contextual proximity. The researchers found an additive effect of positive emotion and reward anticipation on successful incidental memory encoding. Mather and Schoeke [41], using a similar paradigm, also reported that incidental memory encoding was enhanced for positive pictures that were associated with reward anticipation. A more recent study, however, did not find that reward enhanced memory for positive images [63...]. Yan and colleagues [63••] reported main effects of both emotion and reward motivation on memory, but no additive or interactive effects of the two factors. Moreover, memory for negative episodic information has not been observed to be sensitive to reward. Based on findings that negative stimuli tend to be better remembered than neutral or positive stimuli, Shigemune and colleagues [34] hypothesized that rewards would boost memory for negative stimuli, compared to rewarded neutral stimuli or unrewarded negative stimuli, in an intentional encoding paradigm. In line with the findings by Yan et al. [63••], reward and emotion enhanced memory performance separately, but negative rewarded images were not better remembered than negative unrewarded images.

Both emotion and motivation can enhance memory, and under some experimental conditions, when positive images are encoded in close temporal/contextual proximity to a reward cue, this can have an additive effect, such that incidental memory is better when these two

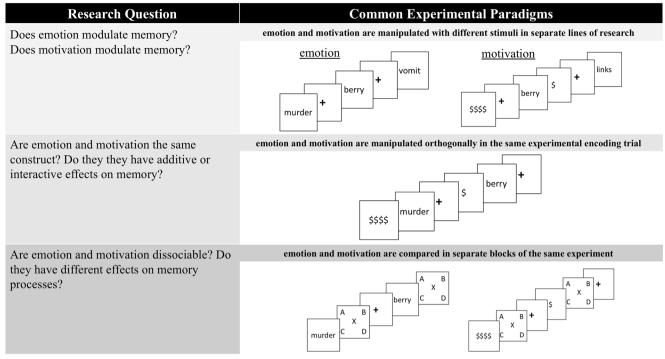


Fig. 1 Common experimental paradigms used to answer various research questions about emotion and reward effects on memory. Note. Depiction of the three research questions detailed in the paper with corresponding experimental paradigms that are commonly employed in the literature. Top Panel: The figure illustrates how questions about emotion and motivation effects on memory have been tested in separate lines of research. The figure depicts (incidental or intentional) encoding trials where emotion is induced with valent words* (e.g., murder, vomit) compared to neutral words (e.g., berry), and motivation is induced with cues at the beginning of each trial indicating a high (\$\$\$) compared to low (\$) reward value for task performance. Memory for the words would be tested on a subsequent memory task (not depicted). Middle Panel: to examine whether emotion and motivation are the same construct, emotion and motivation are induced orthogonally, but within the same experimental trial. The figure depicts (incidental or intentional) encoding trials where emotion is induced with valent words* (e.g., murder) compared to neutral words (e.g., berry), and motivation is induced with cues at the beginning of each trial indicating a high

(\$\$\$\$) compared to low (\$) reward value for task performance. The interactive or additive effects of emotion and motivation on memory for the words would be tested on a subsequent memory task (not depicted). Bottom Panel: to examine whether emotion and motivation are dissociable, their effects on memory are compared in separate trials or blocks of the same experimental task. The figures depict (incidental or intentional) encoding trials where emotion is induced at the beginning of each trial with valent words (e.g., murder) or neutral words (e.g., berry), and motivation is induced with cues at the beginning of each trial indicating a high (\$\$\$\$) compared to low (\$) reward value for task performance. Following the emotion or motivation induction, a stimulus would be flashed in one of the five locations on the screen (e.g., A, B, C, D, or X) and subsequent memory for this stimulus would be tested on a memory task (not depicted). *In this figure, emotion is induced using negative and neutral words, but as described in the current paper, emotional images quite commonly serve as stimuli in the literature, as do emotionally positive stimuli

types of affect are jointly present in the trial. This gives some support to emotion and motivation being distinct and separable processes. If emotion and motivation were relying on the same mechanisms to support successful encoding and episodic memory formation, there would be no advantage to including both in the same trial, but

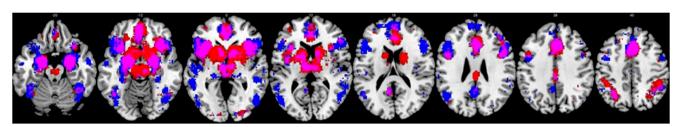


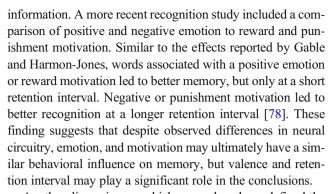
Fig. 2 Neural correlates of "Emotion", "Reward", and their overlap. Note. A search of the Neurosynth [105] (https://neurosynth.org/) database with the terms "emotion" (in blue) and "reward" (in red) suggest separate and overlapping (in purple) neural correlates of these constructs

the boundary conditions on this effect are not sufficiently clear.

How and When Are Emotion and Motivation Dissociable?

The studies detailed in the previous section manipulated emotion and motivation orthogonally within the same trial to examine additive and interactive effects on memory. Despite some claims that emotion and motivation are confounded [55–57], this and other evidence indicates they are dissociable. If emotion and motivation engaged identical neural networks (see Fig. 2), impairment in one domain should be associated with impairment in the other, but this is not always the case. Dysfunctional emotion processing due to amygdala damage is not always linked to reward processing dysfunction [64], and lesions in dopaminergic brain regions in rats can impair motivation to seek out sweet foods, but leave intact positive affect associated with sweetness [65•]. Berridge and colleagues [65•, 66•, 67•, 68•] have reported neurobiological evidence that the circuitry supporting incentive motivation is different from that involved in hedonic (i.e., emotional) experiences: this distinction has been characterized as "wanting" versus "liking", respectively. This distinction lead to the development of incentive-sensitization theory [69] which has been influential for understanding drug addiction and disordered eating, as the theory posits that one can have increased or disordered "wanting" without parallel increases in "liking".

In a thought-provoking review, Chiew and Braver [70] argue that characterizing common and distinct effects of positive emotion and reward motivation is necessary for advancing theories of affect and cognitive control. Indeed, many researchers have done this in the cognitive control domain which have been detailed in a recent review [71•], but similar work in the episodic memory domain is scarce. The few studies that have attempted this have focused on comparing emotion and motivation effects on attentional scope (see Fig. 1, bottom panel). Substantial evidence indicates that emotional valence can modulate the scope of attention, such that positive emotions widen and negative emotions narrow our field of view [72–74]. Valence-driven differences in attentional scope may therefore have downstream effects on episodic memory for central versus peripheral information [75, 76]. To test this hypothesis, Gable and Harmon-Jones [77] compared effects of reward anticipation induced via monetary gains (i.e., "wanting") to positive emotion induced via appetitive images (i.e., "liking"), on incidental memory for neutral words presented in various locations on the screen. Reward motivation and positive emotion had similar effects on attentional scope and incidental memory: both "wanting" and "liking" manipulations at the beginning of each trial narrowed attention, leading to preferential encoding of centrally presented



Another dimension on which researchers have defined the distinction between emotion and motivation is in terms of agency or control [42., 79, 80]. Motivational states are goal-directed and may depend on the perception that deliberate steps or behaviors can help achieve the goal. Emotions, on the other hand, are often associated with lack of control [79]. Emotions are often triggered by an external stimulus² and can drive automatic, spontaneous, and impulsive behaviors [81]. Bowen and Spaniol [42..] compared performance on an incidental memory task in which neutral words were presented in central and peripheral locations on the screen during states of motivation or emotion. During motivation blocks, participants earned or avoided losing money depending on task performance. In emotion blocks, monetary gains and losses were random, akin to the outcomes of playing a slot machine. Similar to the findings by Gable and Harmon-Jones [77], positive valence, whether induced via motivation or emotion, led to similar effects on memory for words presented after the monetary cue, but motivation and emotion effects on memory differed after loss feedback. During motivation blocks, when the participant was in control, but ultimately unsuccessful on the task, memory was better than emotion blocks when the loss was out of the participant's control. Reward motivation narrowed attentional focus and improved memory for central items, perhaps in the service of gaining information to help avoid a controllable loss in the future. This same level of focus did not occur in unsuccessful loss-evoked emotion blocks. Comparisons between emotional and motivational states and influences on cognition are difficult because they are induced and manipulated very differently. Emotion, via pictures or words that evoke negative or positive responses, and motivation, via gain or loss of monetary rewards or points. Bowen and Spaniol equated the experimental conditions using the same stimuli and paradigm (i.e., monetary gains and losses in a reaction time task) to induce both emotional and motivational states, and manipulated participant control over the



² Emotions may not always be triggered by an external event. For example, depressive symptoms may emerge due genetics or hormonal imbalance [106]. Further, impulsivity and lack of control associated with emotion may only be an immediate reaction. After some time and cognitive reappraisal, humans can regulate their emotions quite effectively [107].

outcome. This created high internal validity, but perhaps at the cost of lower external validity.

A final consideration for dissociating emotion and motivation concerns the direction of information processing. In the majority of emotional memory research, participants view affective stimuli, and via bottom-up influences that result from the emotional characteristics of the stimulus [82], this information is prioritized in memory. In studies of motivated-memory, participants view a cue signaling a potential future reward, and via top-down influences of extrinsic motivation [83], the associated information is prioritized in memory. A few recent studies have tested which of these is prioritized in memory when pitted against one another. Eich and Castel [84] examined how well older and younger adults could cognitively control their memory when bottom-up emotional information was competing for cognitive resources against top-down, goal-relevant reward information. To do this, emotional and neutral words were paired with a value ranging from 1 to 12, and participants were instructed to remember the words, but to focus on those associated with a high value to maximize their points. Both groups effectively prioritized high over low value items during intentional encoding, in line with their goals, even in the face of emotionally salient distraction. Sleep also seems to support the prioritization of motivationally relevant information: when top-down (reward) and bottom-up (emotion) goals are present for the same stimulus, memory for top-down information is enhanced after sleep, suggesting that motivation and emotion are not given the same status during memory consolidation [85]. These findings dovetail with the results of Bowen and Spaniol. In all cases, motivation had stronger effects on memory compared to emotion. These three findings also fit with many empirical studies and cognitive theories detailing whether and how emotion and motivation compete for perceptual resources and cognitive control during information processing [71, 86] and whether this prioritization of one type of affect over the other depends on task demands and goal-relevance of the affect [87, 88].

Future Directions

This paper details the few memory studies that have examined interactions between emotion and motivation, or compared their effects by inducing them separately within the same experiment using the same experimental task. In addition to much-needed replication, the results leave many unanswered questions. For instance, additive effects of emotion and motivation on episodic memory emerged during incidental encoding [41, 62], but not during intentional memory formation [34, 63]. If emotion and motivation are in fact separable constructs, why do additive effects emerge only when participants are unaware that their memory will be tested? Further, these effects seem specific to reward motivation and positive

emotion, but not negative emotion, perhaps pointing to a valence congruency effect. Recent neuroimaging work revealed a potential shared valence mechanism across motivation and emotion [89]. However, when comparing emotion and motivation effects on memory, there is reason to speculate that negative emotion and reward motivation would have similar effects on memory despite their valence differences. Traditionally, it was thought that negative emotion narrowed and positive emotion broadened attentional scope [72, 90, 91], but more recent findings indicate factors beyond valence may account for this effect, given that (positive) reward anticipation can also narrow attention [42., 92-95]. In younger adults, negative emotion enhances subjective and sometimes objective aspects of memory compared to positive emotion [6], while rewards seem to be superior to punishment for declarative memory formation [32] and lead to enhanced recollection compared to losses [63...]. One overarching methodological question for comparisons of emotion and motivation is to establish which approach to take—tight internal control, matching the emotion, and motivation conditions as closely as possible [42...], or potentially more externally valid paradigms, involving emotional stimuli and monetary rewards and losses [77]? Each approach can contribute something unique, but choosing one over the other may depend on the particular research questions.

Implications

The large majority of research on emotion and motivation has been carried out in parallel lines of study. Currently, there is no theoretical consensus on whether emotion and motivation are separable or the same construct, but see Cromwell et al. [58•] for a new perspective on this idea. Using episodic memory as a way to compare and test interactive effects of emotion and motivation may move us closer to an understanding of how and when they are common or dissociable. Further, deciding how best to define emotion and motivation has been an enduring debate, but considering them together within the same experimental context may elucidate characteristics about these constructs that can be used to help refine their definitions.

In addition to theoretical importance, there are significant implications for understanding the emotion-motivationmemory relationships. Below are four areas where this research could have substantial practical importance.

 Education. There is a longstanding debate about whether extrinsic rewards undermine a student's intrinsic interest in a subject [83, 96]. A review paper by Hidi [10] focused on motivation and learning in an educational context, nicely articulates both sides of that debate. If it is the case that extrinsic rewards undermine intrinsic enthusiasm for



a subject, it might be beneficial to incorporate extrinsic rewards when students have low intrinsic motivation or a negative reaction to a subject. Many students suffer from math anxiety—a "feeling of tension, apprehension, or fear that interferes with math performance" p. 181 [97]. Exploration into whether extrinsic reward motivation could override these negative emotions would be beneficial to student academic performance. There is some evidence that already supports this idea for boring information [98].

- 2) Aging. Aging is associated with well-documented declines in declarative memory, but reward sensitivity [30, 37, 46, 99, 100] and emotional functioning [5] remain relatively intact in healthy aging. Building on the strengths that older adults already possess, future work on how emotion and motivation might work together or distinctly to improve cognition, could stimulate the development of nonpharmacological memory interventions.
- 3) Dopamine deficiencies. Dopamine deficiencies, such as in Parkinson's disease, can lead to cognitive [101] and reward-learning [102, 103] deficits. To potentially counteract this dysfunction, Ridderinkhof and colleagues [102] assigned one group of medicated Parkinson's patients to watch an emotionally positive (Charlie Chaplin) video and another to watch a neutral video. The positive affect induced by the amusing content in the Charlie Chaplin clip led to better performance on a subsequent rewarded cognitive task. The ability to rescue performance on reward-learning tasks by tapping into phasic dopamine release by inducing positive affect, may be a beneficial avenue of research for other conditions characterized by dopamine deficiencies such as older age and addiction.
- 4) Anxiety and depression. Cognitive, emotional, and motivational impairments are defining symptoms of anxiety and depression, as well as an array of other psychological disorders. A review by Crocker and colleagues [104] notes that most psychopathology research has focused on emotion-cognition interactions without examining motivational factors, despite extensive evidence that motivation is related to the emotional and cognitive symptoms. Studying emotion-motivation-cognition interactions in healthy individuals will provide a basis for understanding how these processes can go awry in psychopathology, informing treatment-based research.

Conclusions

Emotion and motivation are similar constructs, but their influences on memory have largely been investigated in separate lines of research. The studies detailed in this review form marked exceptions that have incorporated both affective and motivational significance in the same experimental paradigm. The findings suggest that these two types of affect interact, and can have similar and distinct modulatory influences on memory processes. There continue to be theoretical debates about whether emotion and motivation are different constructs, and additionally, whether they can be separated, but the findings from the episodic memory literature reviewed here indicate growing support that they are dissociable. There is still much to be learned about emotion-motivation-memory interactions and studies aimed to integrate them would have theoretical impact for all three domains. This work would serve practical and clinical importance, aiding in elucidating mechanisms to target for interventions ranging from education to psychological disorders.

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Compliance with Ethical Standards

Conflict of Interest The authors declare that they have no conflict of interest.

References

Papers of particular interest, published recently, have been highlighted as:

- Of importance
- •• Of major importance
 - Farr E Salman Rushdie discusses creativity and digital scholarship [internet]. Emory Univ 2012. Available from: https://www. youtube.com/watch?v=kmb1oQcRmkM&feature=emb_logo. Accessed 8 Oct 2020.
 - 2.•• Madan CR. Motivated cognition: effects of reward, emotion, and other motivational factors across a variety of cognitive domains. Collabra Psychol. 2017;3:1-14. https://doi.org/10.1525/collabra. 111. This is an extensive review paper that considers a broad range of social, emotional and motivational influences on a variety of functions including motor response, attention, memory and decision making.
 - Hamann SB. Towards understanding emotion's effects on memory. Emot Rev. 2009;1:114–5. https://doi.org/10.1177/1754073908100433.
 - Mather M, Sutherland M. Arousal-biased competition in perception and memory. Perspect Psychol Sci. 2011;6:114

 –33. https://doi.org/10.1177/1745691611400234.
 - Mather M. The affective neuroscience of aging. Annu Rev Psychol. 2016;67:213–38. https://doi.org/10.1146/annurevpsych-122414-033540.
 - Bowen HJ, Kark SM, Kensinger EA. NEVER forget: negative emotional valence enhances recapitulation. Psychon Bull Rev. 2018;25:870–91. https://doi.org/10.3758/s13423-017-1313-9.



- Mather M, Sutherland M. Disentangling the effects of arousal and valence on memory for intrinsic details. Emot Rev. 2009;1:118–9. https://doi.org/10.1177/1754073908100435.
- Kensinger EA. Remembering the details: effects of emotion. Emot Rev. 2009;1:99–113. https://doi.org/10.1177/1754073908100432
- Murty VP, Dickerson KC. Motivational influences on memory. 2016. p. 203-27. https://doi.org/10.1108/S0749-742320160000019019.
- Hidi S. Revisiting the role of rewards in motivation and learning: implications of neuroscientific research. Educ Psychol Rev. 2016;28:61–93. https://doi.org/10.1007/s10648-015-9307-5
- Miendlarzewska EA, Bavelier D, Schwartz S. Influence of reward motivation on human declarative memory. Neurosci Biobehav Rev. 2016;61:156–76. https://doi.org/10.1016/j.neubiorev.2015. 11.015.
- 12.• Gruber MJ, Ritchey M. Episodic memory modulation: how emotion and motivation shape the encoding and storage of salient memories. In: Poeppel D, Gazzaniga MS, Mangun GR, editors. Cogn Neurosci. 6th ed. Cambridge: the MIT press; 2019. p. 257–64. In this paper, the authors review in parallel, how emotion and motivation have been show to influence memory encoding and consolidation processes. The authors also detail the different neural mechansims and neurotransmitters involved in these processes.
- LaBar KS, Mesulam MM, Gitelman DR, Weintraub S. Emotional curiosity: modulation of visuospatial attention by arousal is preserved in aging and early-stage Alzheimer's disease. Neuropsychologia. 2000;38:1734–40. https://doi.org/10.1016/ S0028-3932(00)00077-4
- McGaugh JL. The amygdala modulates the consolidation of memories of emotionally arousing experiences. Annu Rev Neurosci. 2004;27:1–28. https://doi.org/10.1146/annurev.neuro.27.070203. 144157
- Bowen HJ, Kensinger EA. Recapitulation of emotional source context during memory retrieval. Cortex. 2017;91:142–56. https://doi.org/10.1016/j.cortex.2016.11.004
- Bowen HJ, Kensinger EA. Memory-related functional connectivity in visual processing regions varies by prior emotional context. Neuroreport. 2017;28:808–13. https://doi.org/10.1097/WNR.0000000000000829
- Kark SM, Kensinger EA. Effect of emotional valence on retrievalrelated recapitulation of encoding activity in the ventral visual stream. Neuropsychologia. 2015;78:221–30 https://doi.org/10. 1016/j.neuropsychologia.2015.10.014
- Bowen HJ, Fields EC, Kensinger EA. Prior emotional context modulates early event-related potentials to neutral retrieval cues. J Cogn Neurosci. 2019; 31:1755-1767. https://doi.org/10.1162/ jocn_a_01451.
- Phelps EA, Sharot T. How (and why) emotion enhances the subjective sense of recollection. 2008;17:147–52. https://doi.org/ 10.1111/j.1467-8721.2008.00565.x.
- Levine LJ, Pizarro DA. Emotion and memory research: a grumpy overview. Soc Cogn. 2004;22:530–54. https://doi.org/10.1521/ soco.22.5.530.50767.
- Xie W, Zhang W. Negative emotion enhances mnemonic precision and subjective feelings of remembering in visual long-term memory. Cognition. 2017;166:73–83. https://doi.org/10.1016/j.cognition.2017.05.025.
- Talarico JM, Rubin DC. Confidence, not consistency, characterizes flashbulb memories. Psychol Sci. 2003;14:455–61. https://doi.org/10.1111/1467-9280.02453.
- LeDoux JE. Emotion: clues from the brain. Annu Rev Psychol. 1995;46:209–35. https://doi.org/10.1146/annurev.ps.46.020195. 001233.

- Rolls ET. Limbic systems for emotion and for memory, but no single limbic system. Cortex. 2015;62:119–57 https://doi.org/10. 1016/j.cortex.2013.12.005.
- Phan KL, Wager T, Taylor SF, Liberzon I. Functional neuroanatomy of emotion: a meta-analysis of emotion activation studies in PET and fMRI. Neuroimage. 2002;16:331–48. https://doi.org/10. 1006/nimg.2002.1087.
- LaBar KS, Cabeza R. Cognitive neuroscience of emotional memory. Nat Rev Neurosci. 2006;7:54

 –64. https://doi.org/10.1038/ nm1825.
- Murty VP, Ritchey M, Adcock RA, LaBar KS. Reprint of: fMRI studies of successful emotional memory encoding: a quantitative meta-analysis. Neuropsychologia. 2011;49:695–705. https://doi.org/10.1016/j.neuropsychologia.2011.02.031.
- Buchanan TW. Retrieval of emotional memories. Psychol Bull. 2007;133:761–79. https://doi.org/10.1037/0033-2909.133.5.761.
- Tyng CM, Amin HU, Saad MNM, Malik AS. The influences of emotion on learning and memory. Front Psychol. 2017;8. https:// doi.org/10.3389/fpsyg.2017.01454/full.
- Spaniol J, Schain C, Bowen HJ. Reward-enhanced memory in younger and older adults. J Gerontol B Psychol Sci Soc Sci. 2014;69:730–40 https://doi.org/10.1093/geronb/gbt044.
- Adcock RA, Thangavel A, Whitfield-Gabrieli S, Knutson B, Gabrieli JDE. Reward-motivated learning: mesolimbic activation precedes memory formation. Neuron. 2006;50:507–17. https:// doi.org/10.1016/j.neuron.2006.03.036.
- Murty VP, LaBar KS, Hamilton DA, Adcock RA. Is all motivation good for learning? Dissociable influences of approach and avoidance motivation in declarative memory. Learn Mem. 2011;18:712–7. https://doi.org/10.1101/lm.023549.111
- Castel AD, Humphreys KL, Lee SS, Galván A, Balota DA, McCabe DP. The development of memory efficiency and valuedirected remembering across the life span: a cross-sectional study of memory and selectivity. Dev Psychol. 2011;47:1553–64. https://doi.org/10.1037/a0025623.
- 34. Shigemune Y, Abe N, Suzuki M, Ueno A, Mori E, Tashiro M, et al. Effects of emotion and reward motivation on neural correlates of episodic memory encoding: a PET study. Neurosci Res. 2010;67:72–9. https://doi.org/10.1016/j.neures.2010.01.003.
- Cohen MS, Rissman J, Suthana NA, Castel AD, Knowlton BJ. Value-based modulation of memory encoding involves strategic engagement of fronto-temporal semantic processing regions. Cogn Affect Behav Neurosci. 2014;14:578–92. https://doi.org/ 10.3758/s13415-014-0275-x
- Madan CR, Spetch ML. Is the enhancement of memory due to reward driven by value or salience? Acta Psychol. 2012;139:343– 9. https://doi.org/10.1016/j.actpsy.2011.12.010..
- Bowen HJ, Ford JH, Grady CL, Spaniol J. Fronto-striatal functional connectivity supports reward-enhanced memory in older adults. Neurobiol Aging. 2020;90;1-12. https://doi.org/10.1016/j.neurobiolaging.2020.02.013.
- Cohen MS, Cheng LY, Paller KA, Reber PJ. Separate memoryenhancing effects of reward and strategic encoding. J Cogn Neurosci. 2019;1–16. https://doi.org/10.1162/jocn_a_01438.
- Shigemune Y, Tsukiura T, Nouchi R, Kambara T, Kawashima R. Neural mechanisms underlying the reward-related enhancement of motivation when remembering episodic memories with high difficulty. Hum Brain Mapp. 2017;3443:3428–43. https://doi. org/10.1002/hbm.23599.
- Bowen HJ, Kensinger EA. Cash or credit? Compensation in psychology studies: motivation matters. Collabra Psychol. 2017;3:12. https://doi.org/10.1525/collabra.77/
- Mather M, Schoeke A. Positive outcomes enhance incidental learning for both younger and older adults. Front Neurosci. 2011;5:1–10. https://doi.org/10.3389/fnins.2011.00129.



- 42.•• Bowen HJ, Spaniol J. Effects of emotion and motivation on memory dissociate in the context of losses? Learn Motiv. 2017;58:77-87. https://doi.org/10.1016/j.lmot.2017.05.003. This is one of the first empirical studies to have systematically compared emotion and motivation effects on episodic memory using tight internal control. The findings indicate that emotion and motivation may be similar during states of reward and positive affect, but dissociate during losses and negative affect.
- Schultz W. Multiple reward signals in the brain. Nat Rev Neurosci. 2000;1:199–207. https://doi.org/10.1038/35044563.
- Mowrer SM, Jahn AA, Abduljalil A, Cunningham WA. The value of success: acquiring gains, avoiding losses, and simply being successful. PLoS One. 2011;6:e25307. https://doi.org/10.1371/ journal.pone.0025307
- Rademacher L, Krach S, Kohls G, Irmak A, Gründer G, Spreckelmeyer KN. Dissociation of neural networks for anticipation and consumption of monetary and social rewards. Neuroimage. 2010;49:3276–85. https://doi.org/10.1016/j. neuroimage.2009.10.089.
- Spaniol J, Bowen HJ, Wegier P, Grady C. Neural responses to monetary incentives in younger and older adults. Brain Res. 2015;1612:70–82. https://doi.org/10.1016/j.brainres.2014.09.063.
- Arias-Carrión O, Stamelou M, Murillo-Rodríguez E, Menéndez-González M, Pöppel E. Dopaminergic reward system: a short integrative review. Int Arch Med. 2010;3:24. https://doi.org/10.1186/1755-7682-3-24.
- Knutson B, Adams CM, Fong GW, Hommer D. Anticipation of increasing monetary reward selectively recruits nucleus accumbens. J Neurosci. 2001;21:RC159. https://doi.org/10.1523/ JNEUROSCI.21-16-j0002.2001.
- Wittmann BC, Schott BH, Guderian S, Frey JU, Heinze HJ, Düzel E. Reward-related fMRI activation of dopaminergic midbrain is associated with enhanced hippocampus-dependent long-term memory formation. Neuron. 2005;45:459–67. https://doi.org/10. 1016/j.neuron.2005.01.010.
- Shigemune Y, Tsukiura T, Kambara T, Kawashima R. Remembering with gains and losses: effects of monetary reward and punishment on successful encoding activation of source memories. Cereb Cortex. 2014;24:1319–31. https://doi.org/10. 1093/cercor/bhs415.
- Bowen HJ, Grady CL, Spaniol J. Age differences in the neural response to negative feedback. Neuropsychol Dev Cogn B Aging Neuropsychol Cogn. 2019;26:463–85. https://doi.org/10.1080/ 13825585.2018.1475003.
- Knutson B, Fong GW, Adams CM, Varner JL, Hommer D. Dissociation of reward anticipation and outcome with eventrelated fMRI. Neuroreport. 2001;12:3683–7. https://doi.org/10. 1097/00001756-200112040-00016
- Shohamy D, Adcock RA. Dopamine and adaptive memory. Trends Cogn Sci. 2010;14:464

 72. https://doi.org/10.1016/j.tics. 2010.08.002.
- Stanek JK, Dickerson KC, Chiew KS, Clement NJ, Adcock RA. Expected reward value and reward uncertainty have temporally dissociable effects on memory formation. J Cogn Neurosci. 2019;31:1443–54. https://doi.org/10.1162/jocn_a_01411
- Schomaker J, Wittmann BC. Memory performance for everyday motivational and neutral objects is dissociable from attention. Front Behav Neurosci. 2017;11:1–13. https://doi.org/10.3389/fnbeh.2017.00121/full.
- Laming DRJ. On the behavioural interpretation of neurophysiological observation. Behav Brain Sci. 2000;23: S0140525X00392421. https://doi.org/10.1017/ S0140525X00392421.

- Rolls ET. Précis of the brain and emotion. Behav Brain Sci. 2000;23:177–91 discussion 192-233. https://doi.org/10.1017/ s0140525x00002429.
- 58.• Cromwell HC, Abe N, Barrett KC, Caldwell-Harris C, Gendolla GHE, Koncz R, et al. Mapping the interconnected neural systems underlying motivation and emotion: a key step toward understanding the human affectome. Neurosci Biobehav Rev. 2020;113: 204–26. https://doi.org/10.1016/j.neubiorev.2020.02.032. A comprehensive review paper focused on emotion and motivation including behavioral and neuroimaging research. The authors conclude that emotion and motivation merge into a single construct supported by overlapping neural mechanisms.
- Young CB, Nusslock R. Positive mood enhances reward-related neural activity. Soc Cogn Affect Neurosci. 2016;11:934

 44. https://doi.org/10.1093/scan/nsw012
- Speer ME, Bhanji JP, Delgado MR. Savoring the past: positive memories evoke value representations in the striatum. Neuron. 2014;84:847–56. https://doi.org/10.1016/j.neuron.2014.09.028.
- Goschke T, Bolte A. Emotional modulation of control dilemmas: the role of positive affect, reward, and dopamine in cognitive stability and flexibility. Neuropsychologia. 2014;62:403–23. https://doi.org/10.1016/j.neuropsychologia.2014.07.015.
- Wittmann BC, Schiltz K, Boehler CN, Düzel E. Mesolimbic interaction of emotional valence and reward improves memory formation. Neuropsychologia. 2008;46:1000–8. https://doi.org/10.1016/j.neuropsychologia.2007.11.020.
- 63. •• Yan C, Liu F, Li Y, Zhang Q, Cui L. Mutual influence of reward anticipation and emotion on brain activity during memory retrieval. Front Psychol. 2017;8:1873. https://doi.org/10.3389/fpsyg. 2017.01873. One of the only ERP studies to investigate emotion and motivation effects on memory. Participants completed an intentional memory encoding of emotional images under states of reward anticipation. Reward and negative emotion improved recognition memory performance, but there was no interaction between these two types of affect.
- Izquierdo A, Suda RK, Murray EA. Comparison of the effects of bilateral orbital prefrontal cortex lesions and amygdala lesions on emotional responses in rhesus monkeys. J Neurosci. 2005;25: 8534–42. https://doi.org/10.1523/JNEUROSCI.1232-05.2005.
- 65. Berridge KC. Evolving concepts of emotion and motivation. Front Psychol. 2018;9:1–20. https://doi.org/10.3389/fpsyg.2018.01647. A history of how researchers have thought about, defined and empirically tested emotion and motivation, from animal to human models. Berridge also discusses a review of recent empirical findings and applications of these constructs.
- Berridge KC, Robinson TE. Parsing reward. Trends Neurosci. 2003;26:507–13. https://doi.org/10.1016/S0166-2236(03)00233-9
- Berridge KC, Robinson TE, Aldridge JW. Dissecting components of reward: 'liking', 'wanting', and learning. Curr Opin Pharmacol. 2009;9:65–73. https://doi.org/10.1016/j.coph.2008.12.014.
- Berridge KC. Food reward: brain substrates of wanting and liking. Neurosci Biobehav Rev. 1996;20:1–25. https://doi.org/10.1016/ 0149-7634(95)00033-b.
- Berridge KC, Robinson TE. Liking, wanting, and the incentivesensitization theory of addiction. Am Psychol. 2016;71:670–9. https://doi.org/10.1037/amp0000059.
- Chiew KS, Braver TS. Positive affect versus reward: emotional and motivational influences on cognitive control. Front Psychol. 2011;2:1–10. https://doi.org/10.3389/fpsyg.2011.00279/abstract.
- 71.• Padmala S, Sambuco N, Pessoa L. Interactions between reward motivation and emotional processing. Prog Brain Res. 2019;247: 1–21. https://doi.org/10.1016/bs.pbr.2019.03.023. A recent review article of empirical investigations of emotion and



- motivation effects on cognitive control, as well as a discussion of the "dual competition framwork" and how emotion and motivation compete for processesing and cognitive resources.
- Gasper K, Clore GL. Attending to the big picture: mood and global versus local processing of visual information. Psychol Sci [internet]. 2002;13:34–40. https://doi.org/10.1111/1467-9280. 00406
- Fredrickson BL. The broaden-and-build theory of positive emotions. Philos Trans R Soc Lond Ser B Biol Sci. 2004;359:1367

 78. https://doi.org/10.1098/rstb.2004.1512.
- Rowe G, Hirsh JB, Anderson AK. Positive affect increases the breadth of attentional selection. Proc Natl Acad Sci [Internet]. 2007;104:383–8. https://doi.org/10.1073/pnas.0605198104.
- Waring JD, Kensinger EA. Effects of emotional valence and arousal upon memory trade-offs with aging. Psychol Aging. 2009;24:412–22. https://doi.org/10.1037/a0015526.
- Riggs L, McQuiggan DA, Farb N, Anderson AK, Ryan JD. The role of overt attention in emotion-modulated memory. Emotion. 2011;11:776–85. https://doi.org/10.1037/a0022591.
- Gable PA, Harmon-Jones E. The effect of low versus high approach-motivated positive affect on memory for peripherally versus centrally presented information. Emotion. 2010;10:599– 603. https://doi.org/10.1037/a0018426.
- Sun Q, Gu S, Yang J. Context and time matter: effects of emotion and motivation on episodic memory overtime. Neural Plast. 2018;2018:1–13. https://doi.org/10.1155/2018/7051925.
- Roseman IJ. Motivations and emotivations: approach, avoidance, and other tendencies in motivated and emotional behavior. In: Elliot AJ, editor. Handb Approach Avoid Motiv. New York: Psychology Press; 2008. p. 343–66.
- Chiew KS, Braver TS. Dissociable influences of reward motivation and positive emotion on cognitive control. Cogn Affect Behav Neurosci. 2014;14:509–29. https://doi.org/10.3758/ s13415-014-0280-0.
- Ariely D, Loewenstein G. The heat of the moment: the effect of sexual arousal on sexual decision making. J Behav Decis Mak. 2006;19:87–98. https://doi.org/10.1002/bdm.501.
- McRae K, Misra S, Prasad AK, Pereira SC, Gross JJ. Bottom-up and top-down emotion generation: implications for emotion regulation. Soc Cogn Affect Neurosci. 2012;7:253–62. https://doi.org/ 10.1093/scan/nsq103
- Ryan R, Deci E. Intrinsic and extrinsic motivations: classic definitions and new directions. Contemp Educ Psychol. 2000;25:54

 67. https://doi.org/10.1006/ceps.1999.1020.
- Eich TS, Castel AD. The cognitive control of emotional versus value-based information in younger and older adults. Psychol Aging [Internet]. 2016;31:503–12. https://doi.org/10.1037/ pag0000106.
- Bennion KA, Payne JD, Kensinger EA. The impact of napping on memory for future-relevant stimuli: prioritization among multiple salience cues. Behav Neurosci. 2016;130:281–9. https://doi.org/ 10.1037/bne0000142.
- Pessoa L. How do emotion and motivation direct executive control? Trends Cogn Sci. 2009;13:160–6. https://doi.org/10.1016/j.tics.2009.01.006.
- 87.• Park HRP, Kostandyan M, Boehler CN, Krebs RM. Winning smiles: Signalling reward by overlapping and non-overlapping emotional valence differentially affects performance and neural activity. Neuropsychologia. 2019;122:28–37. https://doi.org/10.1016/j.neuropsychologia.2018.11.018. This neuroimaging study included emotional and motivation manipulations that were both equally task relevant. Like prior work on memory, the authors found reward-related positive stimuli enhanced

- performance, but reward-related negative and neutral stimuli led to performance deficits.
- Wei P, Kang G. Task relevance regulates the interaction between reward expectation and emotion. Exp Brain Res. 2014;232:1783– 91. https://doi.org/10.1007/s00221-014-7823870-8.
- Park HRP, Kostandyan M, Boehler CN, Krebs RM. Smiling faces and cash bonuses: exploring common affective coding across positive and negative emotional and motivational stimuli using fMRI. Cogn Affect Behav Neurosci. 2018;18:550–63. https://doi.org/10. 3758/s13415-018-0587-3.
- Friedman RS, Förster J. Implicit affective cues and attentional tuning: an integrative review. Psychol Bull. 2010;136:875–93. https://doi.org/10.1037/a0020495.
- 91. Fredrickson BL. The role of positive emotions in positive psychology. The broaden-and-build theory of positive emotions. Am Psychol. 2001;56(3):218–26. https://doi.org/10.1037/0003-066X. 56.3.218.
- Harmon-Jones E, Gable PA. Incorporating motivational intensity and direction into the study of emotions: implications for brain mechanisms of emotion and cognition-emotion interactions. Neth J Psychol. 2008;64:132–42. https://doi.org/10.1007/ BF03076416.
- Gable PA, Harmon-Jones E. Approach-motivated positive affect reduces breadth of attention. Psychol Sci. 2008;19:476–82. https:// doi.org/10.1111/j.1467-9280.2008.02112.x.
- 94. Gable PA, Harmon-Jones E. The blues broaden, but the nasty narrows: attentional consequences of negative affects low and high in motivational intensity. Psychol Sci a J Am Psychol Soc / APS. 2010;21:211-5. https://doi.org/10.1177/0956797609359622.
- Sadowski S, Fennis BM, van Ittersum K. Losses tune differently than gains: how gains and losses shape attentional scope and influence goal pursuit. Cognit Emot. 2020;6:1–18. https://doi.org/ 10.1080/02699931.2020.1760214.
- Deci EL. Effects of externally mediated rewards on intrinsic motivation. J Pers Soc Psychol. 1971;18:105–15 https://doi.org/10. 1037/h0030644.
- Ashcraft MH. Math anxiety and its cognitive consequences. Curr Dir Psychol Sci. 2002;11:181–5. https://doi.org/10.3758/s13415-015-0370-7.
- Murayama K, Kuhbandner C. Money enhances memory consolidation but only for boring material. Cognition. 2011;119:120–4. https://doi.org/10.1016/j.cognition.2011.01.001.
- Castel AD. The Adaptive and Strategic Use of Memory By Older adults: evaluative processing and value-directed remembering. In: Benjamin AS, Ross B, editors. Psychol Learn Motiv. 1st ed. Academic Press; 2007. p. 225–70. https://doi.org/10.1016/ S0079-7421(07)48006-9.
- Castel AD, Benjamin AS, Craik FIM, Watkins MJ. The effects of aging on selectivity and control in short-term recall. Mem Cogn. 2002;30:1078–85. https://doi.org/10.3758/bf03194325.
- Kaasinen V, Rinne JO. Functional imaging studies of dopamine system and cognition in normal aging and Parkinson's disease. Neurosci Biobehav Rev. 2002;26:785–93. https://doi.org/10. 1016/s0149-7634(02)00065-9.
- 102. Ridderinkhof KR, van Wouwe NC, Band GPH, Wylie SA, Van der Stigchel S, Van Hees P, et al. A tribute to Charlie Chaplin: induced positive affect improves reward-based decision-learning in Parkinson's disease. Front Psychol. 2012;3:1–10. https://doi.org/10.3389/fpsyg.2012.00185.
- Eppinger B, Hammerer D, Shu-Chen L. Neuromodulation of reward based learning and decision making in human aging. Ann N Y Acad Sci. 2011;1235:1–17. https://doi.org/10.1111/j.1749-6632.2011.06230.x.



- Crocker LD, Heller W, Warren SL, O'Hare AJ, Infantolino ZP, Miller GA. Relationships among cognition, emotion, and motivation: implications for intervention and neuroplasticity in psychopathology. Front Hum Neurosci. 2013;7:261. https://doi.org/10. 3389/fnhum.2013.00261.
- Yarkoni T, Poldrack RA, Nichols TE, Van Essen DC, Wager TD. Large-scale automated synthesis of human functional neuroimaging data. Nat Methods. 2011;8:665–70. https://doi.org/10.1038/nmeth.1635.
- Beck AT, Alford BA. Depression causes and treatment. 2nd ed. Philidelpia: University of Pennsylvania Press; 2009. https://doi. org/10.1080/15323269.2010.492268.
- Gross JJ. Emotion regulation: affective, cognitive, and social consequences. Psychophysiology. 2002;39:281–91. https://doi.org/10.1017/S0048577201393198.

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