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Asymmetric effects of emotion on mnemonic interference

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ABSTRACT

Emotional experiences can strengthen memories so that they can be used to guide future behavior. Emotional arousal, mediated by the amygdala, is thought to modulate storage by the hippocampus, which may encode unique episodic memories via pattern separation - the process by which similar memories are stored using non-overlapping representations. While prior work has examined mnemonic interference due to similarity and emotional modulation of memory independently, examining the mechanisms by which emotion influences mnemonic interference has not been previously accomplished in humans. To this end, we developed an emotional memory task where emotional content and stimulus similarity were varied to examine the effect of emotion on fine mnemonic discrimination (a putative behavioral correlate of hippocampal pattern separation). When tested immediately after encoding, discrimination was reduced for similar emotional items compared to similar neutral items, consistent with a reduced bias towards pattern separation. After 24 h, recognition of emotional target items was preserved compared to neutral items, whereas similar emotional item discrimination was further diminished. This suggests a potential mechanism for the emotional modulation of memory with a selective remembering of gist, as well as a selective forgetting of detail, indicating an emotion-induced reduction in pattern separation. This can potentially increase the effective signal-to-noise ratio in any given situation to promote survival. Furthermore, we found that individuals with depressive symptoms hyper-discriminate negative items, which correlated with their symptom severity. This suggests that utilizing mnemonic discrimination paradigms allows us to tease apart the nuances of disorders with aberrant emotional mnemonic processing.

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1. Introduction

Emotions color our memories and can afford them a special status that preserves them from loss and forgetting. This relationship is thought to be adaptive; the association of memories with positive or negative affect allows them to more successfully guide future action. While studies in animals have reliably demonstrated a facilitatory effect of arousal on memory consolidation (McGaugh, 2004), studies in humans suggest a more complicated picture. Flashbulb memories (memories for the circumstances in which one heard about a newsworthy event) initially suggested that memory was better for emotional events and their context compared to neutral events (Brown & Kulik, 1977). These memories were thought to be vivid due to inclusion of many peripheral details. However, Heuer and Reisberg (1990) showed that while emotion leads to vivid recollections, these recollections are not completely accurate and may result from post hoc reconstructions of the emotional event. Thus, the hallmark of an emotional memory may be the subjective vividness with which it is remembered rather than the accuracy with which it is retained (Kensinger, 2009).

More recently, several studies have suggested that emotion's effects on memory are asymmetrical, such that emotional modulation of memory for the gist is enhanced, while memory for details is impaired (Kensinger, 2009; Loftus, Loftus, & Messo, 1987; Mather & Sutherland, 2011). Such selectivity suggests an emotion-induced memory trade-off, where individuals remember the central emotional content of an experience but often forget the details (Buchanan & Adolphs, 2002). An example of this phenomenon is the "weapon focus" effect, where eye-witnesses often recall the weapon used in a crime with great detail but fail to encode (or perhaps more quickly forget) peripheral details such



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as the perpetrator's clothing (Loftus et al., 1987). Typically these effects are most robust after a delay, where emotional arousal can influence the consolidation of information (McGaugh, 2004). However, several studies have shown that explicit memory for emotional stimuli can be enhanced even when tested immediately, which suggests that emotion affects both encoding and consolidation mechanisms (Hamann, 2001).

The effect of emotional arousal on memory is thought to be mediated by the influence of the amygdala on hippocampal processing (McGaugh, 2004). The amygdala is promiscuous in influencing the consolidation of memory for many kinds of motivationally arousing experiences, either appetitive (i.e. positive) or aversive (i.e. negative) (McGaugh, 2002, 2004). This is thought to occur through the amygdala's ability to modulate hippocampal representations. The hippocampus is known to play a critical role in the encoding and storage of episodic memories (Squire, 1992). While there are several levels at which hippocampal functions can be described, many computational models have ascribed particular computational functions to subregions of the hippocampus in service of episodic memory. David Marr (1971) first suggested that the recurrent collaterals in the hippocampal CA3 enabled this region to act as an auto-associative network capable of pattern completion (the process by which previously stored representations are retrieved when presented with partial or degraded cues). In contrast, upstream of the CA3, the dentate gyrus (DG) uses a sparse firing pattern among its granule cells, which allows the region to perform pattern separation - the process of reducing interference among similar inputs by using non-overlapping representations (McClelland, McNaughton, & O'Reilly, 1995; O'Reilly and Norman, 2002; Shapiro & Olton, 1994; Treves & Rolls, 1994; Yassa & Stark, 2011).

While the effect of amygdala-mediated emotional arousal on hippocampal episodic memory has long been observed both in animal and human studies (Dolcos, LaBar, & Cabeza, 2004; McGaugh, 2004), the exact mechanism for this effect has remained quite elusive. The computational descriptions of hippocampal function offer a potential mechanistic account by which information storage may be modulated (i.e. either by enhancing pattern separation or pattern completion). Using this framework, we can reframe the question "How does emotion enhance gist memory and weaken detail memory?" into a more directed mechanistic hypothesis: "Does emotional arousal facilitate or impede pattern separation?"

While we cannot directly make inferences about the computational process, we make the assumption that pattern separation will have a behavioral consequence, namely mnemonic discrimination among similar stimuli. This logic has been previously applied to many studies examining hippocampal function (Hunsaker & Kesner, 2013; Yassa & Stark, 2011). In a recent study, we examined the effect of emotional arousal on discrimination (Segal, Stark, Kattan, Stark, & Yassa, 2012) and demonstrated that increased emotional arousal (measured using salivary alpha amylase, a biomarker for endogenous peripheral noradrenergic activation) was correlated with enhanced mnemonic discrimination for similar neutral objects. These findings suggest that emotion may modulate mnemonic discrimination abilities when interference is high (i.e. when test items are similar to study items), which is thought to rely on hippocampal pattern separation (Yassa & Stark, 2011). However, this prior study only evaluated emotion as a pre-study state effect (i.e. a state of increased arousal could have enhanced attention or increased vigilance) and not on a trial-by-trial basis (thereby losing stimulus specificity). In addition, the study only investigated the immediate effects of emotional arousal on memory, whereas many studies of emotional memory have tested participants after a delay to allow for consolidation to occur.

In the current study, we systematically examined the effect of emotional modulation on individual stimuli (transient effects) using a paradigm where both emotional content (negative, neutral, positive) and stimulus similarity (high and low) were varied in a parametric fashion, and testing was conducted both immediately and after a 24-h delay. Given the wealth of recent empirical data in favor of the role of the hippocampus in reducing mnemonic interference (Yassa & Stark, 2011), the current investigation offers an alternative conceptual framework by which to examine the impact of emotion on hippocampal computations. We hypothesized that emotional targets (i.e. repeated items) would be better remembered while emotional lures (i.e. similar but not identical items) would be more difficult to discriminate when tested immediately and that this effect would be exaggerated after a 24-h delay. Stimulus similarity was manipulated to create highly interfering test stimuli, with the high and low similarity conditions expected to alter performance on the task, where highly similar items should be more difficult to discriminate than low similarity items. We did not have any strong behavioral hypotheses for whether these similarity conditions would vary with emotion.

We also tested the utility of this approach in examining individuals with depressive symptoms. Depression is a neuropsychiatric phenotype involving a recognized disturbance in emotional memory processing. Many studies of major depressive disorder (MDD) have documented general deficits in episodic memory (Airaksinen, Wahlin, Forsell, & Larsson, 2007; Airaksinen, Wahlin, Larsson, & Forsell, 2006; Dere, Pause, & Pietrowsky, 2010). In addition, depressed individuals tend to better remember negative items compared to neutral or positive items (Gordon, Barnett, Cooper, Tran, & Williams, 2008; Haas & Canli, 2008; Hasler, Drevets, Manji, & Charney, 2004; Watkins, Martin, & Stern, 2000; Watkins, Vache, Verney, Muller, & Mathews, 1996). We examined these behavioral aberrations using our emotional discrimination task in a sample of individuals exhibiting depressive symptoms. Our results shed new light on how emotion affects mnemonic computations and how these processes may be affected in depression.

2. Materials and Methods

2.1. Participants

Participants were recruited from Johns Hopkins University and received either course credit or monetary remuneration for their participation for the primary experiments. In the immediate condition, 24 participants were tested (all mean age \pm SD, 21 \pm 3, 16 female). In the 24-h delayed condition, 14 participants were tested (20 \pm 2, 6 female). In the depressive symptom condition, 15 participants were tested (22 \pm 4, 11 female). Participants with depressive symptoms (DS) were recruited through local campus announcements and posted flyers. Supplementary experiments required additional participants (demographics listed in respective sections). Informed consent was obtained from all participants, with all procedures approved by the Johns Hopkins University Institutional Review Board.

2.2. Inclusion/exclusion criteria

All participants were screened against self-reported major medical, psychiatric, and substance use comorbidity. Participants did not receive a diagnostic psychiatric evaluation as part of this study. The Beck Depression Inventory-II was given to all participants. Assignment to healthy versus depressive symptom group was based on BDI-II cutoff (BDI-II < 7 = healthy group, BDI-II > 15 = depressive symptom group). These cutoff criteria were based on the BDI-II symptom severity scale in which 16 is the cutoff for a mild mood disturbance (scores above 16 are suggestive of clinical depression; the higher the score indicates greater severity Download English Version:

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