A retrieved context theory of memory in emotional disorders

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Abstract

Learning and memory play a central role in psychopathology, particularly in depression and posttraumatic stress disorder. We present a new, transdiagnostic theory of how memory and mood interact in emotional disorders. Drawing upon retrieved-context models of episodic memory, we propose that memories form associations with the contexts in which they are encoded, including emotional valence and arousal. Later, encountering contextual cues retrieves their associated memories, which in turn reactivate the context that was present during encoding. We first show how our retrieved-context model accounts for findings regarding the organization of emotional memories in list-learning experiments. We then show how this model predicts clinical phenomena, including persistent negative mood after chronic stressors, intrusive memories of painful events, and the efficacy of cognitive-behavioral therapies.

Introduction

Over 70% of adults will experience traumatic stress at some point in their lifetime, including threatened or actual physical assault, sexual violence, motor vehicle accidents, and natural disasters (Benjet et al., 2016). Following trauma exposure, 20-32% of adults suffer distressing, intrusive memories of the event, hyperarousal, avoidance of event reminders, and persistent negative mood (Brewin, Andrews, Rose, & Kirk, 1999). Trauma-exposed adults also commonly experience negative mood, decreased motivation, and disrupted sleep or appetite (Goenjian et al., 2001). Historically, the Diagnostic and Statistical Manual of

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Mental Disorders (DSM) has divided these symptoms into diagnostic categories of post-traumatic stress disorder (PTSD) or major depressive disorder (MDD), according to the prominence of memory versus mood disturbances, respectively (American Psychiatric Association, 2013). However, although memory intrusions are not among the diagnostic criteria for MDD, patients with depression also report high rates of intrusive memories, replete with sensory and reliving experiences (Reynolds & Brewin, 1999). Conversely, although PTSD is not considered to be a mood disorder, affective symptoms are part of the disorder and as many as 50-75% of patients have co-occurring MDD (K. T. Brady, Killeen, Brewerton, & Lucerini, 2000). The high comorbidity and symptom overlap between these disorders has led to a search for transdiagnostic processes (Insel et al., 2010; Sanislow et al., 2010) that hold promise for the development of more efficient and efficacious treatments. Here we develop a transdiagnostic, computational model of memory in emotional disorders. This model describes how distressing events interact with the memory system, as well as the mechanisms that produce the negative mood and intrusive memories that cut across both depression and PTSD.

Research implicates learning and memory as a transdiagnostic process underlying psychopathology (Beck, Rush, Shaw, & Emery, 1979; Bower, 1981; Brewin, 2006). Patients with PTSD experience intrusive memories of traumatic events (Ehlers, Hackmann, & Michael, 2004), but patients with depression, social anxiety, and a wide range of other emotional disorders also report high rates of vivid, intrusive memories of painful events (Berntsen, 2010; Day, Holmes, & Hackmann, 2004; Hackmann, Clark, & McManus, 2000; Muse, Mcmanus, Hackmann, Williams, & Williams, 2010; Osman, Cooper, Hackmann, & Veale, 2004; Price, Veale, & Brewin, 2012; Reynolds & Brewin, 1999; Speckens, Hackmann, Ehlers, & Cuthbert, 2007). In addition, patients with anxiety and depression tend to recall negative events more frequently than positive events, implicating mechanisms of *mood-congruent recall* (Matt, Vazquez, & Campbell, 1992; P. C. Watkins, Mathews, Williamson, & Fuller, 1992). Here, mood-congruent recall refers to better recall for memories whose emotional valence that matches the current emotional context. Further, during anxiety treatment, patients benefit most when therapeutic interventions take place in an emotional context that will match subsequent retrieval contexts, suggesting processes of *emotion-state dependent recall* (Craske et al., 2008).

Despite these findings, current theories of learning and memory in emotional disorders do not describe whether and how each of these processes – intrusive memories of painful events, mood-congruent recall, emotion-state dependent recall – interact (Brewin, 2014; Rubin, Berntsen, & Bohni, 2008; L. A. Brown, Zandberg, & Foa, 2019). In addition, there are outstanding questions about the role of valence, meaning the attractive ("positive") or repellent ("negative") properties of a stimulus, and arousal, meaning the emotional intensity or degree of activation of the sympathetic nervous system due to a stimulus (Barrett, 1998; Russell, 1980; M. M. Bradley, Greenwald, Petry, & Lang, 1992; T. F. Brady, Konkle, Alvarez, & Oliva, 2008), in human memory and in emotional disorders. Leading theories of memory in PTSD have identified that high negative arousal during an event changes the formation of that memory and its subsequent retrieval, resulting in intrusive memories (Brewin, 2014; Rubin et al., 2008; Rubin, Dennis, & Beckham, 2011). However, these theories differ regarding whether negative arousal results in intrusive memories by impairing (Brewin, 2014) or enhancing (Rubin et al., 2008, 2011) a new memory's association to

its encoding context. Further, these approaches differ regarding whether it is specifically negatively valent arousal that leads to intrusive memories, by disrupting memory-context associations (Brewin, 2014), or whether intrusive memories arise due to the degree of emotional arousal, frequency of rehearsal, and centrality to the person's life story, regardless of the event's negative or positive properties (Rubin et al., 2008, 2011). Resolving these questions is vital to improved understanding of how painful memories operate in and contribute to emotional disorders, and thereby, for generating new treatment avenues.

Computational models are designed to clarify exactly these types of questions. By building a model of the human memory system, we can propose and test, what underlying cognitive processes would need to operate to produce the observed behavior or reportable thoughts and emotions? For example, computational models have identified that context operates as a driving force in human episodic memory, or memory for personally experienced events (Howard & Kahana, 2002a; Lohnas, Polyn, & Kahana, 2015; Healey & Kahana, 2016; Polyn, Norman, & Kahana, 2009; Talmi, Lohnas, & Daw, 2019; Moscovitch, Cabeza, Winocur, & Nadel, 2016). In retrieved-context theories of human memory (Howard & Kahana, 2002a; Lohnas et al., 2015; Healey & Kahana, 2014; Polyn et al., 2009; Talmi et al., 2019), the brain creates networks of associations between the contents of a memory and its context, or the internal or external surroundings (the time or place, the person's emotional or physiological state) that were present just before or while the event took place. These contextual cues then reactivate their associated memories, and in turn, recalling a memory reactivates a mental representation of its associated contextual elements.

However, existing computational models of episodic memory either omit emotion from the model (Howard & Kahana, 2002a; Polyn et al., 2009; Lohnas et al., 2015; Healey & Kahana, 2016) or else represent it as being simply "present or absent" (Talmi et al., 2019), devoid of negative and positive dimensions. In addition, such models do not incorporate insights from leading clinical theories of emotional disorders, such as *emotional processing theory* (Foa & Kozak, 1986; L. A. Brown et al., 2019), which have generated the development of highly efficacious treatments for intrusive memories in PTSD (Powers, Halpern, Ferenschak, Gillihan, & Foa, 2010). Conversely, leading clinical theories have focused on conditioning mechanisms and have not incorporated recent theory and modeling work on human episodic memory. As a result, there is currently no computational model of episodic memory in emotional disorders. Combining insights from both computational theories of episodic memory and clinical theories of memory in emotional disorders holds promise for generating new insights and treatment avenues.

In this paper, we draw upon insights from prior clinical theories of memory in emotional disorders (Brewin, 2014; Ehlers & Clark, 2000; Foa & Kozak, 1986; Rauch & Foa, 2006) and join them with computational modeling techniques of emotion in memory (Bower, 1981; Talmi et al., 2019) to develop a new theory of the mutual influence of memory and mood in emotional disorders. We then use this model to simulate the human memory system and test whether our updated theory of emotion in episodic memory can account for the persistent negative mood and intrusive memories observed in clinical settings.

Retrieved-context theory

We propose a new theory of memory in psychopathology that builds upon prior theoretical work on human episodic memory. In retrieved-context models, the context learned

in associated with a memory guides the later activation of that memory and determines whether it will be consciously retrieved (Healey & Kahana, 2016; Howard & Kahana, 2002a; Lohnas et al., 2015; Polyn et al., 2009; Talmi et al., 2019). Each memory's perceptual features, such as sights and sounds, are encoded in a network of associations with the memory's context, such as time of day, physical location, and emotions felt during the event. Later, encountering a similar context cues retrieval of the associated memories in the stored network, activating the memories whose encoded contexts have the highest overlap with the context that is present at the time of retrieval. Once a memory is retrieved, it is reencoded in association with the new context into which it was re-introduced.

The Emotional Context Maintenance and Retrieval (eCMR) model

Talmi et al. (2019) extended earlier retrieved-context models to account for the influence of arousal on recall performance. The eCMR model conceptualized emotion as having a single dimension, the presence or absence of emotional arousal. In eCMR, the presence or absence of emotion is a component of memories and their contexts, and the presence of arousal strengthens the associations between items and their contexts. The resulting model, eCMR, captures key features of emotional memory in laboratory settings (Talmi et al., 2019). However, eCMR has limited ability to describe memory in emotional disorders. First, eCMR treats emotion as either present or absent, without having negative or positive valence. In addition, eCMR resets prior learning at the end of each encoding list. Thus, this model cannot distinguish between recalls from a target vs. non-target prior context, a necessary ability for modeling memory intrusions (Lohnas et al., 2015), which are of interest to accounting for intrusive trauma-memories.

Overview

This paper introduces a new retrieved-context model of emotion and memory (CMR3), that goes beyond previous work in allowing us to simulate a lifetime of memories and to examine the role of intrusions in the dynamics and persistence of affective states. First, we use a comparative modeling approach to determine the representation of emotional valence in the episodic memory system (Experiment 1, Simulation 1). Then, we demonstrate CMR3's ability to account for mood-congruent recall (Simulation 2) and emotion-state dependent recall (Simulation 3). We then test CMR3's ability to account for the effects of environmental stressors on negative mood (Simulation 4) and clarify the model's predictions that repeated stressors will have a greater likelihood of becoming activated as intrusive memories due to being associated with a wider variety of cueing contexts (Simulation 5). Then, we show the model's ability to capture the effectiveness of positive event scheduling, a core component of behavioral activation therapy for depression (Simulation 6). We demonstrate CMR3's ability to predict that high arousal during encoding will lead to the development of intrusive memories (Simulation 7), and then show CMR3's ability to capture the efficacy of prolonged exposure therapy for alleviating intrusive memories of high-arousal negative events (Simulation 9). We conclude with a discussion of how retrieved-context theory relates to current theories of memory in psychopathology and generates novel predictions.

A retrieved-context model of memory and mood

According to retrieved-context theory, when people form memories of new experiences, they encode the memory in association with its contextual information, such as the time and place of the experience, the thoughts and emotions present during the experience, and other internal states. Later, these contexts – such as revisiting a location where an event took place, or having an emotion that was present during the event – can cue recall of associated memories. Once context cues a memory's retrieval, the memory reactivates its associated contexts, thus reinstating thoughts or emotions that were present during the original experience. The network of associations formed between items and past contexts can also encode semantic relationships among items, as items that share meaning tend to occur in similar temporal and semantic contexts (Howard & Kahana, 2002b; Polyn et al., 2009). Together, these episodic (contextual) and semantic (conceptual) associations guide memory retrieval.

Our model introduces two new mechanisms that improve on prior models as follows. First, our model enables memories and their contexts to have negative, positive, and neutral emotional properties (emotional valence). Second, our model enables emotional learning to accrue over a lifetime of experiences. This also allows the model to distinguish between recall of a memory from an intended (target) context versus an unintended (non-target) context, thus allowing the model to distinguish between voluntary and intrusive memories. The ability to make this distinction is critical in characterizing the role of memory in the development and treatment of PTSD.

Model Description

Here we provide a formal description of our model (Figure 1), cast in terms of equations that define the representation of items and the mechanisms that result in memory storage and retrieval. Following earlier formulations of retrieved-context theory, we assume a multidimensional feature representation of items, each denoted by $\mathbf{f}_t$ and a multidimensional representation of context that evolves as a result of each new experience and the memories it evokes (we denote the context at time t as $\mathbf{c}_t$). Our approach inherits the same equations for updating context, associating context and items, and determining recall dynamics as Polyn et al. (2009). We also inherit the additional mechanisms added by Lohnas et al. (2015) to simulate the continuity of memory across lists. We follow Talmi et al. (2019) in modeling emotion as a component of each item vector which then integrates into context. Then, we advance the model by allowing emotion to be not only present or absent as in eCMR, but further, to have positive or negative valence. In addition, we allow learning to accumulate over the course of multiple lists. This has two desirable properties: first, it allows memory to accrue over the course of long periods of time as in CMR2 (Lohnas et al., 2015), rather than a single experimental list. Second, it provides a method by which we can operationalize intrusive memories as instances of recalling an item from a non-target list, a phenomenon that is of great interest in psychopathology but which cannot be captured by a model that resets the memory system at the end of each individual list. We call this updated model CMR3 and present a mathematical description below.

Item Representation. In CMR3, each element of $\mathbf{f}_t$ represents whether that item is present or absent in the current memory episode, and each element of $\mathbf{c}_t$ represents the

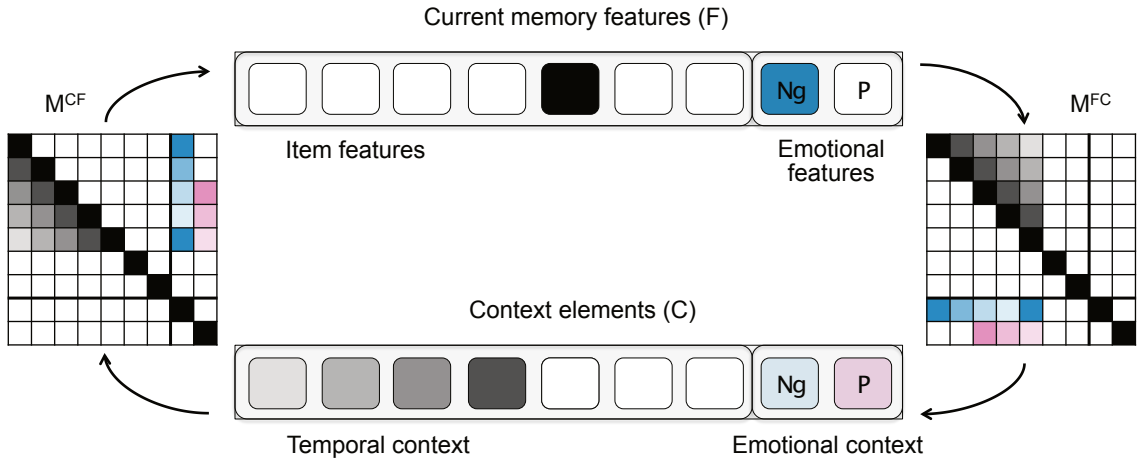

Figure 1. Schematic of how CMR3 models memory encoding and retrieval. The vector F represents event features comprising both item and emotional content. Item features are either present (have a value of1.0, shown in black) or absent (have a value of 0.0, shown in white). Valence is encoded by setting either the Ng cell (where values are shown in blue) or the P cell (where values are shown in pink) to 1.0, indicating negative and positive valence, respectively. Values of 0.0 for both cells, shown in white, indicate neutral valence. The vector C represents context and comprises recent event features(temporal context) and previously evoked emotions (emotional context). The shaded colors represent the decay of context features, which can take any value between 0.0 and 1.0. The F and C vectors interact through two weight matrices, M^{CF} and M^{FC}, which store the strengths of associations between event features and context elements. These associations are also shown in shaded colors to indicate values between 0.0 and 1.0. Context cues memories for recall by activating context-to-item associations stored in M^{CF}. New events update context with their own features, and recalling a memory reactivates its associated context, via item-to-context associations stored in M^{FC}. See text for details.

extent to which prior memories or cognitive states are still active during encoding. In addition to the representations of item features in $\mathbf{f}_t$ and temporal context in $\mathbf{c}_t$, Polyn et al. (2009) introduce an additional subregion in each vector to contain source-memory attributes, such as the encoding task conducted during learning (Polyn et al., 2009) or the presence of emotion (Talmi et al., 2019). In eCMR, emotion is represented as simply present or absent, taking a binary value of 0 or 1 in the source-memory subregion. To model how memory differentially contributes to negative or positive mood, we updated the emotional subregion of both feature and context vectors to contain two cells. In $\mathbf{f}_t$, one cell indicates whether the item is negative, the second whether it is positive, and neutral items have no content in either cell. In $\mathbf{c}_t$, one cell holds the accumulation of negative context and the other holds the accumulation of positive context. We chose two separate cells due to findings that negative and positive emotion may operate via separate cognitive systems (Cacioppo & Berntson, 1994; P. J. Lang, 1995).

List Representation. As in CMR2 (Lohnas et al., 2015), we concatenated all presented lists in both the feature and context vectors, to allow the model to carry information forward that was learned in prior lists. Each list is separated in the feature layer by disruptor items.

These disruptor items induce a shift in temporal context between lists, but they do not form associations with other items in the Hebbian matrices, as described below for true items. We begin each simulation by presenting an initial disruptor item so that the initial context vector is not empty (Lohnas et al., 2015). In addition, we present CMR3 with a disruptor item after each encoding list to model the distractor task used in Experiment 1.

Context-Updating. During encoding, as each item is presented, it enters the current context, causing other contextual elements to decay. Thus, context evolves according to the equation:

$$\mathbf{c}_{t+1} = \rho \mathbf{c}_t + \beta \mathbf{c}^{IN} \tag{1}$$

As such, context becomes a recency-weighted sum of past context states. The features from $\mathbf{f}_t$ that will enter into the new context, represented by the term $\mathbf{c}^{IN}$, are determined by multiplying the weight matrix of item-to-context associations, which we call M^{FC}, by $\mathbf{f}_t$, the vector of current features, and then norming the resulting vector, such that $\mathbf{c}^{IN} = \frac{M^{FC}\mathbf{f}_t}{\|M^{FC}\mathbf{f}_t\|}$. In equation 1, ρ scales the magnitude of prior context so that $\mathbf{c}$ does not grow without bounds (see Howard & Kahana, 2002a). The β parameter determines the rate at which new temporal context enters the updated context vector. This rate differs depending on whether the subject is encoding a new event (β_{enc}), retrieving a new memory (β_{rec}), registering a shift between list contexts (β_{post}), or experiencing a context shift due to a distractor task ($\beta_{distract}$). Emotional context updates according to the same equation, at the rate of β_{emot}.

Encoding. As each newly presented item evolves and updates cognitive context, its features form associations with the elements of context present during encoding. The memory and context representations, $\mathbf{f}_t$ and $\mathbf{c}_t$, interact via two Hebbian associative (outer-product) weight matrices, which model the strength of associations from the studied items to their encoding context, M^{FC}, and from context to associated items, M^{CF}. Because $\mathbf{f}_t$ and $\mathbf{c}_t$ each have two subregions – the first devoted to individual features of the memory, or item features, and its temporal context, and the second consisting of two cells devoted to emotional valence (see item representation), M^{FC} and M^{CF} have corresponding subregions. In the upper-left quadrant, each matrix contains associations between item features, $\mathbf{f}_{items}$, and temporal (or non-emotional) context elements, $\mathbf{c}_{temp}$. In the lower-left quadrant of M^{FC} and the upper-right quadrant of M^{CF}, each matrix contains the associations between item features and emotional context elements, $\mathbf{c}_{emot}$, as below:

$$M^{CF} = \begin{pmatrix} \mathbf{f}_{items}\mathbf{c}_{temp}^{\top} & \mathbf{f}_{items}\mathbf{c}_{emot}^{\top} \\ \mathbf{0} & \mathbf{0} \end{pmatrix} \tag{2}$$

$$M^{FC} = \begin{pmatrix} \mathbf{c}_{items}\mathbf{f}_{temp}^{\top} & \mathbf{0} \\ \mathbf{c}_{items}\mathbf{f}_{emot}^{\top} & \mathbf{0} \end{pmatrix} \tag{3}$$

Prior to the experiment, we initialize each weight matrix as an identity matrix of rank $i+2$, where i is the total number of items presented in the experiment. Two is the number of elements contained in the emotional subregion of the feature and context vectors. In the process, the subregions containing associations between items' temporal features and emotional context are initialized to zero. The pre-experimental Hebbian matrices, called

M^{CF}_{Pre} and M^{FC}_{Pre}, are then scaled by $(1 - \gamma_{CF})$ and M^{CF} by $(1 - \gamma_{FC})$, respectively. The parameters γ_{CF} and γ_{FC} are the learning rates for context-to-item and item-to-context associations, respectively (see Learning Rates, below).

Semantic associations. To represent semantic associations between pairs of items, we add a matrix of inter-item semantic associations, called M^S, to the quadrant in M^{CF}_{Pre} that contains associations between items' temporal features and temporal context (upper-left quadrant). Each entry in this matrix equals the dot product similarity between vector representations of each item's features (Polyn et al., 2009). We define these similarities using Google's Word2Vec algorithm (Word2Vec; Mikolov, Chen, Corrado, & Dean, 2013), which uses the co-occurrence of different words across multiple texts to determine vector representations of each word. The similarity between a pair of items can then be calculated using the dot product between each pair of item vectors. When adding M^S to the initialized M^{CF} , we scale M^S by the parameter s. Thus, s determines the degree to which semantic associations guide the retrieval process.

Learning Rates. New episodic associations accumulate as different memory features and contextual elements are active at the same time. We preserved the learning rule from CMR (Polyn et al., 2009), in which memories form associations with the context at the current time step, rather than at the preceding timestep. Thus, as each new memory is encoded, the change in associations stored in each weight matrix equals:

$$\Delta M^{CF} = \mathbf{f}_t \mathbf{c}_t^\top \tag{4}$$

$$\Delta M^{FC} = \mathbf{c}_t \mathbf{f}_t^\top \tag{5}$$

The rate at which these associations integrate into the M^{FC} and M^{CF} weight matrices is determined by three parameters: γ_{FC}, γ_{CF}, and γ_{emot}. The parameters γ_{CF} and γ_{FC} are the learning rates of new context-to-item and item-to-context associations, respectively. When updating both matrices, γ_{emot} is the learning rate of new associations between item features and emotional context in M^{CF}, which allows memories to form new associations with emotional vs. non-emotional context at different rates. The learning rate in the other quadrants is set to 0.0, since these associations do not contribute to the encoding and retrieval processes in the current model equations (Polyn et al., 2009; Talmi et al., 2019). Thus, before ΔM^{FC} and ΔM^{CF} integrate into M^{FC} and M^{CF}, we scale each ΔM elementwise by its respective matrix of learning rates, L^{FC} and L^{CF}:

$$L^{CF} = \begin{pmatrix} \gamma_{CF} & \gamma_{emot} \\ \mathbf{0} & \mathbf{0} \end{pmatrix} \tag{6}$$

$$L^{FC} = \begin{pmatrix} \gamma_{FC} & \mathbf{0} \\ \gamma_{FC} & \mathbf{0} \end{pmatrix} \tag{7}$$

In addition, to model increased attention to the items at the beginning of lists, each value in equation (4) is scaled by $\phi_t = \phi_S e^{-\phi_D(t-1)+1}$, where ϕ_S scales the overall level of the primacy effect and ϕ_D determines the rate of decay in this primacy effect, as the ith

item is presented. Thus, at a given point in the experiment, the strength of the associations between items and contexts stored in each weight matrix are given by the equations:

$$M^{CF} = M^{CF}_{Pre} + L^{CF} \sum_t \phi_t \mathbf{f}_t \mathbf{c}_t^\top \tag{8}$$

$$M^{FC} = M^{FC}_{Pre} + L^{FC} \sum_t \mathbf{c}_t \mathbf{f}_t^\top \tag{9}$$

Drawing upon work by Talmi et al. (2019), we additionally implement a parameter, ϕ_{emot}, which modulates the strength of context-to-item associations when an emotional item evokes arousal during encoding. For items that evoke no arousal, ϕ_{emot} takes a value of 1.0, and for items that evoke emotional arousal, ϕ_{emot} takes a value greater than 1.0 (Talmi et al., 2019).

Recall. Following the accumulation of feature-to-context associations over the course of multiple items and lists, the model proposes that the context present at retrieval serves to activate its associated memory elements. This takes place by multiplying M^{CF}, by the current context vector at retrieval, $\mathbf{c}_R$. In the resulting vector of item activations, each item is thus activated to the extent that its context during encoding is similar to the context that is present at the start of the retrieval process, such that the vector of item activations is given by:

$$\mathbf{a} = M^{CF} \mathbf{c}_R \tag{10}$$

Thus, each memory's features are activated according to the strength of the dot-product similarity between the context vector present during its encoding and the context that is present during retrieval, as well as the strength of pre-existing semantic associations. The activated elements then enter an evidence accumulation process, in which the evidence for the retrieval of any given item is driven by its activation value in $\mathbf{a}$. On each step of this leaky accumulator process (Usher & McClelland, 2001), the vector of evidence, $\mathbf{x}$, evolves according to the following equation:

$$\mathbf{x}_n = \mathbf{x}_{n-1} - \tau\kappa\mathbf{x}_{n-1} - \lambda\tau N\mathbf{x}_{n-1} + \tau\mathbf{a} + \boldsymbol{\epsilon} \tag{11}$$

That is, the level of evidence on the current step equals the level of evidence on the last step ($\mathbf{x}_{n-1}$), minus the decay in that evidence over time, minus lateral inhibition from other activated items (N is a matrix with 1's along the diagonal and -1's at all other entries, such that the summed activation of other items is subtracted from the given item's activation, and then scaled by λ and the time-decay scalar, τ), plus incoming item activations, and plus noise, ϵ. When the evidence in $\mathbf{x}_n$ for an item i passes a certain threshold, θ_i, that item emerges as a candidate for recall. For computational efficiency, we limit this evidence accumulation race to the 42 (list length x 2) items with the highest activations, since the other items are very unlikely to emerge as successful candidates for recall (Lohnas et al., 2015).

This item then updates the $\mathbf{f}_t$ vector with its features, and the item's associated context is then retrieved by multiplying M^{FC} by the newly updated $\mathbf{f}_t$ vector. If the recalled item's evoked context, $\mathbf{c}^{IN}$, is sufficiently similar to the current context ($\mathbf{c}^{IN} \cdot \mathbf{c}_t > \mathbf{c}_{thresh}$),

with $\mathbf{c}_{thresh}$ being a threshold scalar), then that item is reinstated into $\mathbf{f}_t$. Whether or not the retrieved item is reinstated, it cues its associated context, which evolves the context vector according to the same equations that update $\mathbf{c}_t$ during encoding. Once an item has been retrieved, the threshold of evidence needed to subsequently recall this just-retrieved item is equal to the threshold $\theta_i = 1 + \omega\alpha^j$, where j represents the number of times that a different item has been subsequently retrieved. Here, $\alpha = [0.0, 1.0)$, such that ω raises the absolute level of the threshold, and α decays this newly raised threshold each time the given item is reactivated.

Experiment 1: The role of emotional valence in memory

To develop a model of how episodic memory processes can promote negative versus positive emotion in emotional disorders, it is crucial to understand how emotional valence is represented in human memory and, further, how it may guide and be evoked by the process of recalling a memory. In their retrieved context model of emotional memory, Talmi et al. (2019) modeled emotion as a binary source attribute whose value would indicate the presence or absence of emotional content in items and their contexts. In free recall tasks, however, subjects tend to recall negative, positive, and neutral items in clusters together with other items that have the same valence (Long, Danoff, & Kahana, 2015). This *emotional clustering effect* suggests that not only the presence of emotion, but also the valence of that emotion, guides the organization and retrieval of items in memory. Here, we first sought to replicate the emotional clustering effect in an independent free recall dataset. Then, in Simulation 1, we fit the observed data using two variants of the retrieved context theory: one in which a single binary features indicates whether a memory possesses emotional information (Talmi et al., 2019) and another in which two binary attributes separately indicate whether a memory possesses positive or negative information (the current CMR3 model). We then assessed the two model variants by comparing their ability to fit emotional clustering effects, and other benchmark phenomena, in free recall.

Subjects and Stimuli

We fit the model to data from Experiment 4 of the Penn Electrophysiology of Encoding and Retrieval Study (Kahana, Aggarwal, & Phan, 2018), an ongoing project to collect a large set of free recall data within and across subjects. The full dataset consisted of 120 adults. Among these, 97 subjects completed the full 24 sessions of delayed free recall. The mean age among completers was 22.26 (SEM = 3.1), and reported genders were 51.5% female, 47.5% male, 1.0% other. In each session, subjects studied 24 lists of 24 unique nouns (576 words total) drawn from a subset of 1638 nouns from the University of South Florida word pool (D. L. Nelson, McEvoy, & Schreiber, 2004). See Kahana et al. (2018) for full details of the experiment stimuli and methods. To assess the valence of each word, we used ratings from a prior norming study (Long et al., 2015). In this study, 120 subjects on Amazon's Mechanical Turk (MTURK; Mason & Suri, 2012) generated valence ratings for each item, rating them on a scale from 1-9, where 1 indicated negative valence and 9 indicated positive valence. Words were binned as negative if their valence rating fell below 4, neutral if between 4-6, and positive if above 6. The resulting valences of the 864 words in the experiment word pool were 25.6% positive, 8.9% negative, and 65.5% neutral.

Method

To test the effects of emotional valence on episodic memory, we presented subjects with a multi-trial delayed free recall task, as described above. In a free recall task, subjects study lists of items (here, words). At the end of each study list, subjects then recall as many words as they can, in any order. Because subjects must recall words from the most recent list, rather than all words they have ever learned in their lifetime, this task measures the ability to localize memory to a specific context (i.e., this specific list, in this specific session). Because subjects may recall the study words in any order (i.e., freely), the order in which these words are recalled suggests how the items were organized in memory. Finally, in a "delayed" free recall task, the experimenter places a distractor task (i.e., a delay) after each study list and just prior to the recall period. This reduces the recency effect, or better recall for the last 3-4 items on the list, thus preventing these items from being overrepresented in the subsequent analyses. Here, subjects completed a distractor task of 16 seconds of mental addition.

Behavioral Analyses

In this experiment, we sought to replicate the emotional clustering effect. This replication not only served to establish the reliability of the emotional clustering phenomena, but it also allowed us to obtain individual subject parameter sets for use in subsequent simulations of theoretically-generated data (see Simulations 2-8). We designed PEERS Experiment 4 to comprise sufficient data to allow for stable modeling at the individual subject level (i.e., each subject contributed data from 576 lists obtained across 24 experimental sessions).

To evaluate the effect of emotional valence on recall organization we conducted a conditional probability analysis of transitions among items according to their positive, negative, or neutral valence (for full methods, see Long et al., 2015). Following Long et al. (2015), we adjusted probabilities to account for different rates of negative, positive, and neutral items in each study list. We then examined subjects' tendencies to transition between same-valent or differently-valent items, with higher probabilities for same-valent items indicating a higher tendency to cluster these items together during recall.

Next, we assessed the presence of classic, non-emotional patterns in free recall. These included the *serial position curve* (SPC), or how an item's probability of being recalled changes as a function of its presentation order during study (Murdock, 1962). The SPC allowed us to assess *primacy* and *recency* effects, or subjects' tendencies to recall the first and most recent items that they have seen, respectively. Second, we calculated the *probability of first recall* (PFR), or each item's probability of being first-recalled, plotted as a function of its serial position during study. This allowed us to assess what processes guide the start of subjects' recall outputs. Third, we used conditional probability analyses to calculate the tendency of items to cluster during recall to cluster according to their temporal proximity to one another during study (*temporal contiguity*; Kahana, 1996).

In addition, we used conditional probability analyses to measure subjects' tendency to cluster items during recall according to their semantic relations (*semantic clustering*; Howard & Kahana, 2002b). To represent semantic relations among the words, we used Word2Vec, which is a method of estimating the representations of words in vector space,

or word "embeddings" (Mikolov et al., 2013). Word2Vec identifies the semantic meaning of a word based on what other words accompany it across many different settings in which it is used. Using machine-learning, Word2Vec trains on a database of online texts and then generates vectors representing the dimensions of each word based on the other words that typically accompany it. The inter-item similarity for each pair of words is then calculated as the dot-product between each word-vector in the pair. Using Word2Vec, we generated inter-item similarities for each pair of words in the 1,638 noun word pool. Finally, we calculated the average rate at which subjects mistakenly recalled items from lists preceding the target list (*prior-list intrusions*, or PLI's), and mistaken recalls of items that were never presented during the experiment (*extra-list intrusions*, or ELI's). For each behavioral analysis, we first averaged each effect across lists within session, and then across sessions within each subject.

Results

We assessed the patterns of recall that characterized the behavioral data across multiple sessions of delayed free recall (Figure 2). The lag-conditional response probability (Lag-CRP) analysis showed that subjects had a tendency to cluster their recalls according to how close in time those items were encoded relative to one another (temporal clustering). Subjects also showed a tendency to cluster their recalls according to how semantically similar those items were (semantic clustering). The serial position curve (SPC), or the probability of recall for each item based on where it was presented in the study list, and the probability of first recall (PFR), revealed both recency and primacy effects. That is, subjects were most likely to begin recall with the last item presented or the first item presented, and they were also more likely to recall these items in general. As expected based on previous research (Kahana, Dolan, Sauder, & Wingfield, 2005; Zaromb et al., 2006), our healthy young adult subjects committed low rates of PLI's and ELI's.

In addition, we replicated findings by Long et al. (2015), that subjects had a small, but significant tendency to recall items in clusters of the same emotional valence (Figure 3). That is, upon recalling a negative item, subjects were more likely to next recall another negative item than a positive item, and upon recalling a positive item, subjects were more likely to next recall another positive item than a negative item (Figures 3). To test the significance of this effect, we conducted a 3 (Initial Item Valence: Negative, Positive, or Neutral) x 3 (Transition-Item Valence: Negative, Positive, or Neutral) linear mixed effects model predicting transition probabilities (lme4 R package; Bates, Mächler, Bolker, & Walker, 2015). We set neutral valence as the base category, and we used a random intercept to account for the dependency of observations within each subject. The fixed-effects estimates and significance testing using the Satterthwaite's method for approximating degrees of freedom (lmerTest R package; Kuznetsova, Brockhoff, & Christensen, 2017) are presented in Table 1. The resulting interactions indicated that negative items were significantly more likely to be recalled together with other negative items than with non-negative items, $\beta = .057$, $t(768) = 35.1$, $p < 10^{-16}$, and positive items were significantly more likely to be recalled together with other positive items than with non-positive items, $\beta = .021$, $t(768) = 12.8$, $p < 10^{-16}$. Taken together, our results replicate findings that positive and negative items tend to cluster together with same-valent items during recall (Long et al., 2015). Next, we use a computational approach to identify which representation of emotion in memory is

Table 1: Transition probabilities regressed on initial-item valence and next-item valence.

		β	SE	t	LR$\chi^2(df)$
Step 0					
	Intercept	.070***	.002	52.42	
Step 1					87.16(4)***
	Negative Initial Item	.013***	.001	9.00	
	Positive Initial Item	.001	.001	0.96	
	Negative Next-Item	.010***	.001	6.78	
	Positive Next-Item	.006***	.001	4.01	
Step 2					1,147.9(4)***
	Negative Initial Item x Negative Next-Item	.057***	.002	35.14	
	Negative Initial Item x Positive Next-Item	.000	.002	-0.22	
	Positive Initial Item x Negative Next-Item	.001	.002	0.81	
	Positive Initial Item x Positive Next-Item	.021***	.002	12.77	

optimal to predict this effect.

Modeling emotional valence in memory

In retrieved-context models, emotional valence – the negative or positive emotional content of a memory – might serve one of several roles. As proposed in spreading activation models, emotional valence might serve as part of a memory's semantic content, contributing to how similar the features are of one memory to another (Bower, 1981). Alternatively, emotion might serve as a type of episodic context, yet have broad effects on memory, such that the valence of the emotion does not play a role (Talmi et al., 2019). Third, emotional valence might serve as a type of episodic context, such that negative or positive emotional states can become associated with an event and later serve as retrieval cues. To determine the optimal representation of emotion in memory, we fit CMR2, eCMR, and CMR3 to the behavioral effects observed in Experiment 1 and tested differences between each model's ability to capture these patterns. This allowed us to compare three possible representations of emotion in memory encoding and retrieval processes. In CMR2 (Lohnas et al., 2015), we implemented emotion solely as part of items' semantic content: that is, as a component of inter-item semantic associations. In eCMR (Talmi et al., 2019), we additionally included an item's status as emotional versus neutral (i.e., the presence or absence of emotional content) as a part of item and context features. Because we were interested in capturing patterns of item intrusions across lists, and the original eCMR does not have multilist capabilities, we fitted eCMR with multilist capabilities as in CMR2 and CMR3. In CMR3 (see *Model Overview*), we additionally included emotional valence as part of item and context features.

Model Specification

To isolate the effects of emotional valence, we held the arousal parameter, ϕ_{emot} (Talmi et al., 2019), constant at 1.0 for each model. At this value, arousal neither enhances or weakens the context-to-item associations in M^{CF}. This allowed us to test each model's

ability to capture emotional patterns in the behavioral data solely due to how it represents emotion's dimensions in the feature and context vectors. In addition, the words presented in the free recall tasks have emotional valence properties but likely induce minimal or absent levels of arousal during the free recall task (Long et al., 2015). As in the behavioral analyses in Experiment 1, we used Word2Vec (Mikolov et al., 2013) to generate inter-item similarities for each pair of items, which were added on to the pre-experimental M^{CF} matrix that represents associations between items and contexts.

Simulation 1

Method. We sought to test each model's ability to fit the variability in the dataset within each subject, as well as the aggregate behavioral patterns taken across the dataset. Therefore, we obtained parameter fits for each model to each individual subject's data. Obtaining parameter fits to individual subjects served two purposes. First, for each model, we used the resulting sets of parameters to generate three simulated datasets, comprised of the responses predicted by each model (CMR2, eCMR, or CMR3) for each subject. Then, on each simulated dataset of "virtual subjects," we repeated the full behavioral analyses that we ran on the empirical data. This enabled us to test each model's ability to fit the aggregate behavioral responses observed in the original data. Second, obtaining the best-fitting parameters to each individual subject allowed us to examine the predictions of retrieved-context theory for how different people, whose minds operate according to different cognitive parameters, respond to life stressors with quick recovery, vs. negative mood or intrusive memories (Simulations 2-8).

To obtain the best-fitting parameters for CMR2, eCMR, and CMR3 for each subject, we used a particle swarm with 200 particles evolved over 30 iterations. In each iteration, the model generates the predicted outputs for subject when the model is outfitted with the given set of parameters ("particle"). Then the algorithm calculates a goodness-of-fit index for each particle that quantifies the error between the model predictions and the data, to identify which parameter set produced the best fit. For our fit index, we used the χ^2 error, defined as the sum of squared residuals, with each squared residual normed by the unbiased sample variance of the corresponding data point (Bevington & Robinson, 2003). After the χ^2 error for each particle is determined, the optimal parameter set is identified as the one having the lowest χ^2 error in this iteration, and other parameters move their values closer to the current optimal value. Over the course of iterations, the particles converge on an optimal set of parameters, thereby minimizing the χ^2 error. The 56 points contributing to the χ^2 error for each model fit were the first 15 and last 3 positions of the SPC; the first 15 positions of the PFR; the inner 6 points of the lag-CRP curve (lags of -3, -2, -1, 1, 2, and 3); the 9 conditional probabilities of transitioning among negative, positive, and neutral item types (negative-to-negative, negative-to-positive, negative-to-neutral, and so forth); all 6 points on the semantic CRP curve; the frequency of PLI's per list (1 data point); and the frequency of ELI's per list (1 data point).

Results and Discussion

In order to determine how best to represent emotional valence in CMR, we fit three models to the data from each individual subject. The first model, CMR2 (Lohnas et al., 2015), represented emotional valence solely as a contributor to items' semantic associations

with one another. In the second model, eCMR, an item's emotional content is represented as a binary value, being either present or absent in item features and episodic source context. Finally, in the new model we present in this paper, CMR3, we enabled items to have negative or positive valence. To obtain the best-fitting parameters for each model, fit to each subject, we minimized the χ^2 error between each model's predictions and the actual data for that subject. At the end of the particle swarm process, the mean χ^2 error across model fits to individual subjects was 36.60 (SEM = 4.95) for CMR2, 30.45 (SEM = 2.05) for eCMR, and 29.74 (SEM = 1.64) for CMR3, where lower χ^2 error values indicate better model fits. Degrees of freedom for the χ^2 error values were determined by n – m, where n equals the number of data points fit (56 points) and m equals the number of free parameters in each model (15 for CMR2 and 17 for eCMR and CMR3). Thus, for 97 subjects, CMR2 provided 86 model fits with non-significant $\chi^2(41)$ error; eCMR provided 92 model fits with non-significant $\chi^2(39)$ error; and CMR3 provided 90 model fits with non-significant $\chi^2(39)$ error. The means and standard errors of the sets of parameters obtained for CMR2, eCMR, and CMR3, taken across individual-subject fits, are presented in Table 2.

Next, we used these sets of parameters to simulate three full datasets, with each dataset indicating what the data would look like if subjects' cognitive operations followed the rules of the given model. Having generated the dataset predicted by each model, we assessed each model's ability to predict the aggregate behavioral effects that we observed in the actual data (Figures 2 and 3). Using each simulated dataset, we repeated the behavioral analyses conducted in Experiment 1, and compared the results to those obtained from the empirical data. The graphs for each behavioral analysis are presented in Figures 2 and 3. To assess each model's ability to fit the aggregate data, we calculated three measures of fit: (1) the same χ^2 goodness of fit index that was minimized while fitting the model; (2) the Bayesian Information Criterion (BIC) to account for the different number of parameters across models (Kahana, Zhou, Geller, & Sekuler, 2007; Polyn et al., 2009; Schwarz, 1978); and (3) the RMSE, to identify which specific behavioral analyses determined each model's overall ability to fit the data. We calculated each goodness-of-fit test with respect to all data points in all analyses, $n = 75$, to obtain a total measure of each model's ability to fit the aggregate behavioral effects.

The resulting χ^2 error values were $\chi^2(60) = 74.1$, $p = .10$ for CMR2, $\chi^2(58) = 55.2$, $p = .58$ for eCMR, and $\chi^2(58) = 56.7$, $p = .52$ for CMR3, indicating that all three model fits had non-significant error. For direct model comparisons, it is not valid to directly compare the size of χ^2 error values because eCMR and CMR3 have two more parameters than CMR2, which gives them an advantage over CMR2 in their ability to fit the data. Therefore, we calculated the Bayesian Information Criterion (BIC) values (Kahana et al., 2007; Polyn et al., 2009; Schwarz, 1978) for each model's fits to the aggregate data. The BIC accounts for each model's ability to fit the data while penalizing models that have a greater number of parameters, thus placing the three models on equal footing for comparison. Under the assumption of normally distributed residuals, the BIC formula simplifies to:

$$BIC = kln(n) + nln(\frac{RSS}{n}) \tag{12}$$

Here, k represents the number of free parameters in the model, n represents the number of data points, and RSS is the residual sum of squares. To ensure that all points

Table 2: Best-fitting parameters for each model, averaged across individual-subject fits.

	CMR2		eCMR		CMR3	
	Mean	SEM	Mean	SEM	Mean	SEM
β_{enc}	.298	.008	.295	.008	.286	.007
β_{rec}	.713	.013	.717	.013	.701	.012
$\beta_{distract}$	.458	.018	.481	.020	.453	.020
β_{post}	.672	.021	.675	.025	.733	.020
β_{emot}	–	–	.369	.018	.322	.016
γ_{FC}	.799	.010	.800	.010	.813	.009
γ_{CF}	.872	.009	.845	.010	.869	.009
γ_{emot}	–	–	.394	.025	.417	.026
ϕ_S	1.413	.074	1.009	.064	.957	.072
ϕ_D	.611	.042	.747	.037	.728	.037
κ	.257	.012	.279	.013	.293	.012
η	.184	.010	.181	.010	.189	.010
λ	.118	.010	.115	.011	.125	.010
s	1.044	.041	1.049	.039	1.117	.049
ω	22.821	.383	22.702	.406	22.605	.382
α	.934	.006	.958	.0006	.954	.006
c_{thresh}	.339	.018	.991	.038	.992	.038

Note. β_{enc} = drift rate for temporal context during encoding. β_{rec} = drift rate for temporal context during recall. $\beta_{distract}$ = drift rate for temporal context during a distractor item or shift between mental tasks. β_{post} = drift rate for temporal context at the end of a recall session. β_{emot} = drift rate for emotional context. γ_{FC} = learning rate for item-to-temporal context associations. γ_{CF} = learning rate for temporal context-to-item associations. γ_{emot} = learning rate for emotional context-to-item associations. ϕ_S scales the primacy effect and ϕ_D determines its rate of decay over the presentation of new items. κ = rate of evidence decay in the leaky accumulator due to the passage of time. η = width of the normal distribution of noise values for each item's recall evidence in the leaky accumulator. λ = degree of lateral inhibition between items in the leaky accumulator. s = scales the strength of inter-item semantic associations. ω scales the raised threshold for item repetition, and α scales the decay in that threshold as subsequent items are recalled. c_{thresh} = threshold of similarity between an item's encoding and retrieval contexts needed in order to consider the item a correct recall.

Table 3: RMSE's for individual behavioral analyses.

	CMR2	eCMR	CMR3
Total	.064	.061	.058
Emotional Clustering	.007	.008	.006
SPC	.025	.028	.027
PFR	.059	.038	.037
Left CRP	.036	.030	.031
Right CRP	.043	.050	.053
Semantic CRP	.084	.076	.076
ELI's	.325	.322	.325
PLI's	.098	.098	.098

Note. Total: All data points. Emotional Clustering: Emotional clustering effect. SPC: Serial position curve. PFR: Probability of first recall. Left CRP: Negative lag values of the Lag-Conditional Response Probability graph. Right CRP: Positive lag values of the Lag-Conditional Response Probability graph. Semantic CRP: Semantic conditional response probability graph. ELI's: Frequency of extra-list intrusions per list. PLI's: Frequency of prior-list intrusions per list.

contribute equally to model fits, we multiplied the emotional clustering effect by a factor of 10 to place it on the same scale as the other data points from the set of behavioral analyses (Polyn et al., 2009). This was not necessary for the χ^2 error values because norming the squared residuals by the unbiased sample variance in the data (Bevington & Robinson, 2003) already sets the contributing residuals to comparable scales. The resulting BIC's were -347.06 for CMR2, -345.65 for eCMR, and -353.82 for CMR3, where lower (i.e., more-negative) values represent improved model fits. The results indicate that CMR3 provided the best balance of model parsimony and error minimization, followed by CMR2 and then eCMR.

To identify which behavioral effects distinguished each model's ability to fit the aggregate data, we calculated RMSE values for each behavioral analysis (Table 3). For the total RMSE, taken across all points in all graphs (N = 75), CMR3 provided the smallest RMSE, followed by CMR2, and then eCMR, where smaller values indicate better model fit. Comparing eCMR and CMR3, eCMR provided lower RMSE's for the positive lags of the Lag-CRP and the frequency of extra-list intrusions. Conversely, CMR3 provided the lowest RMSE for the emotional clustering effect, followed by CMR2 and then eCMR. CMR2 provided worse fits to the semantic clustering effect and the probability of first recall, suggesting that the model may have had to sacrifice fits to these data in its attempts to capture emotional clustering patterns.

Visual inspection of Figures 3 and 4 confirms that all three models provided comparable fits to non-emotional memory effects but differed in their ability to capture the emotional clustering effect, the key effect of interest in this dataset for developing a model of emotional memory. To clarify why CMR3 provided optimal fits to the emotional clustering effect, we assessed the tendency of each model to predict the two core aspects of this

effect: (1) the tendency of same-valent items to cluster together during recall, and (2) the tendency of oppositely-valent items to not cluster together during recall.

Figure 3, Panel B, displays the tendencies of each model to over-predict or under-predict item clustering according to the emotional valences of just-recalled and next-recalled items. By not including emotion as a type of episodic features and contexts, CMR2 under-predicted the tendency of same-valent items to cluster together. However, by not differentiating between items of different valences, eCMR over-predicted the tendency of opposite-valent items to cluster together. In CMR3, allowing the emotional content of items and contexts to have both negative and positive emotional valence best captured the tendency of same-valent items to cluster together and the tendency of oppositely-valent items to not cluster together.

In sum, prior theorists have proposed that emotion serves as a feature of items' representations and their contexts (Talmi et al., 2019), or alternatively, that it serves as a type of semantic information about an item (Bower, 1981). However, neither theory has yet been tested by quantitative model fits to empirical data. In this paper, we conducted explicit model comparisons between CMR2 (emotion as semantic-information only), eCMR (representing emotion as present or absent in item features and their contexts, but not having multiple valences), and CMR3 (representing emotion in item features and their contexts, and allowing it to have positive or negative valence). Our results demonstrated that emotion serves as an element of items' episodic features and contexts, as proposed by Talmi et al. (2019) but not tested via quantitative fits in that paper.

Moreover, we show that to capture the effects of emotion on free recall, it is important to represent emotion as having positive and negative valence. First, including emotional valence improved the empirical fits presented above. Whereas CMR3 and eCMR yielded equivalent fits for the χ^2 fit index, the RMSE indices indicated that this was due to eCMR having better performance on non-emotional patterns in the data and CMR3 having better performance on emotional patterns in the data. Overall, CMR3 yielded an improvement in fit according to its BIC and total RMSE value. Second, including emotional valence in the model is necessary to allow retrieved-context theory to predict the activation of negative vs. positive emotional context when retrieving a given memory. In the subsequent sections, we show how the new retrieved-context theory, developed above and formalized in CMR3, can capture patterns of negative vs. positive mood and memory in emotional disorders.

Mood-congruent recall

In the prior section of this paper, we used comparative model fits to test how best to represent emotion in episodic memory. Next, we present a series of simulations testing the model's ability to predict patterns of memory and emotion that are relevant to psychopathology. We begin by evaluating the model's ability to account for mood-congruent and emotion-state dependent recall. Then, we present a new theory of how these principles contribute to negative mood and intrusive memories as transdiagnostic processes, with a focus on patterns in major depression and PTSD.

Motivation

A patient in a depressive episode may readily recall memories of loss or failure, while memories of happy events elude him (Teasdale & Russell, 1983). Yet, once recovered, this

patient may tend to recall positive memories and have difficulty remembering the events that occurred while they were depressed. This phenomenon, mood-congruent recall (MCR), refers to higher rates of recall for memories whose emotional attributes match those of the person's current emotional state. MCR has been observed widely across both clinical and healthy populations: e.g., for sadness and loss-related stimuli in patients with depression (B. P. Bradley, Mogg, & Williams, 1995; Teasdale & Fogarty, 1979; P. C. Watkins et al., 1992), for threat-related stimuli in patients with anxiety (Mathews, Mogg, May, & Eysenck, 1989, but see Bradley et al., 1995) and patients with PTSD (Paunovic, Lundh, & Öst, 2002), and for positive stimuli in healthy subjects (P. C. Watkins et al., 1992). Here, we sought to test whether retrieved-context theory can account for the process of mood-congruent recall.

Simulation 2

Method. We tested CMR3's ability to predict mood-congruent recall (MCR). Specifically, we simulated the results from a series of free recall experiments in which MCR would be expected to occur. First, we simulated 97 virtual subjects by specifying the model with each set of parameters generated while fitting CMR3 to the behavioral data in Experiment 1. Each set of parameters defines the virtual subject's memory system, determining the responses that the model (i.e., the virtual subject) will give while completing the simulated task. Then, we presented each virtual subject with the following task. The simulated task consisted of 60 encoding lists, with each containing a randomly permuted mixture of positive (30%), negative (30%), and neutral (40%) items.

To ensure that negative, positive, and neutral items would all have equivalent semantic structures, we drew the inter-item similarity for each pair of items at random and without replacement from a normal distribution ($\mu = .2, \sigma = 0.5$). A value of -1.0 represents maximum dissimilarity, and 1.0 represents maximum similarity. To simulate a set of unique items, no item pairs were assigned an inter-item similarity of 1.0. Finally, we set the s parameter equal to 0.15, which scaled down the inter-item semantic similarities by that value. This allowed the model outputs to more strongly reflect the episodic dynamics of interest.

In this task, each virtual subject began studying each list in a neutral state. That is, we set the virtual subject's context vector to contain no emotional content. After each encoding list, and prior to the free recall section, we simulated a mood induction. That is, after each list, we set the subject's context vector to contain negative (20 lists), neutral (20 lists), or positive (20 lists) emotional content. The model then predicted the subject's responses during a free recall session, in which emotional context was allowed to evolve naturally in response to the emotional content of the retrieved items. We then ran this simulation for each of the 97 sets of parameters obtained in the fits to behavioral data in Simulation 1. Across simulations, we analyzed the probability of recall for positive, negative, and neutral stimuli, conditional upon the type of mood induction prior to recall.

Results and Discussion. Using the sets of parameters obtained in Simulation 1, we simulated a set of 97 virtual subjects by specifying CMR3 with each set of parameters and obtaining the model-predicted output for a virtual recall task. Specifically, we assessed the model-predicted effects of mood state during retrieval on the recall of emotionally valent and neutral items. Across parameter sets, model predicted that negative or positive mood

states cue more-frequent recall of items that match the current emotional state (Figure 5, A). Further, the model predicted that, during a neutral mood, emotional items were more likely to be recalled overall, with probabilities of 0.66 (SEM = .021) for negative items, 0.65 (SEM = .023) for positive items, and 0.61 (SEM = .024) for neutral items. This matches findings that in laboratory tasks lacking mood induction manipulations, and in which most subjects likely have neutral mood during the task, emotional items have a recall advantage over neutral items (Long et al., 2015; Siddiqui & Unsworth, 2011; Talmi et al., 2019). In CMR3, this occurs because studying or recalling an item evokes emotional context consistent with its emotional valence, and these emotional features serve as the input to the context updating equation. As a result, items that induce a particular emotional context during their encoding have a heightened match when the emotional context evoked by the pre-recall mood induction has matching emotional elements. Next, we examine the model's ability to predict a related effect, emotion-state dependent recall.

Emotion-state dependent recall

Motivation

Whereas patients learn new skills and insights in a calm, therapeutic setting, they must often recall these skills for use in settings fraught with intense emotion. Emotion-state dependent recall refers to better recall of learned items or associations when they are retrieved in a context similar to that in which they were encoded. Emotion-state-dependent recall is a variant of the more general state-dependent recall effect, in which information learned in one environment or state is better recalled in a matching state (Godden & Baddeley, 1975; Smith & Vela, 2001). Whereas laboratory studies of emotion-state dependent recall have yielded mixed findings (Bower & Mayer, 1985; Eich, 1995), the dependency of new learning on emotional context is routinely observed in clinical settings (Craske et al., 2008). Patients with anxiety who form new associations between feared stimuli and neutral outcomes often find that when encountering these stimuli in new contexts, the associated anxiety reemerges (Craske et al., 2008). Here, we tested whether CMR3 can account for emotion-state dependent recall.

Simulation 3

Method. We simulated a delayed free recall task consisting of 60 lists of 10 neutral items. We simulated mood inductions (1) at the beginning of each encoding list and (2) immediately prior to recall. The order of mood inductions in each session was randomized, such that 30 lists had matching encoding and retrieval contexts (15 negative-negative, 15 positive-positive) and 30 lists had mis-matched encoding and retrieval contexts (15 negative-positive, 15 positive-negative). We then calculated the model-predicted recall probabilities and response times conditional upon matching negative, matching positive, mismatched negative-positive, and mismatched positive-negative, encoding and retrieval contexts. Finally, we ran this simulation with each set of parameters obtained by fitting CMR3 to individual subjects' behavioral data in Simulation 1.

Results and Discussion. In this simulation, we sought to determine whether CMR3 can predict emotion-state dependent recall, or improved recall of new learning that occurred

in an emotional state that matches that present during encoding. Specifically, we tested whether virtual subjects recalled neutral items better when their emotional state during retrieval matched the emotional state that was present during encoding. The model-predicted recall probabilities for neutral items encoded and retrieved in matching emotional states were .67 (SEM = .027) for negative states and .69 (SEM = .025) for positive states. The recall probability for neutral items encoded in a negative state and retrieved in a positive state was 0.41 (SEM = .033), and the recall probability for neutral items encoded in a positive state and retrieved in a negative state was 0.38 (SEM = .035). This decrease in recall for neutral items in non-matching (vs. matching) emotional states during encoding and retrieval reflects the model's core prediction: an item's activation for retrieval depends on the similarity between the current context and the context associated with that item during encoding. In CMR3, emotional content is part of those contexts. Thus, the model can account for findings that new learning in clinical settings is enhanced when patients learn new material or associations in an emotional state that matches the emotional state in which they will later need to activate the new learning (Craske et al., 2008).

Effects of frequent, unique stressors on mood

A core feature of major depressive disorder (MDD) is negative mood that persists for two weeks or longer (American Psychiatric Association, 2013). Stressful life events are a major precipitant for MDD, with the likelihood of a depressive episode increasing according to the frequency of recent stressors (Kendler, Karkowski, & Prescott, 1998). Even types of depression considered to be more biologically based are often precipitated by a severe event or major difficulty, particularly for the first major depressive episode (G. W. Brown, Harris, & Hepworth, 1994; Johnson & Roberts, 1995). Early developmental stressors, such as childhood abuse and neglect, also contribute to later risk of depression in adulthood (Jaffee et al., 2002; Kendler et al., 1998, 1995), perhaps in part by influencing how individuals recall their experiences and respond to new events. Here, we test the ability of retrieved-context theory to characterize how the frequency of prior and recent stressors can lead to the development and persistence of negative mood.

Simulation 4

To model the effects of stressors on persistent mood, we again modeled a group of virtual subjects, for whom we then simulated a series of lifetime events. As in Simulations 2 and 3, we constructed each virtual subject by using the CMR3 model, specified by the best-fitting parameters obtained when fitting CMR3 to that subject's individual recall dynamics from the empirical data (see Simulation 1). The model equations thus defined how each virtual subject would respond to new events and recall old ones. As a brief review, in CMR3, each new event introduces its emotional features into the current context and then becomes associated with this temporal, emotional, and spatial context during encoding. Later, encountering a retrieval context that is highly similar to the temporal, perceptual, spatial, or semantic elements of prior contexts reactivates the memories associated with these contexts. When the activated memories are retrieved, they reinstate the context that was present during their encoding. The memory is then re-encoded together with its old context and the new context into which it was retrieved. This updated context serves as the retrieval cue for the next memory.

Using these operations, we modeled how each of the 97 virtual subjects would respond to three different conditions of life events. Unlike in the prior simulations, here an event does not represent a list item experienced during an experimental task. Rather, we conceive of the events in this simulation as modeling actual events that might occur in the real world. We assigned different properties to each event, including the type of emotional valence and the event's semantic relatedness to other events. For simplicity, we allowed each event to have only one valence: either negative, positive, or neutral. To simulate event properties and semantic associations, we drew values for inter-event similarities at random and without replacement from a normal distribution ($\mu = 0.2$, $\sigma = 0.5$), with positive values indicating similarity and negative values indicating dissimilarity. Although all events in this simulation are abstract, to provide a concrete example, a birthday party and an engagement party might have a positive similarity of 0.8. In comparison, going swimming and filling out a tax form might be more dissimilar, with a score of -0.2. No event pairs were allowed to have a perfect similarity of 1.0, to ensure that all simulated events would be unique. In addition, we set the parameter that controls how much semantic associations guide the retrieval process, s, to a value of 0.15. Drawing the inter-event similarity values for all events from the same distribution, regardless of their emotional content, and holding s constant across all virtual subjects allowed us to control whether the results of our simulations could be accounted for just due to the semantic associations among events.

For each virtual subject, we simulated a life-course of events, which began with a "developmental period" simulating the initial events experienced by each virtual subject. Each developmental period consisted of 50 sets, or "lists," of 10 encoding events. Then, we varied the contents of each virtual subject's developmental period across three conditions. Each condition varied the frequency of stressors, and in the process, the ratio of negative to positive events. In the Low-Frequency condition, lists contained 40% neutral, 30% negative, and 30% positive events, resulting in a 1:1 ratio of negative-to-positive events. In the Moderate-Frequency condition, we increased the frequency of negative encoding events, such that lists contained 20% neutral, 60% negative, and 20% positive events, resulting in a 3:1 ratio of negative to positive events. In the High-Frequency condition, we further increased the frequency of negative events, such that lists consisted of 20% neutral, 70% negative, and 10% positive events, resulting in a 7:1 ratio of negative to positive events. Each "list" (i.e., sequence) of encoding events was followed by a free recall period, to model instances in which virtual subjects might spontaneously recollect these prior events. After the developmental period, we presented a neutral period. This neutral period consisted of 30 lists of 10 new, unique encoding events, 100% of which had neutral valence. This allowed us to isolate the effects of prior learning during the developmental period on later mood and memory retrieval, without needing to filter out the effects of new emotional events.

Method. Because each virtual subject is defined as a set of distinct parameters, this allowed us to run each condition for each virtual subject. As we presented the simulated encoding events to each virtual subject, we tracked the model-predicted levels of negative and positive emotion evoked by each event. In addition, during the session of free recall after each list, we calculated the proportion of correctly recalled events (i.e., events that had occurred in the prior, target encoding list), the number of response repetitions (i.e., events that were correctly recalled, but recalled more than once within each simulation period),

and the rate of memory intrusions (i.e., events that were recalled but that had occurred in a non-target encoding list) that occurred within each simulation period. All recall metrics were averaged across lists within each period in the simulation.

Results and Discussion. In this simulation, we sought to test CMR3's predictions of how developmental learning histories affect subsequent mood and memory retrieval. In Figure 5, we first illustrate the dynamics of emotion in each "experimental" condition for one virtual subject, with the subject's cognitive operations defined by the parameters estimated by fitting CMR3 to the recall dynamics observed in a free recall dataset (see Simulation 1). The three sample developmental paths shown in Figure 5 illustrate how the same set of parameters responds to three different developmental learning histories to determine the subject's mood state in response to encoding and retrieval events. Each panel depicts the model-predicted mood for the same parameter set over the course of encoding and retrieval events for each of three conditions: low, medium, and high frequencies of stressors during the developmental period.

Within each panel, the graph shows model-predicted mood over the course of four simulated periods of time. The first two periods, the developmental and neutral periods, show the output of the simulations conducted in this section (Effects of unique, frequent stressors on mood). In the developmental period (Figure 6, developmental period) we show the model-predicted mood while encountering low, medium, or high frequencies of stressors during early learning. In the neutral period (Figure 6, neutral period) we show the model-predicted mood once these stressors have abated and the model is encountering only new, neutral events. The latter two periods of each panel, the treatment and post-treatment periods, show the virtual subject's response to a simulated course of positive event scheduling, a highly efficacious component of behavioral activation therapy which we discuss further in Behavioral Activation Therapy (Simulation 6).

In each panel, height on the graph represents the level of model-predicted mood, calculated as the difference between the amount of positive emotion and negative emotion contained in the emotional valence subregion of the context vector at that point in the simulation. The color of each point on the graph represents the type of event, whether an encoding event or a retrieval event, that evoked the current mood state. Blue represents a negative event, pink a positive event, and gray a neutral event. Each simulation run has the same number of encoding events; however, because CMR3 models recall as a noisy process, the number of recalled events differs in each simulation, and as a result, the length of each simulation differs across panels.

Mood. In Figure 6, we present the mean level of mood, averaged across virtual subjects, within each period of the low-frequency stressors condition, the medium-frequency stressors condition, and the high-frequency stressors condition. As the frequency of developmental stressors increased, the model predicted an increase in mean levels of negative emotion and a decrease in mean levels of positive emotion during the developmental period (Figure 7, Panel A). Further, the emotional context that accrued during the developmental period persisted into the neutral period, even though the virtual subjects rarely recalled events from the developmental period (Figure 7, Panel B). Instead of mood persisting due to recall of prior negative experiences, recalling the recent neutral events evoked the emotional context with which they had been encoded, which reflected the levels of negative or

positive emotion evoked and accrued during the developmental period. That is, the negative emotion from recent stressors generalized to neutral events, causing them to reactivate negative mood even once all stressors, and active memories thereof, had abated.

Recall. In Figure 7, we present the mean levels of types of recall outputs within each period (Panels B-D), averaged across virtual subjects. During the neutral period, in which the virtual subjects experienced persistent low mood due to the prior stressors, the model predicted decreased probability of correct recall relative to the prior developmental period (Figure 7, Panel B). However, when mood elevated during the treatment period of the simulation introduced in a subsequent section (Figure 7, Panel A; see methods in Behavioral Activation Therapy, Simulation 6), the probability of correct recall also increased (Figure 7, Panel B).

One theory of reduced recall of recent neutral or positive events during a depressive episode is impairment of the neural structures that support the memory system (Austin, Mitchell, & Goodwin, 2001; Bremner, Vythilingam, Vermetten, Vaccarino, & Charney, 2004). However, our simulations demonstrate reduced correct recall rates of recent events during a state of persistent negative emotion (Figure 7, Panel B) while using the same set of parameters for each virtual subject, throughout all periods of each simulation. Our results propose an alternative, or perhaps complementary, explanation for reduced memory during a depressive episode. Specifically, mood-congruent recall processes and interference from prior negative memories, which are activated by the patient's mood state, should decrease recall for any non-mood congruent memories, including neutral or positive stimuli. Considering that the stimuli in cognitive tests are often designed to be neutral, our simulations suggest the importance of future research to test whether findings of reduced memory in depressed patients may reflect the mismatch between items' emotional properties and the subject's emotional state, rather than (or perhaps as a compounding factor to) damage to the memory system.

Repeated stressors

In human memory, repetition is a powerful force. Repeated events have higher rates of recall, particularly when the events are spaced out over time (Madigan, 1969; Melton, 1970). Repeated exposure to severe, traumatic stressors is associated with depressive symptoms (Herman, 1992) and more varied and severe PTSD symptoms (Briere, Kaltman, & Green, 2008; Cloitre et al., 2009). Even mild stressors, when repeated, can lead to depression-like effects in animal models, including learned helplessness and decreased pleasure-seeking behaviors (Cabib & Puglisi-Allegra, 1996; Willner, 1997). In human adults, daily hassles are associated with the persistence of clinically significant distress (Depue & Monroe, 1986). Here, we used CMR3 to test novel predictions about how spaced repetitions of mild stressors might perpetuate negative mood by amplifying the activation of memories for repeated stressors.

Simulation 5

Method. We repeated the methods in Simulation 4, including the emotional composition of lists in the developmental and neutral periods in three separate conditions: Low-, Moderate-, and High-Frequency stressors (see Simulation 4 for full methods). However, in

this simulation, we selected one negative event to repeat across lists, at a frequency of every other list. As in Simulation 4, we followed each developmental period with a period of 100% neutral events. The absence of any new emotional learning during this period allowed us to isolate how the prior, repeated stressor affects subsequent mood and recall without confounds due to new emotional events.

Results. In this simulation, we sought to determine the predictions of retrieved-context theory for the effects of stressor repetition on emotion and memory outcomes. In particular, we tested the effects of repeating one stressor during the developmental period on mood and correct recall during the later neutral period, when the virtual subjects were encountering only new, neutral events. During the neutral period, virtual subjects recalled the memory of the repeated-stressor, even though neither the repeated-stressor nor other negative events had been presented during the neutral period (Figure 8). In comparison, no stressors had intruded into the neutral period during the Frequent Stressors simulation (Simulation 4), in which all negative events were unique, and in which arousal was held constant for all events (for the role of high arousal during encoding on intrusive memories, see Intrusive Memories, Simulation 7). Thus, spaced repetitions predisposed the repeated-stressor event to intrude into memory in later time periods of the simulation.

Upon analyzing the patterns of intrusion, two groups emerged. During the neutral period, one group exhibited stressor-memory intrusions at a frequency greater than one intrusion per list (High-Intrusions Group, n = 12). The second group exhibited stressor-memory intrusions at a frequency near zero (Low-Intrusions Group, N = 85). The latter group exhibited a more favorable mood (Figure 8, Panel A) as well as greater responsiveness to the subsequent simulation of positive event scheduling, a core component of behavioral activation therapy for depression (see Simulation 6: Behavioral Activation Therapy). That is, when the repeated-stressor intruded into memory during the neutral period, it evoked negative mood. Further, the degree of negative emotion that it evoked increased as the frequency of stressors in the surrounding context increased during the developmental period. This is evident in that the rate of stressor-memory intrusions was constant across conditions (Figure 8, Panel D), yet within both groups, virtual subjects still exhibited greater or lower levels of negative mood depending on which condition they were in, or which composition of "background events" had been present when the repeating stressor was encoded. Virtual subjects exposed to high, vs. moderate or low, rates of contextual stressor events had lower mood when the memory of the repeated stressor intruded (Figure 8, A). Thus, the stressor memory evoked greater negative emotion during intrusions when it had been encoded against multiple backdrops of other negative events.

Virtual subjects had similar patterns of correct recall, regardless of whether they were in the High-intrusions vs. Low-intrusions group (Figure 8B). However, virtual subjects in the High-Intrusions group had a better probability of correct recall in the neutral period if their developmental period had contained few stressors. In Figure 8C, the higher rate of repetitions for the High-Intrusions group during the developmental period reflects repeated memories of the repeated-stressor event. This is because during the developmental period, in which the repeated stressor was actually occurring, it is considered a correct recall.

Overall, CMR3 predicts that repeating a stressor has two effects. First, repetition associates the stressor with a wider variety of contexts, thus increasing the potential re-

trieval cues that can prompt recalling the stressor. This raises the probability of recalling the stressor and primes it for activation in contexts where it does not belong (i.e., as a memory intrusion). Importantly, the principles of mood-congruent recall predict that reactivating negative context will not only increase the probability of recalling subsequent negative memories, but further, will decrease the probability of recalling positive memories that might otherwise lift mood (see Simulation 2). Second, the emotion evoked by the recall of a stressful event reflects not only the details of that event, but further, of the emotional backdrop of other contextual events that were occurring while the memory was encoded. That is, our simulations predicted that the ratio of negative to positive events in the surrounding context during the encoding of a repeated-stressor will influence the subsequent mood that it later evokes. If the repeated stressor is encoded over multiple negative contexts, it will evoke high levels of negative emotion when recalled; but if it is encoded over multiple neutral or positive contexts, then these other contexts will become associated with the memory of the event. As a result, even though the events' own features are negative, the model predicts that associations with more positive emotional contexts will reduce the degree of negative emotion evoked when the stressor-memory is recalled. Thus, retrieved-context theory can begin to provide a quantitative rationale for how factors like social support can contribute to reduced distress and resilience to psychopathology in the aftermath of a stressful event (Brewin, Andrews, & Valentine, 2000).

Behavioral Activation Therapy

In clinical psychology, a theory of psychopathology must account not only for risk and maintaining factors, but also for what interventions reduce symptoms and by what mechanisms. Thus, we sought to determine whether CMR3 could predict the efficacy of positive event scheduling, which is a core component of Behavioral Activation Therapy (BAT). BAT is an efficacious treatment for depression based on learning and conditioning principles. A core component of BAT that drove much of its early efficacy research is "positive event scheduling." In positive event scheduling, therapists help patients increase the frequency of reinforcing experiences that they have on a daily basis, including re-engaging with positive and meaningful activities (Beck et al., 1979; Jacobson et al., 1996; Lewinsohn, Sullivan, & Grosscap, 1980). Positive event scheduling helps patients correct learned associations between neutral stimuli and punishing outcomes (Kanter et al., 2010) and helps patients re-engage with opportunities for positive emotion (Jacobson, Martell, & Dimidjian, 2001). In recent developments, BAT has added new components designed to help patients reduce their internal avoidance of thoughts and emotional experiences, with the goal of helping patients fully experience and emotionally benefit from positive activities (Dimidjian et al., 2006).

Here, we tested the ability of retrieved-context theory to account for this core component of BAT: a mood boost in response to a greater ratio of new, fully experienced positive events. First, we indirectly manipulated virtual subjects' mood to increasingly negative mood states, following the procedures in Simulation 4 (Frequent, unique stressors) and in Simulation 5 (Repeated stressors). After the simulation resulted in neutral, negative, or very negative mood states across virtual subjects, we then simulated an intervention of positive event scheduling and examined the model-predicted effects on mood, both during the treatment period and during a recovery period afterward. Simulating a positive event

scheduling intervention as a supplemental simulation to both Simulation 4 and Simulation 5 allowed us to examine the conditions under which CMR3 predicts that positive event scheduling may be most effective. That is, it enabled us to compare this intervention's effectiveness when negative mood has generalized to neutral events (Simulation 4) versus when negative mood is driven by intrusive memories of negative events (Simulation 5).

Simulation 6

Method. We extended Simulation 4 (Persistent Negative Emotion) and Simulation 5 (Repeated Stressors) by adding two additional periods in the simulation. After each virtual subject experienced the given developmental period and acquired a persistent mood state during the neutral period, we introduced a treatment period. During the treatment period, we presented the model with 20 lists of positive event scheduling. We operationalized positive event scheduling as a series of 20 lists, each with a list length of 10 events, that contained an increased, 3:1 ratio of positive to negative events (list composition: 30% positive, 10% negative, 60% neutral). After each treatment period, we presented each model with a series of 60 lists of a recovery period, in which the lists of encoding events were largely neutral with a small, balanced proportion of positive and negative events (80% neutral, 10% negative, 10% positive). This enabled us to assess whether the model could predict a sustained response to treatment, as well as to test the model's predictions regarding the conditions leading to relapse. As in the prior simulations, we tracked the model-predicted mood and recall patterns during the treatment and recovery periods.

Results. In this simulation, we sought to test CMR3's ability to predict efficacy of positive event scheduling, a component of behavioral activation therapy (BAT), for alleviating negative mood in major depressive disorder (Lewinsohn et al., 1980). During the treatment epoch, the model predicted improved mood for all patients in Simulation 4, in which all stressors were unique, for all frequencies of negative developmental events (Figure 7, Panel A). In the recovery period after the treatment period, all patients in Simulation 4 sustained recovery, which we operationalized as having an average mood (Positive – Negative context values) at or above 0.0 (as opposed to negative values). We considered an average mood level of 0.0 given that the recovery period consisted mainly of neutral events (80% of events), with a small and equal mixture of positive (10%) and negative (10%) events. CMR3 predicted that BAT would lift mood and that, in the absence of further high-frequencies of stressors, or of new repeated stressors, this mood improvement would be maintained over time (Figure 7, Panel A). In the CMR3 framework, this occurs because positive events evoke positive emotional context, which begins to alleviate the negative context lingering from prior stressors. Over time, new events bind to a progressively less-negative, and eventually positive, emotional context. New events thereby reactivate more positive emotional contexts when they are later recalled.

By contrast, in the Repeated Stressors simulation (Simulation 5), CMR3 predicted that BAT did produce sustained mood improvements in virtual subjects who continued to experience high rates of stressor-memory intrusions of the repeated event. Although the high rates of positive events during the treatment period temporarily lifted mood (Figure 8, Panel A), intrusive memories of negative events continued to evoke negative context. In a retrieved-context framework, negative context both worsens mood and, due to mood-

congruent recall, reduces recall of recent positive events (see *Mood-congruent recall*, Simulation 2), consistent with findings in depressed participants (R. E. Nelson & Craighead, 1977). As a result, the virtual subjects experienced blunted emotional responses to positive events in the long-term. Thus, retrieved-context theory predicts that repeated stressors can lead to intrusive memories and consistent activation of associated negative emotion that blunt positive emotional responding, and thus interfere with BAT for the treatment of depression if the intrusive memories are not themselves addressed. Treatments that directly target intrusive memories in depression have shown promising results (Brewin et al., 2009), as have treatments targeting perseveration about distressing memories in the context of rumination (E. R. Watkins et al., 2011). Our findings in this simulation provide independent corroboration that such approaches might facilitate the efficacy of cognitive-behavioral therapy when distressing memory-intrusions are prominent. Next, we examine the model's ability to characterize the mechanisms of intrusive memories of high-arousal negative stressors.

Intrusive Memories

Motivation

In the aftermath of extreme or traumatic stress, patients with PTSD report that memory intrusions constitute their most distressing symptom (Ehlers & Steil, 1995). For intrusive memories in PTSD, stimuli whose features strongly overlap with the stimuli that directly preceded the event serve as a strong cue of memory intrusions (Ehlers et al., 2004). Such stimuli, here called "trauma cues," often share little or no semantic similarity to the event itself (Ehlers & Clark, 2000). For example, a patient who was assaulted near a water fountain may experience flashbacks when hearing the sound of running water, even though there is no semantic association between water and assault. The tendency of contextual cues, including perceptual, temporal, and spatial elements of context, to activate trauma-memory intrusions is best known in PTSD. However, intrusive memories of painful events are found in numerous disorders beyond PTSD (Brewin, Gregory, Lipton, & Burgess, 2010; Hackmann et al., 2000; Muse et al., 2010) and often involve stressors not traditionally considered to be traumatic, such as social rejection or perceived failure (A. D. Williams & Moulds, 2007).

Here, we examined whether CMR3 can predict intrusive recall of a high-arousal stressful event as the result of encounters with associated trauma cues. For the sake of brevity, we will refer to a high-arousal stressful event as a "trauma event" in this simulation. However, note that this simulation does not distinguish between trauma vs. non-trauma events. Rather, this simulation modes the effects of high-arousal during encoding as a general principle of the episodic memory system, affecting memories quantitatively (that is, having the same effect for all memories, but with this effect amplified according to how much arousal is present during encoding) rather than qualitatively (that is, affecting only memories of a specific "trauma category"). Retrieved-context theory thus predicts that any high-arousal, negative event has the potential to lead to subsequent intrusive memories, with a higher probability of this outcome as the level of negative arousal during encoding increases. In addition, we sought to identify whether CMR3 could predict that approaching, rather than avoiding, trauma cues leads to a reduction in intrusive memories – the principle that forms the basis for exposure therapy for PTSD (Foa & Kozak, 1986; Powers et al., 2010).

An advantage of CMR3 for modeling memory intrusions is that this model distinguishes among three types of recall outputs: (1) memories associated to the current context (correct recalls), (2) involuntary memories, or memories the patient spontaneously recalls that are associated to a non-target (i.e., not intended) prior context, and which the subject recognizes as being distinct from correct recalls (i.e., memories that come from the intended recall context), and (3) involuntary memories associated to a non-target prior context, and which the patient does not recognize as being distinct from correct recalls. Thus, in our model, intrusive memories are spontaneous memories from non-target (i.e., not intended) recall contexts that virtual subjects can either recognize or not recognize as such.

Providing a framework in which intrusive memories are, broadly, memories that a patient recalls from a non-target context, enables our model to simultaneously describe not only clinical findings, but also instances in which intrusive memories arise in daily life (Berntsen, 2010; Staugaard & Berntsen, 2014) and in the laboratory (Zaromb et al., 2006; Roediger & McDermott, 1995). For example, in daily life, vivid intrusive memories are not limited to traumatic or even negative events (Berntsen, 2010; Staugaard & Berntsen, 2014). Indeed, "flashbacks" of positive and neutral events occur frequently, and can be highly vivid with intense emotional impact (Berntsen & Rubin, 2002). Thus, our model predicts involuntary memories to the extent that the current state of context is a potent retrieval cue for a particular episode in one's life, or alternatively, has particularly strong semantic associations to the current context (Lohnas et al., 2015). Our model then predicts whether a subject is aware that a memory is an intrusion (i.e., not recalled from the intended, or "target," context) based on whether this memory's reactivated context is sufficiently similar to the target context.

Simulation 7

Method. This simulation follows the same format as Simulation 4. First, we presented virtual subjects with a developmental period of 50 lists of 10 encoding events, with all developmental periods containing 40% neutral, 30% positive, and 30% negative events. During this developmental period, we selected one negative event at random to serve as a traumatic event, or "trauma event." To model the traumatic event, we assigned a value greater than 1.0 to the arousal parameter, ϕ_{emot}. Having been introduced to retrieved-context models by Talmi et al. (2019), ϕ_{emot} scales the strengths of the new context-to-event associations that form in M^{CF} during encoding (equation 4). If ϕ_{emot} is greater than 1.0, then it amplifies these associations; if it is less than 1.0, then it attenuates these associations. To test the effects of temporal context on cueing trauma-memory intrusions, we set ϕ_{emot} to 5.0, because this value resulted in good variability of trauma-memory intrusion rates across virtual subjects (Figure 9).

Whereas in prior simulations we varied the contents of the developmental period, here we kept the developmental period consistent across conditions. After each developmental period, we presented virtual subjects with a neutral period consisting of 110 lists of new, unique neutral events. This allowed for 10 lists of neutral-only events after the developmental period, followed by 100 lists of the intervention for each neutral period condition. During the neutral period, we simulated three conditions, during which virtual subjects could either approach or avoid trauma cues, modeled as the three neutral stimuli that had directly preceded the traumatic event during encoding. In the *Avoidance* condition, virtual

subjects did not approach any trauma cues after the traumatic event. In the *Single Exposure* condition, virtual subjects approached trauma cues once, which we modeled by embedding the set of trauma cues as new encoding events during a single list in the neutral period. In the *Repeated Exposures* condition, virtual subjects approached trauma cues eight times, for the approximate number of weeks that patients are encouraged to engage in vivo exposure exercises during a course of prolonged exposure therapy (Foa, Hembree, & Rothbaum, 2007). We modeled this by embedding the three trauma cues as new encoding events at eight regular intervals. The Avoidance, Single Exposure, and Repeated Exposures conditions allowed us to test the model's ability to capture a dose-response relationship between the number of times a virtual patient approached versus avoided trauma cues.

Results. In this simulation, we sought to determine whether retrieved-context theory could predict the effects of "trauma cues," or stimuli whose features are similar to those that directly preceded a traumatic event, on cueing intrusive recall of that event (Ehlers & Clark, 2000). Figure 8 shows the rate of trauma-memory intrusions for each virtual subject during the neutral period that followed exposure to the traumatic event. At the selected level of arousal ($\phi_{emot} = 5.0$), the model predicted that all subjects would spontaneously recall the traumatic event for a short time after exposure. However, by the neutral period, two groups emerged. For one group, comprising 85 of the 97 virtual subjects (87.6%), trauma-memory intrusions had subsided to fewer than one intrusion per recall list by the start of the neutral-events period (Low-Intrusions Group). In the second group that emerged during our simulation, 12 virtual subjects (12.4% of the sample) continued to experience trauma-memory intrusions at least once per recall list by the start of the neutral-events only period (High-Intrusions Group). This is not far from rates of chronic PTSD after trauma exposure in real participants, which typically range from 5-10% but can be higher depending on the type and severity of the trauma (Bonanno, Westphal, & Mancini, 2011).

Next, we assessed the model-predicted effects of encounters with trauma cues, defined as the three neutral stimuli that had directly preceded the traumatic event during encoding. In the Avoidance condition, virtual subjects approached no trauma cues; in the Single-Exposure condition, virtual subjects approached trauma cues once; and in the Multiple-Exposures condition, virtual subjects approached trauma cues eight times. For each condition, we examined the simulated rates of trauma-memory intrusions (Figure 10), the probability of correct recalls of non-trauma events (Figure 11), and mood (Figure 12) at each timepoint.

Recall. The resulting memory and mood patterns depended on whether the virtual subject was experiencing infrequent intrusions (Low-Intrusions Group) versus frequent intrusions (High-Intrusions Group). In the Low-Intrusions group, approaching the trauma cues in both Single-Exposure and Multiple-Exposure conditions resulted in a minimal increase in trauma-memory intrusions at the first exposure timepoint (T_1), shown in Figure 10, Panel A. Otherwise, there was no change in trauma-memory intrusions in any condition over the course of the eight timepoints (T_{1-8}). By contrast, the High-Intrusions group showed a dose-response relationship between the number of trauma-cue exposures and reductions in trauma-memory intrusions. Trauma-memory intrusions persisted in the Avoidance and Single-Exposure conditions (Figure 10, Panel B). However, in the Multiple-Exposure condition, the initial elevation in trauma-memory intrusions during the early

exposures (T_{1-2}) declined, by the third exposure, to rates comparable with those in the single-exposure group. By exposures 5-8, virtual subjects in the Multiple-Exposure condition achieved rates of trauma-memory intrusions comparable to those in the Low-Intrusions comparison group. As re-encountering the trauma cues associated them with more varied non-trauma contexts, the cues became associated with and began to evoke a wider variety of recall outputs, thereby decreasing their tendency to cue recall of the trauma event. Accordingly, the trauma cues' reactivating a wider variety of non-traumatic contexts decreased the probability of correct recall of other stimuli from the most recently presented (target) context (Figure 11).

Mood. In the High-Intrusions group, mood showed little improvement in the Avoidance and Single-Exposure conditions. In the Multiple-Exposure condition, mood also showed little improvement until trauma-memory intrusions began to substantially decrease at timepoint T_4. As the frequency of trauma-memory intrusions decreased more substantially at timepoints T_{4-5}, the model predicted an improvement in mood (Figure 12). The Low-Intrusions group also experienced an increase in positive mood as the result of multiple encounters with trauma cues. This occurred because prior to their association with the traumatic event, the neutral trauma cues had been associated with a mildly positive context evoked by an earlier, positive stimulus. Thus, as the trauma cues became decoupled from the traumatic event due to forming associations with new neutral and positive contexts, their tendency to reactivate the trauma-memory decreased, and they instead began to evoke the positive contexts with which they had previously been associated.

The CMR3 model equations produced this effect by re-associating trauma cues with new neutral or positive contexts, not by replacing or altering prior associations. By predicting symptom change as the result of adding new associations to the trauma memory, rather than replacing old ones, CMR3 provides independent corroboration of emerging findings that, even after successful exposure treatment, patients' fear responses can reemerge when they encounter previously-feared stimuli in contexts where new learning did not take place (Craske et al., 2008). Retrieved-context theory aligns with these prior findings by proposing that the old responses associated with the distressing stimulus are still latent and can later reemerge if either (a) the patient encounters a contextual cue that is more strongly associated with the old responses than with new responses, or (b) the current context contains few elements of the context in which learning the new responses took place.

What is novel in retrieved-context theory is the proposed mechanism: namely, that the restructuring of memory-to-context associations is mediated by the episodic memory system, rather than by systems involved in fear-conditioning. This allows our theory to account for the finding that stimuli similar to those that preceded the traumatic event serve to cue trauma-memory intrusions (Ehlers et al., 2004). Further, our theory can account for the observations that avoiding trauma cues perpetuates symptoms, and that in vivo exposure to trauma cues can reduce the frequency of intrusive memories (Foa & Kozak, 1986). However, our theory goes one step beyond fear-conditioning theories to propose a novel account of how, by restructuring episodic association networks in memory, trauma survivors can not only habituate, but also, recover prior enjoyment of trauma-associated stimuli (e.g., as in the case of a survivor of sexual assault who recovers feelings of joy and affection in romantic relationships).

This framework can also account for how interpersonal differences can moderate the frequency and emotional experience of intrusive memories. For example, emotion dysregulation, or difficulties understanding and regulating the intensity and valence of one's emotional experiences, can serve as a risk factor for the development of PTSD and can lead to more extreme responses to trauma cues (Tull, Barrett, McMillan, & Roemer, 2007; Tull, Berghoff, Wheeless, Cohen, & Gratz, 2018; Messman-Moore, Walsh, & DiLillo, 2010). To assess how emotion dysregulation moderates the dynamics of intrusive memories, we repeated Simulation 7 while modeling two groups of virtual subjects: (1) virtual patients with heightened emotion dysregulation (High Emotion Dysregulation group), and (2) virtual patients with low emotion dysregulation (Low Emotion Dysregulation group).

We modeled emotion regulation ability as the rate of updating of emotional context, β_{emot}, meaning how swiftly the emotional contents of new events enter and update the emotional components of patients' internal contextual states. In the High Emotion Dysregulation group, we set $\beta_{emot} = .8$ for all virtual subjects, whereas in the Low Emotion Dysregulation group, we set $\beta_{emot} = .3$ for all virtual subjects. In the post-trauma "Neutral events period," among virtual subjects who experienced frequent trauma-memory intrusions (See Simulation 7 methods), the High Emotion Dysregulation group experienced higher rates of intrusive memories of traumatic events (Mean trauma-memory intrusions = 6.82, SEM = 1.20) than the Low Emotion Dysregulation group (Mean trauma-memory intrusions = 4.92, SEM = 1.10). In the post-trauma "Neutral events period," the High Emotion Dysregulation group experienced more severe negative emotional responses to trauma-memory intrusions (Mean mood = -0.44, SEM = 0.04), relative to the Low Emotion Dysregulation group (Mean mood = -0.13, SEM = 0.05).

The model framework predicts these results due to two factors. First, heightened emotion dysregulation led to a greater tendency to recall negative memories when experiencing a negative mood state (mood-congruent recall). Second, heightened emotion dysregulation led to a greater tendency to recall memories (regardless of valence) that had been encoded with a matching, negative emotional background context (emotion-state dependent recall).

Intrusive Memories: Vividness and Nowness

Motivation

Vividness. A hallmark feature of intrusive memories in PTSD is heightened degrees of sensory features during recall. Indeed, vivid, highly visual memories occur widely across emotional disorders beyond both PTSD and depression (Reynolds & Brewin, 1999), including social phobia (Hackmann et al., 2000), obsessive compulsive disorder (Speckens et al., 2007), health anxiety (Muse et al., 2010), body dysmorphic disorder (Osman et al., 2004), and agoraphobia (Day et al., 2004). Direct comparison between intrusive memories in patients with depression, PTSD, and controls suggests that vividness and nowness may not reflect distinct qualitative features of memory in PTSD, but rather, may vary quantitatively, perhaps with the types of events that lead to intrusive memories in PTSD being particularly emotionally intense (Rubin et al., 2008, 2011). The autobiographical memory theory of PTSD (Rubin et al., 2008, 2011) proposes that the intensity of emotional arousal during a new event predisposes an event to a strongly encoded memory trace, thereby increasing its salience, vividness, and tendency to be cued for spontaneous recall as a memory intrusion.

Importantly, this framework's process is transdiagnostic: it can account not only for the occurrence of vivid, intrusive memories of painful events in PTSD, but further, across a wide array of emotional disorders as described above.

Nowness. Intrusive trauma memories are also characterized by a greater sense of "nowness," or a feeling that the memory is happening again in the here-and-now. Since the classic work of Tulving (1972), episodic memory has been conceptualized as a form of "mental time travel" due to the ability of even neutral memories to reinstate the context of prior events and thereby transport the rememberer back in time. Recent work has conceptualized mental time travel as the degree of similarity between current context and the context that was present at the time of encoding (Howard, Shankar, Aue, & Criss, 2015). In retrieved-context theory, we can operationalize the degree of perceived "nowness" by how closely a memory's reinstated context matches the subject's current temporal context. In prior retrieved-context models, this same similarity metric has also served to determine whether a subject can distinguish when a memory has been retrieved from the current target context, versus being recalled as an intrusion from a distant lure context (Lohnas et al., 2015).

Below, we combine formalized principles of *Autobiographical Memory Theory* of PTSD together with classic principles of mental time travel in episodic memory literature. These principles arise naturally from our model equations in CMR3, as well as in recent work demonstrating this model's ability to account for properties of intrusive recall (Lohnas et al., 2015). We show how the resulting model simulations predicts that the intensity of emotional arousal during encoding predisposes a memory to be recalled more vividly and with a heightened sense of "nowness," or the perception that the memory sources from the immediate and most-recent context.

Simulation 8

Method. In Simulation 7, we observed that heightened negative arousal during encoding increased the model-predicted rates of trauma-memory intrusions. Here, we examine the model's predictions for how the degree of negative arousal at encoding influences an intrusive memory's qualitative properties: vividness and nowness. In this simulation, we operationalized vividness as the magnitude of the activation of different memory features during the recall process (E.q. 10). We operationalized "nowness" as the degree to which the context that is reactivated during a memory's retrieval matches the current context state, evaluated as the dot-product similarity between these two context vectors $\mathbf{c}^{IN} \cdot \mathbf{c}_t$. As in the core model equations, higher dot-product similarity values indicate a lesser awareness that a memory-intrusion does not belong to the immediate temporal context (i.e., higher "nowness"). Since the CMR3 model context vectors represent two subregions, each of which is updated and normed separately, the total contextual similarity value ranges between 0.0 and 2.0. We measured how vividness and nowness vary as a function of ϕ_{emot}, the arousal parameter that scales the strength of context-to-item associations. To ensure a sufficient sample of trauma-memory intrusions for analyses, we varied ϕ_{emot} from 2.0 to 5.0, since at a level of 1.0 (i.e., a value determining that there is no effect of arousal on memory), the virtual subjects committed zero trauma-memory intrusions to analyze. As in the prior intrusive recall simulation (Simulation 7), we randomly assigned 30% of items in each list of 10 items to be negative, 30% to be positive, and 40% to be neutral. We set the trauma

item to occur in the middle of its list, at position 6 out of 10 positions.

Results. The simulation revealed that at heightened levels of negative arousal during the trauma, the virtual subjects experienced the trauma-memory intrusion with a greater sense of vividness (Figure 13, Panel A) and "nowness" (Figure 13, Panel B). In terms of our operationalized metrics of these qualities, negative arousal during encoding subsequently increased both the magnitude of reactivation of a memory's features (vividness) and the match between the memory's reactivated context and its retrieval context (nowness). Thus, the model predicted that high arousal during encoding would increase virtual subjects' probability of (mis)perceiving that the trauma memory occurred in the most-recent, just-experienced list. This occurs for three reasons. First, retrieved-context theory proposes that negative arousal strengthens associations between the memory and its context during encoding. Second, when heightened negative arousal primes the memory system's associative networks, trauma-memories require lower levels of associated contextual cues to reactivate them, and the trauma-memory begins to intrude more frequently. Thus, new contexts already contain elements of trauma-associated context reactivated by prior trauma-memory intrusions. In addition, patients might introduce and consistently refresh the presence of trauma-associated context by ruminating about the trauma (Michael, Halligan, Clark, & Ehlers, 2007). Third, because traumatic events evoke strong negative emotional context, recalling a traumatic memory flavors the current context with negative features. The current context becomes more negative; thus, the emotional context present just prior to retrieval is a stronger match for the negative emotional context of the memory. In addition, because the current context becomes more negative, it is more likely to cue the reactivation of further negative memory-intrusions due to mood-congruent recall, which in turn flavor context with their own negative features, creating a snowball effect.

Prolonged Exposure Therapy

Motivation

Among multiple efficacious treatments for trauma-memory intrusions and other symptoms in PTSD (Tran & Gregor, 2016), one particularly efficacious treatment is prolonged exposure therapy, or PE (PE; Foa & Kozak, 1986; Powers et al., 2010). Exposure-based treatments match the efficacy of other treatments for PTSD and, when study quality is accounted for, slightly outperform them (Tran & Gregor, 2016). Prolonged exposure therapy has two core components. During in vivo exposure exercises, patients systematically approach feared stimuli that they have been avoiding due to their associations with the traumatic event (see Intrusive Memories). Second, during imaginal exposure exercises, patients intentionally reactivate the traumatic memory and imagine it as though it is happening again in the here-and-now.

Despite its strong empirical support, the precise mechanisms by which PE improves PTSD symptoms remain an active area of research (Rupp, Doebler, Ehring, & Vossbeck-Elsebusch, 2017). Although symptom improvement has been attributed to principles of fear conditioning and extinction, symptom reduction is not associated with the duration or degree of habituation achieved within individual exposure exercises (Craske et al., 2008; Jaycox, Foa, & Morral, 1998). Rather, symptom reduction is most strongly associated

with the degree of habituation achieved across sessions, with either weak or no associations to habituation within-session (Rupp et al., 2017; Jaycox et al., 1998). This finding has raised concerns about circularity: for example, that "those who habituate, habituate," or that habituation is incidental to the success of exposure-based treatments (Brewin, 2006). In addition, the degree of initial fear activation during an exposure exercise, a core tenet of fear-conditioning theories of how PE works, is not consistently associated with PTSD symptom improvement (Rupp et al., 2017). Here, we test the ability of CMR3 to account for the efficacy of PE via the mechanism of restructuring episodic context associations, and in particular, to account for a pattern of reduced negative emotion in response to trauma memories that occurs across, rather than within, treatment sessions.

Simulation 9

Method. In this simulation, we repeated the methods from Simulation 7 (Intrusive Memories). We presented a developmental period consisting of 50 lists of 10 encoding events. Each encoding list contained 40% neutral, 30% positive, and 30% negative events and was followed by a simulated free recall session. During the developmental period, we randomly selected a negative event to serve as the trauma event. This time, we amplified the strength of the encoded associations between the trauma event and its context by a factor of $\phi_{emot} = 50.0$. We selected this high value to ensure that all subjects would experience trauma-memory intrusions in the subsequent neutral period.

After the developmental period in each simulation, we presented a neutral period consisting of 110 lists of neutral events. In the neutral period, we presented one of four conditions: (1) the Baseline condition, (2) the Imaginal Exposure condition, (3) the Positive Events control condition, and (4) the Re-encoding control condition. During the Baseline condition, the neutral period consisted solely of new, neutral events. The *Baseline* condition served as a manipulation check to ensure that the chosen level of arousal resulted in high rates of trauma-memory intrusions for all virtual subjects. During the *Imaginal Exposure* condition, we simulated the re-encoding of traumatic memories in safe, therapeutic contexts. We simulated this by re-introducing the trauma-memory at five regular intervals during the neutral period as a new encoding event. Prior to the re-encoding of the trauma memory, we modeled a safe context by introducing a positively valent stimulus. Because patients' negative affect tends to increase in anticipation of the imaginal exposure exercise, we introduced the positive stimulus several stimuli prior to the re-encoding of the trauma memory, such that positive affect would decrease as the moment of re-encoding the trauma memory approached.

To clarify the mechanisms of any change observed in the Imaginal Exposure condition, we included two control conditions. The first control was a Positive Events condition, in which we introduced a new, positive event at identical intervals (i.e., every 20 lists) in the neutral period as the re-encoding of the trauma event during the Imaginal Exposure condition. The *Positive Events* condition served as a control to verify that the Imaginal Exposure condition did not reduce negative emotion simply due to the positive events that preceded re-encoding of the trauma memory. The second control was a *Re-Encoding* condition, in which we introduced the trauma memory as a new encoding event at the same 5 regular intervals in the neutral period. However, unlike in the Imaginal Exposure condition, we did not evoke a less-negative context prior to its encoding. This served to test

whether simply re-encoding the memory in new contexts would promote mood recovery, regardless of the emotional content of those new contexts. As in the prior simulation, we calculated the average mood within each period, the rate of correct recalls of non-trauma events, and the rate of trauma-memory intrusions.

Results. In this simulation, we sought to test whether CMR3 could predict the finding that exposure to the trauma memory reduces the negative emotion evoked by the memory when it is recalled. In addition, we sought to determine whether CMR3 could predict the finding that reduced negative emotion across, but not within, such exposure exercises is associated with symptom improvement (Jaycox et al., 1998; Craske et al., 2008). Below, we outline the model-predicted mood and recall patterns resulting from a simulation of imaginal exposure to a trauma memory.

Mood patterns. The results for an individual virtual subject are shown in Figure 12, and the aggregated effects across virtual subjects are shown in Figure 13. First, as a manipulation check, we confirmed that the trauma event evoked severe and persistent negative emotion during the developmental period at the selected level of arousal ($\phi_{emot} = 50.0$). In the Baseline Condition, the trauma event resulted in high rates of recurrent memory intrusions throughout the subsequent neutral period. Without intervention, the repeated memory intrusions evoked negative context, which resulted in negative mood that persisted for the remainder of the neutral period (Figure 14, Panel A; Figure 15), as occurred in Simulation 5 (Repeated Stressors). Next, in the Positive Control Condition, we presented positive events at 5 regular intervals. Each event briefly instated a positive context when it occurred, but continued intrusions of the trauma-memory returned mood to a negative baseline each time (Figure 14, Panel B; Figure 15). In the Re-encoding condition, we presented the trauma event for re-encoding at the same 5 regular intervals, which resulted in no mood improvements (Figure 15). Finally, in the Imaginal Exposure condition, we first induced less-negative contexts and then paired these with a subsequent presentation of the trauma memory as an encoding event. Over the course of the five re-encodings of the trauma memory, the trauma memory began to associate with the new less-negative contexts. After each intentional re-presentation of the trauma memory, the subsequent trauma-memory intrusions evoked progressively reduced negative emotion, until mood stabilized near a neutral value of 0.0 (Figure 14, Panel C; Figure 15).

Because the trauma memory reinstates its old associated context when first retrieved, CMR3 predicts that its new updated context will not be evoked until the next time the memory is retrieved. Thus, the phenomenon of reduced negative emotion, or apparent habituation, across rather than within sessions of imaginal exposure emerged naturally from the model. This effect can be observed in Figure 12 (Panel B), and in Figure 13. Whereas the mean level of emotion becomes less negative after each re-encoding of the trauma memory (i.e., after each virtual PE session) designated by the vertical lines, the degree of negative emotion evoked by the memory during its reactivations stays level within each session. That is, during the current session, the memory evokes the negative context that had previously been associated with it. Then, each time the trauma memory is re-encoded in association with a less-negative context, it updates its associated affect and thus will evoke less-negative context the next time it is retrieved, resulting in an across-session reduction in negative affect.

Recall patterns. The high value of the arousal parameter, $\phi_{emot} = 50.0$, which strengthened the context-to-event associations during encoding, resulted in high rates of trauma-memory intrusions. The rate of trauma-memory intrusions remained essentially constant throughout timepoints of the simulation, with minimal variability across virtual subjects. Therefore, we report the mean frequency of trauma-memory intrusions across the timepoints in each condition: the mean frequency was 13.8 (SEM = .003) for the Baseline and Positive-Events simulations and 14.0 (SEM = .020) for the Re-Encoding and Imaginal Exposure simulations. Due to the very high rates of intrusions induced by the high arousal level used in this simulation, the probability of correct recall was low, and also consistent across simulations. The mean probability of correct recall across timepoints was .020 (SEM = .0003) for the Baseline and Positive Events simulations and .010 (SEM = .0020) for the Re-Encoding and Imaginal Exposure simulations.

Thus, the simulations predict a slight increase in trauma-memory intrusions for the two conditions that involved a re-presentation of the traumatic memory, and concurrently, a slight decrease in probability of recalling other events. This is consistent with findings that although imaginal exposure is efficacious for alleviating negative affect, the re-presentation of the traumatic memory may initially result in a slight elevation in trauma-memory intrusions in a minority of patients (Foa, Zoellner, Feeny, Hembree, & Alvarez-Conrad, 2002). In CMR3, a decreased probability of recalling nontraumatic stimuli, together with greater activation of the trauma-memory, occurs because the activated trauma-related context is dissimilar to the context of nontraumatic or neutral events, and therefore is less able to cue recall of these stimuli.

General Discussion

Emotional disorders, particularly depression but also including anxiety and PTSD, are the leading source of disability worldwide (World Health Organization, 2017). Their high comorbidity has generated a search for transdiagnostic processes (Insel et al., 2010). Such processes, which contribute to negative emotion across disorders, can point to more efficacious treatments for patients with complex diagnoses. Learning and memory processes have long been implicated as one such mechanism. For example, research on classical conditioning has fueled a number of treatment protocols for depression and PTSD, including behavioral activation therapy (Beck et al., 1979) and prolonged exposure therapy (Foa & Kozak, 1986). However, many phenomena remain unexplained, including why patients sometimes experience negative emotion without any active negative cognitions, and why exposure therapies are so effective for treating PTSD yet are weakly associated with their proposed mechanisms (Rupp et al., 2017). In addition, the precise manner in which high-arousal negative emotion influences the episodic memory system, which supports memory for personally-experienced events, is an active area of research.

In this article, we proposed a new theory of how episodic memory processes interact with mood to produce psychopathology, which we formalize in a computational model called CMR3. The model we develop benefits greatly from prior work on context maintenance and retrieval (CMR) models, particularly the eCMR model developed by Talmi and colleagues (2019), who first conceptualized emotion as a component of memories and their contexts. In addition, we draw upon major advances by prior theories of memory and emotion in clinical disorders, particularly major depression and posttraumatic stress disorder (Bower,

1981; Brewin, 2006, 2014; Ehlers & Clark, 2000; Foa & Kozak, 1986; Rubin et al., 2008, 2011). The theory we develop benefits from the insights of this work while introducing novel processes that account for both classic and previously unexplained phenomena of memory in emotional disorders.

Retrieved-context theory of memory in emotional disorders. Retrieved-context theories of memory propose two core operations. First, memories form associations with their contexts during encoding. Later, new contexts serve as cues for memory retrieval by activating these networks to retrieve memories that were associated with similar contexts. Once a memory is retrieved, it reactivates elements of its encoding context, which can in turn cue other memories. The memory, its old context, and its new context, are then re-encoded together as part of a recursive process that updates the memory to associate it with new information. Recently, Talmi et al. (2019) broke new ground by conceptualizing emotion as a component of memories and their contexts. However, the ability of eCMR to capture phenomena in clinical disorders is limited by two features. First, eCMR models emotion as a single-dimensional construct, without having positive or negative valence, such that the model cannot predict what differentially leads to the activation of negative versus positive emotional context. Second, eCMR limits the effects of prior learning to a single experimental list, such that emotional learning could not accrue over the course of a patient's lifespan. Further, eCMR cannot distinguish between a target vs. non-target prior context, a necessary condition to modeling intrusive memories of distressing events, a core phenomenon of interest in PTSD and other disorders.

In this paper, we introduced a new retrieved-context theory of memory in mood, which we formalized as a mathematical model called CMR3. In CMR3, we introduced emotional valence as a property of both memories and mood states (Figure 1), and we introduced the multilist capabilities of CMR2 (Lohnas et al., 2015). This allows CMR3 to model how memories from a non-target context can intrude into the current context, as well as how emotional learning accrues and influences behavior throughout a patient's lifespan. To empirically test how to represent emotional valence in CMR3, we compared the fits of three retrieved-context models: (1) CMR2, which represents emotion as a type of semantic content; (2) eCMR, which additionally represents emotion as present or absent in memories and their contexts, but with no valence; and (3) CMR3, which represents emotion as multivalent. To enable a direct comparison between each model, we coded a version of eCMR that has multilist capabilities, thus allowing it to predict recall intrusions alongside CMR2 and CMR3. Further, to isolate the effects of the representation of emotional valence in fitting the data, we held the effects of arousal constant in the model, $\phi_{emot} = 1.0$. CMR3 provided the best fits to the aggregate behavioral responses (see Modeling Emotional Memory), indicating that emotional valence functions as a component of both memories and their contexts, not just as semantic content, and that it is important to include it in the model. It is also important to include emotional valence in the model for theoretical purposes, since a model of emotion in clinical disorders cannot function without the ability to differentiate between the effects of positive and negative experiences.

Transdiagnostic framework

In this paper, we have sometimes used the language of diagnostic categories, particularly major depression and PTSD. This approach has allowed us to guide our theory by

drawing upon a wealth of literature examining memory and mood in specific disorders. However, retrieved-context theory reflects recent initiatives to use findings and methods from cognitive neuroscience to identify the basic processes that cut across disorders (Montague, Dolan, Friston, & Dayan, 2012; Sanislow et al., 2010). This approach is consistent with findings that disorders characterized by persistent negative emotion are highly comorbid (K. T. Brady et al., 2000; Kessler, Chiu, Demler, & Walters, 2005), and that memory disturbances, such as intrusive memories of painful events, occur widely across emotional disorders (Brewin et al., 2010; Day et al., 2004; Hackmann et al., 2000; Osman et al., 2004; Speckens et al., 2007). We propose a framework in which intrusive memories and negative mood result from basic processes of cognition and emotion, occurring more often under some conditions, such as patterns of environmental stress interacting with a person's individual characteristics, but not constrained to a specific DSM-5 disorder. We outline retrieved-context theory's framework and proposed processes below.

Mood-congruent and Emotion-state dependent recall

In characterizing memory processes in emotional disorders, we began by demonstrating how retrieved-context theory can account for the interplay of mood and emotion in psychopathology. Using the match between encoding and retrieval contexts, CMR3 accounted for mood-congruent recall (Simulation 2) and emotion-state dependent recall (Simulation 3). In mood-congruent recall, items whose valence matches that of the retrieval context will have introduced that valence into their encoding contexts, and thus will have a stronger activation to promote their retrieval. In emotion-state dependent recall, neutral items are better recalled if the emotional context present during encoding contexts matches the emotional context present during retrieval. Although emotion-state dependent learning is observed inconsistently in laboratory settings with healthy participants (Eich, 1995), its influence appears more strongly in clinical populations (Craske et al., 2008). Retrieved-context theory is consistent with findings that new learning in exposure-based treatments for anxiety disorders is enhanced when new learning occurs in the same emotional context in which it will later be retrieved (Craske et al., 2008).

In his prior spreading activation theory, Bower (1981) proposed that mood-congruent and emotion-state dependent memory occur because emotional valence serves as an node in semantic networks. A positive or negative emotion thus activates semantically associated memories, which tend to share the same emotional properties due to semantic relatedness. In CMR3, because emotional valence also serves as a part of a memory's episodic context, it can become associated with stimuli that themselves are neutral and have no semantic relation with negative emotion. This aspect of our theory is important for allowing CMR3 to model the generalization of negative affect to neutral events (Simulation 4) and how stimuli that have little semantic association to a traumatic event, but that preceded the event, can later cue intrusive memories and trauma-associated affect (Simulation 7). We discuss our model's predictions of these phenomena below.

Persistent Negative Emotion

Retrieved-context theory predicts that emotional context can linger after an event and thus bind to new events, even if these new events are neutral (Simulation 4). Thus, when stressors occur and induce negative emotion, memories of the new events that follow are

encoded in association with the lingering negative emotion. Whereas the subsequent events may be experienced as neutral or positive during their encoding, the emotion that they evoke when later retrieved becomes more negative due to the negative emotional context present during encoding. The ability of negative emotion to bind to later events can explain how a depressed patient might experience a positive event as enjoyable while experiencing it, but later recall the event as having been more negative, since memory of the event activates not only its positive properties but further, the negative context with which it had become associated. Further, this mechanism can account for the phenomenon of "affect before cognition," in which patients report experiencing negative emotion without having any active thoughts or memories about a stressor, especially when stimuli associated with prior negative events are present (Ehlers & Clark, 2000).

Repeated stressors

Retrieved-context theory predicts that repetition has powerful effects on memory. Spaced repetitions of stressors associate the event with a larger number of contexts that can later serve as cues to activate the memory for spontaneous retrieval (Lohnas, Polyn, & Kahana, 2011; Madigan, 1969; Melton, 1970). Retrieved-context theory proposes that repetition, either by experiencing the stressful event multiple times (Simulation 5), or through repeated rehearsal and re-encoding of the memory in many different contexts, will increase the chance that the memory may be cued for retrieval into a context in which it does not belong. Indeed, rumination, which includes the repetitive rehearsal and elaboration upon negative memories, is associated with and can prompt intrusive memories in PTSD (Michael et al., 2007). Our simulations are consistent with a core tenet of the Autobiographical Memory Theory (AMT) of intrusive memories in PTSD, which proposes that repeated rehearsal of distressing memories can lead to intrusive memories by amplifying the memory's accessibility (Rubin et al., 2011). We extend the AMT by proposing a novel mechanism for this process: that repeated rehearsal associates the memory with multiple contexts, thus increasing the probability that future contexts will contain some element of the memory's associated cues and thereby activate it for recall in contexts where the memory otherwise does not belong.

Behavioral Activation Therapy

Retrieved-context theory predicts that increasing the ratio of positive to negative events, a core component of behavioral activation therapy (Beck et al., 1979; Jacobson et al., 1996; Lewinsohn et al., 1980), results in sustained mood improvement (Simulation 6). However, the model predicts that increasing the ratio of positive events is most effective when a patient's negative emotion is the result of the generalization of negative emotion to neutral events. When negative mood results from intrusive negative memories, our simulations predict that patients will initially have a short-term positive response to positive events, but will experience blunted responsiveness to positive events in the long run as memory intrusions reactivate negative emotional context. As such, retrieved-context theory highlights the importance of addressing intrusive memories in major depression. Treatments targeting this symptom have shown promising results (Brewin et al., 2009).

Intrusive memories of high-arousal, negative events

Intrusive memories occur prominently in PTSD, but they also occur widely across other disorders (Berntsen, 2010; Day et al., 2004; Hackmann et al., 2000; Muse et al., 2010; Osman et al., 2004; Price et al., 2012; Reynolds & Brewin, 1999; Speckens et al., 2007) and for painful events not traditionally categorized as traumatic (Brozovich & Heimberg, 2008; A. D. Williams & Moulds, 2007). Prior theories, such as the Autobiographical Memory Theory (Rubin et al., 2011), have proposed that high emotional intensity, or emotional arousal, strengthens the accessibility of a memory, thereby predisposing it to spontaneously activate. We extend this theory by proposing that high emotional arousal during encoding is the driving mechanism, serving to strengthen the associations between an event and its context during encoding, as introduced in the eCMR model (Talmi et al., 2019). In a retrieved-context framework, strengthened context-to-event associations potentiate the memory for retrieval, since lower levels of associated context is needed to cue these associations. Further, strengthened associations strengthen the probability that unrelated contexts will contain enough elements of associated context to trigger the memory (see Simulations 7 and 8).

To allow the model to distinguish between recalling an event from a target context (voluntary recall) versus from a non-target context (a memory intrusion), we combined the high-arousal mechanism of eCMR (Talmi et al., 2019) with the multilist capabilities of CMR2 (Lohnas et al., 2015). The new model, CMR3, can account for findings that encountering stimuli whose features are similar to the perceptual, spatial, and temporal context that directly preceded the traumatic event cue heightened rates of trauma-memory intrusions (Simulation 7), even if the stimuli have no semantic relationship to the event (Ehlers & Clark, 2000; Ehlers et al., 2004). Accordingly, CMR3 proposes that re-associating the temporal context of a traumatic memory with new neutral or positive contexts, as occurs during in vivo exposure exercises, will lead these cues to eventually evoke affect, cognitions, and memories that are not associated with the traumatic event (Simulation 7). This theory is consistent with theories that extinction occurs by encoding new associations that exist alongside the feared stimulus' prior associations (Foa & McNally, 1996). In addition, retrieved-context theory predicts that old associations can still be reactivated when the feared stimuli are encountered in contexts that are dissimilar to the contexts in which new learning has taken place (Craske et al., 2008).

Although such contextual cues can include environmental stimuli such as sights, smells, or sounds, our modeling approach also includes an internal contextual representation that does not map directly on to observable attributes in the environment or even in the subject's conscious awareness. Our modeling approach follows a substantial body of prior theoretical work going back to Estes (1950), in which context is generally not part of one's conscious awareness. Rather, context is an amalgam of internal (latent) features. Context is a combined representation of recent perceptual, spatial, emotional and temporal experiences that need not have any specific interpretation, but which together form a general internal mental state, and whose dynamics of forming associations with other contextual states govern associative learning and retrieval.

Intrusive memories when fear is not the primary emotion

Patients with PTSD often report that primary emotional responses other than fear, such as shame or sadness, are associated with their traumatic event (Resick & Schnicke, 1992). In addition, patients with depression often report vivid memory-intrusions characterized by intense negative emotion other than fear (Kuyken & Brewin, 1994; Reynolds & Brewin, 1999). Retrieved-context theory predicts the development of intrusive memories when high-arousal negative emotion is present during encoding, without constraints for what type of emotion must be present.

Retrieved-context draws insights from the framework of Emotional Processing Theory (EPT), the theory underlying prolonged exposure therapy (Foa & Kozak, 1986; L. A. Brown et al., 2019). Based in Lang's bioinformational theroy of emotion (1979), and principles of classical conditioning, EPT proposes the existence of cognitive "emotion networks" that hold associations between unconditioned stimuli (trauma cues), conditioned responses to those stimuli (fear and avoidance), and cognitions about the meaning of those stimuli, such as "the world is dangerous" and "I am vulnerable" (L. A. Brown et al., 2019). Whereas EPT focuses on the role of fear-conditioning and extinction learning in the respective development and recovery from PTSD, the theory also handles the contributions from other emotional structures, such as associations with guilt, shame, and grief. EPT proposes two mechanisms by which prolonged exposure therapy (PE) reduces fear and avoidance of trauma-associated stimuli, as well as reduced distress while recalling the trauma memory. First, EPT proposes that in vivo and imaginal exposures activate the emotion structure. Then, EPT proposes that the patient must integrate competing associations into the network.

Retrieved-context theory draws insights from EPT and other fear-learning or conditioning models, but our model differs from conditioning frameworks in the following ways. First, traditional conditioning theories represent context as consisting of external, environmental stimuli (Gershman, Blei, & Niv, 2010; Redish, Jensen, Johnson, & Kurth-Nelson, 2007). In retrieved-context models (formalized here as CMR3), context consists of a continuously updating internal representation of recently encountered external features in the environment, as well as recent internal cognitive states (Polyn et al., 2009) and emotional states (Talmi et al., 2019). Thus, contextual associations represent bindings between memory elements and context representations, rather than between pairs of stimuli. Unlike traditional conditioning models, in which new learning changes the set of previously learned associations, the retrieved-context model retains all previously learned associations and also stores all new associations that the subject learns as time continues. All stored associations then combine at retrieval into a shared memory representation based on the current state of context. Thus, in CMR3, context is recursive. That is, a patient's internal context also includes memories that have been recently retrieved, which flavor the patient's context with their reactivated contents and thereby become a part of a new memory trace.

As a result, retrieved-context theory accounts for several new phenomena. First, grounding our model in episodic memory mechanisms can help explain qualitative changes in intrusive trauma memories over time. These include the vividness of the memory, which we model through the activation of the memory's features by encountering a new matching context. In addition, retrieved-context theory characterizes the increased "nowness" of a trauma memory through Tulving's classic mechanism of "mental time travel," linking

our understanding of traumatic memories with basic memory literature on how people experience themselves being transported back in time when they recall a specific memory. We model this as the similarity between the memory's encoding context and the retrieval context in which the patient recalls it. Finally, retrieved-context theory can account for why rumination might itself generate intrusions (Michael et al., 2007), since rehearsing trauma-associated content infuses the patient's context with those trauma-related elements, thus increasing the probability of cuing a trauma-memory associated to those elements.

Further, retrieved-context theory can account for new learning that occurs even when patients do not experience a "prediction error," or violation of expectations, during an individual therapy session. Conditioning models of emotion in clinical disorders propose that new learning depends on prediction errors, or the difference between the predicted and actual contingencies when a stimulus occurs (Eldar, Rutledge, Dolan, & Niv, 2016). Learning-based clinical theory also proposes that learning takes place as patients encounter a feared stimulus, activate their fear structure, and receive disconfirming information (L. A. Brown et al., 2019), such as finding that their fear habituates or reduces. However, clinical findings indicate that feared stimuli, like a trauma memory, still evoke progressively less-negative emotion across sessions even when retrieving the memory confirms patient's predictions by being exactly as distressing as predicted – that is, even when a decrease in negative emotional responding to the memory within-session is not achieved (Jaycox et al., 1998). Retrieved-context theory accounts for this finding through the proposed mechanism of associating the memory to new, less-negative contexts, which importantly can have less-negative properties in our model even if the patient themself is experiencing high negative affect. We detail this further below using the example of prolonged exposure therapy.

Prolonged Exposure Therapy (PE)

In PE, patients vividly reimagine and reactivate trauma memories for a prolonged period across multiple therapeutic sessions. Numerous studies have demonstrated that PE constitutes a highly efficacious treatment for PTSD (Powers et al., 2010; Tran & Gregor, 2016). Consistent with these findings, retrieved-context theory of emotional memory predicts a decrease in negative affect due to the repeated reactivation and re-encoding of negative memories in new, safe or neutral contexts (see Simulation 9). Lane, Ryan, Nadel, and Greenberg (2015) interpret the effectiveness of PE as arising from therapy-induced "reconsolidation" of trauma memories. Here reconsolidation refers to the idea that there is a single copy of a given memory, and that reactivating this memory and then reencoding it alters its contents.

In contrast, retrieved-context theory proposes that each time a memory is re-experienced, its retrieved associations update the current state of context, and new associations form between the item's features and the updated representation of context (i.e., the new experience updates both the context vector, $\mathbf{c}$, and the associative matrices, M^{FC} and M^{CF}). As such, our model maintains the original associations stored in memory but adds new associations based on the re-experienced memory. Recovery from PTSD occurs as patients repeatedly reactivate the memory and then successively re-encode it in association with new, safe contexts. In CMR3, retrieval cues reactivate not only the original memory trace, but also, all of the newer memory traces. At the time of retrieval, the full set of memory traces and their associated contexts combine. Thus, throughout treatment,

retrieving the trauma memory reactivates not only the original context associated to the first memory trace, but also, an amalgam of the many newly associated, safe contexts that are associated with the trauma-memory's subsequent traces, resulting in reduced distress.

Importantly, the finding that PTSD symptom reduction in prolonged exposure therapy is associated with apparent habituation (i.e., a decrease in negative affect due to reactivating the traumatic memory) across, but not within, treatment sessions (Jaycox et al., 1998; Rupp et al., 2017) emerges naturally from our model (Simulation 9). In an episodic memory framework, treatment first activates the memory and then re-encodes it in association with a changed emotional context. The updated emotional context is only reactivated the next time the memory is retrieved, such that negative affect decreases across rather than within sessions (Simulation 9). Further, within an individual session of PE, the memory may be rehearsed multiple times. Although reductions in negative emotional responding to the trauma memory occur inconsistently among PTSD patients within-sessions, such within-session reductions can still be helpful when they do occur (Bluett, Zoellner, & Feeny, 2014). Retrieved-context theory can also account for this effect, in that within-session reductions in distress would promote the re-association of the memory to less negative contexts on a micro level. Retrieved-context theory can further account for the greater effects of across-session effects, as spaced rather than massed repetitions associate the memory with a wider and more diverse variety of new contexts enhance new learning (Lohnas et al., 2011; Madigan, 1969; Melton, 1970).

Retrieved-context theory's prediction of PE's efficacy, even under conditions in which patients experience very high levels of distress, distinguishes it from *dual-representation theory*. Dual-representation theory (DRT) introduced a major advance in theories of memory in PTSD by proposing that high emotional arousal during encoding influences the strength of the associations between traumatic memories and their temporal contexts (Brewin, 2014; Brewin et al., 2010). Specifically, DRT proposes that high arousal disrupts the associations between events' perceptual features and their spatiotemporal contexts (Brewin, 2014; Bisby, Horner, Bush, & Burgess, 2018).

Accordingly, DRT predicts that the same intense distress which disrupted episodic memories' ability to bind to their encoding contexts while experiencing the event should do the same during treatments that involve high levels of negative emotion. Indeed, the laboratory studies used as the basis for dual-representation theory propose that negative arousal disrupts associative memory even at the level of viewing negative images that are not personally relevant (Bisby et al., 2018; Bisby & Burgess, 2014). Thus, a resulting prediction of DRT is that, during in vivo or imaginal exposure exercises, the therapist must carefully manage a patient's distress to prevent the disruption of the process of re-binding the trauma memory's features to its original encoding context (or perhaps to safe elements of the novel context), such as by providing a reassuring and supportive context for new learning to take place.

Here, the predictions of DRT and retrieved-context theory diverge with respect to clinical literature. As demonstrated via simulations in the Prolonged Exposure Therapy section (Simulation 9), retrieved-context theory predicts that high negative arousal during imaginal exposures is not iatrogenic, and may even benefit new learning by strengthening context-to-item associations. In clinical literature, high levels of negative emotion and negative physiological arousal during exposure-based treatments are either associated with

better treatment outcomes (Craske et al., 2008; Kircanski et al., 2012; A. J. Lang & Craske, 2000), including in PE (Jaycox et al., 1998), or else have no relation with treatment outcomes (Rupp et al., 2017). Both phenomena are consistent with retrieved-context theory but inconsistent with a theoretical approach that distress exceeding a given level during treatment is iatrogenic. Regarding the associated concern that high negative arousal might disrupt memory (re)formation by inducing dissociation, patients with high (vs. low) rates of dissociation either show equal gains during PE (Hagenaars, van Minnen, & Hoogduin, 2010) or else do not benefit any less from a course of PE than from comparison treatments that are designed to reduce distress and dissociative responses (Burton, Feeny, Connell, & Zoellner, 2018; Wolf, Lunney, & Schnurr, 2016).

However, it is not sufficient for retrieved-context theory to account for these clinical findings. Retrieved-context theory must also demonstrate its ability to predict laboratory findings that negative arousal during encoding appears to disrupt the formation of associations between visual stimuli and their contexts. Indeed, laboratory findings of stronger associations between pairs of neutral stimuli during recall, and weaker associations between negative and neutral stimuli (Bisby et al., 2018). However, these studies did not control for greater semantic relatedness among pairs of negative (vs. pairs of neutral) stimuli (Talmi & Moscovitch, 2004). AS a result, this pattern of results may be accounted for by the classic "fan effect" (Anderson, 1974). Because neutral items have weaker semantic associations to other neutral items, as well as to items of negative or positive valences, the associations that neutral items form to other neutral items during the experiment will have less competition from prior, long-standing associations. Conversely, negative items have stronger pre-experimental associations to other negative items that will compete for retrieval, and thus impair recall, of new associates learned during the experimental context. Further, in *Modeling Emotional Memory* (Simulation 1), we show how retrieved-context theory similarly predicts the tendency of emotional items to selectively cluster together with same-valent items during a laboratory free recall task, as well as the clustering of semantic associates.

Efficacy of cognitive behavioral therapies for PTSD

Considering emotion as a type of episodic context also enables retrieved-context theory to account for the efficacy of treatments like Cognitive Processing Therapy for PTSD, which are equally efficacious as PE (Rizvi, Vogt, & Resick, 2009). Our theory predicts that modifying the negative emotional context associated with a traumatic event, as occurs through restructuring maladaptive cognitions in cognitive processing therapy (Resick & Schnicke, 1992), should result in the trauma memory being re-encoded with the new less-negative context. This will both result in an apparent habituation effect and also reduce the tendency for intrusive memories cued by a match between the current emotional state and the emotions that were present during encoding (see Mood-congruent Recall, Simulation 2). Overall, retrieved-context theory proposes two treatment routes for PTSD: modifying the context-to-memory associations in the emotion network, as in PE (Foa & Kozak, 1986) and modifying the contents of the emotional context associated with the traumatic memory, as in CPT (Resick & Schnicke, 1992).

Limitations

The utility of our model depends on whether list-learning experiments can be considered to be an adequate basis for a model of human memory. This is the core challenge for all modeling work: finding a paradigm simple enough to be tractable for developing a model in its early stages, yet complex enough to ultimately extend its predictions to multidimensional, real-world experience. As in classic work by George Box, "All models are wrong, but some are useful" (Box, 1979). Certainly, learning and recalling lists of words in the lab, and testing subjects' abilities to localize their recalls to a specific list context, lacks the complexity of real-world emotional events. At the same time, the list-learning paradigm has served as a powerful tool for isolating core principles of human memory, including primacy, recency, temporal and semantic contiguity effects (Kahana, 1996; Murdock, 1967; Howard & Kahana, 2002b; Sederberg, Miller, Howard, & Kahana, 2010), which have replicated in studies of memory for complex events in the real world (Jansari & Parkin, 1996; Loftus & Fathi, 1985; Moreton & Ward, 2010; Uitvlugt & Healey, 2019; Healey, Long, & Kahana, 2019). We view the model's current setup just as a needed starting point for more realistic models of human experience and suggest that future work based on ecological momentary assessment could lead to deeper insights into the mechanisms of memory for emotional events, and particularly, how this process unfolds in emotional disorders in patients' natural environments.

A second limitation is that, whereas retrieved-context theory has some advantages over dual-representation theory in its ability to predict PE treatment effects, dual-representation theory was developed to characterize the internal consistency of traumatic memories (Brewin, 2014), which CMR3 does not fully address. In CMR3, events are represented either on the level of individual stimuli, or a larger event can be presented as a series of stimuli (a "list"), from which the model predicts the retrieval of multiple elements. In Intrusive Memories (Simulation 7), CMR3 demonstrates how high arousal negative emotion during encoding of a list of stimuli can predispose trauma-related stimuli for intrusive memories (Figure 10), while decreasing the probability of correct recall of other stimuli (Figure 11). However, even when conceptualizing an event as a set or list of stimuli, in CMR3 each stimulus is presented one at a time. Further, CMR3 does not currently differentiate among the modalities of each stimulus, i.e., whether they are visual, auditory, internal physiological sensations, and so forth (but see recent updates implementing stimulus modality in the CMR family of models as a type of source context; Pazdera & Kahana, Submitted). It may be the case that CMR3 provides a strong account of the associations between distinct stimuli and traumatic events, whereas dual-representation theory may provide a stronger account of the internal consistency of the different perceptual experiences that make up a memory across different modalities. Empirical testing of both models, beyond the simulation work presented in this paper, will shed light.

Further, a core phenomenon shared by both major depression and PTSD is overgeneral memory, likely related to or perhaps a consequence of deficits in context discrimination abilities (J. M. G. Williams et al., 2007). This is typically assessed by providing participants with verbal cues and asking them to report an autobiographical memory associated with each cue, after which responses are categorized as specific (memories tied to a specific time and place) versus overly general (memories of patterns or categories of events that are

not recalled in association with specific temporal or spatial contexts). A central feature of CMR3 is its ability to account for intrusive thoughts, and in particular intrusive thoughts that share a common emotional context (e.g., negative or positive). An individual who has experienced many examples of negative events that all share some common categorical information will tend to intrusively activate the representations of negative experiences and their categories across time. Because thoughts become memories in our model, the mixing of these negative representations across varied temporal contexts will tend to form a web of associations across lists, much as in an experiment in which subjects experience repeated items from the same categories across lists (e.g., Postman, 1976; Anderson & Bower, 1972). Such manipulations cause high levels of associative interference and frequent intrusions. If the negative categories constitute the repeated items, reactivation of these categories will lead to higher levels of recall, whereas associative interference will lead to lower levels of event-specific recall. This is analogous to the effects of repetition in word lists, as reported by Zaromb et al. (2006). In that study, repeating items across lists led to higher recall of the repeated items at the expense of a greater tendency to intrude memories from non-target contexts, and subsequently terminate recall (see, also, Miller, Weidemann, & Kahana, 2012). Although we could imagine this mechanism potentially producing overgeneral memory in depressed patients, a proper modeling exercise would require experimental data in which depressed patients experimentally study lists of category-exemplar pairs of varying valence/arousal and show improved memory for the categories but impaired memory for the examples. We suggest this as an interesting direction for future work.

A fourth limitation lies in one of our model's strengths, which is the ability to predict a wide array of phenomena in emotional disorders without making strict assumptions about what type of emotion is being experienced. This allows it to account for patterns of comorbidity between mood and stress disorders, as well as how intrusive memories can occur for many types of distressing events. However, in real life, emotion is a complex, multivariate construct whose attributes extend beyond negative-positive valence and low-high arousal. For example, anger and fear are both negatively valent and high-arousal emotions, yet they have distinct subjective experiences, action tendencies (avoid vs. approach; Carver & Harmon-Jones, 2009), and neural patterns (Kragel & LaBar, 2015). In the current version of CMR3, the effects of fear and anger would be indistinguishable. In addition, not all negative emotional states induce high arousal: for example, disgust may be associated with reduced physiological arousal (Ekman, Levenson, & Friesen, 1983). Future research is needed to characterize the full dimensionality and role of emotion in the memory system. Similarly, further research is needed to determine the precise relationship between arousal and the learning rate for new associations during encoding. One could easily introduce a non-linear relation between arousal and learning rate, as in the classic Yerkes-Dodson (1908) results, and perhaps this would be a fruitful direction for future work. Or, perhaps under extreme levels of arousal, there is a more systemic shutdown of the cognitive system, as suggested by dual-representation theorists.

Finally, CMR3 represents mood and memory outcomes as the result of different processes in a simulated mind that are constrained by sets of parameter values, which determine how strongly each process will operate for a given individual. For example, CMR3 can represent an individual with heightened emotional sensitivity by setting the value of β_{emot}, the rate at which emotional information enters and updates the cognitive system, to a higher

value. However, the model does not explain what led to a particular set of parameter values in the first place. The future development of retrieved-context theory will benefit from insights from biological and developmental models of how patients acquire distinct cognitive parameters innately and throughout development.

Conclusion

Retrieved-context theory proposes a parsimonious account of episodic memory that generates persistent negative emotion, intrusive memories, and their co-occurrence. This paper presents the first transdiagnostic, computational model of memory and mood in emotional disorders as these phenomena unfold over time. By fitting the model to empirical data and conducting simulations, we can test whether the predictions of narrative theories, when constrained by their proposed operations, map on to empirical literature. Together with recent initiatives to use computational modeling to characterize clinical phenomena (Bennett, Silverstein, & Niv, 2019; Montague et al., 2012), we propose that developing a clinical theory will benefit from testing whether, given an appropriate set of inputs, a formal model generated from that theory can capture and predict behavioral patterns from experimental and clinical paradigms. The resulting model should be able to predict the efficacy of existing treatments. In addition, the model must do so via mechanisms that map on to our understanding of human cognition and neural architecture. In this paper, we accomplish the first two criteria and lay a foundation for empirical work to accomplish the third. We hope this new framework will be used to refine and challenge the retrieved-context model, thus ultimately improving our understanding of memory and mood in psychopathology.

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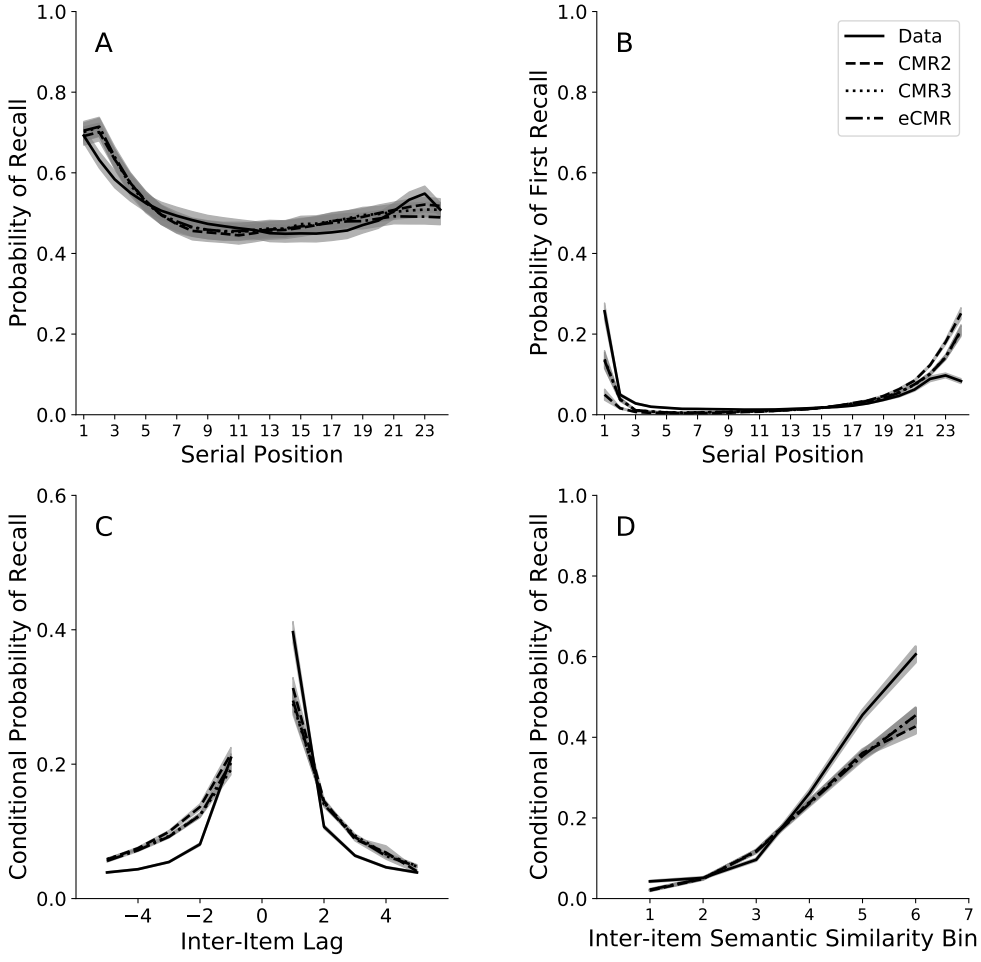

Figure 2. Modeling the organization of memories during free recall. We fit CMR2, eCMR, and CMR3 to serial position effects and to temporal, semantic, and emotional clustering in a delayed free recall task. **A.** The serial position curve, which plots recall probability as a function of items' presentation order during encoding, illustrates the mnemonic benefits for early and late list positions (primacy and recency). **B.** The probability of first recall curve plots the probability that an item will be recalled first as a function of an items' presentation order during encoding. **C.** The lag conditional response probability graph represents the tendency of items to cluster during recall according to their proximity to one another during encoding. For an example, the value at a lag of +2 is the probability that, given the recall of item A, the item that is recalled directly after item A was encoded 2 positions after item A during study. **D.** The semantic conditional response probability curve represents the tendency of items to cluster during recall according to their semantic similarity to one another. The curve depicts the probability that, given the recall of item A, the item recalled right after item A has a certain level of similarity with A, plotted against the median value of each bin.

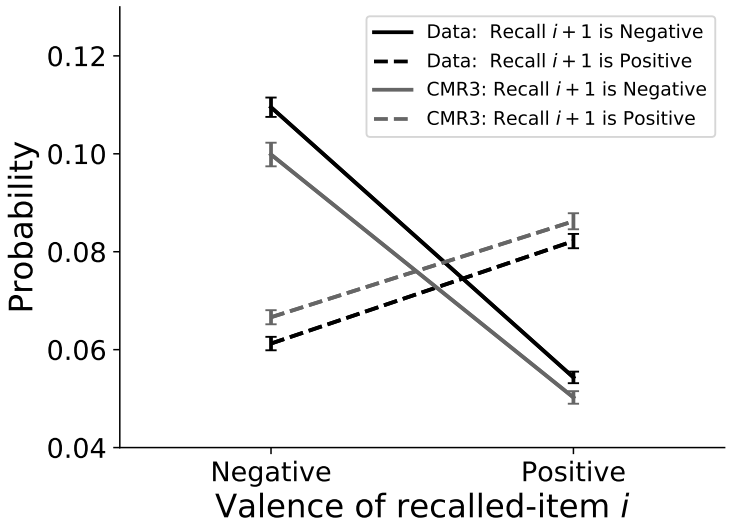

Figure 3. Modeling the organization of memories during free recall, continued. The emotional clustering effect represents the tendency of items to cluster during recall according to their emotional valence. This figure shows the fit of CMR3 to the emotional clustering effect in the data. The graph plots the conditional probability of recalling an item $i+1$ that is either negative or positive, depending on whether the recalled-item i directly preceding it was negative vs. positive. Solid lines represent the tendency to transition to a negative item, and dashed lines represent the tendency to transition to a positive item.

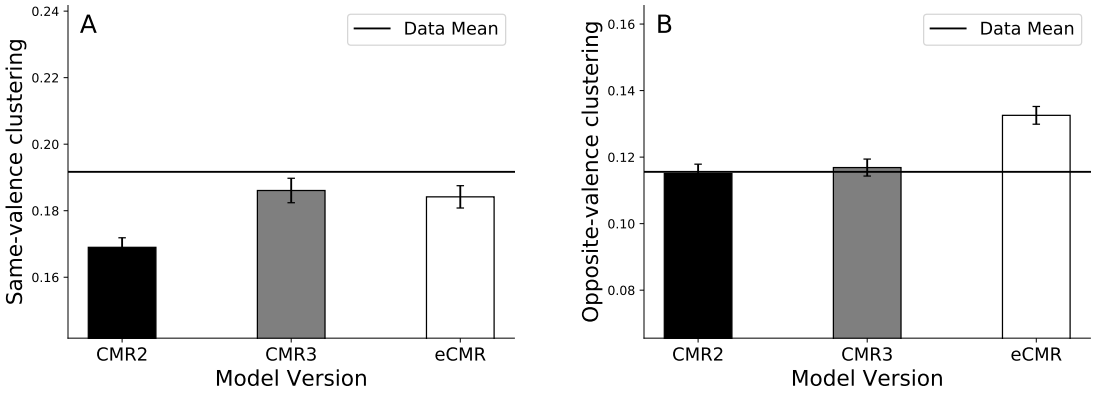

Figure 4. Modeling the organization of memories during free recall, continued. The emotional clustering effect represents the tendency of items to cluster during recall according to their emotional valence. This figure shows the model-predicted degree of clustering among **A.** same-valent and **B.** oppositely-valent items for CMR2 (black bars), CMR3 (gray bars), and eCMR (white bars). Error bars represent the standard error of the mean.

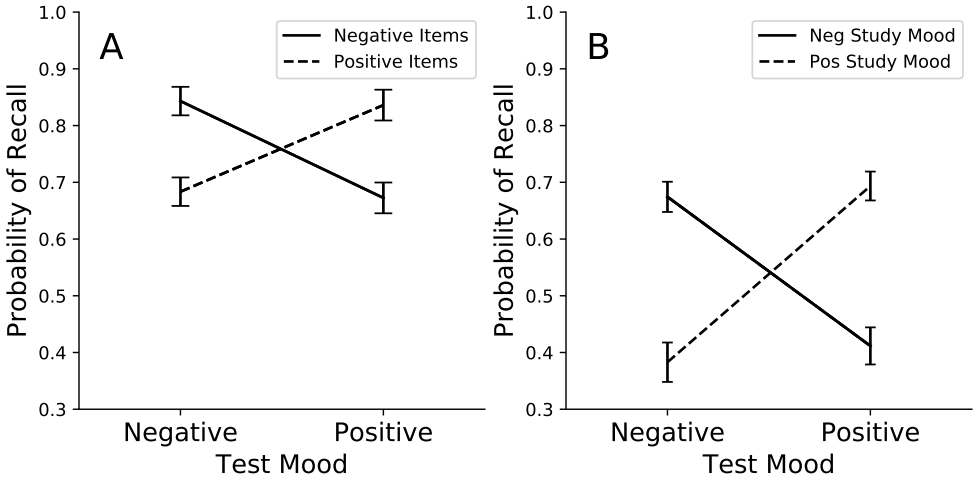

Figure 5. Simulating Mood-congruent and Emotion-state Dependent Recall. Using parameters obtained from the behavioral fits in Simulation 1, we used CMR3 to predict recall outputs based on two factors: (1) the match between an item's valence and the emotional state during retrieval (mood-congruent recall), and (2) the match between the emotional state during encoding and retrieval, regardless of the item's valence (emotion-state dependent recall). **A.** Mean probability of recalling a negative item (solid lines)or a positive item (dashed lines), depending on the valence of the recall context, which is marked on the horizontal axis. **B.** Mean probability of recalling a neutral item depending on whether it was encoded and retrieved in matching versus non-matching emotional states. The valence of emotion during retrieval, or Test mood, is marked on the horizontal axis. Solid lines represent negative mood during study, and dashed lines represent positive mood during study. Error bars represent +/-the standard error of the mean, calculated across all parameter sets' predictions.

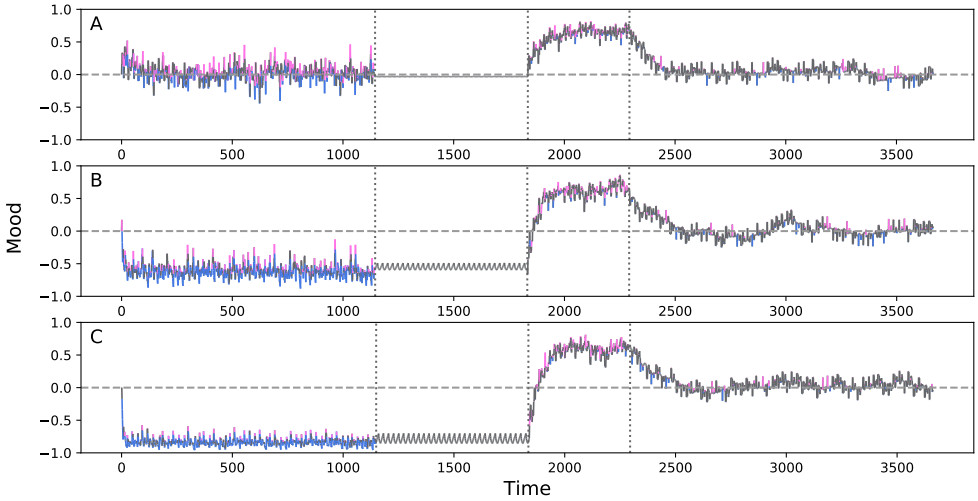

Figure 6. Simulating the effects of stressor frequency. Each panel illustrates the evolution of model-simulated mood across four periods, marked by vertical lines: (1) A developmental period, in which a virtual subject experienced a mixture of both emotional and neutral events, (2) A neutral period, in which a virtual subject experienced solely unique, neutral events, (3) A simulated course of positive event scheduling, a component of behavioral activation therapy in which a virtual subject experienced a heightened rate of positive events (30% positive, 60% neutral, 10% negative), and finally (4) A recovery period comprised of predominately neutral events (80% neutral, 10% negative, 10% positive). The beginning of each period is marked by a vertical dotted line. Across panels A-C we varied the ratio of positive to neutral events during the developmental period, with 30% negative and 30% positive in panel A, 60% negative and 20% positive in panel B, and 70% negative and 10% positive in panel C. The height on the graph represents the level of model-simulated mood (minimum of -1.0, maximum of 1.0), and the color on the graph represents the emotional valence of the encoded or retrieved event that evoked that level of mood (pink = positive, blue = negative, gray = neutral).

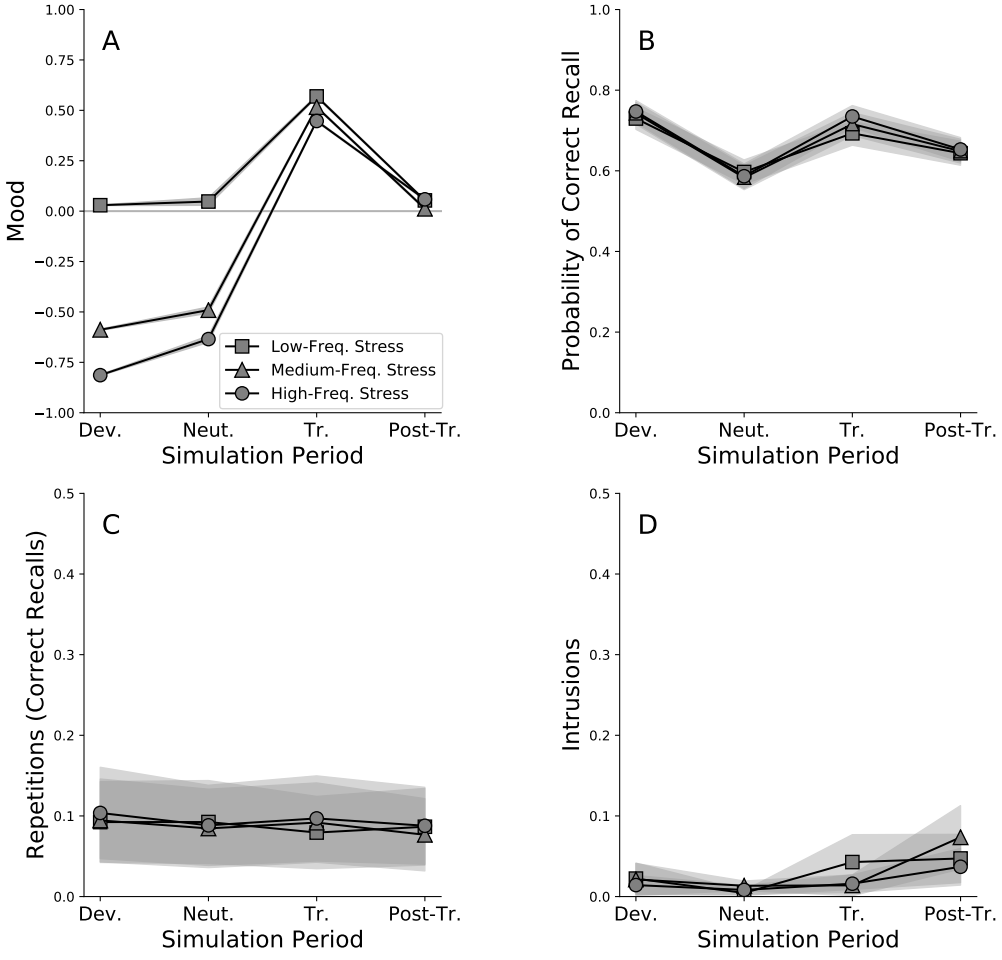

Figure 7. Aggregated results for the simulation of stressor frequency effects. This figure presents the model-predicted patterns of mood and recall for Simulation 4, aggregated across the results for all virtual subjects (i.e., parameter sets). Results are presented for each stage of the simulation, averaged within each stage. In the first condition (square markers), each virtual subject experienced an even mixture of negative and positive events during the developmental period (30% negative, 30% positive events, 1:1 ratio). In the second condition (triangle markers), the virtual subject experienced a moderate frequency of stressors during the developmental period (60% negative, 20% positive events, 3:1 ratio). In the third condition (circle markers), the virtual subject experienced a high frequency of stressors during the developmental period (70% negative, 10% positive events, 7:1 ratio). After the developmental period, all virtual subjects experienced a neutral period (100% neutral events), followed by a "treatment period" containing a simulation of positive event scheduling, a component of behavioral activation therapy (10% negative, 30% positive events). Finally, the simulation concluded with a post-treatument period (10% negative, 10% positive events). **A.** Mean levels of virtual subjects' mood at each stage of the simulation. **B.** The probability of correct recall at each stage of the simulation. **C.** The mean number of repetitions per list at each stage of the simulation. **D.** The mean number of intrusions per list at each stage of the simulation. Error regions represent +/-the standard error of the mean, calculated across all parameter sets' predictions. Dev. = Developmental period. Neut. = Neutral period. Tx = Treatment period. Post-Tx = Post-treatment period.

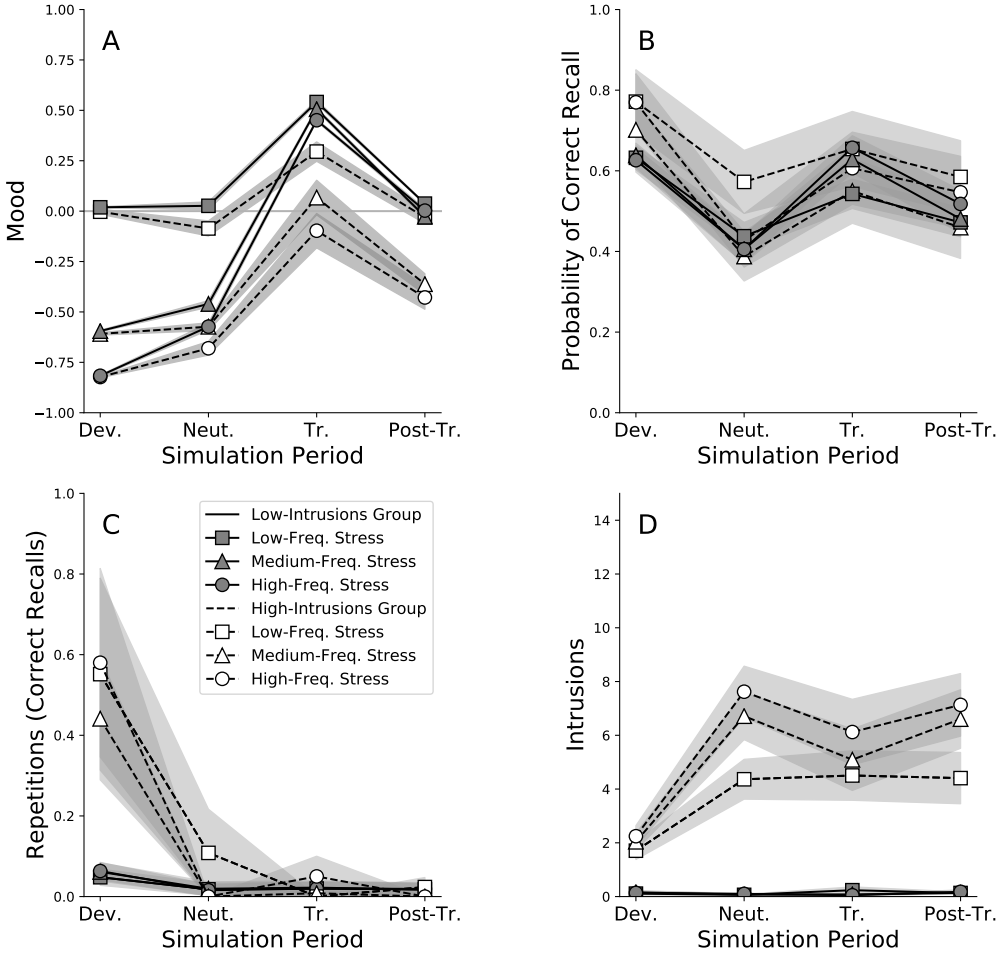

Figure 8. Aggregated results for the simulation of stressor repetition effects. This figure presents the model-predicted patterns of mood and recall for Simulation 5, aggregated across the results for all virtual subjects (i.e., parameter sets). In the first condition (square markers), each virtual subject experienced an even mixture of negative and positive events during the developmental period (30% negative, 30% positive events, 1:1 ratio). In the second condition (triangle markers), the virtual subject experienced a moderate frequency of stressors during the developmental period (60% negative, 20% positive events, 3:1 ratio). In the third condition (circle markers), the virtual subject experienced a high frequency of stressors during the developmental period (70% negative, 10% positive events, 7:1 ratio). In each condition, one negative event was selected to repeat every 10 lists. After the developmental period, all virtual subjects experienced a neutral period (100% neutral events), followed by a "treatment period" containing a simulation of positive event scheduling, a component of behavioral activation therapy (10% negative, 30% positive events). Finally, the simulation concluded with a post-treatment period (10% negative, 10% positive events). **A.** Virtual subjects' mood, averaged within each stage of the simulation. **B.** The probability of correct recall at each stage of the simulation. **C.** The number of repetitions per list, averaged within each stage. **D.** The number of intrusions per list, averaged within each stage of the simulation. Solid lines show virtual subjects with low counts of intrusions (Low-Intrusions Group) and dashed lines show virtual subjects with high counts of intrusions (High-Intrusions Group). Error regions represent +/- the standard error of the mean, calculated across all parameter sets' predictions. Dev. = Developmental period. Neut. = Neutral period. Tx = Treatment period. Post-Tx = Post-treatment period.

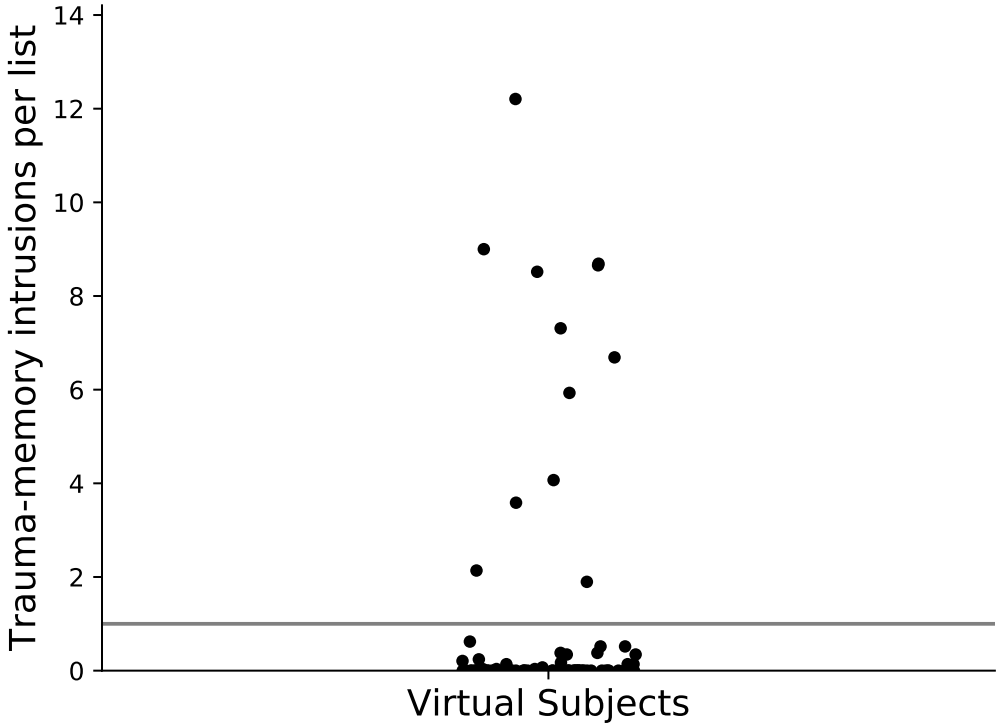

Figure 9. Rate of trauma-memory intrusions per list for each virtual subject. The modal virtual subject had fewer than 1.0 such intrusions per list during the period of neutral events following their traumatic event (Low-Intrusions Group), whereas 12 virtual subjects had more than 1.0 such intrusions per list during the period of neutral events following their traumatic event (High-Intrusions Group). The horizontal line is a reference line, height equal to 1.0.

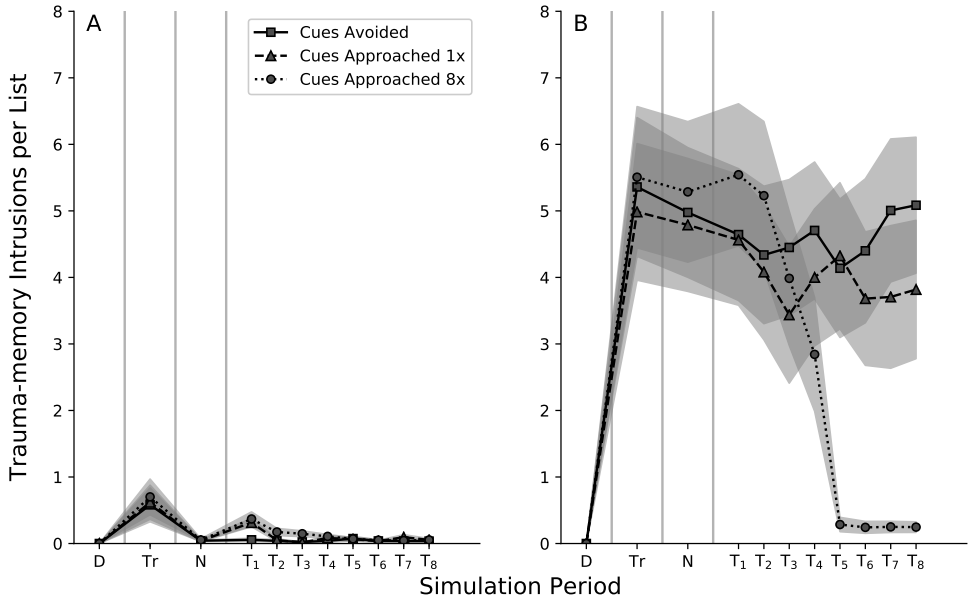

Figure 10. Aggregated results for simulating the effects of temporal context on trauma-memory intrusions. This figure presents the model-predicted patterns of trauma-memory intrusions resulting from encoding a traumatic event, aggregated across the results for all virtual subjects (i.e., parameter sets). Panel A shows results for the "Low-Intrusions Group," or virtual subjects who had low rates of trauma-memory intrusions after their traumatic event. Panel B shows results for the "High-Intrusions Group," or virtual subjects who had high rates of trauma-memory intrusions after their traumatic event. The markers represent one of three conditions. Condition 1 (square markers) is a baseline condition, in which the neutral period consists solely of unique, neutral events. Condition 2 (triangle markers) is a single exposure to a set of three trauma cues, or the nonnegative stimuli that preceded the traumatic event during encoding the neutral period. Condition 3 (circle markers) is eight exposures to the same set of three, nonnegative trauma cues. D = Developmental Period. Tr = The portion of the developmental period after the traumatic event occurs. N = The neutral period prior to the re-encounters with trauma cues. T_{1-8} = each of the eight time-points at which a virtual subject has an opportunity to either approach or avoid trauma cues.

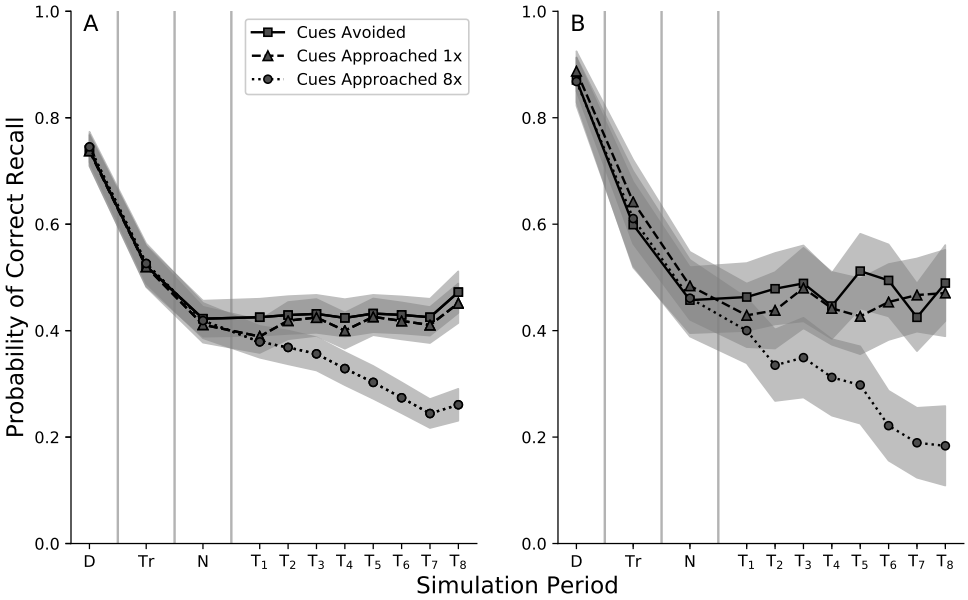

Figure 11. Aggregated results for simulating the effects of temporal context on correct recall. This figure presents the model-predicted patterns of correct recall of recent events after encoding a traumatic event, aggregated across the results for all virtual subjects (i.e., parameter sets). Panel A shows results for the "Low-Intrusions Group," or virtual subjects who had low rates of trauma-memory intrusions after their traumatic event. Panel B shows results for the "High-Intrusions Group," or virtual subjects who had high rates of trauma-memory intrusions after their traumatic event. The markers represent one of three conditions. Condition 1 is a baseline condition (square markers), in which the neutral period consists solely of unique, neutral events. Condition 2 is a single exposure to a set of three trauma cues, or the nonnegative stimuli that preceded the traumatic event during encoding the neutral period (triangle markers). Condition 3 is eight exposures to the same set of three, nonnegative trauma cues (circle markers). D = Developmental Period. Tr = The part of the developmental period after the traumatic event occurs. N = The neutral period prior to the re-encounters with trauma cues. T_{1-8} = each of the eight time-points at which a virtual subject has an opportunity to either approach or avoid trauma cues.

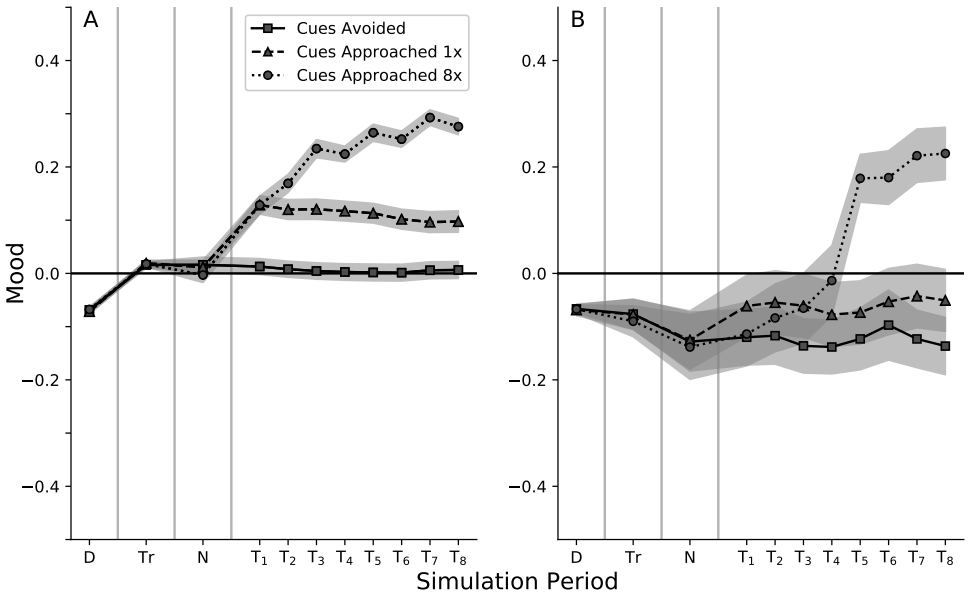

Figure 12. Aggregated results for simulating the effects of temporal context on mood. This figure presents the model-predicted patterns of mood resulting from encoding a traumatic event, aggregated across the results for all virtual subjects (i.e., parameter sets). Panel A shows results for the "Low-Intrusions Group," or virtual subjects who had low rates of trauma-memory intrusions after their traumatic event. Panel B shows results for the "High-Intrusions Group," or virtual subjects who had high rates of trauma-memory intrusions after their traumatic event. The markers represent one of three conditions. Condition 1 (square markers) is a baseline condition, in which the neutral period consists solely of unique, neutral events. Condition 2 (triangle markers) is a single exposure to a set of three trauma cues, or the nonnegative stimuli that preceded the traumatic event during encoding the neutral period. Condition 3 (circle markers) is eight exposures to the same set of three, nonnegative trauma cues. D = Developmental Period. Tr = The part of the developmental period after the traumatic event occurs. N = The neutral period prior to the re-encounters with trauma cues. T_{1-8} = each of the eight time-points at which a virtual subject has an opportunity to either approach or avoid trauma cues.

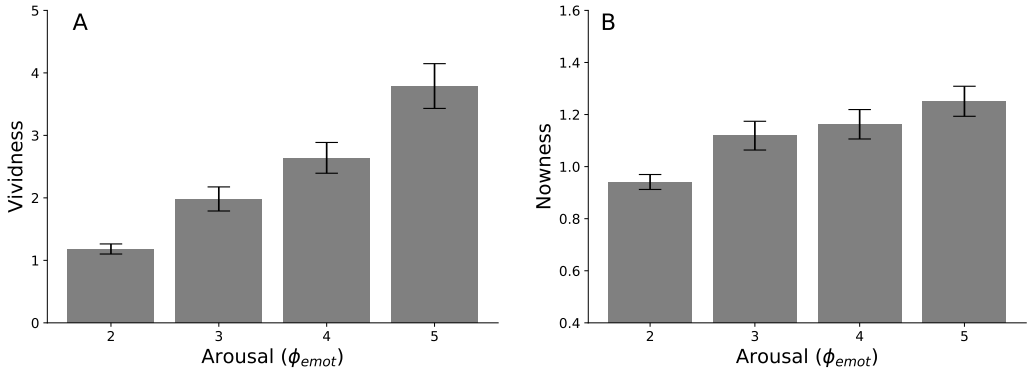

Figure 13. Effects of negative arousal on memory vividness and "nowness." To simulate arousal we varied the learning rate for the associations between context features and item features during encoding (ϕ_{emot}). We then define vividness as the activation of a retrieved memory's features, and we define nowness as the similarity between current context and retrieved context. **A.** Vividness increases with the simulated arousal during the initial encounter with a subsequently remembered experience. **B.** Nowness also increases with the simulated arousal of an experience. Error regions represent +/- 1 *S.E.M.* across the values for each of 97 virtual subjects.

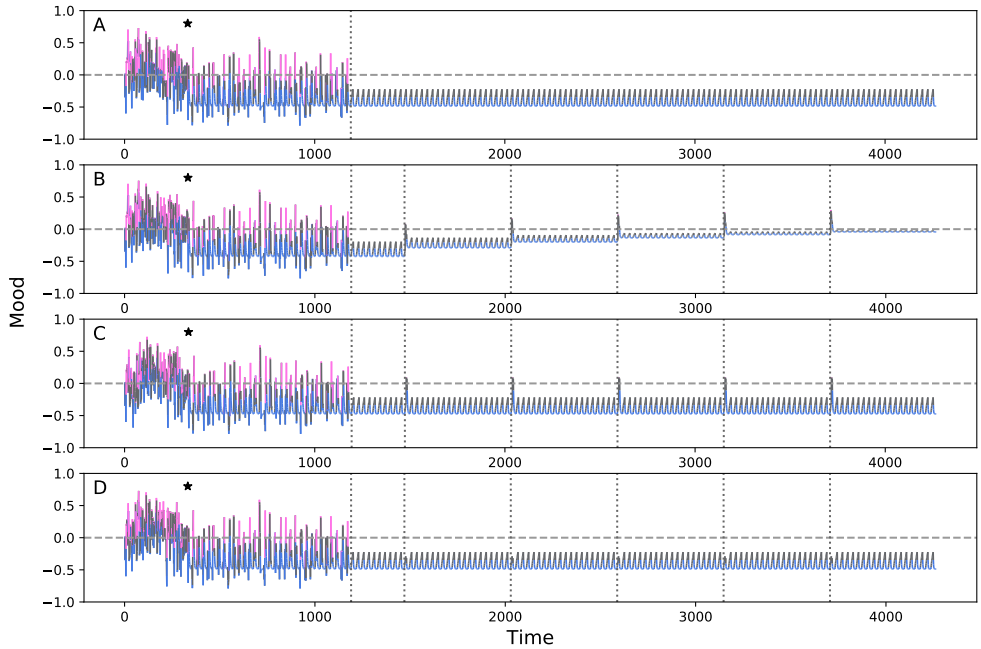

Figure 14. Simulating the effects of trauma and imaginal exposure therapy on intrusive memories. Each panel illustrates the evolution of model-simulated mood across two periods: (1) A developmental period, in which a virtual subject experienced an even mixture of negative and positive life events (30% negative, 30% positive), with one high-arousal negative event (ϕ_{emot} = 50.0) at the location of the asterisk (*), followed by (2) A neutral period, in which a virtual subject experienced solely unique, neutral events (100% neutral). In panel A, the neutral period consisted solely of new, neutral events with no intervention (Baseline). In panel B, the neutral period simulated 5 sessions of imaginal exposure therapy: a less-negative context was evoked by introducing a positive event every 20 lists, this time followed immediately by a re-presentation of the trauma-event as an encoding event (Full treatment). In panel C, the neutral period introduced 5 positive events every 20 lists, marked by vertical dotted lines (Positive-Context Only). In panel D, the neutral period reintroduced the high-arousal negative event 5 times, every 20 lists, marked by vertical dotted lines, without any change in emotional context prior to reencoding (Reencoding Only). The height on the graph represents the level of model-simulated mood (minimum of -1.0, maximum of 1.0). The variability of model-simulated mood in the neutral period reflects the degree of negative emotion evoked by each memory intrusion. The color on the graph represents the emotional valence of the encoded or retrieved event that evoked that level of mood (pink = positive, blue = negative, gray = neutral).

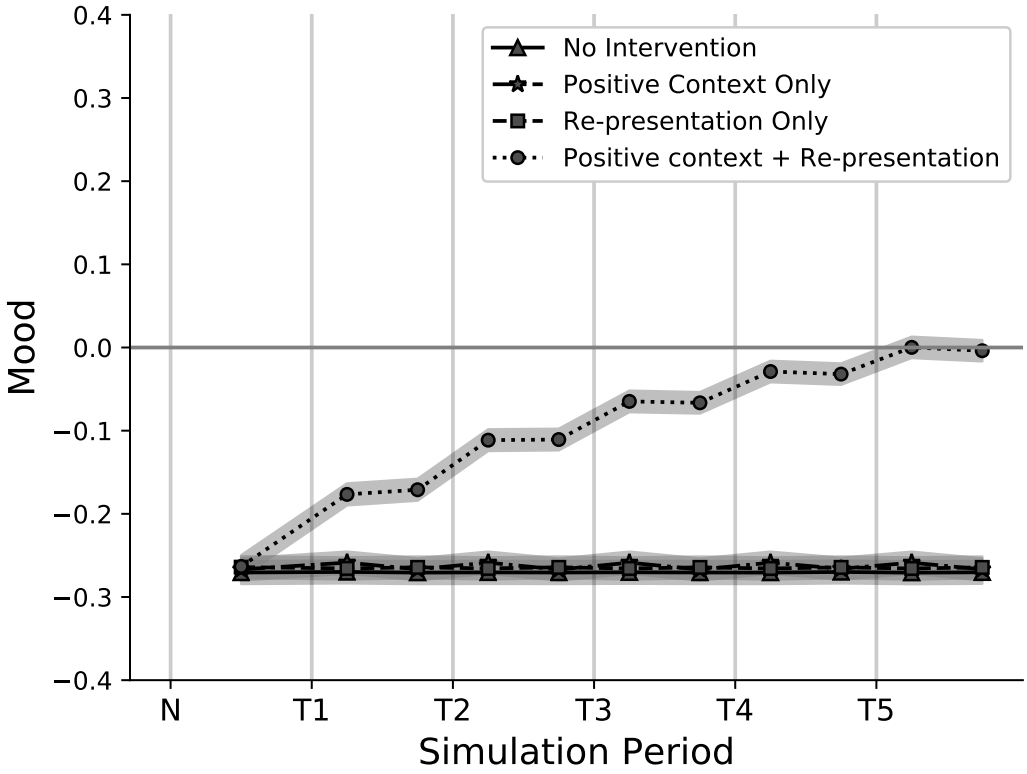

Figure 15. Aggregated results for the simulation of trauma exposure and imaginal exposure therapy. This figure presents the model-predicted patterns of mood for each of four conditions, aggregated across the results for all virtual subjects (i.e., parameter sets). Each virtual subject experienced a developmental period, consisting of an even mixture of negative and positive life events (30% negative, 30% positive), with one high-arousal negative event (ϕ_{emot} = 50.0), and (2) A neutral period, which consisted solely of unique, neutral events (100% neutral). In Condition 1 (triangle markers), a baseline condition, the neutral period consists solely of unique, neutral events. In Condition 2 (star markers), the neutral period additionally introduces 5 positive events every 20 lists. In Condition 3 (square markers), the neutral period instead introduces 5 re-encodings of the traumatic memory every 20 lists, with no changes to the surrounding emotional context. In Condition 4 (circle markers), the neutral period simulates 5 sessions of imaginal exposure therapy: less-negative context is again evoked by introducing a positive event every 20 lists, this time followed by a re-presentation of the traumatic event for re-encoding. The beginning and end of each simulated treatment session are marked by vertical lines. Between these lines, the first data point represents the mean level of mood present during the first half of the session, whereas the second data point represents the mean level of mood present during the second half of the session. N = The neutral period after the traumatic event has occurred. T1-T5 = each of the five timepoints at which a virtual subject receives the given intervention for that condition.