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Dissociation of immediate and delayed effects of emotional arousal on episodic memory



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ABSTRACT

Emotionally arousing events are usually better remembered than neutral ones. This phenomenon is in humans mostly studied by presenting mixed lists of neutral and emotional items. An emotional enhancement of memory is observed in these studies often already immediately after encoding and increases with longer delays and consolidation. A large body of animal research showed that the more efficient consolidation of emotionally arousing events is based on an activation of the central noradrenergic system and the amygdala (Modulation Hypothesis; Roozendaal & McGaugh, 2011). The immediately superior recognition of emotional items is attributed primarily to their attraction of attention during encoding which is also thought to be based on the amygdala and the central noradrenergic system. To investigate whether the amygdala and noradrenergic system support memory encoding and consolidation via shared neural substrates and processes a large sample of participants (n = 690) encoded neutral and arousing pictures. Their memory was tested immediately and after a consolidation delay. In addition, they were genotyped in two relevant polymorphisms (α_{2B} -adrenergic receptor and serotonin transporter). Memory for negative and positive emotional pictures was enhanced at both time points where these enhancements were correlated (immediate r = 0.60 and delayed test r = 0.46). Critically, the effects of emotional arousal on encoding and consolidation correlated only very low (negative r = 0.14 and positive r = 0.03 pictures) suggesting partly distinct underlying processes consistent with a functional heterogeneity of the central noradrenergic system. No effect of genotype on either effect was observed.

1. Introduction

1.1. Enhanced consolidation of emotionally arousing events

Emotionally arousing events are usually remembered better than neutral ones, a phenomenon called the emotional enhancement of memory (EEM). A large body of animal data have shown that the EEM is caused by a rise in peripheral stress hormone levels induced by an emotionally arousing event which activates the central noradrenergic (NOR) system, based in the locus coeruleus (LC) via ascending fibers (Modulation Hypothesis; McIntyre, McGaugh, & Williams, 2012). The LC projects to nearly all brain areas including the basolateral amygdala (BLA) which in turn modulates memory formation in the hippocampus. Both tonic and phasic activations of the BLA result in an EEM; for example, a brief electrical stimulation of the BLA also produces a stimulus-specific EEM, observed in the altered exploration of neutral objects that preceded the BLA stimulation (Bass, Nizam, Partain, Wang, & Manns, 2014; Bass, Partain, & Manns, 2012). Critically, the EEM that results from an increase in stress hormone levels and BLA activations is not observed immediately but only after a consolidation delay – consistent with the *Emotional Synaptic Tagging Hypothesis* (Bergado, Lucas, & Richter-Levin, 2011; McReynolds & McIntyre, 2012).

1.2. Studies in humans on the emotional enhancement of memories

The majority of studies on the EEM in humans, in particular nearly all fMRI experiments, investigate the effect of emotional arousal on memory formation by presenting mixed lists of emotional and neutral items. Better memory for emotional items is thought to be a laboratory measure of the EEM. At the neural level the EEM is associated with greater activity in the amygdala, hippocampus, and parahippocampus, in addition to visual, prefrontal, and parietal areas (Dolcos, Denkova, & Dolcos, 2012; LaBar & Cabeza, 2006; Murty, Ritchey, Adcock, & LaBar, 2010). Thus, the behavioral and neural results appear similar to what has been described in the animal literature on the EEM.

Yet there are critical differences between human fMRI studies of the EEM and animal studies. The rapid stimulus-specific EEM in fMRI-studies is comparable to stimulus-specific EEM elicited by electrical BLA

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stimulation or by a direct NOR infusions into the BLA (shown to enhances memory for previously-explored objects, Barsegyan, McGaugh, & Roozendaal, 2014; Bass et al., 2012), but it cannot be caused by a relatively slow, sluggish systemic increase in stress hormone levels, which characterizes the majority of animal research on EEM. Human fMRI studies also contrast with stimulus-specific animal experiments. While in these experiments the target stimuli are neutral objects, human fMRI studies compare neutral stimuli to stimuli that themselves evoke emotional arousal as a result of their semantic evaluation, and are hence already differentially encoded. Most importantly, in these experiments an EEM is often observed also when memory is tested almost immediately after encoding (Murty et al., 2010; Talmi & McGarry, 2012), an effect that cannot be caused by more efficient consolidation (Talmi, 2013).

1.3. Immediately enhanced emotional memories

Immediate EEM has been explained in cognitive psychology by three characteristics of emotional stimuli. In particular, emotional stimuli are semantically more closely related, they are more distinct and attract more selective attention (Sommer, Glascher, Moritz, & Buchel, 2008; Talmi, 2013). Memory undoubtedly benefits from the attention emotionally-arousing stimuli capture during encoding. Enhanced attention to such stimuli, as reflected, for instance, in more fixations, results in deeper processing during encoding and better immediate memory (Bradley, Houbova, Miccoli, Costa, & Lang, 2011; Kang, Wang, Surina, & Lü, 2014; Miendlarzewska, van Elswijk, Cannistraci, & van Ee, 2013; Sharot & Phelps, 2004; Talmi, Anderson, Riggs, Caplan, & Moscovitch, 2008). Moreover, enhanced attention to emotional stimuli during encoding is also consistent with the more frequent experience of recollection during the recognition of emotional items (Kensinger, Clarke, & Corkin, 2003; Kensinger & Corkin, 2003). Critically, the enhanced immediate recollection of emotional items correlates with amygdala activity during encoding (Kensinger, Addis, & Atapattu, 2011) implicating an encoding related effect that is independent from the more liberal response bias which is induced by their higher semantic relatedness and influences the recognition of emotional stimuli (Dougal & Rotello, 2007). While increased attention can increase episodic memory in recognition as well as in free recall tests, the other characteristics of emotional stimuli known to increase immediate memory, i.e. their higher semantic relatedness and distinctiveness, might primarily enhance recall but not recognition accuracy. Taken together, the EEM observed in recognition tests after a study-test delay too short for consolidation probably mainly reflects increased attention to emotionally-arousing stimuli during encoding (Hamann, 2001; Todd, Palombo, Levine, & Anderson, 2011). Interestingly, studies that elevated arousal only after initial processing of neutral stimuli and observed no immediate but only enhanced delayed memory have suggested a partial independence of arousal-induced processes on encoding and consolidation (Bass et al., 2012; Inman et al., 2017; Schwarze, Bingel, & Sommer, 2012).

1.4. Aim of the current study: do the effects of emotional arousal on consolidation and immediate memory rely on the same neural substrate?

The current study aimed to further characterize the relationship between the effect of emotional arousal on immediate and delayed recognition. In particular, we aimed to find out whether both effects rely on the same neural substrate. The current experimental approach follows the rationale that if both effects stem from the same underlying neural circuits, their magnitudes should be correlated across participants. Therefore, we administered an emotional memory paradigm with immediate and delayed recognition tests to a large sample of participants and correlated the immediate and delayed EEM. In order to be maximally sensitive to differences in the effects of arousal the EEMs were assessed not only as differences in recognition accuracy (corrected hit rate and d-prime) but also in terms of response bias, discriminability (bias-corrected accuracy), and the separate contributions of arousal to familiarity and recollection (White, Kapucu, Bruno, Rotello, & Ratcliff, 2014; Yonelinas, 1994). In order to illuminate potential reasons for differences in immediate and delayed EEMs across participants they were characterized by several neuropsychological tests and relevant questionnaires.

In addition, volunteers were genotyped in two polymorphisms in the genes coding for the α_{2B} -noradrenergic receptor and the serotonin transporter in order to associate the immediate and delayed EEM with the different genotypes. The first polymorphism reduces the α_{2B} -noradrenergic receptor functionality and is in a complete linkage disequilibrium with a polymorphism that results in less transcription of the α_{2B} -noradrenergic receptor (Crassous et al., 2010; Nguyen, Kassimatis, & Lymperopoulos, 2011; Salim, Desai, Taneja, & Eikenburg, 2009; Small, Brown, Forbes, & Liggett, 2001). Carriers of the allele are expected therefore to have fewer and less functional α_{2B} -noradrenergic receptors. This variant has been associated with the greater vividness of processing emotional stimuli, the attraction of selective attention and the immediate EEM in free recall (de Ouervain et al., 2007; Rasch et al., 2009; Todd et al., 2013, 2015). The polymorphism in the gene coding for the serotonin transporter has been associated with attentional bias to negative stimuli and greater amygdala reactivity (Bevilacqua & Goldman, 2011; Canli, Ferri, & Duman, 2009; Munafò, Brown, & Hariri, 2008). The rationale of this complementary experimental approach was that an association of both the immediate and delayed EEM with these polymorphisms would suggest shared underlying neural substrates.

2. Methods

2.1. Participants

The present emotional memory data were taken from a sample of 690 young healthy adults, who took part in a larger test and questionnaire battery to phenotype participants with respect to a variety of cognitive and affective characteristics. 44 participants were excluded due to incomplete data or below chance performance, resulting in a sample of n = 646 (464 females, age range 18–36 y, mean 24.4 y).

2.2. Emotional memory paradigm

Stimulus material were 240 pictures of different valence and arousal levels (80 negative, 80 positive, 80 neutral) taken from the IAPS and the internet. An independent sample (n = 52) rated valence and arousal of all pictures using respective 9-step SAM scales (Fig. 1A; Bradley & Lang, 1994). Means of arousal and valence between negative (valence: 2.05; arousal: 6.99), neutral (6.05; 3.11) and positive pictures (7.75; 3.51) were different at p < 0.0001 (except positive arousal greater than neutral p < 0.01). Note that the average arousal and valence difference between emotional and neutral items were less pronounced for positive than for negative pictures. The pictures were matched between emotional categories so that each category contained an equal number of pictures with a similar content (e.g. two interacting humans, an animal, food). Within each category pictures with similar content were for each participant individually pseudorandomly assigned to target and lures.

Participants incidentally encoded the mixed list of emotionally arousing and neutral pictures (40 negative, 40 positive and 40 neutral) by rating on a 6 point Likert scale whether the picture would be suitable for a news magazine. Participants sat within normal distance of a 24'' monitor and responded via keyboard arrow keys to the task presented with Presentation software (Neurobehavioral Systems). Color photographs of size 375×280 pixel were presented at the center of the screen on a black background for 1 s, followed by a 2-s rating interval and a 3 s active baseline task (three runs of a left/right button press in response to an arrow). 10 min later, filled with a divided attention task

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