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Research Focus

Make mild moments memorable: add a little arousal

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In a recent paper Anderson and colleagues reported that emotionally arousing stimuli enhance long-term memory of immediately preceding neutral stimuli. The findings fit well with the perseveration-consolidation hypothesis and with extensive evidence from both human and animal studies indicating that arousal-induced modulation of memory is mediated by β-noradrenergic activation of the amygdala.

As we know from our own experiences and the findings of many studies, emotionally arousing experiences are well-remembered [1]. The selectivity that arousal creates is generally beneficial, as emotionally arousing events in our lives are worth remembering so that they can be savored and/or instructive. Research investigating why emotional arousal enhances memory has focused on three possible influences. First, emotional arousal might increase the attention given to experiences during their encoding [2]. Second, memories of arousing experiences might be strengthened by subsequent rehearsing [3]. The third influence was suggested by Müller and Pilzecker's hypothesis [4] that neural processes initiated by an experience perseverate and consolidate over time: emotional arousal could activate neurobiological processes that modulate the consolidation of memories of recent experiences. The recent finding of Anderson *et al.* [5] that emotionally arousing stimuli enhance memory of previously presented neutral stimuli offers novel and compelling evidence to support Müller and Pilzecker's 'perseveration-consolidation' hypothesis.

Stress, brain activation and lasting memory

Considerable evidence from both animal and human experiments also supports the perseveration-consolidation hypothesis. The adrenal stress hormones, adrenaline and corticosterone (cortisol in humans), normally released by emotional arousal enhance long-term memory when administered to rats or mice shortly after a training experience [6]. These stress hormones influence noradrenergic activation within the amygdala, and amygdala activity in turn modulates memory processing in other brain regions, including (but not restricted to) the hippocampus [7–9]. Human studies have also reported that memory is enhanced by administering adrenaline shortly after learning or by inducing stressful conditions that release adrenaline [10,11]. Drugs that prevent the actions of adrenaline (β-adrenergic antagonists) block the memory-enhancement induced by emotional arousal [6,10,11] (Figure 1).

Further evidence comes from human brain imaging studies (PET and fMRI) which have found that stimuli that induce emotional arousal activate the amygdala (and hippocampal region) and that the degree of amygdala activation during encoding correlates highly with subsequent long-term memory of the stimuli [12–14]. There are, however, limitations of such findings that constrain their contribution to understanding the influence of emotional arousal on memory. Because the imaging studies examined amygdala activity induced during encoding, the activity might have reflected increased attentional processing engaged by examining the stimuli. Second, because the studies investigated only the memories of the stimuli used to induce the emotional arousal they did not ask whether emotionally arousing stimuli could also have enhanced memory of less emotional stimuli experienced before the arousing stimuli. That question needs to be asked in order to exclude stimulus encoding processes as a basis for the enhancing effects of emotional arousal on subsequent remembrance, and to determine whether such arousal influences consolidation of recent experiences.

Preserving the uneventful recent past

The study by Anderson *et al.* [5] asked that question. In a first experiment, pictures were used to induce emotional arousal – both positive and negative – and pictures of human faces and houses obtained from other sources were used as neutral stimuli. In a series of presentations in a single session, neutral stimuli were presented either 4 or 9 s before arousing (or neutral) stimuli. The subjects rated the intensity of emotional arousal induced by each emotional picture and the memorability of the neutral pictures. A week later they were shown a series of faces, houses and scenes (including foils) and asked whether the images were remembered, familiar or new.

Consistent with the findings of many previous studies, memory for the emotional pictures varied directly with their emotional ratings. More importantly, memory of neutral pictures preceding the emotional pictures by 4 s also varied directly with the emotional intensity of the emotional pictures. No effect was seen with the longer delay interval of 9 s. For both the emotionally arousing pictures and the neutral pictures followed by arousing pictures, specific recollection of the pictures, but not judgment of familiarity, was directly related to degree of arousal of the emotional pictures. The findings of a second

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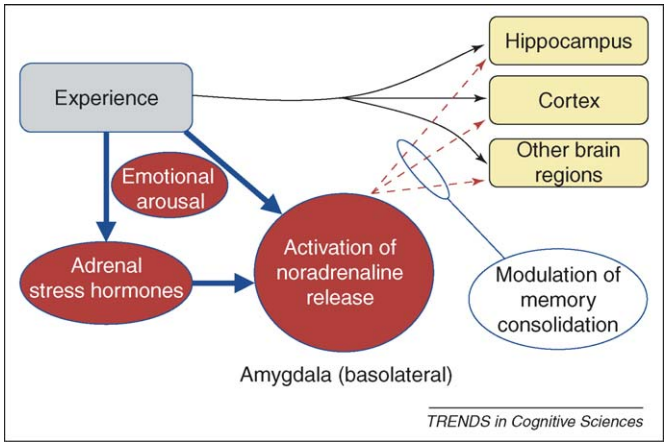

Figure 1. Schematic representation of modulation of memory consolidation by emotional arousal-induced release of adrenal stress hormones and noradrenergic activation of the amygdala. Emotional arousal activates the release of noradrenaline in the basolateral amygdala as well as the release of adrenal stress hormones. The stress hormones then provide increased and sustained noradrenergic activation in the amygdala. The amygdala activation modulates memory consolidation via projections to other brain systems processing memory.

experiment using the same general procedures indicated that, although increasing the distinctiveness of pictures increased their recollection, distinctiveness per se did not increase the recollection of neutral pictures that were presented before the distinctive pictures. Arousal was the crucial factor in enhancing memory for the neutral pictures. In summary, the findings of Anderson *et al*. [5] clearly support the conclusion that, 'Nondistinct stimuli may be endowed with enhanced recollective experience when arousal is manipulated after encoding has passed.' ([5], p. 1600).

The long and the short of it

The findings of Anderson *et al*. [5] might seem to fit well with those of animal and human studies reporting that post-learning administration of stress hormones normally released by emotional arousal enhances long-term memory [6,10]. However, as noted, the emotional pictures influenced memory of the preceding pictures only when they occurred within 4 s. By contrast, in the studies of the effects of post-learning administration of stress hormones the intervals between learning and treatment are typically no shorter than 30 s and, in animals given a single training trial, enhanced memory is readily obtained with treatment delays of several minutes (Figure 2). As Anderson *et al.* [5] pointed out, it is unlikely that adrenal stress hormones played a role in mediating the effects seen in their study simply because stress hormone release is probably too slow to influence amygdala functioning within the 4 s window of effectiveness. Also, as peripherally released stress hormones remain active for many minutes, they would have been influential during the presentation of neutral as well as emotional stimuli. Thus, such findings would seem to question an interpretation suggesting that the emotional picture memory-enhancement and stress-hormone induced memory enhancement have a common basis.

Emotionally arousing findings: β-adrenergic activation

Other findings, however, point to a possible common basis. As noted above, the findings of animal studies indicate that noradrenergic activation of the amygdala is necessary to enable stress-hormone-induced memory enhancement. Furthermore, when assessed during encoding, PET imaging of amygdala activity (assessed following many minutes of arousal) and event-related fMRI of amygdala activity induced by single items both predict long-term memory of the arousing stimuli [12–14]. And, importantly, β-adrenergic antagonists (e.g. propranolol) block the stress hormone modulation of memory consolidation in animals, as well as the increase in amygdala activity and enhanced retention induced by emotional stimuli obtained in fMRI studies [15,16]. Thus, β-adrenergic activation of the amygdala appears to be essential for the short-latency modulation induced by brief and mild emotional arousal such as that seen in the Anderson *et al.* [5] study, as well as the effects found in animal and human studies that have used longer intervals of time between learning and stress hormone administration.

The difference in the time scales of the effects of emotional arousal on memory of preceding events seen in the

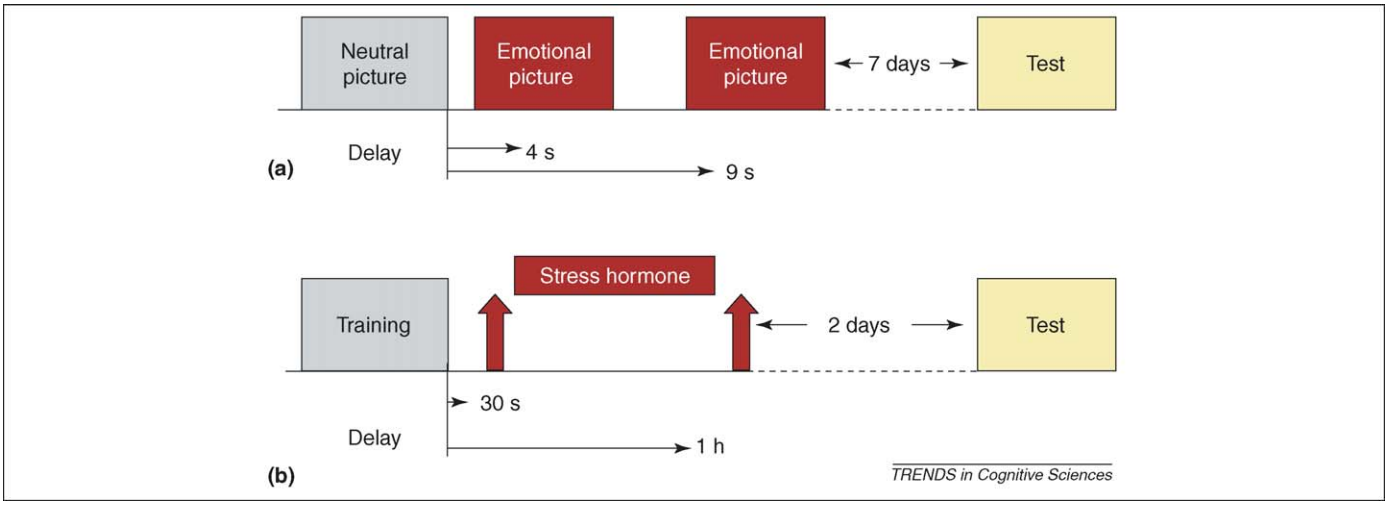

Figure 2. Experimental procedures of the Anderson *et al.* [5] study and a typical animal experiment investigating stress hormone effects on memory consolidation. In the Anderson *et al.* experiment **(a)** emotionally arousing pictures were presented either 4 s or 9 s after neutral pictures and memory was tested a week later. In typical animal studies **(b)**, stress hormones are administered either within a minute after a single training trial or at a delay of an hour (or longer) after the training and memory is tested 2 days later.

study by Anderson *et al.* [5] and those obtained in PET studies and experiments investigating the effects of stress hormones administered after learning may well reflect different degrees of emotional arousal. The degree of emotional arousal induced by training very significantly influences amygdala activity, as assessed by the release of noradrenaline within the amygdala and firing of amygdala neurons [17,18]. Thus, emotional stimuli that induce greater emotional arousal than those used by Anderson *et al.* [5] should modulate the memory of insignificant stimuli appearing at intervals longer than those used in their study. Such enhancement would be expected both because of the rapid increase amygdala activity induced by the emotional experience as well as the subsequent influence of stress hormones on amygdala activity mediated by β-adrenergic activation. Although it is possible that a sustained increase in emotional arousal during the encoding session may have enhanced memory of the neutral stimuli (as well as the emotional stimuli) presented throughout the session, the design of the study did not enable examination of this possibility. Subsequent research stimulated by the Anderson *et al.* [5] findings will no doubt shed more light on this emotionally arousing issue.

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Experiments on the emergence of human communication

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Children learn language from their parents and then use the acquired system throughout the rest of their life with little change. At least that is commonly assumed. But a recent paper by Galantucci adds to the growing evidence that adults (and children) are able to create and negotiate complex communication systems from scratch and relatively quickly, without a prior model. This raises questions of what cognitive mechanisms are implied in this joint construction of communication systems, and what the implications are for the origins of human language.

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Galantucci's recent paper on how human communication systems emerge [1] is remarkable in many ways. His ingenious experimental design allows the systematic collection of data on how humans invent and implicitly negotiate a shared communication system. The data confirm some earlier findings from studies of natural dialogue, such as the importance of alignment and innovation. They also show that differences in social intelligence can have a big impact on success in communication.

Lessons from the study of natural dialogue

Until recently, empirical data on whether and how humans can create a shared communication system was extremely rare. We essentially had to make do with unique 'natural'