# Dissociating Enhancing and Impairing Effects of Emotion on Cognition

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#### Abstract

Emotion is a "double-edged sword" that can either enhance or hinder various aspects of our cognition and behavior. The emotional charge of an event can increase attention to and memory for that event, whereas task-irrelevant emotional information may lead to increased distraction and impaired performance in ongoing cognitive tasks. These opposing effects of emotion can be identified at different levels, both within the same cognitive process and across different processes, and could also be identified at more general levels, such as in the case of the response to stress. The present review discusses emerging evidence regarding factors that influence opposite effects of emotion on cognition in healthy functioning, and how they may be linked to clinical conditions. These issues are important for understanding mechanisms of emotion-cognition interactions in healthy functioning and in emotional disturbances, where both of these effects are exacerbated and tend to co-occur. Overall, the present review highlights the need to consider the various factors that can influence enhancing or impairing effects of emotion on cognition, in studies investigating emotion-cognition interactions.

#### INTRODUCTION

Emotion is a "double-edged sword" that can either enhance or hinder various aspects of our cognition and behavior. The emotional charge of an event can lead to enhanced memory for that event, whereas task-irrelevant emotional information may lead to increased distraction and impaired cognitive performance. These opposing effects of emotion can be identified at different levels. For instance, the same emotionally arousing event can lead to opposite effects on different aspects *within* the same process (episodic memory—EM). Being accosted at gunpoint may increase memory for aspects that are *central* to the event (e.g., the color of the gun), while impairing memory for *peripheral* details (e.g., the way the aggressor was dressed or even details regarding his identity). Emotional information can also lead to opposing effects *across* 

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different cognitive processes: emotional distraction can impair ongoing cognitive processing, while also enhancing the long-term memory for the distracters themselves. For example, passing the scene of a tragic accident while driving may temporarily distract us from the main task, while also leading to better memory for that particular driving experience. Furthermore, in a larger context of the response to stress, emotional responses associated with optimal levels of stress (eustress) may increase performance (e.g., positive emotions associated with wedding preparations), whereas emotions associated with exposure to high levels of stress (e.g., overwhelming worry in the anticipation of a difficult exam), can impair performance. Clarification of these issues has relevance for understanding the mechanisms of emotion-cognition interactions in healthy functioning as well as in emotional disturbances, where these opposing effects of emotion are exacerbated and deleterious.

The present review discusses emerging evidence regarding opposing effects of emotion on cognition in healthy functioning. The first section discusses evidence from studies dissociating the enhancing and impairing effects of emotion *within* the same cognitive process, the second section discusses emerging evidence from studies investigating enhancing and impairing effects *across* different processes, and the third section presents evidence from studies examining the emotion's impact at a more *general* level, reflected in the response to stress. The review ends with concluding remarks and a brief discussion of open issues and future directions.

## CUTTING-EDGE RESEARCH

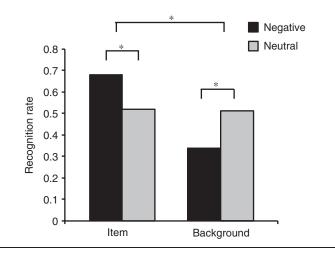
DISSOCIATING BETWEEN OPPOSING EFFECTS OF EMOTION WITHIN THE EPISODIC MEMORY (EM)

While there is strong evidence from both animal (McGaugh, 2004) and human research (Dolcos, LaBar, & Cabeza, 2006; Dolcos, Denkova, & Dolcos, 2012) that emotional events are overall better remembered than the neutral events, there is also evidence that not all aspects of an event benefit from such enhancement. The effects of emotion on EM in humans have been typically investigated using experimenter-generated stimuli, such as lists of words or sets of pictures, varying in emotional arousal and valence, which are encoded in laboratory settings and retrieved at different intervals following encoding (e.g., minutes, hours, and days). Such investigations have provided strong evidence that the memory-enhancing effect of emotion can be attributed to the involvement of the amygdala (AMY) and its interaction with memory-related medial temporal lobe (MTL) regions (hippocampus—HC and the associated entorhinal, perirhinal, and parahippocampal cortices). Moreover, it can also benefit from the engagement of brain regions associated with higher order cognitive processes (e.g., the prefrontal cortex, PFC and parietal cortex, PC) (Dolcos & Denkova, 2008; Dolcos *et al.*, 2012).

The enhancement of memory by emotion has been typically observed for isolated emotional items and their intrinsic properties, while memory for other extrinsic aspects and contextual details of the emotional event are not enhanced and can be even impaired (Kensinger, 2009; Mather, 2007). Enhancing versus impairing effects of emotion on EM have been identified in terms of central versus peripheral, high versus low priority, and item versus associations dichotomies, which will be discussed below.

The Central versus Peripheral Trade-Off in the Impact of Emotion on Memory. The observation that emotion enhances memory for central aspects, while impairing memory for peripheral details has been initially reported in the eyewitness memory literature, which has put forward the term "weapon focus effect", reflecting the tendency in crime witnesses to focus on the weapon, at the expense of other details of the event (Christianson, 1992; Loftus, Loftus, & Messo, 1987). More recent research investigating the impact of emotion on memory has referred to this phenomenon as the central versus peripheral trade-off, in which memory for central aspects of a stimulus is enhanced while memory for the peripheral details is reduced (Kensinger, 2009). This effect is typically investigated by presenting pictures of emotionally aversive objects against neutral backgrounds (e.g., a snake by a river) and pictures of neutral objects against neutral backgrounds (e.g., a chipmunk in a forest). Such investigations revealed better memory for emotional than for neutral objects, but worse memory for backgrounds of emotional objects than for backgrounds of neutral objects (Figure 1) (Kensinger, Garoff-Eaton, & Schacter, 2007a, 2007b; Waring, Payne, Schacter, & Kensinger, 2010). At the neural level, AMY has been involved only in memory-enhancing effects for aspects that are intrinsically linked to the emotional item itself, such as its physical appearance, but not for all aspects of an emotional event, such as its context in the case of source memory paradigms (Dougal, Phelps, & Davachi, 2007; Kensinger et al., 2007a, 2007b; Kensinger & Schacter, 2006).

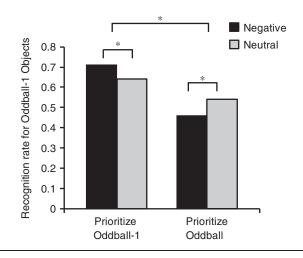
*The Role of Prioritization in the Impact of Emotion on Memory.* Complementary evidence suggests that opposing effects of emotion on memory can be related to prioritization processes, as emphasized in the so-called *ABC (Arousal-Biased Competition) Theory* (Mather & Sutherland, 2011). According to this model, emotional arousal enhances encoding of high priority information at the expense of low priority information (Mather & Sutherland, 2011). In a series of studies, Mather and colleagues showed that presentation



**Figure 1** Recognition accuracy for items and backgrounds revealing a central versus peripheral memory trade-off. While negative items were better remembered than neutral items, backgrounds previously presented with negative items were worse recognized than those presented with neutral items.\* Denotes significant differences. Adapted from Waring, Payne, Schacter & Kensinger (2010).

of emotional images can enhance memory for preceding neutral objects, when people prioritize these objects (prioritized preceding objects), but can impair memory for preceding neutral objects when people do not prioritize these objects (nonprioritized preceding objects) (Figure 2) (Lee, Itti, & Mather, 2012; Lee, Sakaki, Cheng, Velasco, & Mather, 2014; Sakaki, Fryer, & Mather, 2014). Of note, priority can be assigned by bottom-up salience (e.g., emotional) or by top-down (goal-relevant) relevance (Lee *et al.*, 2012; Sakaki *et al.*, 2014). At the neural level, evidence points to dissociable AMY involvement according to whether information is prioritized or not (Lee *et al.*, 2014). Importantly, the ABC model can be linked to accounts considering motivational factors to understand the impact of emotion on memory (Levine & Edelstein, 2009; Sander, Grandjean, & Scherer, 2005).

Unitization versus Complex Associations in the Impact of Emotion on Memory. Another potential explanation of the opposite effects of emotion on EM (Chiu, Dolcos, Gonsalves, & Cohen, 2013) can be linked to the dissociation between memory for isolated items and memory for relations among items (relational or associative memory) (Cohen *et al.*, 1999; Eichenbaum & Cohen, 2001). There is growing evidence from both animal and human memory research that different memory-related MTL regions can play differential roles in memory for item versus associations (e.g., memory for an object, such as a tennis racquet and memory for the association



**Figure 2** The effect of prioritization on memory performance in an oddball task. Negative compared to neutral images lead to better memory for the preceding neutral objects (Oddball-1) when participants prioritized those objects ('Prioritize Oddball-1' condition), but worse memory when they did not prioritize those objects ('Prioritize Oddball' condition). \*Denotes significant differences. Adapted from Sakaki, Fryer & Mather (2014).

between the object and its color, size, or context, such as the red racquet in a car trunk). Whereas the perirhinal cortex (PRC) is important for the encoding of individual items or objects from an experience, the HC is important for binding distinct item representations into memory (Davachi, Mitchell, & Wagner, 2003; Ranganath, Cohen, Dam, & D'Esposito, 2004; Tubridy & Davachi, 2011). Further evidence also revealed that the PRC may also contribute to some simpler forms of associative learning (Staresina & Davachi, 2010), based on unitization, which involves representation of the separate components as a single unit (Graf & Schacter, 1989). The unitization involves for instance assembling together different aspects of an object into a single representation (e.g., association between an object and its color, as in the example above-the red tennis racquet). Therefore memory for isolated items as well as memory for unitized items can be mediated by similar mechanisms, unlike memory representations involving more complex associations of different components of an event, as well as associations between temporally separate events, which rely on HC-dependent mechanisms (Ezzyat & Davachi, 2014). Considering such possible dissociations in the available evidence, Chiu et al. (2013) propose that emotion leads to memory enhancement of separate as well as unitized items, but it impairs more complex HC-dependent memory representations. However, this emerging possible dissociation has not been directly tested, empirically. One potential way of testing it would involve manipulation of the emotional valence (*negative vs. neutral*) of the objects (e.g., handgun vs. tennis racquet) and the association demands—i.e., *unitization*, involving "fusing" an object and its color into one single representation (such as the silver handgun) versus *complex associations*, involving spatial, situational, and temporal information (such as the handgun in the taxi cab, at the gas station, early in the morning).

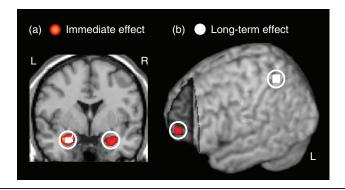
Overall, the opposing effects of emotion on EM have been identified in terms of central vs. peripheral, high vs. low priority, and item vs. associations dichotomies. Further research should consider such dissociations, particularly to better delineate the impact of emotion and the associated neural mechanisms, according to the type of associations, and to better understand its modulation by previous memory representations (Sakaki, Ycaza-Herrera, & Mather, 2014).

## DISSOCIATING OPPOSING EFFECTS OF EMOTION ACROSS COGNITIVE PROCESSES

Emerging evidence also suggests that opposite effects of emotion can be identified according to the distinction between *immediate* (impairing) and *long-term* (enhancing) effects of distracting emotional information, across different cognitive processes. Specifically, there is evidence that task-irrelevant emotional distracters can impair ongoing cognitive processing (e.g., perceptual), while also leading to enhancement of memory for the distracters themselves. These studies provide neural support for opposing effects of emotion in real-life situations, where task-irrelevant emotional information (the scene of a tragic accident while driving) may temporarily distract us from the main task (driving), while also leading to better memory for the distracting information (the crashed vehicles).

*Opposing Effects of Emotion on Perception versus Episodic Memory.* Evidence from a recent investigation suggests that emotional distraction can produce an immediate impairing effect on lower-level perceptual processing, while leading to long-term enhancement of memory for the distracters themselves (Shafer & Dolcos, 2012). Importantly, this study provides evidence that immediate/impairing and long-term/enhancing effects of emotional distraction are differentially influenced by the availability of processing resources. Specifically, while the strongest immediate impairment of emotional distraction occurred when processing load was low, and thus there were more processing resources available, the strongest enhancement of EM for the emotional distracters occurred when processing resources were least available (high load).

At the neural level, dissociation between these two opposing effects was observed in both basic AMY-HC mechanisms and in higher-order cognitive brain regions (medial PFC and PC). Specifically, the results point to possible hemispheric dissociation identified in the AMY-HC mechanisms, with bilateral engagement for the impairing effect and left-sided engagement for the memory enhancement by emotion (Figure 3). This finding can be linked to evidence suggesting greater engagement of the left AMY in more elaborative processing of the emotional stimuli, which also contributes to enhanced memory (Glascher & Adolphs, 2003; Phelps et al., 2001). Of note, these dissociations were observed within AMY-HC areas involved in both effects, but areas dissociating between the two opposing were also identified outside of the MTL. Specifically, medial PFC was associated only with the immediate/impairing effect on perception, and the superior PC was associated only with the long-term/enhancing effect on memory (Figure 3). Given that medial PFC is sensitive to emotional stimuli (Keightley et al., 2003; Scheuerecker et al., 2007) and superior PC is part of the goal-relevant attentional network (Corbetta & Shulman, 2002), the contribution of these regions to the opposing effects can be attributed to increased emotional and goal-relevant processing of the distracters, respectively.



**Figure 3** Dissociation between immediate and long-term effects of emotional distraction in basic emotional and higher-order cognitive brain regions. (a) A coronal view of the amygdala (AMY), illustrating bilateral activation linked to immediate/impairing effect of emotion (in red) and a left-lateralized pattern of activation linked to long-term/enhancing effect of emotion (in white); a subregion of the left AMY also predicted enhanced long-term impact, reflected in positive correlation with EM performance. (b) A tridimensional view of the brain illustrating a specific area of the medial prefrontal cortex (medial PFC) involved only in the immediate impairment of perception (in red) and an area of the superior parietal cortex (superior PC) involved only in the long-term enhancement of EM (in white). R = Right hemisphere, L = Left hemisphere. Adapted from Shafer and Dolcos (2012).

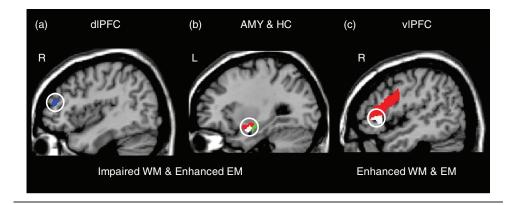
*Opposing Effects of Emotion on Working Memory versus Episodic Memory.* Emotional distraction can produce detrimental effects not only in tasks involving simpler cognitive processing but also in tasks involving more complex processing, such as working memory (WM) (Dolcos, Diaz-Granados, Wang, & McCarthy, 2008; Dolcos & McCarthy, 2006; Dolcos, Miller, Kragel, Jha, & McCarthy, 2007). Evidence from a recent study concomitantly investigating opposing effects of emotional distraction within the same participants revealed that emotional distracters presented during the delay interval between memoranda and probes in a WM task produced immediate impairing effects on WM performance, while being remembered better in a long-term memory task (Dolcos *et al.,* 2013). These findings provide evidence that emotional distracters divert processing resources from the main WM task and impair WM performance (Dolcos & McCarthy, 2006), while simultaneously initiating processing that leads to better memory for the distracters themselves (Dolcos *et al.,* 2013).

At the brain level, trials associated with both effects (impaired WM and enhanced EM) were associated with decreased activity in dorsolateral PFC, dlPFC (linked to immediate/detrimental impact on WM performance) versus increased response in MTL regions (linked to long-term/increased EM performance) (Figure 4). Of note, the same AMY region was linked to both of these opposing effects. Interestingly, trials associated with enhanced EM performance for emotional distracters that did not disrupt WM performance were linked to increased involvement of top-down PFC mechanisms (i.e., ventrolateral PFC, vlPFC). This suggests that enhanced EM performance for emotional distracters also benefits from the engagement of coping strategies engaged to deal with the presence of emotional distraction during the WM task (Dolcos *et al.*, 2013), possibly reflecting deeper encoding owing to more elaborative processing of the distracters (Dillon, Ritchey, Johnson, & LaBar, 2007).

Collectively, these findings demonstrate that the immediate impairing impact of emotional distraction on perception or WM and the long-term enhancing impact of emotion on EM are mediated by overlapping and dissociable neural systems, involving both bottom-up and top-down mechanisms (Dolcos & Denkova, 2014; Dolcos *et al.*, 2014, 2015).

#### Dissociating between Opposing Effects of Emotion in the Response to Stress

The impact of emotion on cognition can also be investigated in the context of the response to stress. Stressful experiences trigger the activation of the hypothalamus-pituitary-adrenal (HPA) axis (Joels & Baram, 2009; Lupien, Maheu, Tu, Fiocco, & Schramek, 2007), which affects the functioning of both brain regions involved in emotion processing (AMY) (Roozendaal, McEwen,



**Figure 4** Brain activity linked to working memory (WM) impairment and/or episodic memory (EM) enhancement by emotional distraction. (a) greater deactivation in the dorsolateral prefrontal cortex (dIPFC, blue blob) and (b) increased activity in both AMY (red blob) and HC (green blob) were linked to impaired WM but enhanced EM performance. (c) increased activity in the ventrolateral prefrontal cortex (vIPFC, red blob) was also linked to enhanced WM and EM. Interestingly, subregions of the AMY and vIPFC (white blobs) also had differential contribution to the impact of emotional distraction on WM, with AMY activity predicting impaired WM performance (showing negative correlation) and vIPFC predicting enhanced WM performance (showing positive correlation). R = Right hemisphere, L = Left hemisphere. Adapted from Dolcos *et al.* (2013).

& Chattarji, 2009) and regions involved in cognitive processing (HC and PFC) (Lupien, McEwen, Gunnar, & Heim, 2009; Roozendaal *et al.*, 2009). These regions are also among the brain areas most sensitive to stress hormones, due to high density of glucocorticoid receptors, and hence not surprisingly they are also the main brain structures involved in emotional learning and memory. There is a large body of evidence from animal and human research showing that stress can have both beneficial and deleterious effects on learning and memory (Lupien *et al.*, 2007; McEwen, 2007; Roozendaal *et al.*, 2009). As we will discuss below, the specific effects of stress on cognition have been linked to various factors, including the duration of the exposure (acute vs. chronic), the level of stress (high vs. low), and the level of stress controllability.

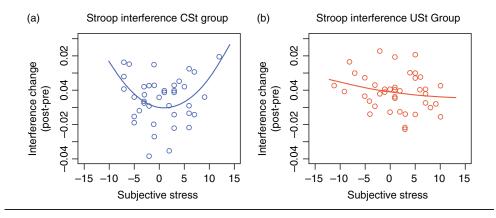
Acute versus Chronic Stress and High versus Optimal Level of Stress. Acute stress can lead to *transient* hyperarousal, which promotes threat detection and memory for emotional events through the involvement of the AMY and its connections with memory-related brain structures (McGaugh, 2000, 2004), and hence can have adaptive outcome (Dolcos, 2014; Henckens *et al.*, 2012). By contrast, repeated exposure to stress (chronic stress) can lead to a state of *continuous* physiological arousal and have deleterious effects on

HC (Roozendaal *et al.*, 2009) and PFC regions (Arnsten, 2000, 2009; Hains & Arnsten, 2008), hence leading to maladaptive outcomes. Converging evidence from human and animal studies suggests that the effect of acute stress on cognition, specifically on memory, follows an inverted U-shape function, with moderate level of stress leading to memory enhancement and too low or too high levels of stress leading to memory impairment (Diamond, Campbell, Park, Halonen, & Zoladz, 2007; Park *et al.*, 2006; Sandi & Pinelo-Nava, 2007). Interestingly, similar effects were also observed in the hippocampal function, in response to stress (Nadel & Jacobs, 1998). Noteworthy, highly intense acute emotional events and/or chronic exposure to stressful experiences can lead to mood and anxiety disorders, such as depression and posttraumatic stress disorder (PTSD).

*Presence versus Absence of Controllability in the Response to Stress.* Interestingly, recent evidence shows that the effects of stress on cognition are not only influenced by the duration of the exposure and level of stress, but also by other factors, such as subjective or objective *controllability* of the stress (Buetti & Lleras, 2012; Henderson, Snyder, Gupta, & Banich, 2012; Mereu & Lleras, 2013). Emerging evidence shows that the presence of controllability can improve cognitive performance, whereas situations extreme subjective experience of stress in uncontrollable situations can have detrimental effects on cognitive functioning. For instance, the study by Henderson *et al.* (2012) provides evidence that controllable stress that was experienced as moderately intense was linked to improved performance (reduced interference in a Stroop task), whereas exposure to uncontrollable stress or extreme subjective response to stress impairs performance (Figure 5).

At the neural level, the presence of controllability has been associated with the involvement of the ventromedial PFC (vmPFC), linked to the presence of control, which very likely inhibits stress responses in the AMY and leads to resilient behavior (Kerr, McLaren, Mathy, & Nitschke, 2012). Of note, decreased activity in vmPFC has also been observed during repeated stressful tasks in subjects who had experienced early-life stress (Wang, Paul, Stanton, Greeson, & Smoski, 2013), which could be linked to the feeling of (un)controllability in these subjects.

Overall, available evidence suggests that optimal and controllable levels of stress can have beneficial effects on cognition and behavior, whereas extreme and repeated stress impairs cognition and may lead to the development of affective disturbances. Neurally, the actual presence or subjective feeling of control over stressful situations engages PFC mechanisms that regulate emotional responses in the AMY.



**Figure 5** Stroop interference as a function of controllability and subjective stress. (a) in the group with controllable stress (CSt), moderate levels of subjective stress were related to improved Stroop performance (reduced interference), while low or high levels of subjective stress were related to impaired Stroop performance. (b) in the group with uncontrollable stress (USt), subjective stress was not related to Stroop performance. From Henderson, *et al.* 2012.

#### CONCLUSIONS AND KEY ISSUES FOR FUTURE RESEARCH

The overarching goal of the present review was to highlight emerging findings from studies investigating opposing effects of emotion on cognition. Available research provides evidence that the enhancing vs. impairing effects of emotions within the same cognitive process, such as EM, can be attributed to different accounts (central vs. peripheral trade-off, high vs. low prioritization of information processing, and item encoding vs. formation of complex association). Emerging research also provides evidence that the opposing effects across cognitive processes can be linked to dissociations between immediate/impairing versus long-term/enhancing effects, which are mediated by dissociable and common neural mechanisms, involving bottom-up and top-down processes. Finally, extant evidence regarding the impact of stress, shows that its effects on cognition have been linked to such factors as the duration of the exposure (acute vs. chronic), the level of stress (high vs. low), and the level of stress controllability.

Despite significant progress in clarifying the mechanisms underlying opposing effects of emotion, several issues still need clarification in future research. **First**, the opposing effects of emotion on cognition have been investigated mainly in laboratory settings, using typical laboratory *micro*events (e.g., emotional pictures), and hence the impact of emotion on real-life personal events (e.g., emotional autobiographical memories) remains unclear. **Second**, although the influence of the attentional resources on the impact of emotional distraction on lower-level perceptual processes has

been investigated, it is unknown how manipulation of attentional resources within higher-level cognitive processes influences the opposing effects of emotion. **Third**, concomitant investigations of opposing effects of emotion should also be considered in the case of affective disturbances, such as PTSD, where these effects are exacerbated, deleterious, and tend to co-occur. Related to the first point above, it is possible that uncontrollable recollection of long-term representations of traumatic events can act as powerful *internal* distracters, which can severely impair performance in current activities (Dolcos, 2013). Clarification of these issues is important for understanding mechanisms of emotion-cognition interactions both in healthy functioning and in emotional disturbances.

## REFERENCES

- Arnsten, A. F. (2000). Stress impairs prefrontal cortical function in rats and monkeys: Role of dopamine D1 and norepinephrine alpha-1 receptor mechanisms. *Progress in Brain Research*, *126*, 183–192.
- Arnsten, A. F. (2009). Stress signalling pathways that impair prefrontal cortex structure and function. *Nature Reviews Neuroscience*, 10(6), 410–422.
- Buetti, S., & Lleras, A. (2012). Perceiving control over aversive and fearful events can alter how we experience those events: An investigation of time perception in spider-fearful individuals. *Frontiers in Psychology*, *3*.
- Chiu, Y. C., Dolcos, F., Gonsalves, B. D., & Cohen, N. J. (2013). On opposing effects of emotion on contextual or relational memory. *Frontiers in Psychology*, 4, 103. doi:10.3389/fpsyg.2013.00103
- Christianson, S. A. (1992). Emotional stress and eyewitness memory: A critical review. *Psychological Bulletin*, 112(2), 284–309.
- Cohen, N. J., Ryan, J., Hunt, C., Romine, L., Wszalek, T., & Nash, C. (1999). Hippocampal system and declarative (relational) memory: Summarizing the data from functional neuroimaging studies. *Hippocampus*, 9(1), 83–98.
- Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience*, *3*(3), 201–215.
- Davachi, L., Mitchell, J. P., & Wagner, A. D. (2003). Multiple routes to memory: Distinct medial temporal lobe processes build item and source memories. *Proceedings* of the National Academy of Sciences of the United States of America, 100(4), 2157–2162.
- Diamond, D. M., Campbell, A. M., Park, C. R., Halonen, J., & Zoladz, P. R. (2007). The temporal dynamics model of emotional memory processing: A synthesis on the neurobiological basis of stress-induced amnesia, flashbulb and traumatic memories, and the Yerkes-Dodson law. *Neural Plasticity*, 2007, 33, 60803.
- Dillon, D. G., Ritchey, M., Johnson, B. D., & LaBar, K. S. (2007). Dissociable effects of conscious emotion regulation strategies on explicit and implicit memory. *Emotion*, 7(2), 354–365.
- Dolcos, F. (2013). Linking enhancing and impairing effects of emotion the case of PTSD. *Frontiers in Integrative Neuroscience*, 7, 26.

- Dolcos, F. (2014). The fast and the slow sides of Cortisol's effects on emotional interference and sustained attention. *Frontiers in Neuroscience*, *8*, 268. doi:10.3389/fnins.2014.00268
- Dolcos, F., & Denkova, E. (2008). Neural correlates of encoding emotional memories: A review of functional neuroimaging evidence. *Cell Science Reviews*, 5(2), 78–122.
- Dolcos, F., & Denkova, E. (2014). Current emotion research in cognitive neuroscience: Linking enhancing and impairing effects of emotion on cognition. *Emotion Review*, *6*, 362–375.
- Dolcos, F., Denkova, E., & Dolcos, S. (2012). Neural correlates of emotional memories: A review of evidence from brain imaging studies. *Psychologia*, 55, 80–111.
- Dolcos, F., Diaz-Granados, P., Wang, L., & McCarthy, G. (2008). Opposing influences of emotional and non-emotional distracters upon sustained prefrontal cortex activity during a delayed-response working memory task. *Neuropsychologia*, 46(1), 326–335.
- Dolcos, F., Iordan, A., Kragel, J., Stokes, J., Campbell, R., McCarthy, G., & Cabeza, R. (2013). Neural correlates of opposing effects of emotional distraction on working memory and episodic memory: An event related fMRI investigation. *Frontiers in Psychology*, 4.
- Dolcos, F., LaBar, K. S., & Cabeza, R. (2006). The memory-enhancing effect of emotion: Functional neuroimaging evidence. In B. Uttl, N. Ohta & A. L. Siegenthaler (Eds.), *Memory and emotion: Interdisciplinary perspectives* (pp. 107–133). Malden, MA: Blackwell Publishing.
- Dolcos, F., & McCarthy, G. (2006). Brain systems mediating cognitive interference by emotional distraction. *Journal of Neuroscience*, 26(7), 2072–2079.
- Dolcos, F., Miller, B., Kragel, P., Jha, A., & McCarthy, G. (2007). Regional brain differences in the effect of distraction during the delay interval of a working memory task. *Brain Research*, 1152, 171–181.
- Dolcos, F., Wang, L., & Mather, M. (2014). Current research and emerging directions in emotion-cognition interactions. *Frontiers in Integrative Neuroscience*, 8, 83. doi:10.3389/fnint.2014.00083
- Dolcos, F., Wang, L., & Mather, M. (Eds.) (2015). Current Research and Emerging Directions in Emotion-Cognition Interactions. Frontiers E-Book Series, *Frontiers Media SA*. (p. 740, ISBN: 978-2-88919-4384), doi:10.3389/978-2-88919-438-4
- Dougal, S., Phelps, E. A., & Davachi, L. (2007). The role of medial temporal lobe in item recognition and source recollection of emotional stimuli. *Cognitive, Affective,* & *Behavioral Neuroscience,* 7(3), 233–242.
- Eichenbaum, H., & Cohen, N. J. (2001). From conditioning to conscious recollection: Memory systems of the brain. New York, NY: Oxford University Press.
- Ezzyat, Y., & Davachi, L. (2014). Similarity breeds proximity: Pattern similarity within and across contexts is related to later mnemonic judgments of temporal proximity. *Neuron*, *81*(5), 1179–1189.
- Glascher, J., & Adolphs, R. (2003). Processing of the arousal of subliminal and supraliminal emotional stimuli by the human amygdala. *Journal of Neuroscience*, 23(32), 10274–10282.

- Graf, P., & Schacter, D. L. (1989). Unitization and grouping mediate dissociations in memory for new associations. *Journal of Experimental Psychology Learning*, 15, 930–940.
- Hains, A. B., & Arnsten, A. F. (2008). Molecular mechanisms of stress-induced prefrontal cortical impairment: Implications for mental illness. *Learning & Memory*, 15(8), 551–564.
- Henckens, M. J., van Wingen, G. A., Joëls, M., & Fernández, G. (2012). Timedependent effects of cortisol on selective attention and emotional interference: a functional MRI study. *Frontiers in Integrative Neuroscience*, 6, 66. doi:10.3389/ fnint.2012.00066
- Henderson, R. K., Snyder, H. R., Gupta, T., & Banich, M. T. (2012). When does stress help or harm? The effects of stress controllability and subjective stress response on Stroop performance. *Frontiers in Psychology*, *3*, 179.
- Joels, M., & Baram, T. Z. (2009). The neuro-symphony of stress. Nature Reviews Neuroscience, 10(6), 459–466.
- Keightley, M. L., Winocur, G., Graham, S. J., Mayberg, H. S., Hevenor, S. J., & Grady, C. L. (2003). An fMRI study investigating cognitive modulation of brain regions associated with emotional processing of visual stimuli. *Neuropsychologia*, 41(5), 585–596.
- Kensinger, E. A. (2009). Remembering the details: Effects of emotion. *Emotion Review*, *1*(2), 99–113.
- Kensinger, E. A., Garoff-Eaton, R. J., & Schacter, D. L. (2007a). Effects of emotion on memory specificity: Memory trade-offs elicited by negative visually arousing stimuli. *Journal of Memory and Language*, 56, 575–591.
- Kensinger, E. A., Garoff-Eaton, R. J., & Schacter, D. L. (2007b). How negative emotion enhances the visual specificity of a memory. *Journal of Cognitive Neuroscience*, 19(11), 1872–1887.
- Kensinger, E. A., & Schacter, D. L. (2006). Amygdala activity is associated with the successful encoding of item, but not source, information for positive and negative stimuli. *Journal of Neuroscience*, *26*(9), 2564–2570.
- Kerr, D. L., McLaren, D. G., Mathy, R. M., & Nitschke, J. B. (2012). Controllability modulates the anticipatory response in the human ventromedial prefrontal cortex. *Frontiers in Psychology*, *3*, 557.
- Lee, T. H., Itti, L., & Mather, M. (2012). Evidence for arousal-biased competition in perceptual learning. *Frontiers in Psychology*, *3*, 241.
- Lee, T. H., Sakaki, M., Cheng, R., Velasco, R., & Mather, M. (2014). *Emotional arousal amplifies the effects of biased competition in the brain. Social Cognitive & Affective Neu roscience.*
- Levine, L. J., & Edelstein, R. S. (2009). Emotion and memory narrowing: A review and goal-relevance approach. *Cognition & Emotion*, 23(5), 833–875.
- Loftus, E. F., Loftus, G. R., & Messo, J. (1987). Some facts about "weapon focus". Law and Human Behavior, 11, 55–62.
- Lupien, S. J., Maheu, F., Tu, M., Fiocco, A., & Schramek, T. E. (2007). The effects of stress and stress hormones on human cognition: Implications for the field of brain and cognition. *Brain and Cognition*, 65(3), 209–237.

- Lupien, S. J., McEwen, B. S., Gunnar, M. R., & Heim, C. (2009). Effects of stress throughout the lifespan on the brain, behaviour and cognition. *Nature Reviews Neuroscience*, 10(6), 434–445.
- Mather, M. (2007). Emotional arousal and memory binding: An object-based framework. *Perspectives on Psychological Science*, *2*, 33–52.
- Mather, M., & Sutherland, M. R. (2011). Arousal-biased competition in perception and memory. *Perspectives on Psychological Science*, 6(2), 114–133.
- McEwen, B. S. (2007). Physiology and neurobiology of stress and adaptation: Central role of the brain. *Physiological Reviews*, *87*(3), 873–904.
- McGaugh, J. L. (2000). Memory-a century of consolidation. *Science*, 287(5451), 248–251.
- McGaugh, J. L. (2004). The amygdala modulates the consolidation of memories of emotionally arousing experiences. *Annual Review of Neuroscience*, 27, 1–28.
- Mereu, S., & Lleras, A. (2013). Feelings of control restore distorted time perception of emotionally charged events. *Consciousness and Cognition*, 22(1), 306–314.
- Nadel, L., & Jacobs, W. J. (1998). Traumatic memory is special. Current Directions in Psychological Science, 7, 154–157.
- Park, C. R., Campbell, A. M., Woodson, J. C., Smith, T. P., Fleshner, M., & Diamond, D. M. (2006). Permissive influence of stress in the expression of a U-shaped relationship between serum corticosterone levels and spatial memory errors in rats. *Dose Response*, 4(1), 55–74.
- Phelps, E. A., O'Connor, K. J., Gatenby, J. C., Gore, J. C., Grillon, C., & Davis, M. (2001). Activation of the left amygdala to a cognitive representation of fear. *Nature Neuroscience*, 4(4), 437–441.
- Ranganath, C., Cohen, M. X., Dam, C., & D'Esposito, M. (2004). Inferior temporal, prefrontal, and hippocampal contributions to visual working memory maintenance and associative memory retrieval. *Journal of Neuroscience*, 24(16), 3917–3925.
- Roozendaal, B., McEwen, B. S., & Chattarji, S. (2009). Stress, memory and the amygdala. *Nature Reviews Neuroscience*, 10(6), 423–433.
- Sakaki, M., Fryer, K., & Mather, M. (2014). Emotion strengthens high-priority memory traces but weakens low-priority memory traces. *Psychological Science*, 25(2), 387–395.
- Sakaki, M., Ycaza-Herrera, A. E., & Mather, M. (2014). Association learning for emotional harbinger cues: When do previous emotional associations impair and when do they facilitate subsequent learning of new associations? *Emotion*, 14(1), 115–129.
- Sander, D., Grandjean, D., & Scherer, K. R. (2005). A systems approach to appraisal mechanisms in emotion. *Neural Networks*, *18*(4), 317–352.
- Sandi, C., & Pinelo-Nava, M. T. (2007). Stress and memory: Behavioral effects and neurobiological mechanisms. *Neural Plasticity*, 2007, 78970.
- Scheuerecker, J., Frodl, T., Koutsouleris, N., Zetzsche, T., Wiesmann, M., Kleemann, A. M., ..., Meisenzahl, E. M. (2007). Cerebral differences in explicit and implicit emotional processing—an fMRI study. *Neuropsychobiology*, 56(1), 32–39.
- Shafer, A. T., & Dolcos, F. (2012). Neural correlates of opposing effects of emotional distraction on perception and episodic memory: An event-related fMRI investigation. *Frontiers in Integrative Neuroscience*, 6, 70.

- Staresina, B. P., & Davachi, L. (2010). Object unitization and associative memory formation are supported by distinct brain regions. *Journal of Neuroscience*, 30(29), 9890–9897.
- Tubridy, S., & Davachi, L. (2011). Medial temporal lobe contributions to episodic sequence encoding. *Cerebral Cortex*, 21(2), 272–280.
- Wang, L., Paul, N., Stanton, S. J., Greeson, J. M., & Smoski, M. (2013). Loss of sustained activity in the ventromedial prefrontal cortex in response to repeated stress in individuals with early-life emotional abuse: Implications for depression vulnerability. *Frontiers in Psychology*, 4, –320.
- Waring, J. D., Payne, J. D., Schacter, D. L., & Kensinger, E. A. (2010). Impact of individual differences upon emotion-induced memory trade-offs. *Cognition & Emotion*, 24(1), 150–167.

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Florin Dolcos, PhD., is a faculty member in the Psychology Department, the Neuroscience Program, and the Beckman Institute for Advanced Science and Technology at the University of Illinois Urbana-Champaign, where he directs the Social, Cognitive, Personality, and Emotional (SCoPE) Neuroscience Laboratory. His research investigates the neural mechanisms of emotion-cognition interactions in healthy and clinical groups. Dr. Dolcos has been published in a number of high impact journals, including Neuron, Proceedings of the National Academy of Sciences, American Journal of Psychiatry, Journal of Neuroscience, Journal of Cognitive Neuroscience, Psychological Science, Emotion, Social Cognitive, and Affective Neuroscience, NeuroImage, Neurobiology of Aging, Neuroscience & Biobehavioral Reviews, and Cerebral Cortex. Professor Dolcos joined the University of Illinois after an initial faculty appointment in the University of Alberta's Department of Psychiatry, preceded by research training at Duke University and University of Alberta. Dr. Dolcos is also an Associate Editor for the APA journal Emotion, for Psychophysiology, and for the Frontiers Journals Frontiers in Neuroscience-Integrative Neuroscience and Frontiers in Psychology-Emotion Science. In addition, Professor Dolcos has been an Editor and Contributing Author of the Frontiers Special Research Topic titled "The Impact of Emotion on Cognition—Dissociating between Enhancing and Impairing Effects", and of the associated Frontiers E-Book titled "Current Research and Emerging Directions in Emotion-Cognition Interactions." His research has received both national and international supports, from governmental and non-governmental funding agencies. He is the recipient of a Laird Cermak Award for Early Contributions to Memory Research from the Memory Disorders Research Society, a Young Investigator Award from the National Alliance for Research on Schizophrenia and Depression, and a Best Paper Award from the Journal of Cognitive Psychology (Psychology Press). For more information about Professor Dolcos' research, visit: http://dolcoslab.beckman.illinois.edu/.

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**Ekaterina Denkova, PhD.,** is a Senior Scientist at the University of Miami. She has received her PhD from the University of Strasbourg (France), with Professor Liliann Manning, where she performed research in cognitive neuroscience of memory. Then, she joined the University of Alberta (Canada) as a *Wyeth Pharmaceuticals—Canadian Institutes of Health Research Post-Doctoral Fellow*, where she received post-doctoral training in cognitive and affective neurosciences in Professor Florin Dolcos' group. Her research investigates the neural correlates of autobiographical memory in healthy and brain-damaged populations, and how they are influenced by emotion and cognitive control strategies.

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