Introduction

The overarching goal of this review is to discuss emerging evidence regarding factors that influence opposing effects of emotion on cognitive processing at different levels (Fig. 1), and the associated neural mechanisms, and to highlight the need to consider such factors in studies investigating emotion-cognition interactions. These issues have relevance for understanding mechanisms of emotion-cognition interactions in healthy functioning and in emotional disturbances, where such opposing effects of emotion are exacerbated and deleterious.

It is important to clarify upfront that enhancing vs. impairing effects of emotion may be associated with beneficial vs. detrimental effects, respectively, and hence to some extent these notions can be used interchangeably. However, this is not always the case, as dissociations can also be identified. For instance, attending to task-irrelevant emotional distraction may impair performance in cognitive tasks at hand. However, from an evolutionary perspective, having in place neural systems sensitive to emotional

![Fig. 1 Emotion-Cognition Interactions in the Brain and their Relations with Adaptive and Maladaptive Outcomes.](image)
information whose detection and processing are relevant for survival (e.g., in threatening situations) is adaptive and hence beneficial. Therefore, the impairing effects of emotional distraction in this case may be seen as “necessary side-effects” of enhancing effects of emotion on attention and perception, which overall are beneficial for survival. In the case of psychopathology, on the other hand, exacerbation of both enhancing and impairing effects of emotion are context inappropriate and thus indeed detrimental. Specifically, at a basic level, enhanced emotional memory retrieval is beneficial for survival, for instance, if it helps us predict/avoid dangerous situations. However, if it causes suffering, such as in the case of post-traumatic stress disorder (PTSD) patients, who may inappropriately re-experience memories for traumatic events in safe situations, such enhanced memory is maladaptive and hence deleterious. This clarification is important, because a rigid view that impairing effects of emotion (or stress for that matter) on cognition are always detrimental hampers research progress. Hence, in the present discussion, enhancing/impairing effects refer to the impact of emotion on the cognitive processes or performance measures of interest (perception, memory, etc.), rather than to beneficial/detrimental effects in general, or from an evolutionary standpoint.

**Opposing Effects of Emotion Within the Same Cognitive Domain**

Enhancing and impairing effects of emotion can be identified within the same cognitive processes/domains, such as perception and episodic memory (i.e., memory for specific personal events). Opposing effects of emotion in perception can be linked to the context in which emotional information is processed (goal-relevant or irrelevant) (reviewed in Dolcos et al., 2011, 2017a, 2020a, 2017b, Jordan et al., 2013) to the timing of its processing (simultaneous or asynchronous) (Bocanegra and Zeelenberg, 2009a, 2011b; Ciesielski et al., 2010; McHugo et al., 2013; Ohman et al., 2001; Phelps et al., 2006), and to the spatial frequency of visual information (high or low spatial frequency) (Bocanegra and Zeelenberg, 2009b, 2011a; Vuilleumier et al., 2003). Regarding episodic memory, opposing effects of emotion can be attributed to different accounts, including central (enhancing) vs. peripheral (impairing) effects (Kensinger, 2009) and high (enhancing) vs. low prioritization (impairing) of information (Mather and Sutherland, 2011). Moreover, an important emerging topic of research in this area concerns opposing effects of emotion on associative or relational memory (Chiu et al., 2013), where the evidence is mixed (Dolcos et al., 2017b). Clarification of instances where emotion enhances or impairs relational memory is important because this type of memory is differentially affected in neurologically (Alzheimer’s disease), emotional (mood and anxiety disorders), and other disturbances, such as schizophrenia.

Neurally, opposing behavioral effects of emotion on perception are predominately linked to the involvement of the amygdala (AMY), which is sensitive to initial bottom-up prioritization and influences allocation of cortical resources to process emotional information. Similarly, the opposing effects of emotion on episodic memory have been linked to dissociative engagement of the AMY according to the differential impact of arousal on various aspects of the information to be remembered (e.g., central vs. peripheral, and high-vs. low-prioritized). More generic dissociations between singular or unitized items encoding and formation of complex associations, also contribute to the opposing effects of emotion on episodic memory. In this more comprehensive perspective (Chiu et al., 2013), emotion may lead to memory enhancement of separate as well as unitized items, but to impairment of more complex hippocampus (HC)-dependent memory representations. This emerging evidence highlights the importance of considering different aspects of an event and their complex interactions.

For both perception and memory, the factors mentioned above as influencing opposing effects of emotion have been identified through research investigating effects linked to the characteristics of the stimuli, rather than to the emotional state one may be in. Indeed, one’s emotional state can also impact cognition and behavior, and there is evidence that emotional state can affect visual attention and perception. Perhaps the most widely known phenomenon is the influence of mood on attentional scope, with positive mood linked to increased distributed attention and negative mood to more focused attention (Vanlessen et al., 2016; Whitmer and Gotlib, 2013). Another, and perhaps lesser known phenomenon, is the effect of mood and emotional state on perception. Specifically, loudness, height, and distance judgments have all been shown to be influenced by one’s emotional state (Anderson et al., 2011; Rienier et al., 2011; Siegel and Stefanucci, 2011; Stefanucci and Proffitt, 2009; Zadra and Clore, 2011).

Similar to the case of perception and attention, one’s emotional state can also impact episodic memory (Fitzgerald et al., 2011; Greene et al., 2014; Lewis et al., 2005). In short, available research suggests that emotional states can lead to differential effects depending on their congruency with the emotional information to encode and retrieve, a phenomenon known as mood-congruent memory (Blaney, 1986). Namely, memory is enhanced when the mood valence is consistent between encoding and retrieval, or when there is congruency (during encoding or retrieval) between the subject’s mood and the valence of the information to be encoded/retrieved (Fitzgerald et al., 2011). The differential impact of emotional stimuli vs. emotional state is still an open question, as research trying to delineate these effects is scarce (Cohen et al., 2016). Hence, clarification of this issue is a fruitful avenue for further research, both in normal functioning and in affective disorders, which are characterized by an overall negative mood and a negative affective bias in attention, perception, and memory (Drevets, 2001).

The factors reviewed here regarding the impact of emotion on perception and memory may be considered either independently or as interacting with one another. Future research on emotion-perception-attention interactions should consider them and their possible interactions in predicting and interpreting findings regarding opposing effects of emotion on visual processing. Similarly, future research on the impact of emotion on episodic memory should consider the various factors influencing the opposing effects of emotion, to further delineate them and the associated neural correlates, according to the type of memory associations and linked to effects of emotional stimuli vs. emotional states, or to modulations by previous memory representations (Sakaki et al., 2014).
Opposing Effects of Emotion Across Cognitive Domains

There is also emerging evidence of opposing effects of emotion across cognitive processes/domains, which also emphasizes the link and dissociation between immediate and long-term effects of emotional distraction on perception, attention, and working memory (WM) (Dolcos, 2013; Shafer and Dolcos, 2012), on the one hand, and episodic memory, on the other hand. For instance, task-irrelevant emotional information can impair ongoing cognitive processing, while also enhancing long-term memory for the distracters themselves. Seeing 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 totaled cars). Novel brain imaging evidence regarding these phenomena points to both overlapping and dissociable neural mechanisms mediating these opposing effects of emotion (Dolcos et al., 2013; Shafer and Dolcos, 2012), and highlights the role of other factors, such as the load of the main cognitive task (Shafer and Dolcos, 2012; Shafer et al., 2012).

Evidence regarding the neural correlates of the opposing immediate (impairing) impact of emotional distraction on perception or WM and the long-term (enhancing) impact of emotion on episodic memory are mediated by overlapping and dissociable neural systems, involving both bottom-up and top-down mechanisms. Links between the opposing effects of emotion on perception/attention and memory were observed in both basic (AMY) (Anderson and Phelps, 2001; Lim et al., 2009; Phelps et al., 2006) and higher-order processing (e.g., ventrolateral prefrontal cortex, vlPFC) (Dolcos et al., 2020b) regions, showing overlapping effects of emotion on perception and memory, whereas dissociations were observed mainly in higher order cognitive brain regions, showing involvement only in immediate impairing (medial PFC, mPFC) or long-term enhancing (superior parietal cortices, SPC) effects. Given that mPFC is sensitive to emotional stimuli (Keightley et al., 2003; Scheuerecker et al., 2007) and SPC is part of the attentional network (Corbetta and Shulman, 2002), their involvement in the opposing effects can be attributed to increased emotional and goal-relevant processing of the distracters, respectively.

Regarding the link between opposing effects of emotion on WM and episodic memory, at the brain level, trials producing both effects (impaired WM and enhanced episodic memory) were associated with decreased activity in dorsolateral PFC (dlPFC) (linked to immediate/detrimental impact on WM performance) and increased response in medio-temporal lobe (MTL) regions (linked to long-term/increased episodic memory performance) (Dolcos et al., 2013). Of note, the same AMY region was linked to both of these opposing effects. Interestingly, trials associated with enhanced episodic memory performance for emotional distractors that did not disrupt WM performance were linked to increased involvement of top-down PFC mechanisms (i.e., vlPFC). This suggests that enhanced memory performance for emotional distractors also benefits from the engagement of coping mechanisms engaged to deal with the presence of emotional distraction during the WM task (Dolcos et al., 2013), possibly involving deeper encoding due to more elaborative processing of the distracters (Dillon et al., 2007).

Overall, these findings point to the involvement of both bottom-up and top-down mechanisms. Bottom-up AMY-MTL mechanisms are involved in both the impairing and enhancing effects of emotion on perception/WM vs. episodic memory. On the other hand, top-down PFC mechanisms dissociate between the enhancing and impairing effects, pointing to a dorsal-ventral distinction between PFC mechanisms involved in maintenance of goal-relevant information (dlPFC), and the ones involved in coping with emotional distraction linked to enhanced episodic memory for the distractors themselves (vlPFC) (Dolcos et al., 2013).

Opposing Effects of Emotion in the Stress Response

In a larger context of the stress response, emotional stressors can lead to opposing effects depending on the context and degree. Optimal levels of stress may temporarily increase cognitive performance (e.g., nervousness about the outcome of an important exam may motivate us to study harder), whereas high levels of stress can impair performance (e.g., overwhelming worry in the anticipation of or during a difficult exam may impair our ability to stay focused and perform optimally) (Diamond et al., 2007). Moreover, chronic and/or extreme levels of stress can lead to clinical conditions (Arnsten, 2009; Roozendaal et al., 2009), such as PTSD, which are associated with longer-lasting cognitive impairments. An interesting emerging finding in this area points to the role of subjective or objective control upon stressful situations (Henderson et al., 2012; Kerr et al., 2012; Mereu and Lleras, 2013), in determining the beneficial or detrimental impact on cognitive processing. In addition, recent research is also considering the role of individual differences in response to stressors, which can lead to adaptive or maladaptive consequences. Thus, it is important to consider both factors related to the stressors themselves and factors related to variations (personality, genetic) in the individuals’ responses to stressful situations.

Regarding the duration of stressors, opposing effects of acute stress are linked to carefully orchestrated contributions of executive control regions, such as the PFC, and limbic and subcortical structures, such as the AMY. Exposure to acute stress increases activity in brain regions involved in fear and attentional vigilance, at the cost of executive control regions function. This allocation of resources to the affective vs. executive control function reverses, as the stress subsides, normalizing the emotion-cognition balance in the aftermath of stress (Hermans et al., 2014). Notably, while these effects might allow for optimal responding to stressful situations and subsequent recovery in healthy functioning, they are likely impaired in clinical conditions such PTSD, which is characterized by a continuous state of hypervigilance (Dolcos, 2013), as discussed in Section “Linking Opposing Effects of Emotion on Cognition in PTSD” below.

Regarding the level and controllability of stressors, 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 (Buetti and Lleras, 2012; Henderson et al., 2012; Kerr et al., 2012). The opposite effects of stress on cognition are reflected in a differential engagement and interplay between MTL and PFC mechanisms (reviewed in Dolcos et al., 2018). Neurally, the available evidence suggests that the actual presence, or the mere subjective feeling, of control over stressful situations engages ventromedial PFC (vmPFC) mechanisms that regulate emotional reactions in the AMY (Kerr et al., 2012). Controllable anticipatory responses to stressors were associated with increased vmPFC activity, which provides evidence for its involvement in reducing stress responses when stress is controllable, likely by inhibiting AMY responses and promoting resilient behavior. On the other hand, uncontrollable stress engages dorsolateral PFC (dlPFC). Stress induced through exposure to an upsetting, violent film was associated with impaired WM performance and reduced dlPFC activity (Qin et al., 2009). Further support for the role of the dlPFC in the response to uncontrollable stress comes from studies showing that transcranial stimulation of the dlPFC prevents stress-induced WM deficits (Bogdanov and Schwabe, 2016). Together, these findings suggest that the presence of control (or the feeling thereof) during stressful situations engages PFC mechanisms that regulate emotional reactions in AMY, and the engagement of these mechanisms is affected by previous stress history and personality traits.

Regarding individual differences in stress responses, PFC functioning in response to stressors has been also linked to individual variations in personality traits indexing vulnerability to (trait rumination) or resistance against (trait mindfulness) emotional dysregulation (Khawli et al., 2017), as well as to genetic differences associated with susceptibility (COMT Met-homozygotes) or resilience (Val-carriers) to stress (Qin et al., 2012). In addition to its effects on the PFC structures (dlPFC and vmPFC), exposure to stress impairs performance on memory tasks dependent on the hippocampus (Kim and Diamond, 2002; McEwen and Milner, 2007; McEwen and Sapolsky, 1995).

Overall, the opposing effects of acute stress on cognition have been linked to a variety of factors, ranging from the objective properties of the stressors and the subjective experience of stress to individual variations in personality traits and genotype, reflected in a differential engagement and interplay between MTL and PFC mechanisms. Available evidence points to carefully orchestrated neuromodulatory effects on executive control regions such as the PFC, and the limbic and subcortical structures such as the AMY, involved in emotional and attentional vigilance. Initial involvement of the latter comes at the cost of the engagement of the former, but as the stress subsides allocation of resources to the affective and executive control function reverses, hence normalizing the emotion-cognition balance in the aftermath of stress.

**Linking Opposing Effects of Emotion on Cognition in PTSD**

The co-occurrence of enhancing and impairing effects of emotion is probably most evident in affective disturbances, such as PTSD, which are characterized by increased sensitivity to emotional distraction and impaired cognitive control (Hayes et al., 2012). Thus, in this case, both of these opposing effects of emotion are exacerbated and deleterious. For example, uncontrolled recollection of traumatic memories in PTSD may interfere with ongoing cognitive processing. Novel evidence from PTSD studies points to altered interactions between the mechanisms that are typically responsible for enhancing vs. impairing effects of emotion in healthy functioning (Dolcos, 2013). Specifically, there is evidence suggesting that non-specific responses to cues for trauma-related memories, presented as task-irrelevant distraction (Morey et al., 2009), may reflect non-specific initial encoding of memories for the traumatic events due to heightened arousal (Hayes et al., 2011). This suggests a link between the initial impact of emotion influencing episodic memory and the impact of its retrieval triggered by trauma-related pictures presented as task-irrelevant distracters. Specifically, reduced AMY-HC engagement during the formation of memory for trauma-related pictures may be explained by initial non-specific encoding of gist-based representations due to hyperarousal. This, in turn, leads to non-specific responses in dlPFC, when trauma-related and neutral stimuli are presented as task-irrelevant distracters, and to symptoms of hypervigilance, which contribute to the maintenance of a hyperarousal state and to non-specific (re)encoding of traumatic memories, in a continuous vicious cycle (Dolcos, 2013).

Overall, this evidence points to general and specific emotional and cognitive disturbances in PTSD, where the opposing effects of emotion co-occur and are both deleterious. These effects are linked to alterations in the neural circuitry underlying emotion-cognition interactions, and impact both immediate and long-term effects of emotion on working and episodic memory, respectively. These effects also point to alterations of both bottom-up and top-down mechanisms in PTSD.

**Comparing Opposing Effects of Emotion in Healthy Aging vs. Depression**

There is also intriguing converging evidence from across-fields comparisons of findings from groups with opposing emotional biases, such as healthy aging (showing a positive bias; Mather, 2012; Mather and Carstensen, 2005) vs. depression (showing a negative bias; Mayberg, 1997). Interestingly, these opposing biases are linked to opposite effects on the ability to control emotions in these groups—enhanced emotion regulation in healthy aging (Mather, 2012; St. Jacques et al., 2010) vs. impaired emotion control or emotion dysregulation in depression (Mayberg, 1997). Thus, direct comparisons of these groups with opposing emotional biases and emotion regulation abilities, along with studies aiming at elucidating the mechanisms of enhanced emotional resilience in healthy aging, provide an exciting possible research avenue of addressing mental health issues.

Evidence from such groups with opposing emotional biases identify activity in the mPFC/anterior cingulate cortex (ACC) as a biological marker of emotional resilience vs. vulnerability in healthy aging vs. depression, respectively. This evidence links
enhanced response in this region with increased ability to control emotions, characterizing healthy aging, and decreased response with impaired emotion control characterizing depression (Dolcos et al., 2014; Gutjers et al., 2007; Kensinger and Schacter, 2008; Leclerc and Kensinger, 2008; St. Jacques et al., 2010; Tessitore et al., 2005). Importantly, therapeutic interventions improve emotion regulation processes in depressed patients by normalizing activity in these areas (Ritchey et al., 2011). Therefore, direct comparisons of these groups with opposing emotional biases and emotion regulation abilities provide an exciting research avenue in addressing mental health issues associated by emotional dysregulation. Such studies can lead to identification of additional neural markers that can be targeted in therapeutic interventions (Dolcos et al., 2021).

Conclusion

The overarching goal of the present review was to discuss emerging findings from studies identifying enhancing and impairing effects of emotion on cognition at different levels of analysis. Available research provides evidence that these opposing effects of emotions can be observed within the same cognitive domains, across cognitive domains, at the more general level of the response to stressors, as well as within clinical groups and across groups with opposing affective biases. Importantly, these multilevel relations are also influenced by individual differences, which underlines the need for adopting a comprehensive view in studies examining emotion-cognition interactions, in both healthy and clinical populations. The present review emphasizes the need to consider the various factors that can influence opposing effects of emotion on cognition and identifies new avenues for future investigations of emotion-cognition interactions. These issues have relevance for understanding mechanisms of emotion-cognition interactions in healthy functioning and in emotional disturbances, where such opposing effects of emotion tend to be exacerbated and deleterious.

Acknowledgments

During the preparation of this manuscript, FD was supported by a Helen Corley Petit Scholarship in Liberal Arts and Sciences and an Emanuel Donchin Professorial Scholarship in Psychology, from the University of Illinois at Urbana-Champaign.

References


