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The Neurobiology of Emotion–Cognition Interactions

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C14.P1 Emotion and cognition have long been viewed as two separate mental faculties, largely based on subjective differences between emotional and cognitive experience. Yet, an increasing body of research highlights the bidirectional influences between cognitive and emotional systems (1). These recent developments have been made possible by the emergence of powerful new tools for objectively assessing emotion and brain function

C14.P2 This chapter reviews evidence for the mutual modulatory relationships between emotional and cognitive functions, as well as for the neural circuits supporting these relationships. We discuss the influence of emotional information on different aspects of attention. We further elaborate on the flexibility of cognitive biases toward emotional information, as well as the plasticity of the neural connections supporting these biases. We then discuss the influence of cognitive strategies on emotions. Finally, we point to limitations of existing research and suggest future scientific directions. A better understanding of the mutual influences between emotional and cognitive processes is of great theoretical and clinical importance. Such an understanding may also contribute to the development of specific interventions for individuals with prominent emotional and cognitive disturbances, including patients with schizophrenia, substance abuse, and internalizing disorders.

C14.S1 ## The Influence of Emotion on Cognition

C14.S2 ### Biased Attention to Threat

C14.P3 Ample evidence indicates that humans are particularly sensitive to threat-related stimuli (i.e. snakes, spiders, threatening faces [2]), probably owing to the evolutionary importance of selective responses to potentially dangerous aspects of the environment. Biased attention to emotional stimuli can be measured using a

variety of methods that compare reaction time and accuracy rates between neutral and emotional items.

C14.P4 The focus of attention is determined by a delicate balance between *exogenous* (stimulus-driven) and *endogenous* (goal-directed) mechanisms (3). Sussman et al. (4) highlight the influence of goal-directed neurocognitive mechanisms—those related to internal goals, moods, and motivational states (e.g. looking for a friendly face in social gatherings)—on the prioritized perception of relevant stimuli. Such prestimulus factors lead to anticipatory search behaviours that allow fast detection of sources of potential reward or threat. An extended brain network is involved in endogenous processing of emotional stimuli, including frontoparietal (intraparietal sulcus, frontal eye field, and fusiform gyrus), sensory, and limbic regions. Neural circuits that involve limbic areas can facilitate enhanced attention via at least two mechanisms: directly, via projections from the basolateral nucleus of the amygdala to cortical sensory areas (e.g. fusiform face area); and indirectly, via projections to neuromodulatory systems in the basal forebrain and brainstem that, in turn, can modulate sensory cortical areas (i.e. increase the neuronal signal-to-noise ratio [5]). Accumulating evidence highlights the role of the amygdala in biased attention and demonstrates that manipulations that potentiate amygdala reactivity can also enhance attentional bias to threatening stimuli (for details see [5]). For example, Herry et al. (6) used a translational approach in mice and humans to show that unpredictability led to amygdala-dependent avoidance and anxiety behaviours. Amygdala damage in humans was shown to disrupt the prioritized processing of threat-related faces in crowded stimulus arrays (7). The amygdala was also found to play a key role in redirecting gaze (i.e. overt attention) to those features of the face, such as the eyes and the brows, that are most diagnostic of threat, trustworthiness, anger, and fear (8). Furthermore, there is evidence for increased connectivity between frontoparietal and sensory regions and the amygdala in response to informative cues for emotional stimuli (9). There is also evidence for increased connectivity between frontal regions and face-sensitive visual areas when participants must decide whether visual objects are faces or not (10).

C14.P5 Endogenous influences are of major importance when investigating depressed and anxious individuals, who tend to expect increased probability and cost for negative events (i.e. expectancy biases [11]). Indeed, threat sensitivity and maladaptive attention biases are more salient among depressed and anxious individuals (e.g. 12, 13). These biases can be manifested in both covert and overt attention by heightened vigilance to threat, difficulty in disengaging attention from threat, and/or avoidance of threatening stimuli (e.g. 11). Recent views highlight the role of dysfunctional expectancy biases in anxiety. Dysfunctional expectancy has been suggested to be associated with abnormal functioning of prefrontal–limbic–striatal–sensory pathways (14). Indeed, patients with social anxiety disorder showed increased amygdala activation and exaggerated behavioural interference

when performing tasks that assess attentional bias to fear, such as the emotional Stroop or dot-probe tasks (15).

C14.P6 Dysfunctional biases already exist in populations *at risk* for developing psychopathology. For example, individuals with elevated levels of dispositional negativity—those who are prone to more intense, frequent, or persistent negative affect—are more likely to show elevated heightened reactivity to threat-related cues and to be characterized by significant attentional biases to threat (5). From a longitudinal perspective, attentional biases to threat-related cues have been shown to moderate the impact of dispositional negativity on the development of internalizing symptoms among youth. For example, White et al. (16) demonstrated that, among young people with an early childhood history of extreme dispositional negativity, those in the subset that also showed an attentional bias to threat-related cues on the dot-probe task were most likely to exhibit social withdrawal and elevated anxiety symptoms later in development.

C14.S3 The Influence of Threat on Executive Functions

C14.P7 Executive functioning is an umbrella term referring to a set of cognitive processes necessary for controlling behaviour. That is, these processes are essential in monitoring behaviours that facilitate the attainment of chosen goals. One of these functions is *working memory*, which holds important information regarding our current thoughts, feelings, and behaviour by directing attention towards internal representations (17). The capacity of working memory is determined by the ability to filter irrelevant information in the environment (18). However, evidence shows that task-irrelevant emotional information gains prioritized access to working memory (19), an effect that is more robust among individuals with, or dispositioned to, emotional disorders (20). The exaggerated representation of emotional information in working memory disrupts endogenous attention and other control mechanisms. This deficit may be a contributing factor to the heightened negative affect (i.e. anxiety, sadness) characterizing these populations (14). The tendency of anxious individuals to experience heightened distress and intrusive thoughts may be explained by allocation of excess storage capacity to threat, even when it is completely irrelevant to the task at hand and even when it is not present in the external world (21). Once lodged in working memory, threat-related information is poised to bias the stream of information processing (i.e. attention, memory retrieval, and action), thus promoting worry and other maladaptive cognitions (22).

C14.P8 Related to the evidence regarding enhanced distractibility in working memory, various studies have shown a reduced ability to disregard distracting emotional stimuli and to *focus attention* on a target among depressed and anxious individuals (23). The most common method of examining selectiveness of attention

among these populations is the emotional Stroop task (24), in which participants are asked to attend to only one aspect of a written word (e.g. its colour) and ignore its distracting other characteristics (e.g. its emotional meaning). Findings demonstrate that the negative meanings of words interfere with attention among anxious and depressed patients, reflected by longer response latencies compared to healthy controls (25). Similar findings were demonstrated when participants were asked to determine the location of a picture target and to ignore emotional or neutral flankers that could appear in congruent and non-congruent locations (26). Anxious—but not depressed—participants showed attentional interference when faced with negative distractors (27). These findings demonstrate a specific deficiency in selective attention among anxious individuals during threat distraction.

C14.P9 Dysfunctional selective attention has been associated with abnormal activity in prefrontal, limbic, and sensory regions. For example, Mitterschiffthaler et al. (25) employed the emotional Stroop task and found significant engagement of the left rostral anterior cingulate cortex (ACC) and the right precuneus during the presentation of sad words, as well as a positive correlation between rostral ACC activation and response latencies for the sad words among depressed patients compared to controls. Fales et al. (28) reported a combination of enhanced amygdala reactivity and attenuated prefrontal reactivity among depressed patients in trials where they failed to ignore emotional distractors. Likewise, Kaiser et al. (29) showed that the level of depressive symptoms positively predicted the level of activation in the dorsal ACC and posterior cingulate cortex in response to negative distractors on the emotional Stroop, as well as correlating positively with higher connectivity between these areas. The researchers concluded that this connectivity between areas associated with cognitive control and internal attention systems suggests that, when depressed individuals are confronted with negative information, their elevated attention to internal thoughts and their difficulty in adaptively allocating resources in the environment interfere with goal-directed behaviour.

C14.P10 Deficiency in ignoring distractors may be related to a deficit in *cognitive control*, which refers to processes that enable regulating, coordinating, and sequencing thoughts and actions according to behavioural goals that are maintained internally. In situations when conflicting reactions must be modified based on contextual information, the control processes help make our behaviour as adaptive as possible (30). Accumulating evidence shows the disruptive influence of emotional distractors on cognitive control among healthy individuals (31) and even more significantly among depressed and anxious participants (32). In emotional-cued tasks in which individuals must strategically activate proactive control in a particular context (32), depressed as well as highly ruminative or worried individuals showed deficits manifested in longer response latencies or lower accuracy rates relative to healthy participants (e.g. 31, 33). In electrophysiological and

neuroimaging studies of conflict and control, depressed individuals showed attenuated neural responses and anxious participants showed heightened responses compared to healthy controls (for a review see [32]).

C14.S4 ### Flexible Changes in the Relations Between Cognition and Emotion

C14.P11 Accumulating evidence suggests that attentional biases are plastic and can be altered by early and adult life experiences or interventions (34). Type of caregiving and type of parental communication were found to be associated with children's performance on inhibition, working memory, and cognitive flexibility tasks (35). Moreover, there is evidence that clinically effective cognitive behavioural and pharmacological treatments for anxiety also tend to reduce attentional biases to threat-related cues (36).

C14.P12 In light of the above, studies on adult interventions, such as cognitive training of adaptive allocation of attention or improvement of inhibitory functions, aim to reduce attentional biases presented in different mental disorders when reacting to emotional stimuli. In non-clinical samples, attention modification has been shown to reduce distress and behavioural signs of anxiety (e.g. 37). There is also evidence for neural plasticity following the training (e.g. 38). In adult clinical samples, medium-to-small treatment effects have been observed compared to placebo training (34, 39). However, recent reviews highlight some important limitations of existing protocols for attentional bias modification (see discussion in [40]).

C14.S5 ## The Influence of Cognition on Emotion

C14.P13 In daily life, we use a variety of cognitive strategies to regulate our emotions (e.g. 41). There is evidence that circuits involved in attention and working memory play a crucial role in emotion regulation (42). One frequently used and relatively effortless strategy aimed at reducing distress elicited from stimuli in the environment is attentional avoidance/deployment, manifested in shifting of attention away from the source of distress (41). Aue et al. (43) found that participants with arachnophobia who exhibited enhanced activation of the amygdala and dorsal striatum during exposure to spider images also executed more visual avoidance, suggesting that this strategy was aimed at regulating their extreme fear. This finding is in line with evidence highlighting the regulation of subcortical regions during attention avoidance (44). Another strategy considered to be an automatic attentional defence against unpleasant stimuli is repression of negative feelings aroused from emotional content away from awareness (45). Studies

indicate that individuals who frequently exhibit this strategy tend not to recognize and label negative emotions (46) and report experiencing less negative emotion during mood induction. However, they also exhibit various deficiencies in cognitive and social skills, as well as enhanced physiological reactivity (47). Taken together, these findings show the complexity of repression as a strategy for emotion regulation.

C14.P14 Two strategies that require more effort and volition are distraction and reappraisal. Distraction is executed by generating a mental representation of something unrelated to the presented stimuli, while reappraisal involves generating an alternate meaning for the stimuli (48). Strauss et al. (49) pointed out that, while both distraction and reappraisal decrease amygdala response and increase activation in prefrontal and cingulate cortices, distraction leads to a larger decrease in the amygdala and a greater increase in prefrontal and parietal regions. This difference may be due to different demands on attention imposed by each strategy or their influence on different stages of emotion generation. Other strategies for regulating emotional states, such as cognitive reappraisal (50), require making efforts to maintain an explicit regulatory goal or model and depend on a working memory circuit encompassing the lateral prefrontal cortex (PFC) and posterior parietal cortex (PPC) (51). Consistent with this perspective, individual differences in working memory capacity are predictive of reappraisal success (42). Work using transcranial direct-current stimulation demonstrates that the lateral PFC is crucial for emotion regulation (52). In addition, recent evidence shows that the human ability to choose adaptive emotion regulation strategies is flexible, depending on the emotional context (e.g. reappraise when the stimulus is mildly aversive and distract when it is highly aversive [53]).

C14.P15 Ehring et al. (54) suggest that individuals who are vulnerable to depression fail to regulate their emotions successfully and sometimes regulate their emotions in situations when this is not necessary or functional. In addition, even when they do use adaptive strategies, they may extract less benefit from them, as they frequently fail to inhibit negative information (as in the case of repetitive rumination). Johnstone et al. (55) showed abnormal neural reactivity among depressed individuals during failure to regulate emotions. This abnormality was manifested in counterproductive enhanced activation of the right PFC and lack of engagement of left lateral–ventromedial prefrontal circuitry, crucial for the downregulation of amygdala responses to negative stimuli.

C14.S6 ## The Integration of Emotion and Cognition

C14.P16 Accumulating behavioural and neural-based evidence has led to the growing recognition that cognition and emotion are tightly interwoven. Neuroimaging studies demonstrate brain colocalization of key emotional and cognitive processes

(56); electrophysiological studies show that prototypical cognitive control signals (e.g. no-go N2, error-related negativity) systematically covary with emotional traits and states (57); and there is evidence for cognitive biases during negative or threatening states as well as among populations showing abnormal emotions. Indeed, a number of brain regions that are widely conceptualized as 'cognitive' are also involved in emotional processing. For example, the dorsolateral PFC, traditionally considered a key player in reasoning and higher cognition (58), also contributes to the top-down control of emotion and motivated behaviour (51) by gating working memory and focusing attention in the face of emotional distraction (e.g. 59).

C14.P17 Conversely, the amygdala, a canonical 'emotional' region, plays an important role in regulating higher cognitive functions by influencing the brainstem neurotransmitter systems orchestrating the quality of information processing (60). In situations that require rapid and immediate reactions to the environment, the amygdala guides attention and allocates resources from the PFC to adapt behaviour (61).

C14.S7

Conclusions and Future Directions

C14.P18 The findings reviewed here demonstrate that threat-related cues and emotional states influence a variety of attentional and executive functions. Cognitive biases have been demonstrated among healthy individuals, at-risk populations, and psychiatric patients. Other work indicates that executive attention plays a key role in the regulation of emotion. These mutual relationships between emotional and cognitive functions are subserved by a diffused neural network that includes the amygdala, insula, frontoparietal, midcingulate, sensory, and brainstem regions. This robust influence of emotional— mainly negative—information on attentional and executive function is nevertheless plastic and is modulated by experience.

C14.P19 The work we have reviewed suggests that emotion influences a number of specific cognitive processes. However, the vast majority of studies have only examined one cognitive process at a time, leaving the exact nature of the interrelationships unclear. This gap has motivated recent work aimed at understanding relationships between different kinds of emotional biases (11). For example, Everaert et al. (62) demonstrated that deficient inhibitory control over negative items is related to attention bias, which in turn predicts interpretation bias and depressive symptoms. A better understanding of the similarities and differences in processing biases between anxiety and depression may offer important insights for future diagnosis and treatment.

C14.P20 As demonstrated here and elsewhere (1), emotional cues, states, traits, and disorders can profoundly influence key elements of cognition, including orientating,

selective attention, working memory, and cognitive control. There is also evidence that neural pathways involved in expectancy, executive functions, and working memory contribute to the regulation of emotional reactions. Evidence further shows that neural regions (e.g. dorsolateral PFC, middle cingulate cortex) and processes (e.g. attention, working memory, cognitive control) that are conventionally associated with cognition play a central role in emotional states, traits, and disorders. This evidence is in line with a recent model emerging from anatomical and neuroimaging findings. This model proposes that a non-hierarchical diffuse neural network, which includes cortical, thalamic, and midbrain areas, supports bidirectional and non-linear connections between emotion, cognition, motivation, and action (63).

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C14.P21 Open questions remain regarding the dynamic mutual influences of the cognitive and neural systems modulating emotional processing. The development of advanced data acquisition and analysis methods may help to resolve these questions. Exciting developments in neuroimaging analysis offer opportunities for better characterizing the dynamics of valence processing and of interactions between neural networks. Developing a deeper understanding of the interplay between emotion and cognition is a matter of theoretical as well as practical importance. Many of the most common, costly, and challenging neuropsychiatric disorders involve prominent disturbances of both cognition and emotion, suggesting that these disorders can be conceptualized as disorders of the emotional–cognitive brain.

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