

REVIEW

GENETICS OF EMOTION REGULATION

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Abstract—Emotions can be powerful drivers of behavior that may be adaptive or maladaptive for the individual. Thus, the ability to alter one's emotions, to regulate them, should be beneficial to an individual's success of survival and fitness. What is the biological basis of this ability? And what are the biological mechanisms that impart individual differences in the ability to regulate emotion? In this article, we will first introduce readers to the construct of emotion regulation, and the various strategies that individuals may utilize to regulate their emotions. We will then point to evidence that suggests genetic contributions (alongside environmental contributions) to individual differences in emotion regulation. To date, efforts to identify specific genetic mechanisms involved in emotion regulation have focused on common gene variants (i.e. variants that exist in >1% of the population, referred to as polymorphisms) and their association with specific emotion regulation strategies or the neural substrate mediating these strategies. We will discuss these efforts, and conclude with a call to expand the set of experimental paradigms and putative molecular mechanisms, in order to significantly advance our understanding of the molecular mechanisms by which genes are involved in emotion regulation. © 2009 IBRO. Published by Elsevier Ltd. All rights reserved.

Key words: emotion regulation, neuroimaging, gene polymorphism, prefrontal cortex, amygdala, 5-HT transporter.

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Abbreviations: COMT, catechol-O-methyltransferase; DLPFC, dorsolateral prefrontal cortex; DTI, diffusion tensor imaging; G×E, gene-by-environment; HR, heart rate; MAOA, monoamine oxidase A; met, methionine; OFC, orbitofrontal cortex; pACC, perigenual anterior cingulate cortex; PFC, prefrontal cortex; rACC, rostral anterior cingulate cortex; SL, heterozygous short allele carrier; SNP, single nucleotide polymorphism; SS, homozygous short allele carrier; val, valine; VLPFC, ventrolateral prefrontal cortex; VNTR, variable number of tandem repeats; WM, white matter; 5-HTT, 5-HT transporter; 5-HTTLPR, 5-HT transporter-linked polymorphic region.

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THE CONSTRUCT OF EMOTION REGULATION

Individuals differ greatly in their responses to emotional experiences. For example, extroversion and neuroticism represent two fundamental personality traits that reflect, respectively, individual differences in positive and negative feeling states, cognitive styles and attitudes (Costa and McCrae, 1980). Maladaptive responses to emotional stimuli may render individuals vulnerable to various forms of psychopathology. For example, individuals who score high in neuroticism are vulnerable to mood disorders (Kendler et al., 1993a,b). Thus, individuals can benefit greatly from behaviors that regulate emotions to maximize adaptive responses and minimize maladaptive responses to emotional experiences.

Gross proposed a conceptual framework of emotion regulation that considers the temporal aspects of emotion (Gross, 1998). Using this framework, Gross identified antecedent-focused strategies, which an individual may utilize to regulate emotions before they arise, and response-focused strategies, which an individual may utilize once an emotion has begun to unfold. Emotion regulation strategies may involve either automatic/unconscious or voluntary/conscious processes.

We will briefly discuss behavioral data from three emotion regulation strategies, for which there are relevant genetic data (discussed in the next sections). As an example of a form of emotion regulation that is often automatic/unconscious, we will discuss studies assessing attentional bias to emotional stimuli. As two examples of emotion regulation that usually require voluntary/conscious effort, we will discuss studies assessing the costs and benefits of cognitive reappraisal (an antecedent-focused strategy) and suppression (a response-focused strategy). A comprehensive review of this literature is well beyond the scope of this article (interested readers are referred to

authoritative reviews elsewhere (e.g. Gross and Levenson, 1993, 1997; Gross, 1998, 2002, 2007), as is a comprehensive discussion of the patient and animal literature. Instead, the studies discussed below serve as an illustration of the various paradigms that have been used in the study of emotion regulation mostly in non-patient populations and highlight some of the salient findings that have accrued in this literature to date.

Attention to emotional stimuli

A number of studies have investigated individual differences in attentional bias to emotional stimuli using paradigms that assess automatic/unconscious processes. For example, studies using an emotional version of the Stroop task, in which participants are timed to indicate the color in which presented words are printed, have reported that subjects who score high in trait anxiety or neuroticism respond slower to negatively valenced words than to neutral words (Richards et al., 1992; Wells and Matthews, 1994; Derryberry and Reed, 1998), which is interpreted as an attentional bias towards negative stimuli. In anxious individuals (compared to depressed or healthy individuals), this bias can be observed regardless of whether stimuli are presented subliminally or supraliminally (Mogg et al., 1993). In sub-clinical populations, anxiety is correlated with biased Stroop processing of anxiety-related words only for subliminal stimuli (Yovel and Mineka, 2005). There is also evidence supporting a more complex interplay of trait and state variables. For example, one study using an emotional Stroop task found no evidence for state or trait effects on Stroop interference, but did find an interactive effect, such that only high-trait anxiety individuals showed a positive correlation between state anxiety and Stroop interference (Egloff and Hock, 2001).

Another example is the dot-probe paradigm, in which pairs of target stimuli (usually differing in valence) are presented, followed by presentation of a probe stimulus placed in the same location as one of the preceding target stimuli. Measures of participants' reaction times to localize the probe or of their overt orienting responses using eye-tracking methods indicate to which item of the target pair participants attended. This work has found that individuals with high state or trait anxiety exhibit an orienting bias towards threatening facial expressions (Bradley et al., 2000; Mogg et al., 2000). More recent work has extended these findings to show that high-anxious individuals, compared to low-anxious individuals, exhibit a similar attentional bias for both intense fear-related and threat-related facial expressions (Mogg et al., 2007). A recent study (Cooper and Langton, 2006) suggests that low-anxious individuals may also exhibit attentional biases for threatening faces, if they are probed 100 ms after stimulus presentation but not if they are probed 500 ms after stimulus presentation (which is a standard parameter used in dot probe studies).

Electrophysiological evidence for attentional bias comes from studies using event related potentials (ERPs). For example, one study using a spatial cueing task (Fox et al., 2008), in which individuals who were either high or low in

trait anxiety viewed valenced (happy and angry) alongside neutral face stimuli. Only high-anxiety individuals exhibited biased attentional processing, as measured by an enhanced N2-posterior-contralateral component, which is believed to represent attentional processes during visual search.

Taken together, there is ample evidence across paradigms that there are individual differences in subjects' automatic/unconscious attentional bias towards emotional stimuli. The next section will discuss complementary studies that have used paradigms requiring voluntary/conscious effort in emotion-related reappraisal and suppression.

Reappraisal and suppression

Behavioral studies have used a wide range of experimental paradigms to study the emotional, physiological, cognitive, and social consequences of emotion reappraisal and suppression. Reappraisal refers to the strategy of changing one's interpretation of stimuli or situations that may elicit strong (usually negative) emotions in a manner that reduces or alters the emotional experience. Suppression refers to the strategy of inhibiting the behavioral (e.g. facial) expression of one's emotional experience. Perhaps the most seminal contribution to the study of these processes has been made by Gross and colleagues. In the first study of this kind, Gross and Levenson, (1993) presented a film clip selected to elicit strong feelings of disgust and had participants either watch the film without further instruction or with the instruction to suppress the outward expression of their feeling state. The suppression condition was effective in reducing outward expression of emotion, but not in reducing the emotional experience per se; suppression was also associated with evidence for increased sympathetic arousal. Later work replicated and extended these findings to show dissociable consequences of emotion suppression, compared to cognitive reappraisal, during presentation of emotional films and pictures (Gross, 1998). This work discovered that, although both strategies were effective in reducing the expression of emotion, only reappraisal was also effective in reducing the experience of negative emotion.

Studies of the physical consequences of different emotion regulation strategies have found that emotion suppression leads to increased sympathetic activation of the cardiovascular system (Davidson, 1993; Gross and Levenson, 1993, 1997; Gross, 1998). On the other hand, cognitive reappraisal is associated with reduced cardiovascular responding. For example, individuals who scored high in reappraisal exhibited a more adaptive cardiovascular response following an anger provocation paradigm, compared to individuals who scored low in reappraisal (Mauss et al., 2007).

A major cognitive consequence of emotion suppression, but not reappraisal, is the impairment of memory for the details of negative film clips or images (Richards and Gross, 2000, 2006). Indeed, the extent to which memory during emotion suppression is diminished is comparable to a condition in which participants are instructed to distract

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