**CHAPTER 4**

The Neuroscience of Emotion Regulation: Basic Mechanisms and Their Role in Development, Aging, and Psychopathology

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**Abstract**

When life's gentle breezes turn into threatening gales, we humans have a remarkable ability to adapt accordingly. This adaptability grants us a degree of control over not just our circumstances but also our emotional responses to them. We can keep our cool under stress, resist harmful temptations, and emerge resilient from all manner of trials and tribulations. We do so using a diversity of emotion regulation strategies that allow us to alter the nature, magnitude, and duration of our emotional responses in a variety of circumstances. The ability to regulate one's emotions is one of the keys to leading a healthy and productive life and the failure to do so is a hallmark of many types of psychopathology, as well as a normal part of development for children and adolescents. A major motivator of the emerging science of emotion regulation is the need to better understand why and how these failures occur and by the foundation for efforts to improve emotion regulation skills. With this in mind, the goal of this chapter is twofold: In the first section, a model of the cognitive control of emotion in healthy adults is outlined. In the second section, this model is used as a vantage point from which to survey recent efforts to examine emotion regulation in the contexts of development, aging, and psychopathology.

**Key Words:** emotion, emotion regulation, cognitive control, amygdala, prefrontal cortex

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**Cognitive Control of Emotion**

In this initial section of the chapter we outline a model that broadly describes the psychological and neural processes by which cognitive strategies can be used to control our emotions (Figure 4.1). First, we will outline a psychological process model of emotion generation and regulation. Next, we will consider the neural sources of regulation—the regions that generate and regulate the regulatory processes that comprise a given strategy. Finally, we will consider the neural targets of regulation—the regions that are affected by regulatory processes.

**Process Model of Emotion Generation and Regulation**

The time line at the bottom of Figure 4.1A depicts four basic steps involved in the generation of an emotional response (Barrett, Mesquita, Ochsner, & Gross, 2007). In the first step, a stimulus is perceived in its current situational context. The stimulus could be internal in origin, such as a thought, feeling, or sensation, or external, such as a facial expression, gesture, acton, or event. At the second stage, one attends to some of these stimuli or their attributes. The focus of attention determines what information feeds forward to subsequent emotion generation stages. Ignored or unattended stimuli may be either excluded from these subsequent stages or receive reduced processing. The third stage involves appraising the significance of stimuli in terms of their relevance to one's current goals, wants, or needs. According to appraisal theories of emotion, this is the stage at which an emotion takes on high salience (whether it is positive or negative) and its more specific characterization (e.g., anger, fear, sadness) (Schlenker, Schor, & Johnstone, 2001). Finally, in the fourth stage these appraisal codes influence an emotional response, consisting of some combination of emotional experience, emotion-expressive behavior, and autonomic activity. Although these three indicators of emotional response do not always correlate with one another, for reasons that are not perfectly understood (Mauss, Levenson, McCarther, Wilhelm, & Gross, 2005), emotion regulation strategies can effect changes in some or all of them, depending on the strategy.

**EMOTION REGULATION**

Emotion regulation involves the modification of emotional responses through the engagement of top-down control processes. Building on previous work, our model of emotion regulation distinguishes among five classes of strategies whose effects on emotion can be understood in terms of the stage of the emotion generation sequence that they impact (Gross, 1998b). In the present chapter, we focus on conscious, goal-driven regulatory strategies rather than implicit or non-conscious ones because they have been studied far more frequently. As illustrated by the top portion of Figure 4.1A, the first two strategies involve changing the nature of the stimulus inputs to the emotion generation
cycle. In situation selection, one keeps oneself away from stimuli that elicit unwanted emotions and puts oneself in the presence of stimuli that elicit desired emotions. For example, a recovering alcoholic may choose to skip a happy hour with coworkers, or a dieter may stay away from the sections of the grocery store that offer desserts. Situation selection occurs when one is in the presence of a stimulus that elicits an unwanted emotion and one changes something about the situation to alter its impact (Davis, Gross, & Ochsner, 2011). For the recovering alcoholic, this may mean leaving a party when friends begin to become intoxicated.

Given that we cannot always avoid or alter our external circumstances, at times we must regulate our emotions by changing our internal responses. A third strategy, attentional deployment, describes the allocation of attention among stimuli or components of a particular stimulus. This strategy can be further broken down into two subtypes (Ochsner & Gross, 2005). Selective attention involves moving the focus of attention toward or away from stimuli or their attributes (e.g., Anderson, Christoff, Panitz, De Rosa, & Gabrieli, 2005; Edin, Egner, Peraza, Kandel, & Hsch, 2006). For example, the recovering alcoholic may attempt to avert his gaze from an ad on the subway promoting the latest flavored vodka. Distraction involves limiting attentional resources by introducing a competing working-memory demand (e.g., Buhle, Stevens, Friedman, & Wager, 2012; Buhle & Wager, 2009; Kusaka, Heitlier, Schoeffler, Bunge, & Wessa, 2011; McRae et al., 2010). For example, the alcoholic may throw himself into a difficult problem at work when the urge to drink arises.

Cognitive change involves altering the way one thinks about an emotional stimulus so as to alter one's emotional response to it. This change may occur when generating an initial emotional response, as when expecting, beliefs, or moods influence one's appraisal of a stimulus, or subsequently, when one changes the way one thinks about the stimulus (Atlas & Wager, 2012; Buhle & Wager, 2010; Meinert et al., 2011). The most commonly studied exemplar of cognitive change is reappraisal, which involves reinterpreting the meaning of a stimulus, or mentally modifying the emotional relevance of it, in order to change subsequent emotional responses. Reappraisal is one of the most cognitively complex strategies, drawing on language and memory to reference semantic knowledge about the stimulus, working memory to maintain and manipulate appraisals, response selection to pick goal-congruent appraisals, and self-monitoring to ensure that one is reappraising successfully (Ochsner, Bunge, Gross, & Gabrieli, 2002; Ochsner & Gross, 2005).

Reappraisals themselves can be accomplished in a number of ways. Two of the most common subtypes are reinterpreting and distancing. Reinterpreting involves changing how one understands or "interprets" the emotion-dictating situation or stimulus (e.g., Ochsner et al., 2002). In the case of the alcoholic, he might think about how a beer contains many calories, and that turning down a drink will help him achieve his weight loss goals. Distancing involves changing one's personal connection to, or psychological distance from, the emotion-dictating stimulus (e.g., Ochsner et al., 2004). For example, the alcoholic facing a surging desire to drink may reduce the intensity of his emotional response by imagining himself as an objective friend viewing the situation from the outside.

Finally, response modulation strategies target the specific response or emotional behavior. The most commonly studied exemplar is expressive suppression (e.g., Goldin, McRae, Ramel, & Gross, 2008; Gross, 1998a; Hayes et al., 2010), which entails keeping the emotion in check so that an observer cannot detect that one is experiencing an emotion. Because expressive suppression only targets the final stage of the emotion-generations process, it influences emotional experience subdul, if at all (Davis, Seagosh, & Ochsner, 2009; Goldia et al., 2008). However, the effort expended during expressive suppression may increase physiological arousal (Gross, 1998a). Other forms of response modulation, such as expressive enhancement (Bonanno, Papa, Lalande, Wesphal, & Coifman, 2004; Jacobo, Malinowski, Larson, & Davidson, 2000) and expressive change, also exist, but they have received little attention in the neuroimaging literature that far.

The differences among these strategies may lead to differences in long-term efficacy and real-world use. For example, reappraisal, but not distraction, has been shown to have long-lasting effects on one's tendency to have an emotional response to a stimulus (Kross & Ayduk, 2008), presumably because only reappraisal involves an active change in how one represents the affective meaning of that stimulus. However, the active change induced by reappraisal requires engagement with the emotional content, which may be difficult or unappealing. One recent study showed that participants, when allowed to choose which emotion to moderate, preferred a reappraisal strategy to implement, typically used reappraisal in low-intensity negative situations but preferred the distraction-based strategy of distraction in high-intensity negative situations (Bauss, Scheibe, Suri, & Gross, 2011).

Neural Bases of Emotion Regulation

Over the last decade, functional imaging research in healthy human adults has provided tremendous insight into the nature of the source regions that implement regulatory strategies as well as the target systems that are acted upon during reappraisal. This section discusses core conclusions that can be drawn from reappraisal research and a general model of emotion regulation that can be derived from it.

Reappraisal as a Paradigm Case

Reappraisal is an appropriate starting point for developing a model of the cognitive control of emotion, for five reasons. First, because reappraisal is among the most cognitively complex strategies, a model of emotion regulation derived from reappraisal work may be generally applicable to relatively simpler strategies and phenomena. Second, the majority of neuroimaging studies to date have focused on reappraisal. Third, reappraisal is deeply engrained in our culture, as evidenced by countless well-known aphorisms reminding us that "life is what you make of it," "April showers bring forth may flowers," and "it all grist to the mill."

In contrast to other areas of emotion regulation research (see Extending the Model to Other Forms of Emotion Regulation, below) reappraisal studies tend to be more methodologically and conceptually similar to one another and thus provide a stronger base for mechanistic inferences. Finally, reappraisal is an important component of many therapeutic techniques, including cognitive behavioral therapy (Beck, 2005) and dialectical behavioral therapy (Lynch, Trist, Salmon, & Linehan, 2007). With these considerations in mind, we now review the neural systems that have been most consistently observed in studies of reappraisal (Ochsner & Gross, 2008).

Implementation of Reappraisal

Figure 4.18 schematically illustrates the brain systems shown by current research to be involved in the cognitive control of emotion via reappraisal, and Figure 4.2 plots peak activation foci for 43 studies (see Table 4.1) of reappraisal in healthy individuals. As these figures demonstrate, a great deal of evidence now supports the hypothesis that the cognitive regulation of emotion is implemented largely by the same frontospatial control regions that regulate memory, attention, and other thought processes (Ochsner et al., 2002). In this section we consider the possible roles in reappraisal of some of the most commonly observed regions, including dorsolateral prefrontal...
Table 6.1 Studies of Brain Systems Involved in Cognitive Control of Emotion via Reappraisal*

<table>
<thead>
<tr>
<th>Study</th>
<th>Participants</th>
<th>Goal</th>
<th>Valence</th>
<th>Tactic</th>
<th>Amygdala</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bevan et al., 2001</td>
<td>HYA</td>
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<td>Pos</td>
<td>Dist</td>
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</tr>
<tr>
<td>Domes et al., 2010</td>
<td>HYA</td>
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<td>Neg</td>
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<tr>
<td>Eippert et al., 2007</td>
<td>HYA</td>
<td>Both</td>
<td>Neg</td>
<td>Both</td>
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</tr>
<tr>
<td>Erik et al., 2010</td>
<td>HC</td>
<td>Dec</td>
<td>Neg</td>
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</tr>
<tr>
<td>Goldin et al., 2008</td>
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</tr>
<tr>
<td>Haerrski &amp; Humann, 2006</td>
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</tr>
<tr>
<td>Hayes et al., 2010</td>
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<td>Dec</td>
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</tr>
<tr>
<td>Herwig et al., 2007</td>
<td>HYA</td>
<td>Dec</td>
<td>Both</td>
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</tr>
<tr>
<td>Hoffmann et al., 2012</td>
<td>HYA</td>
<td>Dec</td>
<td>Pos (food)</td>
<td>Reint</td>
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</tr>
<tr>
<td>Ichikawa et al., 2011</td>
<td>HYA</td>
<td>Both</td>
<td>Neg (errors)</td>
<td>Reint</td>
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</tr>
<tr>
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<td>HYA</td>
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<td>Both</td>
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</tr>
<tr>
<td>Kim &amp; Humann, 2007</td>
<td>HYA</td>
<td>Dec</td>
<td>Both</td>
<td>Reint</td>
<td>Inc pos only</td>
</tr>
<tr>
<td>Kober et al., 2010</td>
<td>HYA smokers &amp; nonsmokers</td>
<td>Dec</td>
<td>Pos (food/ cigarettes)</td>
<td>Reint</td>
<td>Yes</td>
</tr>
<tr>
<td>Koenigsburg et al., 2010</td>
<td>HYA</td>
<td>Dec</td>
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</tr>
<tr>
<td>Kross et al., 2012</td>
<td>HYA</td>
<td>Dec</td>
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<tr>
<td>Kroo et al., 2009</td>
<td>HYA</td>
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<tr>
<td>Lang et al., 2011</td>
<td>HC</td>
<td>Both</td>
<td>Neg</td>
<td>Dist</td>
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<tr>
<td>Levenson et al., 2003</td>
<td>HYA</td>
<td>Dec</td>
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<tr>
<td>Mak et al., 2009</td>
<td>HYA</td>
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<tr>
<td>McRae et al., 2008</td>
<td>HYA</td>
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<tr>
<td>McRae et al., 2010</td>
<td>HYA</td>
<td>Dec</td>
<td>Neg</td>
<td>Reint</td>
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</tr>
<tr>
<td>McRae, Gross, et al., 2012</td>
<td>Healthy aged 10-22</td>
<td>Dec</td>
<td>Neg</td>
<td>Reint</td>
<td>No</td>
</tr>
<tr>
<td>McRae, Gross, et al., 2012</td>
<td>Divided</td>
<td>Dec</td>
<td>Neg</td>
<td>Reint</td>
<td>Yes</td>
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<tr>
<td>Modin et al., 2010</td>
<td>HYA</td>
<td>Dec</td>
<td>Neg</td>
<td>Reint</td>
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<tr>
<td>New et al., 2009</td>
<td>HC</td>
<td>Both</td>
<td>Neg</td>
<td>Reint</td>
<td>Yes</td>
</tr>
<tr>
<td>Ochsner et al., 2002</td>
<td>HYA</td>
<td>Dec</td>
<td>Neg</td>
<td>Reint</td>
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</tr>
<tr>
<td>Ochsner et al., 2004</td>
<td>HYA</td>
<td>Both</td>
<td>Neg</td>
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<tr>
<td>Ochsner et al., 2009</td>
<td>HYA</td>
<td>Inc</td>
<td>Neg</td>
<td>Both</td>
<td>Yes</td>
</tr>
<tr>
<td>Ochs et al., 2006</td>
<td>HYA</td>
<td>Dec</td>
<td>Both</td>
<td>Unclear</td>
<td>Yes</td>
</tr>
</tbody>
</table>

*Studies are ordered first by alphabetical order and second by year and are listed in the Reference section. Only studies that reported outcomes (e.g., not only functional connectivity or covariational analyses for psychologically healthy individuals) are included here. If a study included a patient sample but still reported results for its healthy adult controls separately, it was included. All studies used event-related designs except the two studies designated by * in the "Timing of reappraisal" column, which indicates that they used a block design. Also, for the attention type column, phrenological terms were drawn from the international affective neuroscience system unless otherwise specified. Unless noted, Participants: HYA = healthy young adult participants typically 18–39 years old. HOA = healthy older adults; participants typically aged 60 years or older. HC = healthy adult control participants matched to patients. Goal = goal pursued by participants to increase or decrease emotional responses. Dec = decrease, Inc = increase, Both = both increase and decrease conditions were used. Valence: positive = positive valued emotional stimulus, Neg = negative, Pos = positive, Both = both positive and negative stimuli were used. Tactic: positive = emotional stimuli used—disengaging or reinterpreting, Both = both disengaging and reinterpreting were used (this only applies to Ochsner et al., 2002; or participants were given choice of distancing or reappraising, Dis = because easier to for psychologically distant. Reap = cognitively reappraise related to either stimulus, where only = just prior to stimulus event and b = in the few seconds after stimulus onset. Amygdala: whether modulation of amygdala was reported.

Table 4.1 (Continued) Designs

<table>
<thead>
<tr>
<th>Study</th>
<th>Participants</th>
<th>Goal</th>
<th>Valence</th>
<th>Tactic</th>
<th>Amygdala</th>
</tr>
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<tr>
<td>Opitz et al., 2012</td>
<td>HYA &amp; HOA</td>
<td>Both</td>
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<td>Plaut et al., 2007</td>
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<tr>
<td>Pujol et al., 2011</td>
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<td>Schott et al., 2010</td>
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<td>Schulz et al., 2010</td>
<td>HC</td>
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<td>Neg</td>
<td>Both</td>
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<td>Sackinger et al., 2009</td>
<td>HYA</td>
<td>Dec</td>
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<td>Uey et al., 2006</td>
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<td>Bush</td>
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<td>Uey et al., 2009</td>
<td>HOA</td>
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<tr>
<td>van Beekum et al., 2007</td>
<td>HOA</td>
<td>Both</td>
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<td>Reint</td>
<td>Dec only</td>
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<td>Walter et al., 2009</td>
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<td>Wiscoff et al., 2010</td>
<td>HYA &amp; HOA</td>
<td>Dec</td>
<td>Both</td>
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cortex (dIPFC), inferior parietal cortex (IPC), dorsal anterior cingulate (dACC) and adjacent posterior medial prefrontal cortex (dmPFC), ventrolateral prefrontal cortex (vPFC), and anterior dmPFC. It is important to note that neuroimaging studies of reappraisal have varied along a number of experimentally significant dimensions, including tactics (reinterpretation or distancing), valence of stimuli and emotions elicited (positive or negative), and modulatory direction (decrease or increase), and a number of studies have even directly examined how altering these dimensions impacts neural responses during reappraisal. In keeping with the scope of this chapter, the present discussion will largely consider reappraisal as a whole, looking at general patterns that are consistent across these variations. We encourage the interested reader to see another review for a more thorough assessment of how parameters differences meaningfully influence patterns of neural recruitment (Ochsner, Silvers, & Bush, 2012).

Dorsolateral Prefrontal Cortex and Inferior Parietal Cortex Together, the dIPFC and IPC are believed to constitute a dorsal frontoparietal network for the
endogenous control of attention and working mem-
(Corbett & Shulman, 2002). While attention and working memory are supported by complex interactions between dACC and IPC, the precise roles they play in these processes are somewhat distinct. On the one hand, dACC appears to play a role in inhibitory control, while IPC is involved in working memory and attentional processes by maintaining goals (Peck, 2011) and monitoring the contents of working memory (Champod & Petrides, 2010). On the other hand, IPC appears to initiate shifts in attention to goal-relevant stimuli (Peck, 2012) and to manipulate components in working memory in accordance with goal states represented in dACC (Champod & Petrides, 2010). In the context of reappraisal, this network may be used to direct attention to reappraisal-relevant stimulus features, to hold in mind reappraisal goals, and to manipulate information during the construction of new appraisals.

**Dorsal Anterior Cingulate and Posterior Dorsomedial Prefrontal Cortex**

Neuroimaging and lesion research has broadly associated the dACC and posterior dmPFC with the initiation and maintenance of controlled pro-
cessing (Bush, Lau, & Paucor, 2000; Ochsner et al., 2001; Fass, 2001). In the most well-known models, dACC and posterior dmPFC direct con-
flicts, cross, or other performance signals, and may then call upon dACC to implement needed control (Botvinick, Braver, Carter, & Cohen, 2001; Botvinick, Cohen, & Carter, 2004; Gehring & Knight, 2000; MacDonald, Cohen, Stenger, & Carter, 2000; Miller, 2008; Miller & Cohen, 2001). In other models, dACC and posterior dmPFC do not play a role in monitoring but are directly responsible for activating and maintaining task rep-
resentations and goals (Stuss & Alexander, 2007). In the context of reappraisal, these regions might track the extent to which one's current reappraisal is changing emotional responses in the intended way and recruit dACC to improve or modify reappraisal processes as necessary (Denny, Silver, & Ochsner, 2009; Ochsner & Banett, 2001; Ochsner & Gross, 2004), or dACC and posterior dmPFC may serve to directly activate and sustain the task representations and goals that are needed to implement reappraisals.

An alternative view of the dACC and posterior dmPFC is that these regions help coordinate appropriate autonomic responses during emotion genera-
tion and regulation. When stimulated, the dACC is one of the few cortical areas that can cause changes in heart rate, respiration, and gastric motility (Bairns & Wynn, 1985; Hurley-Giua & Neafsey, 1986; Karda, Pilgrim, & Epstein, 1990; Pool & Rasmussen, 1989). In both animals and humans, dACC and posterior dmPFC lesions have been shown to alter cardiac and skin conductance responses to stimuli with learned affective and physiological significa-
tance as well as to decrease self-reporting of emo-
tional tasks (Buchanan & Pwll, 1982b; Naccache et al., 2005; Neafsey, 1990; Zahn, Graftam, & Tranel, 1995). Neuroimaging studies also suggest that dACC and posterior dmPFC mediate skin conductance responses to conditioned stimuli and are specifically involved in the acquisition of condi-
tioned aversive responses (Elidn, Egnor, & Kalder, 2011; Schilier & Delgado, 2010). Taken together, these data suggest that the dACC is important for controlling learned physiological responses and may therefore also be critical for modifying physiological responses in the context of reappraisal (e.g., reduc-
ing skin conductance responses to an aversive stim-
ulus that is being reappraised).

**Ventrolateral Prefrontal Cortex**

Left vPFC has been implicated in the selec-
tion of goal-appropriate responses and information from semantic memory (Bader & Wagner, 2007; Thompson-Schill, Bedny, & Goldberg, 2005) and in the production of speech (Bockhheimer, 2002; Huang, Caro, & Caro, 2002), including internal speech (Hinke et al., 1993; Huang & Huo, 2002). In the context of reappraisal, left vPFC may be used to deliberately select semantic elements needed to construct a new stimulus-appropriate, verbally
mediated reappraisal. We would expect this type of semantic selection to be especially important during reinterpretation, a reappraisal tactic that involves changing one's interpretation of the ele-
ments of the situation or stimulus that elicits emo-
tion. Conversely, we would expect less of a need for semantic selection during distorting, a reappraisal tactic that involves changing one's personal connection to, or psychological distance from, the stimulus that elicits emotion. In line with this psychological prediction, reinterpretation engages activity in left vPFC than does distancing (Ochsner et al., 2012).

Right vPFC has been implicated in the inhib-
ition of prepotent, goal-inappropriate responses (Aaron, Robbins, & Poldract, 2004; Kooshi et al., 1999; Lieberman et al., 2007; Ochsner, 2005). In the context of reappraisal, right vPFC may serve to inhibit one's initial appraisal in favor of a goal-congruent reappraisal. Consideration of the type of reappraisal implemented can provide a useful test of this hypothesized function. While decreasing an emotional response without altering its valence typically requires the inhibition of an initial appraisal and its replacement with a less negative alternative, increasing a response would typically only involve amplifying one's initial appraisal, and inhibitory demands should be lower. In keeping with this psychological interpreta-
tion, several studies that compared decreasing and increasing found greater right vPFC activation for the decreasing condition (Kim & Hamson, 2007; Ochsner et al., 2004; Urry, 2009), and this pattern seems to hold across the larger set of studies that have examined decreasing or increasing conditions separately (Ochsner et al., 2012).

**Anterior Dorsolateral Prefrontal Cortex**

Anterior dmPFC has been implicated in the reflec-
tion on and making judgments about the mental states of oneself and others (Amadio & Frith, 2006; Denaro, Kober, Wager, & Ochsner, 2012; Mitchell, 2009; Olson & Ochsner, 2008) (see Chapter 2 in this book). In the context of reappraisal, one pos-
ssibility is that anterior dmPFC might be important for both assessing the effect of one's initial appraisal on one's mental state and assessing one's new mental state following reappraisal. Alternatively, or perhaps additionally, anterior dmPFC might support atten-
tion to and elaboration of emotional states, inten-
tions, and outcomes of the individuals depicted in the photographic stimuli typically used in these studies. This second possibility is consistent with the predominance of anterior dmPFC in reap-
praisal tasks in which the goal is to increase emo-
tion (Ochsner et al., 2012). Of the 12 studies that directly compared increasing emotion to a control condition where participants responded naturally, 6 showed increases in anterior dmPFC (Domes et al., 2010; Ichikawa et al., 2011; Lang et al., 2011; Ochsner et al., 2004, 2009). Of the six that did not, most showed activation in neighboring areas (such as anterior cingulate and paracingulate cortex) (Eppert et al., 2007; New, Fan, et al., 2009; Pinkel, Bedard, Crowley, & Sibley, 2011; Schilier et al., 2010; Urry, 2009; van Reekum et al., 2007).

**Targets of Reappraisal**

In the previous section, we reviewed the regions believed to be responsible for the implementation of reappraisal. These regions can be thought of as targets of reappraisal. But what are the targets of this context? Given that reappraisal effec-
tively modulates self-reported emotional experience as well as other behavioral and physiological corre-
lations of emotion, we would also expect to see modula-
tion in regions involved in generating emotions. In this section, we review the putative target regions that have garnered the most attention in the reap-
praisal literature thus far, including the amygdala, ventral striatum, and insula. As described earlier, neuroimaging studies of reappraisal have varied along a number of dimen-
sions, including tactics, stimulus and emotional valence, and regulatory goals. Again, we will largely consider reappraisal as a whole, looking at patterns that cut across together these different task dimen-
sions. However, we will pay special attention to task differences that occur as a function of valence, as differentially valenced emotions can be expected to involve considerably different appraisal systems. For a more detailed discussion of the variability seen in different types of reappraisal tasks, we direct the interested reader to a recent review by Ochsner et al. (2012).

**Amygdala**

The amygdala is believed to support the detection and appraisal of stimuli relevant to one's current or chronic affective goals (Cunningham, Arduck, John, Mosner, & Middaful, 2011; Cunningham, Van Bavel, & Johnstone, 2008). While the amygdala most consis-
tently has been shown to respond to aversive stimuli such as punishments, fearful facial expressions, and negatively valenced films or images (Neta & Whalen, 2011; Vullersenti & Postoaj, 2007; Whalen et al., 2004), it has also been shown to respond to posi-
tive stimuli, such as rewards, as well as other forms of salience, context-relevant stimuli (Anderson, Christoff, Stappen, et al., 2003; Davis & Whalen, 2001; Hattit & Whalen, 2011; Phillips, 2000).

As can be seen in Figure 4.2B, many studies have reported changes in the amygdala as a consequence of reappraisal. These studies have most typically involved the reduction of negative affect, with a few studies examining, and showing, increases in the amygda when the goal was to increase an emotion or the valence was positive (see Table 4.1). Notably, the few cases in which the modulation of negatively valenced emotions resulted in amygdala modula-
tions were left-lateralized (Herwig et al., 2007; Ohira et al., 2006; Vricona, Sandor, & Vullersenti, 2011; Wiscooff, Lobs, Madden, Cahoon, & Hackett, 2010). While this is consistent with some older hypotheses about valence lateralization (Davidsson & Sutton, 1995), the imaging literature in gen-
eral has not borne this out (Sergerie, Chelousteg, &
Ventricul Striatum
The ventricular striatum is believed to be involved in learning the relationships between cues (ranging from social signals, such as smiling faces, to actions to abstract objects) and rewarding or reinforcing outcomes (Knauss & Cooper, 2005; O'Doherty, 2004; Schultz, 2007).

As can be seen in Figure 4.2B, a number of studies have reported changes in the ventricular striatum as a consequence of reappraaisal. With the amygdala, reappraisal of both positive and negative emotions has been shown to modulate the striatum. However, in contrast to the amygdala, changes in ventricular striatum have been less frequently for negative emotions and more frequently for positive emotions (Ochsner et al., 2012). That said, because only a relatively small number of studies have examined positively valenced emotions, it is far too early to draw firm conclusions. As noted above, an important future direction for reappraisal studies is to more thoroughly examine how valence influences regulatory targets.

Insula
The insular cortex has been theorized to represent a viscerotopic map of ascending inputs from the body (Mckinon & Meulam, 1982) that some believe is essential to negative affective experience in general (Craig, 2009; Wager & Feldman Barrett, 2004). Within the insula, more posterior regions are associated with the representation of sensations from the body, while more anterior regions have been linked to motivational and affective states, such as disgust, that have a strong visceral component (Augustine, 1996; Cahill, Lawrence, & Young, 2001; Critchley, Wiens, Rockenstein, Ohman, & Dolan, 2004; Nitschke, Srinivasan, Miehlkwich, Schaefer, & Davidson, 2006; Wager & Feldman Barrett, 2004). While several studies have reported target-related activity in the posterior insula, only a few studies have reported modulation in anterior insula. One possible explanation for this surprising dearth of findings in the anterior insula may stem from the proximity of this region to VPC regions involved in the implementation of reappraisal. Target regions are typically detected using the reverse contrast used to detect VPC regions. For example, a contrast between reappraisal and a passive-viewing, naturalistic response modality could be used to detect source regions that support the implementation of reappraisal, while the reverse contrast may be used to detect target regions that demonstrate reactivity. As described above and depicted in Figure 4.2A, VPC regions are often activated in the implementation of reappraisal. This increase in activity may overwhelm the activity that would otherwise be observed in adjacent portions of anterior insula.

Other Areas Involved in Reappraisal
Several other areas that appear to be involved in reappraisal do not fit neatly into the source-target dichotomy. One such area is the ventromedial prefrontal cortex (vmPFC), which has been proposed as both a source and target of reappraisal. We will review evidence in support of the hypothesis that modulation of these emotion-processing regions results from earlier modulation of semantic and perceptual representations in temporal and occipital regions known to support perceptual and semantic representations (see Figure 4.1B).

Ventricular Prefrontal Cortex
The vmPFC is hypothesized to integrate mem-
ory and sensory information about current and the medial temporal lobes, affective appraisals of specific stimuli formed by subcortical structures such as the amygdala and ventral striatum, and inputs from other regions that provide information about current and behavioral and motivational goals such as the brainstem and prefrontal cortex (Cunnigham, Johnson, & Wagner, 2011; Deutch, 2006; Fowlers, 2011; Murray, O'Doherty, & Schoenbaum, 2007; Ochsner et al., 2002; Ongur, Ferrari, & Price, 2003; Price, 1999; Raedtke & Murray, 2011; Schoenbaum, Ullsperger, Liu, & D'Esposito, 2011). As such, vmPFC activity may scale with the affective value one attributes to a stimulus in a situational and goal-dependent manner (Oya et al., 2005; Roy, Shankman, & Wager, 2011; Schoenbaum, Dordick, & Stalnaker, 2007; Schoenbaum et al., 2011). Examples of how this includes affective learning, including fear extinction and reversal learning, the finding that vmPFC response to an image of a healthy food is modulated by whether one has the goal to eat healthily (Hare, Cameron, & Rangel, 2009), and the view that vmPFC lesions lead to context-in-
appropriate affective responses in both humans and animals (Beer, Heyerd, Kizil, Scabini, & Knight, 2003; Dumas, 1994; Murray et al., 2007).

In order to understand the functional role that these temporal regions play in reappraisal, at least three issues need to be addressed. First, there is the issue of how consistently these regions are recruited across different types of emotion regulation. It makes theoretical sense that such regions would be important for reappraisal given that reappraisal involves changing the meaning of a stimulus. However, it is less clear whether other regulatory strategies that do not involve changing the meaning of a stimulus might rely on such areas. The fact that direct comparisons between reappraisal and distraction have shown that the two strategies differentially recruit posterior temporal cortex (reappraisal relies on these regions more) supports the notion that activity in this region may differ across regulatory strategies (Kanske et al., 2011; McRae et al., 2010).

Second, there is the question as to what cognitive process or processes are driving activation of these temporal regions. Greater activity might reflect increased attention to perceptual and semantic aspects of stimuli. Alternatively, greater activity may reflect increased retrieval of alternative interpretations of reappraised stimuli, or the process of actively restructuring one's mental image of the stimulus. Future work should attempt to distinguish among these possibilities.

Third is the question of how these temporal regions fit into the neural model of emotion regulation described earlier and depicted in Figure 4.1B. One possibility is that they play an intermediary role between prefrontal control systems and affec-

tive appraisal systems (Ochsner et al., 2002, 2012). According to this view, PFC and parietal regions could change one's mental representation of a stim-
ulus's meaning from the top down, directly alter-
ing perceptual and semantic processing, and then affect the temporal regions. This reappraised representation in turn feeds forward to the amygdala and other structures that trigger affective responses. Because the amygdala now "sees" the reappraised stimulus, its response changes. While consistent with the existing data, these hypotheses have yet to be directly tested.

Extending the Model to Other Forms of Emotion Regulation
The majority of functional imaging studies of emotion regulation have focused on reappraisal. That said, the other four main classes of emotion reg-

ulation strategies diagrammed in Figure 4.1A have been targeted by imaging studies to vmPFC's role in these. Given the robustness of the neurocognitive model
depicted in Figure 4.1B in accounts for reappraisal, the question naturally arises as to whether this model can be generalized to account for other types of emotion regulation strategies. Here, we briefly discuss each of the four other classes of regulation, using the model derived from reappraisal as a starting point for analysis.

SITUATION SELECTION AND MODIFICATION

As discussed above, situation-focusing strategies are effective in certain situations (Davis et al., 2011), they are difficult to study in a neuroimaging context, so little is known about the neural processes involved in humans. In the rodent literature, a typical avoidance conditioning paradigm consists of a rat learning to perform an action that allows it to avoid or remove the presentation of an aversive stimulus (Everitt et al., 1999; LeDoux & Gorman, 2001). In a handful of studies examining avoidance conditioning in humans, it has been shown that avoidance conditions differ in VFCP and IFPC regions of the control system and modulates the amygdala (Delgado, Jou, Ledoux, & Phelps, 2009; Prevost, McCabe, Jessup, Bossaerts, & O’Doherty, 2011; Schlund & Catallol, 2010; Schlund et al., 2010). These findings provide preliminary evidence for the notion that situation selection may depend on systems relevant for maintaining regulatory goals and selecting context-appropriate avoidance responses.

ATTENTIONAL DEPLOYMENT

In comparison to situation selection and modification, there have been numerous human neuroimaging studies of attentional deployment, second in number only to studies of reappraisal. As described above, such research can be broken down into two types of studies. The first type involves the use of selective attention to shift visual-spatial attention away from an affectively valenced stimulus or stimulus attribute and toward a neutral one. The second type focuses on the use of distraction to shift the focus of attention away from an affective stimulus and onto some internally maintained mental representation (e.g., a relevant working memory load, self-generated stimulus-irrelevant thoughts, a pleasant mental image). As has been suggested elsewhere (Busch, Wigger, & Stel, 2010; Oudekerk & Groes, 2005), interpretation of results found in both types of studies is challenged by three issues. First, the vast majority of selective attention studies, and many studies of distraction, use stimuli that do not elicit strong emotional responses, such as facial expressions of emotion. As such, these studies are concerned with the regulation of evaluative judgment or perception rather than with affective responding per se. Second, among the studies that have used highly arousing and affect-inducing stimuli, the stimulus of choice has almost always been physical pain. While the experience of pain has a strong negatively valenced affective component, this component may itself have a distinct neural signature that depends in part on dedicated pain-specific neural pathways (Apathy, Bushnell, Treede, & Zubieta, 2005; Tracey & Manary, 2007). Whether or not regulation of pain is similar to or different from the regulation of negative affective responses more generally remains an empirical question in need of testing. Third, attentional deployment studies tend to be highly heterogeneous, often employing very different methods of controlling the focus and level of attention, often without a clear or consistently defined dependent variable for how well attention was controlled. Despite these limitations, it is worth noting that the control systems and modulation of affect systems (like the amygdala) are often (but not always) reported.

RESPONSE MODULATION

Only two imaging studies have examined response modulation (Goldin et al., 2008; Hayes et al., 2010). Both focused on expressive suppression, the ability to hide behavioral manifestations of emotion (Cozolino, 1998a), asking participants to suppress facial expressions of disgust elicited by a film clip (Goldin et al., 2008; Hayes et al., 2010). Both studies found that expressive suppression activated dorsolateral and ventrolateral PFC regions associated with maintaining goals, response selection, and inhibition (Aron et al., 2004; Badre & Wagner, 2007; Thompson-Schill et al., 2005), and it activated the insula, which is involved in the formation of affective responses. Amygdala findings were more mixed, however, with one study reporting increases (Goldin et al., 2008) and one reporting decreases (Hayes et al., 2010) in activity during suppression. Increases in insula and amygdala fit with psychophysiological studies demonstrating that expressive suppression enhances autonomic measures of emotional responding (Cozolino, 1998a).

In total, the available literature on emotion regulation strategies other than reappraisal is in some cases limited and in other cases somewhat confusing, but in general it supports the idea that all emotion regulation strategies depend on interactions between cognitive control and affective-generative regions.

Emotion Regulation in Development, Aging, and Psychopathology

The first goal of this chapter was to review and synthesize current functional imaging research on emotion regulation in healthy adults. Another important direction for emotion regulation research is the translation of basic findings to special populations. Two domains in which this will probably play particularly significant is understanding (1) how our emotional lives evolve as we grow from childhood through adolescence into adulthood and old age, and (2) how emotional reactivity and regulation are impacted in psychopathology.

Development of Emotion Regulation

There is growing evidence that childhood and adolescence are critical times for development of the emotional regulatory abilities needed to adaptively balance affective impulses and the deleterious health behaviors they can promote. Demands for self-regulation are high in adolescence in particular as individuals experience increased independence, hormonal changes, and a changing social environment (Bakermans-Kranenburg, 2008; Casey, Gere, & Galvan, 2008; Samara, Jones, & Casey, 2010). Most individuals successfully navigate the challenges of adolescence by developing regulatory skills that will help them cope with stresses for the rest of their lives. However, for some individuals adolescence marks the beginning of a lifelong struggle with emotion regulation and mental and physical health. Not only does the peak age of onset for mental illness occur during adolescence (Keeler et al., 2005), but lifelong problems with alcohol and substance abuse, obesity, and eating disorders (Alldao, Nolen-Hoeksema, & Schweitzer, 2010; Baumesiter & Heatherton, 1996; Chandler, Fleckser, & Volkow, 2009; Gupta, Zachary Rosenbluth, Mancini, Cheavens, & Lynch, 2008; Herman, Pories, Lask, & Heatherton, 1987; Houwen & Wiers, 2009; Volkow et al., 2010) often have their origins in adolescence. Thus a critical question is how emotion regulatory mechanisms develop during adolescence when individuals are at greatest risk for developing maladaptive patterns of emotional regulation and unhealthy behaviors.

While a considerable number of behavioral studies have suggested that, on average, adolescents experience more extreme affect (both positive and negative) and more variable mood states in their everyday lives than do adults (Lansoo, Calkszenhimalyi, & Gaal, 1980; Larson, Moeser, Richards, & Wilson, 2002; Larson & Richards, 1994), this work has been somewhat contradictory regarding the reasons for these data. For example, this work does not make clear whether emotional reactivity decreases linearly from childhood to adolescence to adulthood (Carry, Hones, Apter, Edge, & Gross, 2010; Murphy, Eisenberg, Fabes, Shepard, & Guthrie, 1999) whether it changes in a quadratic fashion, with emotionality being higher in adolescents (Casey et al., 2008, 2010) or whether it is both linear and quadratic in nature (Larson et al., 2002; Thomas, De Bellis, Graham, & LaBarr, 2007) (see Figure 4.3).

To address this issue, studies would need to disentangle the developmental trajectories of emotional reactivity and regulation. To date, however, few studies have done so (for notable exceptions, see Murphy et al., 1999; Silk, Steinberg, & Morris, 2003), which makes it difficult to determine whether age-related differences in emotional reactivity are due to differences in bottom-up emotional reactivity or top-down emotion regulation. That said, reappraisal has been examined in limited age groups (Casey et al., 2010; Levenson et al., 2004; Moore, Mitchel, & Zeiss, 1976; Pinkel et al., 2011), with two studies comparing emotional...
reactivity (baseline responsiveness to affective stimuli) and regulation success (the ability to use regulatory strategies to modulate emotional responses) in individuals at the beginning, middle, and end of adolescence (Carneset et al., 2012; Silvers et al., 2012). Both of these studies found that emotional reactivity remains relatively constant across adolescence while regulatory success improves.

Imaging studies have just begun to address the reactivity-regulation issue using a combination of structural and functional methods. In general, what has been most studied under this two-kind of findings, the first from studies of emotional reactivity and the second from studies of the development of control systems. First, volumetric MRI studies indicate that the amygdala increases in size during puberty, with some studies concluding that these changes occur rapidly at the beginning of adolescence before tapering off (Ortby et al., 2009), and others reporting less steady linear increases over the course of adolescence (Giedd et al., 1996; Schumann et al., 2004). These structural findings may help to explain why in functional imaging studies adolescents are particularly sensitive to the motivational properties of affective stimuli (Casey et al., 2006). They show that while the ventral striatum and amygdala respond to the receipt of rewards (Ernst et al., 2005; Galvan et al., 2006; Geyer, Tervoort, Töttösch, Melavou, & Luna, 2009; van Leijenhorst, Crane, & Bunge, 2006; van Leijenhorst et al., 2010) and perception of fear faces (Hare et al., 2008; Killgore & Yurgelun-Todd, 2001, 2003; Monks et al., 2003; Thomas et al., 2001), respectively. Second, there is evidence of structure-function-behavior relationships in “cold” forms of cognitive control (such as working memory and response inhibition) during adolescence. These studies have shown that prefrontal control systems mature later than subcortical systems, with FPC white matter increasing linearly throughout adolescence (Barnea-Goraly et al., 2005; Giedd et al., 1999; Pfefferbaum et al., 1994) and pruning of FPC gray matter starting around puberty and continuing into one’s 20s (Gogtay et al., 2005). Strikingly, these structural changes are paralleled by improved performance on control tasks, with performance improvements correlating with decreases in functional connectivity (Barnea-Goraly et al., 2005; Giedd et al., 1999; Pfefferbaum et al., 1994) and pruning of FPC gray matter starting around puberty and continuing into one’s 20s (Gogtay et al., 2005). Strikingly, these structural changes are paralleled by improved performance on control tasks, with performance improvements correlating with decreases in functional connectivity (Barnea-Goraly et al., 2005; Giedd et al., 1999; Pfefferbaum et al., 1994). Building on these findings, current studies have aimed to examine emotion-regulation processes in adolescence in two ways. First, studies of selective attention have shown that children and adolescents are more susceptible to the influence of affective stimuli than adults, showing age-related inverted-U shaped response patterns in PFC regions known to support emotional regulation (Elliott et al., 2009), along with declines in performance on “cold” cognitive control tasks (e.g., response inhibition) that depend on these regions (Park & Reuter-Lorenz, 2009). How might we reconcile these two observations?

In comparison to younger adults, older adults report less negative affect and show reduced autonomic and amygdala responses to aversive stimuli (Levenson, Carstensen, & Gotman, 1994; St. Jacques, Beuette-Symons, & Cabeza, 2006; Tiit, Levenson, & Carstensen, 2000). Given that the amygdala is structurally intact during aging and that age-related decreases in amygdala activity are often accompanied by enhanced prefrontal control activity (Nashio, Sakai, & Matsumoto, 2012), some investigators have suggested that age-related decreases in negative affect may be driven by the use of top-down regulation strategies. Supporting this notion is the fact that age-related bias toward reporting more positive and less negative emotion in response to stimuli is stronger for low-arousal stimuli for which top-down appraisal processes may play a greater role in generating and regulating emotional experiences (Seissel & Kummeln, 2011). While this evidence is suggestive, only two studies have directly examined whether there are age-related changes in emotional regulation of the amygdala. One found that older adults could successfully decrease amygdala responses to both positive and negative stimuli compared with young adults (Winocur et al., 2010). The other reported no baseline amygdala responses in old or young adults (Opitz, Rauchs, Terry, & Urry, 2012), so regulatory effects could not be examined.

While older adults report that they regularly use reappraisal (Gross et al., 1997), several experimental studies have suggested that they are actually less able to do so (Ochsner & Gross, 2001; Ochsner, Gabrieli, & Gross, 2004; Shiffman, 2007; Silvers et al., 2012). Consequently, another study found that while older adults were unable to effectively use reappraisal to dampen their negative affect, they were able to use reappraisal to improve their positive affect (Opitz et al., 2012). Given that anterior dmPFC has been implicated in regulation of emotion in prior work (Ochsn et al., 2004), we suggest that older adults may be better at reappraising when the reappraisal goals rely on dmPFC-supported processes, in comparison to when reappraisal goals rely on processes supported by dorsal and lateral PFC. Indeed, both older and younger adults recruit dmPFC to a similar degree in several tasks known to involve this area, including making self-referential (Gutman, Kansinger, & Schacter, 2007) or semantic (Richey, Beuette-Symons, Hayes, & Cabeza, 2011) judgments about valenced stimuli, and more generally when viewing positive stimuli (Kensinger & Schacter, 2008; Leclerc & Kansinger, 2008, 2011). Consistent with these hypotheses, two neuroimaging studies of reappraisal in older adults have shown widespread dmPFC activity accompanied by impaired ability to decrease negative emotion (Opitz et al., 2012; Winocur et al., 2010). Furthermore, one of these studies found that activity in a DACC region adjacently to dmPFC in older adults was associated with greater success at increasing negative emotion (Opitz et al., 2012). Taken together, this week suggests that older adults have preserved reappraisal abilities when reappraising using a positivizing tactic or when the reappraisal goal is to increase emotion. However, it also may be the case that older adults struggle to reappraise when asked to use tactics and follow goals that are not consistent with their chronic regulatory tendencies or to draw upon coping strategies that require working memory and response selection processes involved in neutralizing negative emotion that are supported in lateral PFC.

Emotion Regulation in Psychopathology

A second important goal for translational research will be to understand how prefrontal function in the mechanisms of emotion generation and regulation may underlie various forms of psychopathology. This translational direction is being pursued in studies of reappraisal in healthy volunteers with and without disorders (Kendler et al., 2007; Lang et al., 2011; Schachtel et al., 2010; Silvers, Buell, Ochsner, 2011; Silvers et al., 2012).
et al., 2010), to depression (Erk, Mikulich, et al., 2010; Heller et al., 2009) Johnstone et al., 2007) to anxiety disorders (Gould, Manber, Hakimi, Casti, & Gross, 2009; Goldin, Manher-Ball, Werner, Heimberg, & Gras, 2009), including phobia (Herrmann et al., 2009) and post-traumatic stress disorder (Lang et al., 2011; New, Fan, et al., 2009). In the next section of this chapter, we will highlight the research findings to date on the neural bases of emotion regulation in each of these disorders.

**Borderline Personality Disorder**

Emotional instability, particularly in the context of interpersonal relationships, is one of the hallmarks of borderline personality disorder (BPD) ( Gunderson, 2007; Gunderson & Lyons-Ruth, 2008). Not only is this instability a trademark feature of BPD, it is also one of the most deconstructive aspects of this disorder in that it is associated with suicidality, extreme anger, and feelings of emptiness (Koonsingberg et al., 2003; Lindhan, 1993). Structured MII research has linked this tendency to experience heightened emotional reactivity to decreased amygdala and thalamus volumes, regions associated with emotional responding, as well as reduced ACC volumes, a region associated with emotion regulation (Nunes et al., 2009; Ruch et al., 2003; Schmahl, Vermetten, Etinga, & Douglas Bennaim, 2003; Soffot et al., 2012; Tebar et al., van Elle et al., 2003). Building on these findings, (MRI studies have found that individuals with BPD show exaggerated amygdala responses during pre- ventive viewing of emotional stimuli (Donegan et al., 2003; Herpette et al., 2001; Koonsingberg, Siever, et al., 2009; Menningen, Fan, New, Tang, & Siever, 2007; Schnell, Dierich, Schnitter, Daumann, & Herpette, 2007) and atypical prefrontal recruitment during cognitive control tasks (New, Hazlett, et al., 2007; Silverberg et al., 2007; Vollen et al., 2004; Wingfeld et al., 2009).

At present, three studies have assessed the neural correlates of reappraisal in individuals with BPD. While these studies differed in terms of stimulus type (pictures versus emotional scripts), reappraisal goal (increase vs. decrease), and reappraisal tactic (reinterpretation vs. distancing), they all agree that the basic pattern of results is similar: individuals with BPD did not differ from healthy controls on behavioral measures of baseline emotional reactivity or reappraisal success (Koonsingberg, Fan, et al., 2009; Lang et al., 2011). The second, somewhat contradictory pattern, is that in comparison to healthy controls, during reappraisal individuals with BPD showed both heightened amygdala and responses and diminished recruitment of cortical regions involved in cognitive control, including dIPFC, VMPFC, and, to a lesser extent, dACC and anterior dmPFC (Koonsingberg, Fan, et al., 2009; Lang et al., 2011; Schulte et al., 2010). This work has suggested that the tendency to have difficulty in recognizing and expressing emotions, exist in BPD (Beerebam, 1996; Domes, Grab, Köchendoerfer, Heinrichs, & Herpette, 2011) and that high alexithymic traits are also associated with diminished activity in dACC and anterior and posterior dmPFC during mentalizing and emotional interference tasks (McRae, Reitan, Forn, Chen, & Laire, 2008; Morgul et al., 2006, 2007). Taken together, these behavioral and imaging findings suggest that individuals with BPD are less adept than healthy controls at self-monitoring and making online evaluations of reappraisal success and, perhaps, their own emotions more generally.

**Major Depressive Disorder**

Major depressive disorder (MDD) is characterized by prolonged, diathetic mood as well as disrupted motivation, thought (McDermott, Drossard, & Todd, 1997). To date, a central focus of neuroimaging research on MDD has been evaluating whether MDD symptomology is caused by a bottom-up enhancement of responses to negative stimuli, diminished responses to positive stimuli, impaired top-down regulatory ability, or some combination of these three. In keeping with these ideas, IMI work has suggested that individuals with MDD exhibit (1) atypical resting-state activity in anterior dIFC and visual cortex (Kahn & Gallina, 2013), as well as (2) enhanced amygdala and (3) diminished striatal responses to emotional stimuli (Delvecchio et al., 2012; Hamilton et al., 2012). Structural studies also are generally consistent, with two recent meta-analyses showing that individuals with MDD show diminished hippocampal, prefrontal, and orbitofrontal volumes in comparison to healthy controls (Madden, Mano, Munafò, & Anderson 2012; Kempton et al., 2011). Somewhat confusing, however, is a separate meta-analysis focusing specifically on the amygdala, which found that amygdala volumes were reared for individuals with MDD on medication relative to healthy controls but diminished for unmedicated individuals with MDD relative to healthy controls (Hamilton, Stenchever, & Gotth, 2008). These results raise questions about the relationships between structural volumes and functional responsivity that have yet to be resolved.

With this somewhat cloudy picture as a backdrop, it becomes clear that many of the studies on depression and reappraisal in depression. While these studies examined different reappraisal tactics (reinterpretation vs. distancing), goals (increase vs. decrease emotion), and emotional valence (positive vs. negative), three general trends have emerged. First, individuals with MDD do not differ from healthy controls on behavioral measures of reappraisal success (Beeregam, Paquette, & Levesque, 2006; Erk, Mikulich, et al., 2010; although in one study individuals with MDD reported that it was more difficult to reappraise than did healthy controls (Barresi et al., 2010). Second, regulation of subcortical circuits to affective stimuli is impacted by MDD, with one study finding that individuals with MDD fail to sustain ventral striatal responses during up-regulation of positive emotion (Heller et al., 2009), another finding that they show enhanced amygdala responses during down-regulation of negative affect (Beeregam et al., 2006), and yet another finding that individuals with MDD do not show enduring reappraisal-related modulation of the amygdala (Erk, Mikulich, et al., 2010). Third, in three out of the four studies that compared neural responses in a reappraise "respond naturally" contrast in individuals with MDD and healthy controls, depressed individuals recruited larger swaths of PFC during reappraisal than did healthy controls. This suggests less efficiency during emotion regulation in individuals with MDD (Beeregam et al., 2006; Johnstone et al., 2007; Light et al., 2012). Fourth, all studies that examined prefrontal-subcortical interactions found that functional connectivity between the PFC and the amygdala (Erk, Mikulich, et al., 2010; Johnstone et al., 2007) or ventral striatum (Heller et al., 2009) in individuals with MDD was either diminished or showed an opposite pattern of what was observed in healthy controls.

**Phobias, Anxiety Disorders, and PTSD**

State anxiety may be defined as a feeling of agitation or anxiety or arousal caused by the perception of a real or imagined threat (Amatruda, 2008). In anxiety disorders (AD), specific (e.g., social anxiety disorder [SAD]), and some post-traumatic stress disorder (PTSD) or varied (e.g., generalized anxiety disorder [GAD]) triggers chronically activate this anxious state (American Psychiatric Association, 1995). Within this framework, our model of emotion regulation, AD may represent an inability to accurately appraise what is threatening, an inability to reappraise threat, or both.

In support of the appraisal possibility, relatively greater activation of the insula and amygdala has been shown in response to negative or threatening social stimuli across different types of AD (Eskin & Wagner, 2007). These relatively small hyperactivations have been observed in response to negative emotional facial expressions (Blair et al., 2008; Evans et al., 2008; Goldin, Manber, et al., 2009; Klump, Austad, & Phan, 2012; Lausch et al., et al., 2010), during a speech preparation task in individuals with SAD (Lobesbaum et al., 2004), to trauma-themed pictures and scripts for individuals with PTSD (Simmons & Matthews, 2012), and to photogenic stimuli for individuals with spider phobia (Alpers et al., 2009; Caesars et al., 2010; Dilger et al., 2003; Goossens, Schreurs, Peters, Gries, & Sannert, 2007; Larson et al., 2006; Lipka, Milner, & Straub, 2011; Schleier, Schafer, Walter, Stark, & Vaitl, 2005; Schwenckeldecker et al., 2011; Straube, Mentzel, & Milten, 2006; Wendt, Lotze, Weis, Hosten, & Hamm, 2008). It should be noted, however, that a reappraisal-related activity is somewhat different for PTSD than for other ADs in that most ADs are associated with hyperactivation of the insula whereas PTSD is not, nor is PTSD associated with hyperactivation of the entire amygdala, but rather only more ventral portions (Eskin & Wagner, 2007).

GAD is unusual in its lack of specificity for what produces anxious feelings, and it is for this reason that some neuroimaging studies have found anticipation or viewing of fear-related stimuli to elicit greater amygdala responses in GAD (Eskin & Schanberg, 2011; McClare et al., 2007; Nitschke et al., 2009), while others have found no differences in amygdala responses between individuals with GAD and healthy controls (Palm, Elliott, Dockin, & Anderson, 2011). Still others have observed hyporeactive amygdala responses in GAD (Blair et al., 2008).

In summary, inappropriate threat appraisals in AD may be defined as a feeling of agitation or anxiety or arousal caused by the perception of a real or imagined threat (Amatruda, 2008). In anxiety disorders (AD), specific (e.g., social anxiety disorder [SAD]), and some post-traumatic stress disorder (PTSD) or varied (e.g., generalized anxiety disorder [GAD]) triggers chronically activate this anxious state (American Psychiatric Association, 1995). Within this framework, our model of emotion regulation, AD may represent an inability to accurately appraise what is threatening, an inability to reappraise threat, or both.
SUMMARY OF TRANSLATIONAL FINDINGS

Taken together, the translational work to date emphasizes the need to evaluate emotion regulation in development, aging, and psychopathology using converging evidence from the behavioral and fMRI literatures. In doing so, we have already made great strides toward identifying how emotional reactivity and regulation impacts the structure and function of the brain. While much more work still needs to be done, it is clear that breakdowsins in prefrontal control systems and subcortical affective appraisal systems contribute to regulatory failures in the young, the elderly, and the neurologically ill, there is still a need to carefully and precisely characterize the nature of these breakdowsins on a population-by-population basis. Additionally, when looking between these populations that are well-characterized, there is a need to understand why they differ. For example, why does more prefrontal recruitment result in diminished regulatory success in some cases (e.g., MDD) while less recruitment results in diminished regulatory success in other cases (e.g., BPD)? This is just one of many questions that have yet to be fully addressed by translational emotion regulation work.

Summary and Future Directions

The overarching goal of this chapter has been to review and synthesize current functional imaging research on emotion regulation and to apply it to development, aging, and psychopathology. In the first part of this chapter, we outlined a basic model of the processes and neural systems that support emotion generation and regulation. At its core, this model specifies how prefrontal, cingulate, and parietal control systems modulate activity in affective appraisal regions as well as oculomotor/preparatory regions involved in semantic and perceptual representations. Such dynamics may differ across regulatory contexts as a function of one’s goal, tactic, and the nature of the stimulus and emotions being regulated (Ochsner et al., 2012).

With this model in place, the second part of this chapter sought to translate the model to constrain and interpret findings on emotion regulation in development, aging, and clinical populations. This approach is critical both for understanding the mechanisms underlying normal variability and for testing the boundaries of our basic model of emotion regulation.

While this chapter sought to clarify and synthesize our existing knowledge about basic and applied aspects of emotion regulation, it is important to note the limitations of our current knowledge. On the basic side, four questions stand out. First, more direct comparisons of emotion regulation paradigms in terms of goals, tactics, and stimulus types are needed to clarify the basic mechanisms underlying emotion regulation. Second, additional work is needed to determine what roles the brain systems supporting prefrontal play in the biocultural phenomena such as emotional engagement and situational assessment and modification. Third, it will be essential to not only refine our understanding of the distinctions between these breakdowsins on a population-by-population basis. Additionally, when looking between these populations that are well-characterized, there is a need to understand why they differ. For example, why does more prefrontal recruitment result in diminished regulatory success in some cases (e.g., MDD) while less recruitment results in diminished regulatory success in other cases (e.g., BPD)? This is just one of many questions that have yet to be fully addressed by translational emotion regulation work.


