

## Chapter 14

# Emotion regulation across the life span

CHELSEA HELION, SYDNEY M. KRUEGER, AND KEVIN N. OCHSNER\*

*Department of Psychology, Columbia University, New York, NY, United States*

### Abstract

Being able to flexibly regulate one's emotions is critical for adaptive functioning across the life span. The importance of emotion regulation for human cognition has been reflected in the marked increase in the amount of psychologic research on emotion and its regulation in the past two decades. In this chapter, we review theoretical and empirical advances in this research, with a particular focus on the neural bases of emotion regulation. We begin with a brief overview of the field at present and provide a general primer on the behavioral and neuroimaging methods used to study emotion regulation. We then outline the brain regions involved in both triggering and modulating affect, and how they may change throughout development and into old age. Finally, we conclude with a roadmap for the future study of emotion regulation, in particular focusing on how to integrate measures with high ecologic validity (e.g., experience sampling, social emotion regulation) with neuroimaging techniques.

Humanity's capacity to experience—and desire to express—emotion has inspired some of our greatest cultural achievements. From the misery of Picasso's *Guernica*, Romeo's love for Juliet, to Michael's betrayal of Fredo in *The Godfather*, artistic portrayals of the complexity of affective experience are deeply moving and very popular. However, all are also examples of unrestrained emotion leading to unwanted outcomes, as the world's bloodiest wars, most heart-breaking love stories, and deepest regrets are often the result of unchecked emotion gone awry. Given the importance of emotion and the need for its regulation, it is not surprising that the study of emotion regulation has grown exponentially within the past 20 years (Gross and Barrett, 2011; Webb et al., 2012). With the advent of new neuroimaging technologies coupled with advanced analytic techniques, psychologists and neuroscientists have been able to visualize and explore the neural and physiological bases of affective experience and regulation like never before.

In addition to an emphasis on new techniques, there also has been a marked push to study emotion regulation

as it unfolds/develops across the life span (John and Gross, 2004). While most existing research has focused on young adulthood, each stage of human development is characterized by a unique set of socioaffective challenges coupled with physical changes in brain structure and connectivity. With this in mind, psychologists have begun to examine the cognitive and affective processes underlying what successful emotion regulation means at different life stages. This research begins at infancy, finding that early life stress has a meaningful and detrimental influence on prefrontal–subcortical circuitry and regulatory ability (Tottenham et al., 2010; Gee et al., 2013). Another key time period is the transition from childhood to adolescence, when individuals are more sensitive to reward and threat cues but are less able than adults to effectively engage control circuitry (Casey and Jones, 2010). On the other end of the life span, the brain in healthy aging adults undergoes dramatic changes in structure and function in the latter stages of life. The frontal lobes of healthy older adults (ages 60–91) without any signs of Alzheimer's disease or dementia undergo brain atrophy of 0.5% a year (Fjell et al., 2009).

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\*Correspondence to: Kevin N. Ochsner, B.A., M.A., Ph.D., Professor and Chair, Department of Psychology, Columbia University, 1190 Amsterdam Avenue, 369 Schermerhorn Hall, New York, NY 10027, United States. Tel: +1-212-851-9348, Fax: +1-212-854-3609, E-mail: ochsner@psych.columbia.edu

However, despite cognitive decline and cortical thinning in brain regions known to be important for regulation, older adults display greater levels of emotional stability (Carstensen et al., 2000) and report more positive affect in advanced ages (Carstensen et al., 2011), which presents a paradox for regulation researchers—how do elderly individuals manage to do more with seemingly less?

In this chapter, we review advancements that have occurred in the study of emotion regulation within the past decade. We begin with an overview of existing theories of emotion and emotion regulation. We then explore how a converging methods approach (i.e., brain and behavior) has refined these theories and given us new insights into the neural bases of emotion generation and regulation. At each point, we review the existing developmental, young adult, and aging research. Finally, we conclude with where we think the study of emotion regulation is going next and the big questions that remain unexplored.

## WHAT WE TALK ABOUT WHEN WE TALK ABOUT EMOTION REGULATION

One of the most generative models of emotion regulation has been Gross's PROCESS model (1998), which describes six classes of regulatory strategies in terms of the stage of the emotion generation sequence that they impact. These six classes are known as: situation selection, situation modification, attentional control, cognitive change, and response modulation (Gross, 1998; Gross and Thompson, 2007). To date, the most commonly studied forms of regulation have been attention selection, reappraisal, and response modulation (Silvers et al., 2014a), in part because of the relative ease with which they can be studied behaviorally in the laboratory and in part because of the availability of cognitive neuroscience models of their underlying psychological processes (e.g., Ochsner and Gross, 2005; Ochsner et al., 2012). The following paragraphs briefly cover the existing behavioral research that has examined these strategies and their trajectories over the life span.

### Attentional control

Imagine for a moment that you have been asked to give the toast at a close friend's wedding. You've been planning what to say for weeks. Should the toast be funny or serious? Do you share a lengthy college story, or keep it short and sweet? While everyone else seems to be enjoying the reception, you are filled with anxiety about what you will say and how it will be received. To regulate this anxiety, you decide to take out your phone and scroll

through news highlights and check social media. This is an example of a class of strategies that involve controlling the focus of attention, in this case, selectively shifting the focus of one's attention away from the emotion-inducing toast. Individuals tend to favor attentional control when emotional intensity is high, as a way of curbing one's affective response before it gets out of hand, though it may be less effective than reappraisal as a long-term regulation strategy because it may fail to cause changes in the mental representation—and emotional potency—of a stimulus (Ayduk and Kross, 2010; Sheppes et al., 2011). Common tasks used to assess attentional control as a form of emotion regulation include the affective Stroop (Gotlib and McCann, 1984; Hwang et al., 2014), the affective go/no-go (Hare et al., 2005, 2008), and mindfulness meditation (Lutz et al., 2008).

### ATTENTIONAL CONTROL ACROSS THE LIFE SPAN

The ability to successfully engage in attentional control increases across development, paralleling the development of neural networks involved more generally in executive control throughout childhood and adolescence (Rueda et al., 2005). The ability to use attentional control as a form of emotion regulation is maintained in older adults. One study found that older adults were successful at performing an affective flanker task despite declines in performance on other executive functioning tasks, including a nonaffective flanker task (Samanez-Larkin et al., 2010), and older adults can successfully regulate their emotions via distraction but are impaired at reappraisal relative to younger adults (Tucker et al., 2012). In addition, when given the choice between reappraisal and distraction (an attention selection strategy), older adults prefer distraction, which may be an adaptive response to age-related cognitive decline (Scheibe et al., 2015; Mather, 2016). Finally, top-down attention—and attention to positive information in particular—appears to be preserved in aging, which bodes well for attention selection as an effective regulatory strategy across the life span (Madden, 2007; Reed et al., 2014).

### Cognitive change

Rather than reducing the attention paid to a stimulus or shifting it toward a different one, cognitive change takes a markedly different approach to emotion regulation. During the most common exemplar of cognitive change, known as reappraisal, individuals think about the emotion-eliciting stimulus in a way that changes its meaning, thereby changing the subsequent emotional response. To return to the wedding toast example, one could use reappraisal to think about the toast as a way

to express your affection for your friend rather than as a stressful public speaking event (Ochsner and Gross, 2008). Most research examining reappraisal as a regulatory strategy has focused on two distinct variants of it, or reappraisal tactics: (1) reinterpreting the stimulus itself (e.g., “An ambulance will be there soon, so there is nothing to worry about”) and (2) distancing the self from the emotion-eliciting stimulus (e.g., “This is just a picture; I am not a part of this scene”) (Webb et al., 2012).

### REAPPRAISAL ACROSS THE LIFE SPAN

While both reinterpretation and distancing are effective ways of regulating emotion, they may be differentially successful at different developmental stages. Younger individuals have an easier time implementing a distancing approach (Silvers et al., 2017), while in contrast, older adults have a more difficult time using a distancing form of reappraisal and minimizing the importance of a situation (Shiota and Levenson, 2009; Winecoff et al., 2011; Tucker et al., 2012). Instead, older adults are more successful at regulating via reappraisal when instructed to find positivity in a negative situation in order to reduce negative affect (i.e., “positivizing”) (Shiota and Levenson, 2009; Li et al., 2011; Opitz et al., 2014), and this effect is moderated by gender, such that not only do older adults use positive reappraisal more than younger adults, but this effect is also greater for women than for men (Nolen-Hoeksema and Aldao, 2011).

### Response modulation

In contrast to attentional control and cognitive change, which both impact processing of an emotion-eliciting stimulus, response modulation involves regulating behavioral responses to that stimulus. The most studied form of response modulation is expressive suppression, or effortfully keeping oneself from outwardly expressing an emotional response (Gross, 1998). In the wedding toast example, you would attempt to regulate your emotions by suppressing any outward physiological and affective responses—as popular aphorisms instruct, you might “keep a stiff upper lip” so no one could “see you sweat.” In young adults, while suppression is clearly effective in reducing the behavioral manifestation of emotion (e.g., reducing facial expressive behavior; Gross and Levenson, 1993), it has small and inconsistent effects on emotional experience (Goldin et al., 2008), possibly due to reductions in attention to stimuli as one monitors one’s own behavior (Richards and Gross, 1999) or by reducing facial feedback that contributes to the experience of emotion (Davis et al., 2009, 2010).

### RESPONSE MODULATION ACROSS THE LIFE SPAN

Research has found that younger children tend to rely more on suppression compared to adolescents, and that this reliance decreases as individuals get older (Gullone et al., 2010). This trend carries through to later life development as well, with older adults reporting that they rely more on reappraisal compared to suppression in their 60s than they did 40 years earlier (John and Gross, 2004). In addition, there are gender differences in the tendency to rely on response modulation as a regulation strategy; in general, women tend to report using rumination and seek social support, whereas men tend to report engaging in expressive suppression (Zimmermann and Iwanski, 2014). This study also found that the use of more “active” forms of regulation (e.g., seeking social support) tends to decrease with age, while the use of more passive forms of regulation (e.g., withholding a reaction) tends to increase with age. Taken together, this suggests that the older adults may experience less affective reactivity in negative situations.

### MEASURING REAPPRAISAL AND RESPONSE MODULATION BEHAVIORALLY

Most of the studies that have examined reappraisal and suppression have typically relied on self-reported measures of affect to assess whether people successfully execute the strategies. However, there have been notable exceptions, which have relied on physiological measures, including skin-conductance response, facial electromyography (EMG), and startle response, which have all been shown to track with self-report measures (Gross and Levenson, 1993; Jackson et al., 2000; Dillon and LaBar, 2005; Ray et al., 2010). During reappraisal experiments, researchers will often train participants on how to implement either reappraisal (e.g., “when you see this image, try to imagine the situation getting better”) or suppression (e.g., “when you see the image, try to react in such a way that someone would not be able to tell how you are feeling”). During a typical study, participants view emotionally charged images that are preceded by cue words to engage in reappraisal (e.g., “decrease”), engage in expressive suppression (e.g., “suppress”), or to view the image as they would normally (e.g., “look”), and then rate how negative they feel looking at the image (Ochsner et al., 2002). In this case, successful regulation would be indicated by reporting lower levels of negative affect in response to images viewed while reappraising or suppressing, relative to the negativity reported when looking at the picture normally.

## MEASURING THE NEURAL BASES OF EMOTION REGULATION

While there are a number of ways that researchers have used neuroscience methods to study emotion regulation, including electroencephalography (EEG), transcranial magnetic stimulation, positron emission tomography, and others, the majority of the neuroimaging research on emotion regulation has used functional magnetic resonance imaging (fMRI), which will be the primary focus of this chapter.

### Real-time fMRI

Within the past decade, there has been increased interest in studying how receiving “real-time” neurofeedback can increase emotion regulation success. Real-time fMRI (rt-fMRI; [deCharms et al., 2004, 2005](#)) is a method that gives participants moment-by-moment information about their brain activity, often via a numerical or a visual representation about the magnitude of activity in a given region of interest that is identified via a localizer task and tracked/displayed via online analyses ([Sulzer et al., 2013](#); [Emmert et al., 2016](#); [Paret et al., 2016](#)). This method has shown promising results in terms of increasing regulatory success and strengthening cortical–subcortical connectivity during emotion regulation ([Cohen Kadosh et al., 2016](#); [Li et al., 2016](#)).

### Connectivity analyses

The goal of a connectivity analysis (be it functional, effective, or resting state) is to examine the functional relationship between different brain regions at a given time point, or across time. A useful analogy is to think about connectivity as a conversation between brain regions.

#### FUNCTIONAL CONNECTIVITY

Functional connectivity (assessed via methods like psychophysiological interactions and beta-series correlations) examines the interregional conversation as it takes place during a given task. Typically, researchers delineate a seed region of interest, extract the pattern of activity from this region throughout the task, and see if the pattern of activity in other brain regions is temporally correlated with the one observed in the seed region. Psychophysiological interaction (or PPI) analyses ask whether this correlation is stronger in one condition vs another ([Friston et al., 1997](#)). To the extent this is the case, it is inferred that activity in the two regions is related to them both as a function of the psychological operations engaged in one condition vs the other. An important caveat is that—as with all

correlational analyses—observing functional connectivity between two regions cannot determine temporal causality. For example, if a researcher observes functional connectivity between the amygdala and the prefrontal cortex (PFC) during emotion regulation, it would not be possible to determine if activity in the PFC causes and/or precedes the associated pattern in the amygdala (or vice versa). This is where effective connectivity comes in.

#### EFFECTIVE CONNECTIVITY

The goal of effective connectivity is to determine the directionality of the connectivity between brain regions, often relying on Bayesian model comparison to determine best fit for the direction of connectivity between regions. Common ways to assess effective connectivity include dynamic causal modeling (DCM), Granger causality, and structural equation modeling (for a review of the differences between different effective connectivity analyses, see [Friston, 2011](#)).

#### RESTING STATE CONNECTIVITY

Both functional and effective connectivity focus on connectivity during a given experimental task. In contrast, resting state connectivity (rs-fMRI) examines the relationship between activity in different brain regions at “rest,” when an individual lies in the scanner (either with eyes closed or viewing a fixation point/cross) and is allowed to think about whatever they want. As such, it provides insight into how brain regions are interacting with one another during so-called spontaneous cognition—i.e., cognition initiated by the participant and presumably guided by their personal motivations and goals rather than being directed toward the performance of an experimenter-provided task ([Fair et al., 2007](#)). Resting state connectivity analyses take multiple approaches ([Goldenberg and Galván, 2015](#)). This includes region-of-interest (ROI)-based analyses, which examine how spontaneous fluctuations within a particular region at rest are associated with activity in other regions; independent component analysis, which is useful for delineating specific networks (e.g., default mode, sensorimotor), and graph theoretical analyses, which conceptualize distinct brain regions as nodes connected via edges and can be useful in terms of determining which regions of the brain serve as “hubs” for information integration ([Bullmore and Sporns, 2009](#)). Resting state analyses can be particularly useful in studying developmental populations, which can be prone to excessive movement and/or difficulty with sustained task performance ([Uddin et al., 2010](#)). In addition, resting state connectivity analyses are used for measuring rates of cognitive decline or the effects of training interventions, where the relative strength of interregional

connectivity is thought to be indicative of greater brain plasticity and healthier aging (Andrews-Hanna et al., 2007; Li et al., 2014).

### Structural analyses

While the majority of emotion regulation research has focused on functional approaches, there has also been a renewed focus on looking at brain structure and in particular how the physical structure of different regions involved in affective and controlled processes change across the life span. The brain undergoes a great deal of structural change from infancy to young adulthood, in particular, a posterior–anterior pattern of cortical thinning, believed to be a marker of neural efficiency (Gogtay et al., 2004). The healthy adult brain remains relatively stable until around age 50, when it begins to undergo linear declines in structure of both white and gray matter, accompanied by increased cell death, demyelination, and the introduction of disruptive neurofibrillary plaques and tangles (Price et al., 1991; Hedman et al., 2012). Age-related structural decline in nonpathological aging is not uniform across people or within brain regions, with more lateral and dorsal prefrontal brain areas undergoing more drastic decline than medial areas (Raz et al., 2005). Examining brain structure can involve the use of multiple methods, including diffusion tensor imaging, which examines the structure of white matter tracts, coupled with fractional anisotropy, which looks at the direction of the diffusion of water molecules along said tracks (Schwarz et al., 2013), and cortical pattern matching, which examines structural changes in gray matter volume (Gogtay et al., 2004).

## BRAIN REGIONS INVOLVED IN EMOTION REGULATION

### Regions involved in triggering affective responses

Emotion is an essential component of the human experience. From our earliest cry to our last goodbye, emotions imbue our lives with meaning and are essential to our survival. While the exact definition of emotion is an ongoing topic of debate (see, e.g., Adolphs, 2016; Barrett, 2016), for present purposes, we consider emotion to be an evaluative appraisal of a stimulus's meaning that leads to physiological and experiential changes as well as activating response tendencies.

#### Amygdala

The amygdala is one of the primary brain regions involved in triggering an affective response (Ochsner et al., 2009; Lindquist et al., 2012), in large part because it is thought to signal the presence of goal-relevant

stimuli, and emotions arise from appraisals of goal relevance (Sander et al., 2003; Cunningham and Brosch, 2012). As such, it is densely interconnected with brain regions involved in sensory detection, attentional alerting, memory, and associative learning (Davis and Whalen, 2001; Phelps and LeDoux, 2005) and contributes to these behaviors because of its role as a neuromodulatory region that influences the operation of brain systems that process sensory information and consolidate it into memory (Anderson and Phelps, 2001, 2002; Barrett et al., 2007). In this way, the amygdala's role in emotional experience may be indirect rather than direct (Anderson, 2007). The amygdala receives inputs from sensory systems (e.g., visual, auditory, olfactory), and has reciprocal connections with ventromedial areas of the PFC and anterior cingulate (Ghashghaei and Barbas, 2002; Ghashghaei et al., 2007; Barbas et al., 2011; Timbie and Barbas, 2015; Zikopoulos et al., 2017). This speaks to its central role in generating affect as well as guiding attention, memory encoding, and reinforcement learning and, as such, it is a common target for emotion regulation.

### EMOTION REGULATION AND THE AMYGDALA

Given the amygdala's key role in affect generation, it is not surprising that it is one of the primary targets for emotion regulation and that decreases in amygdala activity are often treated as a marker of successful regulation. However, different regulation strategies vary in the extent to which they accomplish this feat. Consistent with the idea that successful downregulation of emotion involves dampening amygdala activity, prior research has found that using selective attention to focus on a nonarousing (vs arousing) section of a negative image led to decreases in amygdala activity (Ferri et al., 2013), and that increased amygdala activity is associated with worse performance on tasks that require inhibition of behavioral responses to negative stimuli (Hare et al., 2005, 2008).

In general, meta-analyses have shown that the use of reappraisal to change one's interpretation has been found to up- vs downregulate amygdala responses as a function of the goals that one has to think about the meaning of a stimulus in ways that amplify vs diminish is emotional impact (reviewed in Buhle et al., 2014). Such effects are thought to follow from reappraisal-related changes in the representation of stimulus meaning. By contrast, although the route by which expressive suppression might impact amygdala is less clear, its impact on the amygdala appears to be different from that of reappraisal. One study directly compared reappraisal and expressive suppression in response to aversive videos, reporting that reappraisal with the goal of diminishing negative

emotion decreased amygdala reactivity, whereas suppression increased amygdala reactivity (Goldin et al., 2008). These differential effects on amygdala activity may be apparent at an individual level, such that chronic use of reappraisal is linked to decreased amygdala activity when viewing negative images without an explicit goal to regulate (Drabant et al., 2009), whereas the chronic use of suppression is associated with heightened amygdala activity when viewing negative stimuli (Vanderhasselt et al., 2013a, b). Some have suggested that reappraisal use and its impact on the amygdala are both trait-like and domain-general—decreases in amygdala activity when regulating responses to negative images predicted decreases in responses to amygdala activity when regulating responses to physical pain 2 years later (Lapate et al., 2012). Interestingly, recent work has found that amygdala activity during reappraisal can be dynamically modulated based on real-time neurofeedback—in one study, researchers presented participants with feedback based on their actual amygdala response while regulating during an fMRI scan—and found receiving feedback on how well one was doing led to significant decreases in amygdala activity during regulation, coupled with increased lateral prefrontal–amygdala connectivity during feedback trials (Sarkheil et al., 2015).

Decreases in amygdala activity during reappraisal are associated with increased connectivity between the amygdala and both the OFC and dorsomedial prefrontal cortex (dmPFC) (Banks et al., 2007). Notably, these regions (dmPFC, middle temporal cortex) are also key regions involved in theory of mind and mentalizing about the self and others, which may speak to the important role that these processes play in successful reappraisal, which often involves reframing a stimulus in terms of its self-relevance. In contrast, decreased amygdala activity during distraction is associated with increased connectivity between the amygdala and the dorsal anterior cingulate (dACC), ventromedial prefrontal cortex (vmPFC), and the right insula (Kanske et al., 2011). Given the dACC's role in detecting and signaling conflict, the vmPFC's role in signaling value, and the insula's role in integrating sensory information, these regions may be involved in signaling the presence of an affective stimulus, deciding its relevance to one's goals, and implementing the appropriate response.

#### AMYGDALA ACTIVITY AND REGULATION ACROSS THE LIFE SPAN

Amygdala reactivity to negative images and facial expressions decreases across the life span (Mather et al., 2004; Gee et al., 2013; Silvers et al., 2017). However, amygdala reactivity to positive stimuli follows a

slightly different trajectory, in that older adults show greater reactivity to positive relative to negative stimuli, a pattern that is reversed in younger adults (Mather et al., 2004). As indicated previously, amygdala–prefrontal connectivity is a critical component of successful emotion regulation and it changes notably throughout the life span. Developmental research has found that structural connectivity between the amygdala and PFC increases linearly throughout childhood into young adulthood (Swartz et al., 2014), and young children show positive amygdala–prefrontal connectivity (that is, as activity in one region increases, so does activity in the other), a pattern that reverses after age 6, suggesting the emergence of a regulatory relationship between the two regions (Gee et al., 2013). The development of a negative amygdala–prefrontal connectivity pattern is accelerated by the absence of a stable primary caregiver during infancy, suggesting that it is a response to early life stress (Tottenham et al., 2012). In terms of healthy aging into older adulthood, resting state functional connectivity shows that density of amygdala-based networks increases with age (Tomasi and Volkow, 2012), and there is evidence for the preservation of amygdala volume and connectivity in old age (Raz et al., 1997; Jernigan et al., 2001; Jiang et al., 2014). Taken together, this suggests that the amygdala goes through many structural and functional changes relatively early in life, and then stabilizes for the duration of the life span.

#### Ventral striatum

The ventral striatum is a subcortical brain region innervated with dopaminergic neurons and involved in tracking the subjective value of stimuli, signaling the presence of/expectation of reward, and encoding errors and outcomes of such predictions (Knutson et al., 2001; Phan et al., 2002; Eldar et al., 2016). It is thus a critical contributor to affective anticipation, showing increased activity when individuals anticipate both rewarding and aversive experiences (Jensen et al., 2003). Further, reactivity to rewarding cues like food and sexual images has been shown to be predictive of both long-term weight gain and sexual desire, respectively (Heatherton and Wagner, 2011; Demos et al., 2012). The ventral striatum also is densely interconnected with the amygdala and vmPFC (Haber and Knutson, 2010), and, through modulatory connections to the central nucleus of the amygdala, plays a critical role in fear learning and extinction retention (Phelps et al., 2004; Schiller and Delgado, 2010). During reappraisal, both the amygdala and the ventral striatum show increased connectivity with the dmPFC/ACC and the lateral PFC (Sripada et al., 2014), and one recent study that examined neurofeedback in striatum found increased striatum–mPFC connectivity

when individuals received feedback and were attempting to regulate it, as compared to trials in which they did not receive feedback (Greer et al., 2014).

### EMOTION REGULATION AND THE VENTRAL STRIATUM

The ventral striatum, like the amygdala, is one of the primary targets for emotion regulation (Ochsner et al., 2012; Buhle et al., 2014). In particular, it is a primary modulation target when individuals are regulating responses to rewarding stimuli (Roitman et al., 2005; Kim and Hamann, 2007; Kober et al., 2010), and it tends to be more active when viewing positive relative to negative and neutral stimuli (Seo et al., 2014). During reappraisal, the striatum can act as a mediator in the relationship between ventrolateral prefrontal cortex (vlPFC) activity and regulation success (Wager et al., 2008), presumably supporting reappraisals that find positive meaning in aversive events. A number of studies have also examined striatal downregulation via reappraisal in decision-making tasks, finding that reappraisal led to decreased activity in the striatum coupled with fewer risky decisions (Martin and Delgado, 2011) and less anger when offered unfair deals in a social interaction (i.e., dictator game) (Grecucci et al., 2013). This indicates that the striatum plays a key role in the successful implementation of affective reappraisal for both positive and negative stimuli and may be involved when putting a “positive spin” on a bad situation (Doré et al., 2017a).

### VENTRAL STRIATUM ACTIVITY AND REGULATION ACROSS THE LIFE SPAN

Adolescents show heightened activity in the striatum relative to children and adults (Geier and Luna, 2009; Somerville and Casey, 2010), which is believed to underlie their increased propensity toward risky behavior (Galvan et al., 2006). There are comparatively fewer published works examining the striatum in aging, but one study found that healthy older adults show less striatal activity when experiencing regret as compared to healthy young and depressed older adults (Brassen et al., 2012). Intriguingly, striatal reactivity and the ability to regulate it may be somewhat stable over the life span—in one study, individuals who had completed the marshmallow task (a task that measures the ability to delay gratification) during childhood were scanned 40 years later while performing a task that requires inhibiting the prepotent impulse to behaviorally respond to affective cues (the affective go/no-go). The researchers found that low-delayers in adolescence (i.e., individuals who were unable to wait for the second treat) showed increased striatal activity when regulating responses toward affectively rewarding stimuli (happy faces) as middle-aged adults (Casey et al., 2011). In terms of

striatal connectivity, the regulatory relationship between the ventral striatum and mPFC develops throughout adolescence, with one study finding that children (relative to young adults) show higher striatal activity during appetitive regulation, coupled with weaker striatal–prefrontal connectivity (Silvers et al., 2014b). This coupling between the striatum and PFC may even be strengthened later in life, with one study finding that, relative to younger adults, older adults show increased connectivity between ventral striatum and mPFC while viewing positive stimuli (Ritchev et al., 2011).

### Insula

The insula is an area critically important for the experience and generation of emotion—it is a hub where somatosensory information is integrated with other types of information to support the interoception and awareness of internal body states, affective experience, and cognitive control (Satpute et al., 2015; Uddin et al., 2017). It is also involved in experiencing empathy for others (Bruneau et al., 2012; Zaki et al., 2016), and is a key player in the “pain” network (Singer et al., 2004). However, while the insula is an important contributor to compassion, it is also implicated in the expression and physiological experience of disgust (Calder et al., 2001). Given its role in disgust and avoidance, it is perhaps not surprising that the insula is engaged across a variety of inhibition tasks (Wager et al., 2005), and may be of particular import for inhibiting responses toward affective stimuli (Shafritz et al., 2006).

The insula is part of the frontoparietal control network, which is involved in goal implementation and attainment (Spreng et al., 2010) and becomes more interconnected and efficient across development (Fair et al., 2008). It sits at the nexus of both affective (i.e., striatum, amygdala) and control (i.e., ACC, vlPFC) regions, and plays diverse roles ranging from affective identification and expression to response inhibition (Wager and Barrett, 2017). The insula serves in so many roles due to its wide-ranging connectivity with different brain regions, and it is parcellated into three subregions: the dACC, the ventral anterior cingulate, and the posterior cingulate. The dACC has many connections to the frontal lobe, anterior cingulate cortex (ACC), and parietal cortex, and plays a key role in cognitive control and executive function (Uddin et al., 2017). The ventral anterior insula also shows connectivity with the frontal lobe and with subcortical regions involved in affect and emotion, underscoring the region’s involvement in socioemotional cognition (Uddin et al., 2014; Nomi et al., 2016). The posterior insula shows increased connectivity with parietal and the temporal cortices and is involved in

interoception and visceral integration (Uddin et al., 2017). The insula, along with the ACC, is part of the so-called “salience” network, thought to be critical for identifying goal-relevant stimuli and guiding attention accordingly (Menon and Uddin, 2010).

### EMOTION REGULATION AND THE INSULA

With regard to its role in emotion regulation, the insula is a bit of a mixed bag, due to functional differences across different subregions. Both the ventral anterior insula and posterior insula can be the target of regulation (Ochsner et al., 2004; Martin and Delgado, 2011; Buhle et al., 2014; Sripada et al., 2014), but the dorsal anterior and posterior insula can also show increased activity during regulation (Koenigsberg et al., 2010; Buhle et al., 2014; Lamke et al., 2014). Consistent with the idea that the insula is critical for attentional control, trait suppression usage (a regulation tactic that requires a great deal of focused attention) is positively correlated with insula volume (Giuliani et al., 2011b). One study that compared distraction (a form of attention selection) to reappraisal (Kanske et al., 2011), found that distraction recruited the dorsal anterior insula to a greater extent during regulation than did reappraisal and that amygdala–insula connectivity during distraction was associated with regulatory success. Paralleling these results, but this time comparing suppression and reappraisal, one study found that dorsal anterior insula activity decreased during reappraisal, but showed increased activity during suppression (Goldin et al., 2008). However, another study found no differences in insula activity when regulating via reappraisal or expressive suppression (Vrtička et al., 2011). Taken together, this suggests that the dorsal anterior insula may play a key role as a regulator in nonreappraisal strategies but may be a noncontributor during reappraisal.

One study that directly examined insula connectivity and emotion regulation in the context of the ultimatum game found that dorsal anterior insula activity when receiving an unfair offer was correlated with explicit ratings of anger, and was exclusively active when reappraising moderately fair and unfair offers as compared to fair offers (Grecucci et al., 2013). Using DCM, they found that when using reappraisal during unfair offers, the inferior frontal gyrus (IFG) and temporoparietal junction (TPJ) modulated activity in the dorsal anterior insula. This suggests that the dorsal anterior insula plays a key role in interpersonal emotion regulation and is modulated by regions involved both in executive control (i.e., IFG) and mentalizing (i.e., TPJ). Thus during at least one form of social emotion regulation, the insula appears to play a role in integrating information about the mental states of others and their intentions with affective experience, in order to inform behavior.

### INSULA ACTIVITY AND REGULATION ACROSS THE LIFE SPAN

In general, connectivity in the frontoparietal network (of which the insula is a key player) declines later in life (He et al., 2014), and decreases in insula volume show interindividual variation in old age (Tisserand et al., 2004; Raz et al., 2010). Older adults do, however, show increased dorsal anterior insula activity to negative stimuli (angry faces) relative to younger adults, a pattern that is reversed in the amygdala (Fischer et al., 2005).

Taken together, all of this information gives an unclear picture of the insula’s role in regulation, both in general and across the life span. While this can be somewhat frustrating, it may speak to the many roles performed by the insula and the complexity of its structure and function across its multiple subnuclei.

### REGIONS INVOLVED IN MODULATING AFFECT

The regions outlined previously are those that are involved in generating emotional states; however, emotion generation and regulation are interconnected processes (Gross and Barrett, 2011). Indeed, our appraisals about a stimulus can both give rise to our affective states and work to regulate them. While regions like the amygdala and striatum signal the presence of an affectively relevant stimulus, these representations are flexible and can be modified based on an individual’s goals and contextual cues. In the next section, we will focus on the brain regions involved in dynamically updating affective appraisals and exerting top-down control over automatic affective responses.

#### Anterior cingulate cortex

The ACC is involved in monitoring performance and signaling conflict between competing responses (MacDonald et al., 2000). Together with the insula it comprises the salience network and is involved in detecting and responding to pain, both for the self and others (Zaki et al., 2009; Menon and Uddin, 2010; Shackman et al., 2011). Recent accounts of ACC function posit that its primary role is computing the expected value of exerting cognitive control, which supports detection of affectively salient stimuli, and subsequently signaling to lateral prefrontal regions the need to exert control over responses to them (Shenhav et al., 2013).

As mentioned previously, the ACC has dense structural connections with the anterior insula. It also has termination points in the amygdala’s basolateral and central nuclei, which underscores its role as signaling the need for vigilance and heightening of arousal (Zikopoulos et al., 2017). Intriguingly, the ACC is also one of the primary



sites for von Economo neurons, a type of neuron that allows for quick signaling and is associated with enhanced executive and socioaffective functioning; it is one of the first areas to deteriorate in the early stages of frontotemporal dementia (Allman et al., 2010). Taken together, these structural features speak to the ACC's important role in human cognition and its role in both affective and cognitive control processes. In terms of functionality, the ACC exhibits functional connectivity with both the insula and lateral regions of the PFC (Shenhav et al., 2013), and structural research has found that smaller dorsal ACC volume is related to difficulties regulating emotion (Giuliani et al., 2011a). ACC connectivity changes markedly across development, beginning as relatively diffuse in childhood and becoming more focalized in adulthood (Kelly et al., 2009).

### EMOTION REGULATION AND THE ACC

In terms of emotion regulation, some have suggested the ACC plays a central role in monitoring regulatory performance and exhibits increased activity during both up- and downregulation of negative emotion via reappraisal (Ochsner et al., 2004; Braunstein et al., 2017). Notably, the ACC also plays a critical role in autonomic control and interoception (Critchley, 2004), indicating that its role in signaling the need for control based on a computation of value may draw on body-state information to determine value and may in turn trigger body-state changes to support subsequent attempts at control. As such, it is interesting that one study found that dACC activity was positively correlated with both pupil dilation and heart rate during reappraisal and served as a marker of cognitive and physiological effort (Urry et al., 2009). This account is consistent with research focusing on more automatic forms of emotion regulation. In one study using the affective go/no-go, individuals showed increased ACC activity when inhibiting automatic responses to affective stimuli (Hare et al., 2005), and research using a variant of the affective Stroop found that the rostral ACC exerted inhibitory control on the amygdala during task performance (Etkin et al., 2006). This indicates that the ACC is one of the key contributors to implementing emotion regulation—it is involved in detecting conflict and signaling the need for ongoing control, and it monitors performance through the regulatory process.

### ACC ACTIVITY AND REGULATION ACROSS THE LIFE SPAN

Prior research has found that children and adolescents engage the ACC to a greater extent than adults in tasks that require cognitive control (Rivera et al., 2005), and

that adolescents exhibit increased ACC activity (relative to adults) when viewing fearful faces/negative stimuli (Blakemore, 2008). One study that examined attention selection across development found that children show increased activity relative to adolescents and young adults in dACC during the affective Stroop task, due to immature functional development and younger individuals needing increased activity to get to the same level of performance (Hwang et al., 2014).

Interestingly, the ACC appears to be the region most associated with positivity bias in attention in aging (Brassen et al., 2011), which is consistent with the research that found that the ACC may be more involved in the regulation of positive relative to negative emotion (Seo et al., 2014). In addition, ACC–lateral prefrontal connectivity during both distancing and positivizing reappraisal is conserved across the life span and there is evidence for increased conservation of gray matter in the ACC relative to other prefrontal regions (Allard and Kensinger, 2014a, b).

### Dorsolateral PFC

The dorsolateral prefrontal cortex (dlPFC) is a hub for executive control processes (Thompson-Schill et al., 2005), and it is one of the regions most commonly recruited during emotion regulation (Buhle et al., 2014). Through connections to parietal control, sensorimotor, temporal, and more medial regions of the PFC, it plays a critical role in response preparation, goal maintenance, and goal-directed cognition (Miller and Cohen, 2001; Badre and D'Esposito, 2007; Arnsten, 2009). During emotion regulation, it communicates with the dmPFC/dACC to monitor conflict and signal the need for behavioral change and can signal parietal control regions to guide attention elsewhere, resulting in downregulation of amygdala activity (Mitchell, 2011). Though we typically think of the dlPFC as an affect-modulating region, it is also involved in the top-down generation of affective states (e.g., experiencing affect via mental simulation) (Otto et al., 2014).

While structural and functional changes occur throughout the whole brain across the life span, it is the lateral prefrontal regions that appear to show the most age-related changes during childhood (Somerville and Casey, 2010). Like the vlPFC, the dlPFC experiences cortical thinning across development, and it is one of the last brain regions to fully mature (Gogtay et al., 2004). Its development is associated with increased ability to exercise cognitive control and to engage in strategic thinking (Steinbeis et al., 2012). While the dlPFC may be one of the last brain regions to fully mature, it is also one of the first to begin

to degrade in old age. The dorsolateral prefrontal and hippocampal regions experience the most atrophy in old age, and depletion of these more lateral brain regions is consistent with reports of age-related decline in executive functioning (Fjell et al., 2009).

### EMOTION REGULATION AND THE dlPFC

Similar to its neighbor the vlPFC, the dlPFC plays a role in regulation via reappraisal of both negative and positive stimuli (Golkar et al., 2012) and during both up- and down-regulation (Ochsner et al., 2012). It is believed to be part of a “regulatory network” (along with the vlPFC and mPFC) that shows heightened activity during regulation regardless of the type of stimuli being regulated (Nelson et al., 2015). Indeed, the dlPFC is not only involved in regulation toward negative affective stimuli but is also involved in regulating striatal activity during reappraisal of financial rewards (Staudinger et al., 2011) and reappraising losses in a gambling task (Sokol-Hessner et al., 2013). It was also involved in regulation across multiple different strategies measured in the same participants (detachment, reinterpretation, expressive suppression, distraction) (Dörfel et al., 2014).

A recent meta-analysis using activation likelihood estimation, found that volitional emotion regulation processes work as follows: first the vlPFC signals the need to regulate, the dlPFC maintains the regulation process, and then modulates the amygdala and ACC (Kohn et al., 2014). However, the direct connections from the dlPFC to amygdala are sparse, so it is believed that the dlPFC modulates amygdala activity through vmPFC, a region critical for proactive control (Whelock et al., 2014) or by modulating activity in posterior cortical regions that represent perceptual and semantic information and send inputs to emotion triggering regions (Ochsner et al., 2012). Differences in dlPFC reactivity to negative stimuli may also underlie individual differences in spontaneous regulation of negative emotion, as one study found that individuals who gave lower negative affect ratings when viewing and rating negative images exhibited increased recruitment of the dlPFC (Silvers et al., 2014b), and individuals who report higher trait reappraisal show increased dlPFC activity when viewing negative relative to positive stimuli (Vanderhasselt et al., 2013a, b). Taken together, this suggests that, during emotion regulation, the dlPFC is involved in exerting top-down control, but also perhaps automatically in generating reappraisals that can alter the current interpretation of one’s affective state.

### dlPFC ACTIVITY AND REGULATION ACROSS THE LIFE SPAN

Children and adolescents show increased activity in dlPFC compared to adults during negative emotion

regulation, suggesting that they may need to recruit more cognitive resources in order to achieve the same regulatory results (Levesque et al., 2004; Geier and Luna, 2009). Similarly, although older adults show reduced activity in the dlPFC during nonemotional working memory tasks (Opitz et al., 2012), they show greater dlPFC activity during reappraisal as compared to attention selection relative to younger adults (Allard and Kensinger, 2014a, b). Intriguingly, the opposite is true for regulation toward appetitive stimuli, at least in childhood and adolescence (Silvers et al., 2014b). Future work should examine the nature of this interaction between age and regulation across both negative and positive stimuli and see if this reversal is also the case for older adults.

### Ventrolateral PFC

The vlPFC is one of the primary regions involved in cognitive control and most commonly during emotion regulation (Berkman and Lieberman, 2009). It is instrumental in implementing goal-directed behavior and guiding retrieval of relevant information from memory (Badre et al., 2005; Badre and Wagner, 2007; Satpute et al., 2014), and in the “top-down” generation of emotion (Ochsner et al., 2009; Otto et al., 2014). It also plays a key role in response inhibition through projections to both the ACC and the insula (Lieberman et al., 2011; Kohn et al., 2014). Through these connections, the vlPFC regulates responses to stimuli that are emotionally distracting and responds to signals from the ACC that current affect is incompatible with desired affect (Mitchell, 2011). The vlPFC has functional connections to the anterior insula, medial PFC, and dorsal regions of the lateral PFC (Menon and Uddin, 2010; Morawetz et al., 2016; Silvers et al., 2017), underscoring its role in response selection based on the detection of internal states and influencing goal-directed cognition. Since it has relatively few direct (i.e., physical) connections to the amygdala, it is believed to modulate amygdala activity indirectly through OFC/mPFC (Mitchell, 2011).

### EMOTION REGULATION AND THE vlPFC

Underscoring its key role in emotion regulation, the vlPFC was one of only three brain regions (along with SMA and anterior insula) that were found to be active regardless of regulation strategy used (reappraisal, attention selection, response modification) in a meta-analysis of emotion regulation studies (Morawetz et al., 2017). However, it appears to be particularly critical for reappraisal that involves reinterpretation relative to other regulation strategies (e.g., detachment) (Ochsner et al., 2009, 2012; Dörfel et al., 2014), which may be related

to its role in semantic retrieval. In addition, it may play a role in “spontaneous” regulation—that is, regulation processes that occur without explicit direction. One study that examined vIPFC and its role in downregulating emotion following interpersonal conflict found that increased vIPFC activity to one’s romantic partner’s negative facial expression was predictive of better coping and well-being following relationship conflict (Hooker et al., 2010). When it comes to reappraisal, the vIPFC seems to be a “jack of all trades,” and is involved in the reappraisal of myriad stimuli, ranging from negative scenes, negative faces (i.e., angry and fearful), to appetitive stimuli (Ochsner et al., 2012; Silvers et al., 2014b; Nelson et al., 2015).

In terms of connectivity during emotion regulation, changes in vIPFC activity during reappraisal were correlated with reported changes in emotional experience, and this relationship between vIPFC activity and regulatory success was mediated by two indirect and independent pathways: (1) through amygdala/insula (leading to less success) and (2) the ventral striatum (leading to increased success) (Wager et al., 2008). One study that used DCM to assess effective connectivity during reappraisal found that, while the dlPFC is active during the initial stages of reappraisal in order to maintain regulation goals in working memory and initially shows positive coupling with the vIPFC, once the vIPFC has selected the chosen appraisal, the vIPFC then exerts an inhibitory effect on the dlPFC, which is no longer needed once the appraisal has been selected (Morawetz et al., 2016). Thus, like its neighbor the dlPFC, the vIPFC plays a flexible and important role in emotion regulation, specifically by generating appraisals to shape the meaning of affective stimuli and selecting the appropriate response in order to achieve one’s regulatory goals.

#### **vIPFC ACTIVITY AND REGULATION ACROSS THE LIFE SPAN**

There is a positive correlation with age and vIPFC activity during response inhibition toward affective faces during early development (Shafritz et al., 2006), suggesting that younger individuals may have more difficulty utilizing this region during regulation. It seems that the capacity for lateral prefrontal (i.e., vIPFC and dlPFC) regions to regulate emotion is rooted in childhood experience, as adults who experienced poverty during childhood show decreased vIPFC activity during reappraisal relative to individuals who did not (Kim et al., 2013). As part of the normal maturational process, lateral prefrontal areas undergo cortical thinning from childhood into early adulthood, and thinning of both the dlPFC and vIPFC is associated with increased use of reappraisal in adolescents (though curiously only in females)

(Vijayakumar et al., 2014). However, when it comes to cortical thinning, too much can be a problem in older age, as both the ventral and dorsal regions of the PFC undergo severe cortical thinning in the aging brain (Fjell, 2010), which may be related to older adults activating the vIPFC less than younger adults when reducing responses to negative emotions. However, this degradation of the vIPFC may be compensated for—while younger adults show stronger ACC-vIPFC/dlPFC activity during reappraisal, older adults instead show stronger acc-vmPFC/OFC connectivity (Allard and Kensinger, 2014a, 2014b), which is consistent with other work showing that older adults recruit the vIPFC less than younger adults during regulation (Wincoff et al., 2011; Opitz et al., 2012), without having significant problems regulating emotion. Further, this vIPFC deficit in old age may be specific to regulating responses to negative stimuli, as one study found that the vIPFC is recruited more during processing and reflecting upon positive images in older adults, as compared to young adults (Ritchey et al., 2011). Taken together, this suggests that the vIPFC is sensitive to early affective inputs and may be of particular importance during emotion regulation in childhood and young adulthood, while being less important for regulation in older adults.

#### **Dorsomedial prefrontal cortex**

The dmPFC is a region that acts as a conduit between cognitive control areas and affect-triggering regions and that plays a role in both generating and regulating emotion (Kober et al., 2008). Similar to the dlPFC, it has dense connections to sensorimotor areas and ACC, and is involved in goal-directed behavior—it works together with the dlPFC in reversal learning, cost/benefit calculation, and together with the ACC signals conflict to the dlPFC and vIPFC (Mitchell, 2011). Like the vmPFC (see the following), it is part of the default mode network and plays a key role in the detection and awareness of one’s own emotional state and the emotional states of others (Ochsner et al., 2004; Lindquist et al., 2012).

#### **EMOTION REGULATION AND THE dmPFC**

In terms of emotion regulation, the dmPFC is recruited across various forms of regulation (e.g., reappraisal, distraction, suppression), and plays a key role in affective elaboration (Buhle et al., 2014; Dörfel et al., 2014), likely because of its role in “mentalizing”—i.e., thinking about mental states, including affective ones (Zaki and Ochsner, 2012). As such, it is not surprising that it is involved in the regulation of both positive and negative emotion (Seo et al., 2014), and is more active during regulation to social (relative to nonsocial) stimuli (Vrtička et al., 2011). The dmPFC acts as a positive mediator

during reappraisal and is one of the regions that—when paired with increased activity in the vlPFC—increases regulatory success (Wager et al., 2008). Like the dlPFC, it is associated with individual differences in responses to negative stimuli, such that increased activity during viewing is associated with lower negative affect ratings (Silvers et al., 2014b). This is consistent with recent research showing that the dmPFC is critical for “endogenous” control, that is, choosing to act rather than being instructed to do so (Kühn et al., 2013); in contrast to the vlPFC, the dmPFC may play a stronger role during upregulation of emotion relative to downregulation (Ochsner et al., 2012).

The dmPFC plays a regulatory role during both reappraisal and distraction and shows increased amygdala connectivity during the implementation of both strategies (Banks et al., 2007). Negative reciprocal dmPFC-amygdala connectivity is correlated with chronic usage of reappraisal (Drabant et al., 2009), and the region may play a central role when regulating responses toward unpredictable negative stimuli (Whealock et al., 2014). It is also one of the regions that is the most malleable to receiving neurofeedback via rt-fMRI, as neurofeedback increases amygdala-dmPFC connectivity during emotion regulation (Li et al., 2016) and the region shows enhanced connectivity with the left amygdala when receiving neurofeedback during the upregulation of positive emotion (Zotov et al., 2013). Taken together, this indicates that once an emotion has been identified, the dmPFC is involved in flexibly shaping the intensity of that emotion based on an individual’s regulatory goals.

#### **dmPFC ACTIVITY AND REGULATION ACROSS THE LIFE SPAN**

The dmPFC plays an increasingly key role in the upregulation of positive emotion via its connections to the ventral striatum from childhood into early adulthood (Silvers et al., 2014b). It also appears to be preserved both in structure and in this regulatory role across the adult life span, as it is involved in emotion regulation toward positive images in both older and younger adults (Winecoff et al., 2011) and both age groups show increased ACC-dmPFC connectivity during reappraisal (Allard and Kensinger, 2014a, 2014b).

#### **Ventromedial prefrontal cortex**

The vmPFC seems to be critically involved in coding the affective value of stimuli within the current situational and temporal context (Ochsner and Gross, 2014; Braunstein et al., 2017). This function is supported by its dense reciprocal connections with amygdala (Ghashghaei et al., 2007) and its connections with other

subcortical (e.g., hippocampus) and posterior cortical regions that encode situation and historical information about a stimulus and how it is being experienced in relationship to other stimuli (Ochsner and Gross, 2014; Braunstein et al., 2017). Given these connectivity patterns, it is not surprising that it plays a key role in fear extinction (Phelps et al., 2004; Schiller and Delgado, 2010), which involves determining how the value of a stimulus has changed over time in relation to expected but omitted negative outcomes, in implementing forms of controlled regulation that depend on making choices about the value of stimuli with respect to changing task goals (Hutcherson et al., 2012), in coding prediction errors and supporting feedback-learning (Mitchell, 2011), in judging the relatedness of stimulus to the self (Kober et al., 2008) and in inferring the mental states of others (Ochsner et al., 2004; Bruneau et al., 2012). Interestingly, one study showed that individuals who were more successful at downregulating their amygdala via reappraisal showed inverse coupling of amygdala and vmPFC, and the strength of this coupling was predictive of cortisol levels longitudinally (Urry et al., 2006). Cognitive depletion can weaken this vmPFC-amygdala connectivity, leading to heightened affective reactivity (Wagner and Heatherton, 2013).

#### **EMOTION REGULATION AND THE vmPFC**

When it comes to emotion regulation, the vmPFC is believed to play a role in deriving affective meaning, through its connections to subcortical (e.g., amygdala) and temporal (e.g., hippocampal) regions (Roy et al., 2012). Activity in vmPFC tends to be inversely correlated with amygdala activity during emotion regulation (Kober et al., 2008), and the activity in the vmPFC is modulated via top-down inputs from the dlPFC, rostral dorsal ACC, and dmPFC, which then regulates amygdala activity (Hartley and Phelps, 2010; Roy et al., 2012). Taken together, this suggests that the vmPFC may play an important role in regulating affect. In addition to being involved in amygdala regulation, it serves a regulatory role for the ventral striatum—one study that investigated the emotion regulation in financial decision-making found increased vmPFC activity when regulating responses to losses (Sokol-Hessner et al., 2013), and it is involved in tracking positive emotion and serves as a valuation region (Winecoff et al., 2013).

While this would seem to suggest that vmPFC plays a critical role in emotion regulation, this is not always the case. Some studies observe decreased vmPFC activity during regulation (Kanske et al., 2011), and a recent meta-analysis found no evidence for consistent involvement of the vmPFC during reappraisal (Buhle et al., 2014). It’s possible that the vmPFC may be chronically

active during both the generation and regulation of affective states during reappraisal, which may account for the lack of a consistent role during the regulation process. Finally, like the dlPFC, vmPFC activity is associated with individual differences in the spontaneous regulation of affect (Silvers et al., 2014b). Regardless of its exact role in emotion regulation, it clearly plays a critical role in affective valuation, as it receives inputs from both the amygdala and ventral striatum, computes information about value, and signals to more lateral prefrontal regions to engage in goal-directed cognition (Ochsner et al., 2012; Braunstein et al., 2017).

#### **vmPFC ACTIVITY AND REGULATION ACROSS THE LIFE SPAN**

Regulatory connectivity between the vmPFC and amygdala develops during late childhood (Gee et al., 2013), but can be accelerated by experiencing early life stress during infancy (Tottenham et al., 2011). Once this association has been established, it persists throughout the life span—in older adults the amygdala and vmPFC are relatively well-preserved relative to the degradation seen in more lateral prefrontal regions (Fjell et al., 2009). In addition, both older and younger adults show increased functional connectivity between ACC and vmPFC during reappraisal (Allard and Kensinger, 2014a, b)—which suggests that the region may be involved in implementing the reappraisal strategy selected by more lateral prefrontal regions across the life span.

### **WHERE DO WE GO FROM HERE?**

As evidenced by the research presented here, emotion regulation is a complex ability that depends on the concerted actions of multiple processes that in turn depend upon networks of brain regions. In the following paragraphs, we briefly outline what we think should be the future focuses of emotion regulation research, how these can inform our current theoretical models, and how to apply these recommendations to studying emotion regulation across the life span.

#### **Increasing ecological validity through experience sampling**

In recent years, there has been a push to combine neuroimaging measures of emotion regulation with more ecologically valid behavioral measurements of emotion generation and regulation. One way this has begun to be addressed is through combining experience sampling methods with neuroimaging. For example, ecological momentary assessment (EMA) (Shiffman et al., 2008) can be used to study thoughts, behaviors and emotions

as they occur in daily life across the adult life span (Carstensen et al., 2000), and there has been a recent increase in the applications of EMA methods, particularly as a tool to measure emotion regulation behavior. EMA enjoys advantages over other lab-based methods because it is ecologically valid and is not subject to the memory biases typical of recall-based experimental designs. By asking people about situations they are actively regulating throughout the day, experimenters have learned that perceived situational controllability interacts with regulatory strategy in such a way that people with high well-being use reappraisal more in situations they perceive as lower in controllability and less in situations they perceive as higher in controllability (Haines et al., 2016). Time-series analyses of EMA responses have also found that for healthy individuals, the use of suppression may be followed by increases in negative affect and decreases in positive affect, whereas reappraisal and social sharing, as regulatory strategies, may be associated with subsequent increases in positive affect (Brans et al., 2013). Additionally, fMRI activity in lab-based tasks has been shown to predict daily life functioning (Falk et al., 2015; Heller et al., 2015). However, the combination of EMA with fMRI measures of brain activity during emotion regulation tasks remains, to our knowledge, an unexplored area of research with the potential to add a great deal to our understanding of brain mechanisms of regulation in and outside of the lab.

#### **New ways of measuring affective behavior**

In addition to improving behavioral measurement outside of the lab, there has also been an uptick in using unobtrusive behavioral measures such as eye tracking and pupil dilation to study emotion regulation within the lab. These more implicit measures aim to minimize demand effects while allowing for a potentially more direct pipeline into physiological responses elicited by affective stimuli and its subsequent regulation. While the use of psychophysiological methods to study emotion is not new (see, e.g., Norman et al., 2014), they have been used to answer new types of questions. For instance, they have offered new insights about how individuals at different developmental stages spontaneously regulate their emotions, finding that older adults spent more time looking at happy faces and less time looking at fearful and angry faces relative to younger adults (Isaacowitz et al., 2006), whereas adolescents exhibit more pupil dilation—a marker of increased attention and cognitive processing—for negative than positive social stimuli relative to younger children (Silk et al., 2012).

### Emotion regulation training and choice

Most of the research thus far has given participants instructions on what strategies to use and when they should be implemented within an experimental setting. While this has given insight into the neural and behavioral architecture of different forms of emotion regulation, it remains unclear to what extent these different strategies are used spontaneously in day-to-day behavior, if choosing to implement a certain strategy versus being directed to implement it changes its efficacy, and if receiving regulation training impacts emotion regulation practices outside of the lab. A few studies have focused on these questions directly and have yielded promising results. When individuals are given a choice in what kind of regulation to implement, they tend to prefer distraction for high-intensity negative images and to choose reappraisal for low-intensity negative images (Sheppes et al., 2014), and recent work examining regulation choice found that PFC-amygdala activity during an initial viewing of negative images predicts the subsequent choice to regulate (Doré et al., 2017b).

Previous research has found that reappraisal training can have lasting effects, as when individuals show decreased amygdala activity to images that have been reappraised multiple times as compared to images that have been reappraised only once (Denny et al., 2015). One study that focused directly on reappraisal training over the long term found that distancing reappraisal may be particularly effective, in that individuals who practiced distancing (as compared to reinterpretation and control groups) reported reduced stress and were less reactive to negative stimuli (Denny et al., 2015). In addition, it seems that training basic nonaffective cognitive control skills can impact emotion regulation ability. One study (Cohen et al., 2016) trained individuals over the course of 2 weeks on a nonaffective Flanker task, designed to increase cognitive control and flexibility. The researchers found that individuals who had received Flanker training showed less affective interference during an image-viewing task, and increased amygdala–prefrontal connectivity. Taken together, this suggests that receiving regulation training may have a positive impact on psychologic well-being.

When discussing emotion regulation training, we would be remiss if we did not mention the advances made in recent years in studying the neural bases of mindfulness and compassion-based meditation training on emotion regulation. Mindfulness and meditation techniques frequently rely on attention selection and cognitive reappraisal working together in order to regulate emotion. One study that examined Focused Attention (FA) meditation—in which individuals actively attend to a certain stimulus (e.g., breathing), and bring

the focus back to the stimulus whenever attention wanders—found that FA led to increased activity in dIPFC and parietal control areas, and decreased amygdala activity (Brefczynski-Lewis et al., 2007; Lutz et al., 2008). Another study found that engaging in mindfulness practices increased prefrontal activity and decreased amygdala and hippocampal activity when viewing negative images, and that individuals that were high in trait mindfulness needed to recruit prefrontal and insula regions less when expecting to view negative stimuli (Lutz et al., 2013). Follow-up research found that cognitive reappraisal and mindfulness recruit similar prefrontal circuitry (Opialla et al., 2014). Interestingly, a study that directly compared mindfulness with suppression found that while both downregulated amygdala activity, the former tended to recruit medial regions of the PFC, whereas the latter tended to recruit dIPFC. Finally, one study contrasted reappraisal with compassion-based regulation, which asks people to focus on and attend to the mental and emotional states of others (Engen and Singer, 2014). This study found that both compassion and reappraisal regulated emotion, but that compassion was more successful than reappraisal when upregulating positive emotion, and reappraisal was more successful than compassion when downregulating negative emotion. Not surprisingly, compassion regulation led to more activity in large swathes of the mPFC, including regions involved in self and social awareness.

### It takes (at least) two: The social regulation of emotion

The majority of emotion regulation research to date has focused on intrapersonal regulation or regulating emotion at the individual level. However, this does not adequately reflect the real world, in which both our emotions and their regulation are meaningfully impacted by the actions of others (Lakey and Orehek, 2011; Aldao, 2013; Reeck et al., 2016). Recent research has begun to address this gap in the literature, finding that regulating others' emotions can benefit the self (Inagaki and Eisenberger, 2012; Doré et al., 2017b) and that taking another person's perspective can modulate both behavioral measures and neural correlates of emotion (Gilead et al., 2016). In addition, there is a growing body of research that has focused on the neural bases of social support and close attachment on emotion regulation (Beckes and Coan, 2012), finding that both actual interaction with a romantic partner (Coan et al., 2006) and passive viewing of a romantic partner's face (Eisenberger et al., 2011) reduces brain activity in regions implicated in stress and arousal (e.g., anterior insula, dACC) when experiencing physical pain. The social regulation of emotion may be of particular import

in studying emotion regulation across development, as children often rely on both implicit and explicit signals from primary caregivers when learning how to react to new affect-eliciting situations. It is also important to study social regulation in older adults, a population faced with increasing health concerns. In difficult times, older adults often rely on their caregivers for emotional support, which can become especially taxing on the caregivers.

### **Individual differences in emotion regulation goals**

In addition to an increased interest in studying interpersonal emotion regulation, there also has also been interest in studying how individual differences impact emotion regulation goals and efficacy. In particular, there has been a push to consider demographics as key contextual features of emotion regulation (Aldao, 2013). Individuals learn how to experience and regulate emotions from others, and different cultural scripts can lead to marked differences in the generation and regulation of specific emotions (Gross and Barrett, 2011). An individual's cultural background can have a meaningful impact on the emotions that are desirable and undesirable (Tsai, 2007), and how effective different strategies will be in terms of creating a desired affective state. Recent research on how emotion regulation goals differ as a function of one's cultural background found that individuals from Asian cultures are less likely to engage in hedonic emotion regulation (upregulating positive emotion and downregulating negative emotion) than European Americans (Miyamoto et al., 2014), and that this difference is reflected in the increased tendency for European Americans to savor positive emotion (Miyamoto and Ma, 2011; Ma et al., 2017). In addition, the negative consequences associated with suppression are moderated by one's cultural background, in that they are stronger for individuals from Western cultures and weaker for individuals from East-Asian cultures (Butler et al., 2007). It seems plausible that this type of difference could be the case for individuals that come from the same culture but grew up in different generations with different norms in terms of communicating and expressing emotion.

### **Multivariate approaches to emotion regulation**

In recent years, there has been increased interest in using multivariate methods to study both emotion and its regulation. These methods include multivoxel pattern analysis (MVPA), representational similarity analysis, and machine learning. In general, the goal of these analyses is to get a better sense of how information is represented in the brain and to use observed brain states to

make better inferences about what participants are experiencing. One study that used MVPA and emotion regulation found evidence for a reappraisal network that includes vIPFC, dlPFC, and parietal control regions, which show similar neural patterns for reappraisal across both static (i.e., negative images) and dynamic (i.e., video) stimuli (Morawetz et al., 2016). In terms of machine learning, Chang et al. (2015), identified a network of regions that together create a neural "signature" for experienced affect and can predict explicit ratings of negative emotion, termed the Picture Induced Negative Emotion Signature (PINES). Recent work examining social regulation of emotion through perspective taking used the neural signature identified in the PINES research and found that this network was sensitive to mental simulation and could be modulated based on regulatory goals (Gilead et al., 2016). We believe that these methods are a promising step forward and will yield new insights on the processes involved in emotion regulation in the coming years.

### **CONCLUSION**

In the show *Star Trek: The Next Generation*, a robot named Data develops feelings for a fellow crewmate. In a show of devotion, he develops a new subroutine in order to guide him in the process of falling in love and connecting with another person emotionally. Unfortunately for Data, he finds that a program built only on logic cannot withstand the vagaries of love, and the relationship ends. While this perhaps seems like a problem that would only befall a robot, we too create routines and programs for how to manage our own and others' emotions, with varying degrees of success. Emotion regulation is complex—it involves learning and applying multiple strategies, with networks of brain regions working together, and how one goes about it can meaningfully change across the life span. At times, the programs that we have created to manage our emotions seem to work beautifully—we get the second marshmallow, successfully hold back our tears, or suppress our laughter at an inappropriate moment. But other times, like Data, our program is insufficient, and we cannot quite handle the affective situation that we have gotten ourselves into. The research discussed earlier has begun to lay out the space for emotion regulation—we have a better understanding of both the programs that are applied for emotion regulation and their components—but, this is only the beginning. By taking a converging-methods approach that examines emotion generation and its regulation at multiple levels of analysis and at different points in the life span, we will be better able to understand and predict when emotions will give to rise to our best or bring out our worst.

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## REFERENCES

- Adolphs R (2016). How should neuroscience study emotions? By distinguishing emotion states, concepts, and experiences. *Soc Cogn Affect Neurosci* 12 (1): 24–31.
- Aldao A (2013). The future of emotion regulation research. *Perspect Psychol Sci* 8 (2): 155–172. <https://doi.org/10.1177/1745691612459518>.
- Allard ES, Kensinger EA (2014a). Age-related differences in functional connectivity during cognitive emotion regulation. *J Gerontol B Psychol Sci Soc Sci* 69 (September): 852–860. <https://doi.org/10.1093/geronb/gbu108>.
- Allard ES, Kensinger EA (2014b). Age-related differences in neural recruitment during the use of cognitive reappraisal and selective attention as emotion regulation strategies. *Front Psycho* 15 (April): 296. <https://doi.org/10.3389/fpsyg.2014.00296>.
- Allman JM, Tetreault NA, Hakeem AY et al. (2010). The von Economo neurons in fronto-insular and anterior cingulate cortex. *Ann N Y Acad Sci* 1225: 59–71. <https://doi.org/10.1111/j.1749-6632.2011.06011.x>.
- Anderson AK (2007). Feeling emotional: the amygdala links emotional perception and experience. *Soc Cogn Affect Neurosci* 2 (2): 71–72. <https://doi.org/10.1093/scan/nsm022>.
- Anderson AK, Phelps EA (2001). Lesions of the human amygdala impair enhanced perception of emotionally salient events. *Nature* 411 (6835): 305–309. <https://doi.org/10.1038/35077083>.
- Anderson AK, Phelps EA (2002). Is the human amygdala critical for the subjective experience of emotion? Evidence of intact dispositional affect in patients with amygdala lesions. *J Cogn Neurosci* 14 (5): 709–720. <https://doi.org/10.1162/08989290260138618>.
- Andrews-Hanna JR, Snyder AZ, Vincent JL et al. (2007). Disruption of large-scale brain systems in advanced aging. *Neuron* 56 (5): 924–935. <https://doi.org/10.1016/j.neuron.2007.10.038>.
- Arnsten AFT (2009). Stress signalling pathways that impair prefrontal cortex structure and function. *Nat Rev Neurosci* 10 (6): 410–422. <https://doi.org/10.1038/nrn2648>.
- Ayduk Ö, Kross E (2010). From a distance: implications of spontaneous self-distancing for adaptive self-reflection. *J Pers Soc Psychol* 98 (5): 809.
- Badre D, D'Esposito M (2007). Functional magnetic resonance imaging evidence for a hierarchical organization of the prefrontal cortex. *J Cogn Neurosci* 19 (12): 1–18. <https://doi.org/10.1007/s11525-006-9103-5>.
- Badre D, Wagner AD (2007). Left ventrolateral prefrontal cortex and the cognitive control of memory. *Neuropsychologia* 45 (13): 2883–2901. <https://doi.org/10.1016/j.neuropsychologia.2007.06.015>.
- Badre D, Poldrack RA, Paré-Blagoev EJ et al. (2005). Dissociable controlled retrieval and generalized selection mechanisms in ventrolateral prefrontal cortex. *Neuron* 47 (6): 907–918.
- Banks SJ, Eddy KT, Angstadt M et al. (2007). Amygdala-frontal connectivity during emotion regulation. *Soc Cogn Affect Neurosci* 2 (4): 303–312. <https://doi.org/10.1093/scan/nsm029>.
- Barbas H, Zikopoulos B, Timbie C (2011). Sensory pathways and emotional context for action in primate prefrontal cortex. *Biol Psychiatry* 69 (12): 1133–1139. <https://doi.org/10.1016/j.biopsych.2010.08.008>.
- Barrett LF (2016). Navigating the science of emotion. In: *Emotion measurement*, Woodhead Publishing, pp. 31–63.
- Barrett LF, Bliss-Moreau E, Duncan SL et al. (2007). The amygdala and the experience of affect. *Soc Cogn Affect Neurosci* 2: 73–83. <https://doi.org/10.1093/scan/nsl042>.
- Beckes L, Coan JA (2012). Social baseline theory and the social regulation of emotion. In: *The science of the couple*, Psychology Press, New York, NY, pp. 81–93.
- Berkman ET, Lieberman MD (2009). Using neuroscience to broaden emotion regulation: theoretical and methodological considerations. *Soc Personal Psychol Compass* 3 (4): 475–493. <https://doi.org/10.1111/j.1751-9004.2009.00186.x>.
- Blakemore S-J (2008). The social brain in adolescence. *Nat Rev Neurosci* 9: 267–277. <https://doi.org/10.1038/nrn2353>.
- Brans K, Koval P, Verduyn P et al. (2013). The regulation of negative and positive affect in daily life. *Emotion* 13 (5): 926–939. <https://doi.org/10.1037/a0032400>.
- Brassen S, Gamer M, Bchel C (2011). Anterior cingulate activation is related to a positivity bias and emotional stability in successful aging. *Biol Psychiatry* 70 (2): 131–137. <https://doi.org/10.1016/j.biopsych.2010.10.013>.
- Brassen S, Gamer M, Peters J et al. (2012). Don't look back in anger! Responsiveness to missed chances in successful and unsuccessful aging. *Science* 336 (6081): 612–614. <https://doi.org/10.1126/science.1217516>.
- Braunstein LM, Gross JJ, Ochsner KN (2017). Explicit and implicit emotion regulation: a multi-level framework. *Soc Cogn Affect Neurosci* 12 (10): 1545–1557.
- Brefczynski-Lewis JA, Lutz A, Schaefer HS et al. (2007). Neural correlates of attentional expertise in long-term meditation practitioners. *Proc Natl Acad Sci* 104 (27): 11483–11488. <https://doi.org/10.1073/pnas.0606552104>.
- Bruneau EG, Pluta A, Saxe R (2012). Distinct roles of the “shared pain” and “theory of mind” networks in processing others' emotional suffering. *Neuropsychologia* 50 (2): 219–231. <https://doi.org/10.1016/j.neuropsychologia.2011.11.008>.
- Buhle JT, Silvers JA, Wager TD et al. (2014). Cognitive reappraisal of emotion: a meta-analysis of human neuroimaging studies. *Cereb Cortex* 1–10. <https://doi.org/10.1093/cercor/bht154>.
- Bullmore E, Sporns O (2009). Complex brain networks: graph theoretical analysis of structural and functional systems. *Nat Rev Neurosci* 10 (4): 312. <https://doi.org/10.1038/nrn2618>.
- Butler Ea, Lee TL, Gross JJ (2007). Emotion regulation and culture: are the social consequences of emotion



- suppression culture-specific? *Emotion* 7 (1): 30–48. <https://doi.org/10.1037/1528-3542.7.1.30>.
- Calder AJ, Lawrence AD, Young AW (2001). Neuropsychology of fear and loathing. *Nat Rev Neurosci* 2 (5): 352–363. <https://doi.org/10.1038/35072584>.
- Carstensen LL, Pasupathi M, Mayr U et al. (2000). Emotional experience in everyday life across the adult life span. *J Pers Soc Psychol* 79 (4): 644–655. <https://doi.org/10.1037/0022-3514.79.4.644>.
- Carstensen LL, Turan B, Scheibe S et al. (2011). Emotional experience improves with age: evidence based on over 10 years of experience sampling. *Psychol Aging* 26 (1): 21–33. <https://doi.org/10.1037/a0021285>.
- Casey BJ, Jones RM (2010). Neurobiology of the adolescent brain and behavior: implications for substance use disorders. *J Am Acad Child Adolesc Psychiatry* 49 (12): 1189–1201. S0890-8567(10)00670-2 [pii]. <https://doi.org/10.1016/j.jaac.2010.08.017>.
- Casey BJ, Somerville LH, Gotlib IH et al. (2011). Behavioral and neural correlates of delay of gratification 40 years later. *Proc Natl Acad Sci* 108 (36): 14998–15003. <https://doi.org/10.1073/pnas.1108561108>.
- Chang LJ, Gianaros PJ, Manuck SB et al. (2015). A sensitive and specific neural signature for picture-induced negative affect. *PLoS Bio* 113 (6): 1–28. <https://doi.org/10.1371/journal.pbio.1002180>.
- Coan JA, Schaefer HS, Davidson RJ (2006). Lending a hand: social regulation of the neural response to threat. *Psychol Sci* 17 (12): 1032–1039. <https://doi.org/10.1111/j.1467-9280.2006.01832.x>.
- Cohen Kadosh K, Luo Q, de Burca C et al. (2016). Using real-time fMRI to influence effective connectivity in the developing emotion regulation network. *Neuroimage* 125: 616–626. <https://doi.org/10.1016/j.neuroimage.2015.09.070>.
- Cohen N, Moyal N, Lichtenstein-Vidne L et al. (2016). Explicit vs. implicit emotional processing: the interaction between processing type and executive control. *Cognit Emot* 30 (2): 325–339.
- Critchley HD (2004). The human cortex responds to an interoceptive challenge. *Proc Natl Acad Sci U S A* 101 (17): 6333–6334. <https://doi.org/10.1073/pnas.0401510101>.
- Cunningham Wa, Brosch T (2012). Motivational salience. *Curr Dir Psychol Sci* 21 (1): 54–59. <https://doi.org/10.1177/0963721411430832>.
- Davis M, Whalen PJ (2001). The amygdala: vigilance and emotion. *Mol Psychiatry* 6 (1): 13–34. <https://doi.org/10.1038/sj.mp.4000812>.
- Davis JI, Senghas A, Ochsner KN (2009). How does facial feedback modulate emotional experience? *J Res Pers* 43 (5): 822–829. <https://doi.org/10.1016/j.jrp.2009.06.005>.
- Davis JI, Senghas A, Brandt F et al. (2010). The effects of BOTOX injections on emotional experience. *Emotion* 10 (3): 433–440. <https://doi.org/10.1037/a0018690>.
- deCharms RC, Christoff K, Glover GH et al. (2004). Learned regulation of spatially localized brain activation using real-time fMRI. *Neuroimage* 21 (1): 436–443. <https://doi.org/10.1016/j.neuroimage.2003.08.041>.
- deCharms RC, Maeda F, Glover GH et al. (2005). Control over brain activation and pain learned by using real-time functional MRI. *Proc Natl Acad Sci* 102 (51): 18626–18631. <https://doi.org/10.1073/pnas.0505210102>.
- Demos KE, Heatherton TF, Kelley WM (2012). Individual differences in nucleus accumbens activity to food and sexual images predict weight gain and sexual behavior. *J Neurosci* 32 (16): 5549–5552. <https://doi.org/10.1523/JNEUROSCI.5958-11.2012>.
- Denny BT, Inhoff MC, Zerubavel N et al. (2015). Getting over it. *Psychol Sci* 26 (9): 1377–1388. <https://doi.org/10.1177/0956797615578863>.
- Dillon DG, LaBar KS (2005). Startle modulation during conscious emotion regulation is arousal-dependent. *Behav Neurosci* 119 (4): 1118–1124. <https://doi.org/10.1037/0735-7044.119.4.1118>.
- Doré BP, Boccagno C, Burr D et al. (2017a). Finding positive meaning in negative experiences engages ventral striatal and ventromedial prefrontal regions associated with reward valuation. *J Cogn Neurosci* 29 (2): 235–244.
- Doré BP, Weber J, Ochsner KN (2017b). Neural predictors of decisions to cognitively control emotion. *J Neurosci* 37 (10): 2580–2588.
- Dörfel D, Lamke JP, Hummel F et al. (2014). Common and differential neural networks of emotion regulation by detachment, reinterpretation, distraction, and expressive suppression: a comparative fMRI investigation. *Neuroimage* 101 (June): 298–309. <https://doi.org/10.1016/j.neuroimage.2014.06.051>.
- Drabant EM, McRae K, Manuck SB et al. (2009). Individual differences in typical reappraisal use predict amygdala and prefrontal responses. *Biol Psychiatry* 65 (5): 367–373. <https://doi.org/10.1016/j.biopsych.2008.09.007>.
- Eisenberger NI, Master SL, Inagaki TK et al. (2011). Attachment figures activate a safety signal-related neural region and reduce pain experience. *Proc Natl Acad Sci U S A* 108 (28): 11721–11726.
- Eldar E, Rutledge RB, Dolan RJ et al. (2016). Mood as representation of momentum. *Trends Cogn Sci* 20 (1): 15–24. <https://doi.org/10.1016/j.tics.2015.07.010>.
- Emmert K, Kopel R, Sulzer J et al. (2016). Meta-analysis of real-time fMRI neurofeedback studies using individual participant data: how is brain regulation mediated? *Neuroimage* 124: 806–812. <https://doi.org/10.1016/j.neuroimage.2015.09.042>.
- Engen HG, Singer T (2014). The neural signatures of compassion-based emotion regulation in expert meditators. In: *Inaugural conference of the society for affective science (SAS)*.
- Etkin A, Egner T, Peraza DM et al. (2006). Resolving emotional conflict: a role for the rostral anterior cingulate cortex in modulating activity in the amygdala. *Neuron* 51 (6): 871–882. <https://doi.org/10.1016/j.neuron.2006.07.029>.
- Fair Da, Dosenbach NUF, Church JA et al. (2007). Development of distinct control networks through segregation and integration. *Proc Natl Acad Sci* 104 (33): 13507–13512. <https://doi.org/10.1073/pnas.0705843104>.
- Fair Da, Cohen AL, Dosenbach NUF et al. (2008). The maturing architecture of the brain's default network. *Proc Natl Acad Sci* 105 (10): 4028–4032. <https://doi.org/10.1073/pnas.0800376105>.

- Falk EB, O'Donnell MB, Cascio CN et al. (2015). Self-affirmation alters the brain's response to health messages and subsequent behavior change. *Proc Natl Acad Sci* 112 (7): 1977–1982. <https://doi.org/10.1073/pnas.1500247112>.
- Ferri J, Schmidt J, Hajcak G et al. (2013). Neural correlates of attentional deployment within unpleasant pictures. *Neuroimage* 70: 268–277. <https://doi.org/10.1016/j.neuroimage.2012.12.030>.
- Fischer H, Sandblom J, Gavazzeni J et al. (2005). Age-differential patterns of brain activation during perception of angry faces. *Neurosci Lett* 386 (2): 99–104.
- Fjell AM (2010). Structural brain changes in aging: courses, causes and cognitive consequences. *Rev Neurosci* 21 (3): 187–221. <https://doi.org/10.1515/REVNEURO.2010.21.3.187>.
- Fjell AM, Westlye LT, Amlien I et al. (2009). High consistency of regional cortical thinning in aging across multiple samples. *Cereb Cortex* 19 (9): 2001–2012. <https://doi.org/10.1093/cercor/bhn232>.
- Friston KJ (2011). Functional and effective connectivity: a review. *Brain Connect* 1 (1): 13–36. <https://doi.org/10.1089/brain.2011.0008>.
- Friston K, Buechel C, Fink G et al. (1997). Psychophysiological and modulatory interactions in neuroimaging. *Neuroimage* 6 (3): 218–229. <https://doi.org/10.1006/nimg.1997.0291>.
- Galvan A, Hare TA, Parra CE et al. (2006). Earlier development of the accumbens relative to orbitofrontal cortex might underlie risk-taking behavior in adolescents. *J Neurosci* 26 (25): 6885–6892. <https://doi.org/10.1523/JNEUROSCI.1062-06.2006>.
- Gee DG, Humphreys KL, Flannery J et al. (2013). A developmental shift from positive to negative connectivity in human amygdala–prefrontal circuitry. *J Neurosci* 33 (10): 4584–4593. <https://doi.org/10.1523/JNEUROSCI.3446-12.2013>.
- Geier C, Luna B (2009). The maturation of incentive processing and cognitive control. *Pharmacol Biochem Behav* 93 (3): 212–221. <https://doi.org/10.1016/j.pbb.2009.01.021>.
- Ghashghaei HT, Barbas H (2002). Pathways for emotion: interactions of prefrontal and anterior temporal pathways in the amygdala of the rhesus monkey. *Neuroscience* 115 (4): 1261–1279. [https://doi.org/10.1016/S0306-4522\(02\)00446-3](https://doi.org/10.1016/S0306-4522(02)00446-3).
- Ghashghaei HT, Hilgetag CC, Barbas H (2007). Sequence of information processing for emotions based on the anatomic dialogue between prefrontal cortex and amygdala. *Neuroimage* 34 (3): 905–923. <https://doi.org/10.1016/j.neuroimage.2006.09.046>.
- Gilead M, Boccagno C, Silverman M et al. (2016). Self-regulation via neural simulation. *Proc Natl Acad Sci* 113 (36): 10037–10042. <https://doi.org/10.1073/pnas.1600159113>.
- Giuliani N, Drabant E, Gross J (2011a). Anterior cingulate cortex volume and emotion regulation: is bigger better? *Biol Psychol* 86 (3): 379–382. <https://doi.org/10.1016/j.biopsycho.2010.11.010>.
- Giuliani NR, Drabant EM, Bhatnagar R et al. (2011b). Emotion regulation and brain plasticity: expressive suppression use predicts anterior insula volume. *Neuroimage* 58 (1): 10–15. <https://doi.org/10.1016/j.neuroimage.2011.06.028>.
- Gogtay N, Giedd JN, Lusk L et al. (2004). Dynamic mapping of human cortical development during childhood through early adulthood. *Proc Natl Acad Sci U S A* 101 (21): 8174–8179. Retrieved from file://c:/My files/RefMan10/RefMan pdfs/16127.pdf.
- Goldenberg D, Galván A (2015). The use of functional and effective connectivity techniques to understand the developing brain. *Dev Cogn Neurosci* 12: 155–164. <https://doi.org/10.1016/j.dcn.2015.01.011>.
- Goldin PR, McRae K, Ramel W et al. (2008). The neural bases of emotion regulation: reappraisal and suppression of negative emotion. *Biol Psychiatry* 63 (6): 577–586. <https://doi.org/10.1016/j.biopsych.2007.05.031>.
- Golkar A, Lonsdorf TB, Olsson A et al. (2012). Distinct contributions of the dorsolateral prefrontal and orbitofrontal cortex during emotion regulation. *PLoS ONE* 7 (11): e48107. <https://doi.org/10.1371/journal.pone.0048107>.
- Gotlib IH, McCann CD (1984). Construct accessibility and depression: an examination of cognitive and affective factors. *J Pers Soc Psychol* 47 (2): 427–439. <https://doi.org/10.1037/0022-3514.47.2.427>.
- Greucci A, Giorgetta C, van't Wout M et al. (2013). Reappraising the ultimatum: an fMRI study of emotion regulation and decision making. *Cereb Cortex* 23 (2): 399–410. <https://doi.org/10.1093/cercor/bhs028>.
- Greer SM, Trujillo AJ, Glover GH et al. (2014). Control of nucleus accumbens activity with neurofeedback. *Neuroimage* 96: 237–244.
- Gross JJ (1998). The emerging field of emotion regulation: an integrative review. *Rev Gen Psychol* 2 (5): 271–299. <https://doi.org/10.1017/S0048577201393198>.
- Gross JJ, Barrett LF (2011). Emotion generation and emotion regulation: one or two depends on your point of view. *Emot Rev* 3 (1): 8–16. <https://doi.org/10.1177/1754073910380974>.
- Gross JJ, Levenson RW (1993). Emotional suppression: physiology, self-report, and expressive behavior. *J Pers Soc Psychol* 64 (6): 970–986. <https://doi.org/10.1037/0022-3514.64.6.970>.
- Gross JJ, Thompson RA (2007). Emotion regulation: conceptual foundations. In: JJ Gross (Ed.), *Handbook of emotion regulation*. Guilford Press, New York, pp. 3–24.
- Gullone E, Hughes EK, King NJ et al. (2010). The normative development of emotion regulation strategy use in children and adolescents: a 2-year follow-up study. *J Child Psychol Psychiatry Allied Discip* 51 (5): 567–574. <https://doi.org/10.1111/j.1469-7610.2009.02183.x>.
- Haber SN, Knutson B (2010). The reward circuit: linking primate anatomy and human imaging. *Neuropsychopharmacology* 35 (1): 4–26. <https://doi.org/10.1038/npp.2009.129>.
- Haines SJ, Gleeson J, Kuppens P et al. (2016). The wisdom to know the difference strategy-situation fit in emotion regulation in daily life is associated with well-being. *Psychol Sci* 27 (12): 1651–1659. <https://doi.org/10.1177/0956797616669086>.
- Hare TA, Tottenham N, Davidson MC et al. (2005). Contributions of amygdala and striatal activity in emotion regulation. *Biol Psychiatry* 57 (6): 624–632. <https://doi.org/10.1016/j.biopsych.2004.12.038>.
- Hare TA, Tottenham N, Galvan A et al. (2008). Biological substrates of emotional reactivity and regulation in adolescence during an emotional Go-Nogo task. *Biol*

- Psychiatry 63 (10): 927–934. <https://doi.org/10.1016/j.biopsych.2008.03.015>.
- Hartley CA, Phelps EA (2010). Changing fear: the neurocircuitry of emotion regulation. *Neuropsychopharmacology* 35 (1): 136–146. <https://doi.org/10.1038/npp.2009.121>.
- He X, Qin W, Liu Y et al. (2014). Abnormal salience network in normal aging and in amnesic mild cognitive impairment and Alzheimer's disease. *Hum Brain Mapp* 35 (7): 3446–3464. <https://doi.org/10.1002/hbm.22414>.
- Heatherton TF, Wagner DD (2011). Cognitive neuroscience of self-regulation failure. *Trends Cogn Sci* 15 (3): 132–139. <https://doi.org/10.1016/j.tics.2010.12.005>.
- Hedman AM, van Haren NEM, Schnack HG et al. (2012). Human brain changes across the life span: a review of 56 longitudinal magnetic resonance imaging studies. *Hum Brain Mapp* 33 (8): 1987–2002. <https://doi.org/10.1002/hbm.21334>.
- Heller AS, Fox AS, Wing EK et al. (2015). The neurodynamics of affect in the laboratory predicts persistence of real-world emotional responses. *J Neurosci* 35 (29): 10503–10509. <https://doi.org/10.1523/jneurosci.0569-15.2015>.
- Hooker CI, Gyurak A, Verosky SC et al. (2010). Neural activity to a partner's facial expression predicts self-regulation after conflict. *Biol Psychiatry* 67 (5): 406–413. <https://doi.org/10.1016/j.biopsych.2009.10.014>.
- Hutcherson CA, Plassmann H, Gross JJ et al. (2012). Cognitive regulation during decision making shifts behavioral control between ventromedial and dorsolateral prefrontal value systems. *J Neurosci* 32 (39): 13543–13554. <https://doi.org/10.1523/JNEUROSCI.6387-11.2012>.
- Hwang S, White SF, Nolan ZT et al. (2014). Neurodevelopmental changes in the responsiveness of systems involved in top down attention and emotional responding. *Neuropsychologia* 62 (1): 277–285. <https://doi.org/10.1016/j.neuropsychologia.2014.08.003>.
- Inagaki TK, Eisenberger NI (2012). Neural correlates of giving support to a loved one. *Psychosom Med* 74 (1): 3–7.
- Isaacowitz DM, Wadlinger HA, Goren D et al. (2006). Selective preference in visual fixation away from negative images in old age? An eye-tracking study. *Psychol Aging* 21 (1): 40.
- Jackson DC, Malmstadt JR, Larson CL et al. (2000). Suppression and enhancement of emotional responses to unpleasant pictures. *Psychophysiology* 37 (4): 515–522. <https://doi.org/10.1111/1469-8986.3740515>.
- Jensen J, McIntosh AR, Crawley AP et al. (2003). Direct activation of the ventral striatum in anticipation of aversive stimuli. *Neuron* 40 (6): 1251–1257. [https://doi.org/10.1016/S0896-6273\(03\)00724-4](https://doi.org/10.1016/S0896-6273(03)00724-4).
- Jernigan TL, Archibald SL, Fennema-Notestine C et al. (2001). Effects of age on tissues and regions of the cerebrum and cerebellum. *Neurobiol Aging* 22 (4): 581–594. [https://doi.org/10.1016/S0197-4580\(01\)00217-2](https://doi.org/10.1016/S0197-4580(01)00217-2).
- Jiang J, Sachdev P, Lipnicki DM et al. (2014). A longitudinal study of brain atrophy over two years in community-dwelling older individuals. *Neuroimage* 86: 203–211. <https://doi.org/10.1016/j.neuroimage.2013.08.022>.
- John OP, Gross JJ (2004). Healthy and unhealthy emotion regulation: personality processes, individual differences, and life span development. *J Pers* 72 (6): 1301–1333. <https://doi.org/10.1111/j.1467-6494.2004.00298.x>.
- Kanske P, Heissler J, Schönfelder S et al. (2011). How to regulate emotion? Neural networks for reappraisal and distraction. *Cereb Cortex* 21 (6): 1379–1388. <https://doi.org/10.1093/cercor/bhq216>.
- Kelly AMC, Di Martino A, Uddin LQ et al. (2009). Development of anterior cingulate functional connectivity from late childhood to early adulthood. *Cereb Cortex* 19 (3): 640–657. <https://doi.org/10.1093/cercor/bhn117>.
- Kim SH, Hamann S (2007). Neural correlates of positive and negative emotion regulation. *J Cogn Neurosci* 19 (5): 776–798. <https://doi.org/10.1162/jocn.2007.19.5.776>.
- Kim P, Evans GW, Angstadt M et al. (2013). Effects of childhood poverty and chronic stress on emotion regulatory brain function in adulthood. *Proc Natl Acad Sci* 110 (46): 18442–18447. <https://doi.org/10.1073/pnas.1308240110>.
- Knutson B, Adams CM, Fong GW et al. (2001). Anticipation of increasing monetary reward selectively recruits nucleus accumbens. *J Neurosci* 21 (16): RC159.
- Kober H, Barrett LF, Joseph J et al. (2008). Functional grouping and cortical–subcortical interactions in emotion: a meta-analysis of neuroimaging studies. *Neuroimage* 42 (2): 998–1031. <https://doi.org/10.1016/j.neuroimage.2008.03.059>.
- Kober H, Mende-Siedlecki P, Kross EF et al. (2010). Prefrontal–striatal pathway underlies cognitive regulation of craving. *Proc Natl Acad Sci* 107 (33): 14811–14816. <https://doi.org/10.1073/pnas.1007779107>.
- Koenigsberg HW, Fan J, Ochsner KN et al. (2010). Neural correlates of using distancing to regulate emotional responses to social situations. *Neuropsychologia* 48 (6): 1813–1822. <https://doi.org/10.1016/j.neuropsychologia.2010.03.002>.
- Kohn N, Eickhoff SB, Scheller M et al. (2014). Neural network of cognitive emotion regulation—an ALE meta-analysis and MACM analysis. *Neuroimage* 87: 345–355. <https://doi.org/10.1016/j.neuroimage.2013.11.001>.
- Kühn S, Brass M, Haggard P (2013). Feeling in control: neural correlates of experience of agency. *Cortex* 49 (7): 1935–1942. <https://doi.org/10.1016/j.cortex.2012.09.002>.
- Lahey B, Orehek E (2011). Relational regulation theory: a new approach to explain the link between perceived social support and mental health. *Psychol Rev* 118 (3): 482–495. <https://doi.org/10.1037/a0023477>.
- Lamke JP, Daniels JK, Dörfel D et al. (2014). The impact of stimulus valence and emotion regulation on sustained brain activation: task-rest switching in emotion. *PLoS ONE* 9 (3): e93098. <https://doi.org/10.1371/journal.pone.0093098>.
- Lapate RC, Lee H, Salomons TV et al. (2012). Amygdalar function reflects common individual differences in emotion and pain regulation success. *J Cogn Neurosci* 24 (1): 148–158. [https://doi.org/10.1162/jocn\\_a\\_00125](https://doi.org/10.1162/jocn_a_00125).
- Levesque J, Joanne Y, Mensour B et al. (2004). Neural basis of emotional self-regulation in childhood. *Neuroscience* 129 (2): 361–369. <https://doi.org/10.1016/j.neuroscience.2004.07.032>.
- Li T, Fung HH, Isaacowitz DM (2011). The role of dispositional reappraisal in the age-related positivity effect. *J Gerontol B Psychol Sci Soc Sci* 66B (1): 56–60. <https://doi.org/10.1093/geronb/gbq074>.

- Li R, Zhu X, Yin S et al. (2014). Multimodal intervention in older adults improves resting-state functional connectivity between the medial prefrontal cortex and medial temporal lobe. *Front Aging Neurosci* 6: 39. <https://doi.org/10.3389/fnagi.2014.00039>.
- Li Z, Tong L, Guan M et al. (2016). Altered resting-state amygdala functional connectivity after real-time fMRI emotion self-regulation training. *Biomed Res Int* 2016: 2719895. <https://doi.org/10.1155/2016/2719895>.
- Lieberman MD, Inagaki TK, Tabibnia G et al. (2011). Subjective responses to emotional stimuli during labeling, reappraisal, and distraction. *Emotion* 11 (3): 468–480. <https://doi.org/10.1037/a0023503>.
- Lindquist KA, Wager TD, Kober H et al. (2012). The brain basis of emotion: a meta-analytic review. *Behav Brain Sci* 35 (3): 121–143. <https://doi.org/10.1016/j.biotechadv.2011.08.021>.
- Lutz A, Slagter Ha, Dunne JD et al. (2008). Attention regulation and monitoring in meditation. *Trends Cogn Sci* 12 (4): 163–169. <https://doi.org/10.1016/j.tics.2008.01.005>.
- Lutz J, Herwig U, Opialla S et al. (2013). Mindfulness and emotion regulation—an fMRI study. *Soc Cogn Affect Neurosci* 9 (6): 776–785. <https://doi.org/10.1093/scan/nst043>.
- Ma X, Tamir M, Miyamoto Y (2017). A socio-cultural instrumental approach to emotion regulation: culture and the regulation of positive emotions. *Emotion* 18 (1): 138–152. <https://doi.org/10.1037/emo0000315>.
- MacDonald AW, Cohen JD, Stenger VA et al. (2000). Dissociating the role of the dorsolateral prefrontal and anterior cingulate cortex in cognitive control. *Science* (New York, NY) 288 (5472): 1835–1838. <https://doi.org/10.1126/science.288.5472.1835>.
- Madden DJ (2007). Aging and visual attention. *Curr Dir Psychol Sci* 16 (2): 70–74. <https://doi.org/10.1111/j.1467-8721.2007.00478.x>.
- Martin LN, Delgado MR (2011). The influence of emotion regulation on decision-making under risk. *J Cogn Neurosci* 23 (9): 2569–2581. <https://doi.org/10.1162/jocn.2011.21618>.
- Mather M (2016). The affective neuroscience of aging. *Annu Rev Psychol* 67: 213–238.
- Mather M, Canli T, English T et al. (2004). Amygdala responses to emotionally valenced stimuli in older and younger adults. *Psychol Sci* 15 (4): 259–263. <https://doi.org/10.1111/j.0956-7976.2004.00662.x>.
- Menon V, Uddin LQ (2010). Saliency, switching, attention and control: a network model of insula function. *Brain Struct Funct* 214 (5–6): 655–667. <https://doi.org/10.1007/s00429-010-0262-0>.
- Miller EK, Cohen JD (2001). An integrative theory of prefrontal cortex function. *Annu Rev Neurosci* 24 (1): 167–202.
- Mitchell DGV (2011). The nexus between decision making and emotion regulation: a review of convergent neurocognitive substrates. *Behav Brain Res* 217 (1): 215–231. <https://doi.org/10.1016/j.bbr.2010.10.030>.
- Miyamoto Y, Ma X (2011). Dampening or savoring positive emotions: a dialectical cultural script guides emotion regulation. *Emotion* 11 (6): 1346.
- Miyamoto Y, Ma X, Petermann AG (2014). Cultural differences in hedonic emotion regulation after a negative event. *Emotion* 14 (4): 804.
- Morawetz C, Bode S, Baudewig J et al. (2016). Neural representation of emotion regulation goals. *Hum Brain Mapp* 37 (2): 600–620. <https://doi.org/10.1002/hbm.23053>.
- Morawetz C, Bode S, Derntl B et al. (2017). The effect of strategies, goals and stimulus material on the neural mechanisms of emotion regulation: a meta-analysis of fMRI studies. *Neurosci Biobehav Rev* 72: 111–128. <https://doi.org/10.1016/j.neubiorev.2016.11.014>.
- Nelson BD, Fitzgerald DA, Klumpp H et al. (2015). Prefrontal engagement by cognitive reappraisal of negative faces. *Behav Brain Res* 279 (November): 218–225. <https://doi.org/10.1016/j.bbr.2014.11.034>.
- Nolen-Hoeksema S, Aldao A (2011). Gender and age differences in emotion regulation strategies and their relationship to depressive symptoms. *Personal Individ Differ* 51 (6): 704–708. <https://doi.org/10.1016/j.paid.2011.06.012>.
- Nomi JS, Farrant K, Damaraju E (2016). Dynamic functional network connectivity reveals unique and overlapping profiles of insula subdivisions dynamic functional network connectivity reveals unique and overlapping profiles of insula subdivisions. *Hum Brain Mapp* 37 (5): 1770–1787. <https://doi.org/10.1002/hbm.23135>.
- Norman GJ, Berntson GG, Cacioppo JT (2014). Emotion, somatovisceral afference, and autonomic regulation. *Emot Rev* 6 (2): 113–123.
- Ochsner KN, Gross JJ (2005). The cognitive control of emotion. *Trends Cogn Sci* 9 (5): 242–249.
- Ochsner KN, Gross JJ (2008). Cognitive emotion regulation: insights from social cognitive and affective neuroscience. *Curr Dir Psychol Sci* 17 (2): 153–158. <https://doi.org/10.1111/j.1467-8721.2008.00566.x>.
- Ochsner KN, Gross JJ (2014). The neural bases of emotion and emotion regulation: a valuation perspective. In: JJ Gross, R Thompson (Eds.), *The handbook of emotion regulation, second edition* Guilford Press, New York, pp. 23–42.
- Ochsner KN, Bunge SA, Gross JJ et al. (2002). Rethinking feelings: an FMRI study of the cognitive regulation of emotion. *J Cogn Neurosci* 14 (8): 1215–1229. <https://doi.org/10.1162/089892902760807212>.
- Ochsner KN, Knierim K, Ludlow DH et al. (2004). Reflecting upon feelings: an fMRI study of neural systems supporting the attribution of emotion to self and other. *J Cogn Neurosci* 16 (10): 1746–1772. <https://doi.org/10.1162/0898929042947829>.
- Ochsner KN, Ray RR, Hughes B et al. (2009). Bottom-up and top-down processes in emotion generation: common and distinct neural mechanisms. *Psychol Sci* 20 (11): 1322–1331. <https://doi.org/10.1111/j.1467-9280.2009.02459.x>.
- Ochsner KN, Silvers JA, Buhle JT (2012). Review and evolving model of the cognitive control of emotion. *Ann N Y Acad Sci* 1251: 1–35. <https://doi.org/10.1111/j.1749-6632.2012.06751.x>.
- Opialla S, Lutz J, Scherpiet S et al. (2014). Neural circuits of emotion regulation: a comparison of mindfulness-based and cognitive reappraisal strategies. *Eur Arch Psychiatry Clin Neurosci* 265 (1): 45–55. <https://doi.org/10.1007/s00406-014-0510-z>.

- Opitz PC, Gross JJ, Urry HL (2012). Selection, optimization, and compensation in the domain of emotion regulation: applications to adolescence, older age, and major depressive disorder. *Soc Personal Psychol Compass* 6 (2): 142–155. <https://doi.org/10.1111/j.1751-9004.2011.00413.x>.
- Opitz PC, Lee IA, Gross JJ et al. (2014). Fluid cognitive ability is a resource for successful emotion regulation in older and younger adults. *Front Psychol* 5: 609. <https://doi.org/10.3389/fpsyg.2014.00609>.
- Otto B, Misra S, Prasad A et al. (2014). Functional overlap of top-down emotion regulation and generation: an fMRI study identifying common neural substrates between cognitive reappraisal and cognitively generated emotions. *Cogn Affect Behav Neurosci* 14 (3): 923–938. <https://doi.org/10.3758/s13415-013-0240-0>.
- Paret C, Ruf M, Gerchen MF et al. (2016). fMRI neurofeedback of amygdala response to aversive stimuli enhances prefrontal–limbic brain connectivity. *Neuroimage* 125: 182–188. <https://doi.org/10.1016/j.neuroimage.2015.10.027>.
- Phan KL, Wager T, Taylor SF et al. (2002). Functional neuroanatomy of emotion: a meta-analysis of emotion activation studies in PET and fMRI. *Neuroimage* 16 (2): 331–348. <https://doi.org/10.1006/nimg.2002.1087>.
- Phelps EA, LeDoux JE (2005). Contributions of the amygdala to emotion processing: from animal models to human behavior. *Neuron* 48 (2): 175–187. <https://doi.org/10.1016/j.neuron.2005.09.025>.
- Phelps EA, Delgado MR, Nearing KI et al. (2004). Extinction learning in humans: role of the amygdala and vmPFC. *Neuron* 43 (6): 897–905.
- Price JL, Davis PB, Morris JC et al. (1991). The distribution of tangles, plaques and related immunohistochemical markers in healthy aging and Alzheimer's disease. *Neurobiol Aging* 12 (4): 295–312. [https://doi.org/10.1016/0197-4580\(91\)90006-6](https://doi.org/10.1016/0197-4580(91)90006-6).
- Ray RD, McRae K, Ochsner KN et al. (2010). Cognitive reappraisal of negative affect: converging evidence from EMG and self-report. *Emotion (Washington, DC)* 10 (4): 587–592. <https://doi.org/10.1037/a0019015>.
- Raz N, Gunning FM, Head D et al. (1997). Selective aging of the human cerebral cortex observed in vivo: differential vulnerability of the prefrontal gray matter. *Cereb Cortex* 7 (3): 268–282. <https://doi.org/10.1093/cercor/7.3.268>.
- Raz N, Lindenberger U, Rodrigue KM et al. (2005). Regional brain changes in aging healthy adults: general trends, individual differences and modifiers. *Cereb Cortex* 15 (11): 1676–1689. <https://doi.org/10.1093/cercor/bhi044>.
- Raz N, Ghisletta P, Rodrigue KM et al. (2010). Trajectories of brain aging in middle-aged and older adults: regional and individual differences. *Neuroimage* 51 (2): 501–511. <https://doi.org/10.1016/j.neuroimage.2010.03.020>.
- Reeck C, Ames DR, Ochsner KN (2016). The social regulation of emotion: an integrative, cross-disciplinary model. *Trends Cogn Sci* 20 (1): 47–63. <https://doi.org/10.1016/j.tics.2015.09.003>.
- Reed AE, Chan L, Mikels JA (2014). Meta-analysis of the age-related positivity effect: age differences in preferences for positive over negative information. *Psychol Aging* 29 (1): 1–15. <https://doi.org/10.1037/a0035194>.
- Richards JM, Gross JJ (1999). Composure at any cost? The cognitive consequences of emotion suppression. *Pers Soc Psychol Bull* 25 (8): 1033–1044. <https://doi.org/10.1177/01461672992511010>.
- Ritche M, Bessette-Symons B, Hayes SM et al. (2011). Emotion processing in the aging brain is modulated by semantic elaboration. *Neuropsychologia* 49 (4): 640–650. <https://doi.org/10.1016/j.neuropsychologia.2010.09.009>.
- Rivera SM, Reiss AL, Eckert MA et al. (2005). Developmental changes in mental arithmetic: evidence for increased functional specialization in the left inferior parietal cortex. *Cereb Cortex (New York, NY: 1991)* 15 (11): 1779–1790. <https://doi.org/10.1093/cercor/bhi055>.
- Roitman MF, Wheeler RA, Carelli RM (2005). Nucleus accumbens neurons are innately tuned for rewarding and aversive taste stimuli, encode their predictors, and are linked to motor output. *Neuron* 45 (4): 587–597. <https://doi.org/10.1016/j.neuron.2004.12.055>.
- Roy M, Shohamy D, Wager TD (2012). Ventromedial prefrontal-subcortical systems and the generation of affective meaning. *Trends Cogn Sci* 16 (3): 147–156.
- Rueda MR, Posner MI, Rothbart MK (2005). The development of executive attention: contributions to the emergence of self-regulation. *Dev Neuropsychol* 28 (2): 573–594. [https://doi.org/10.1207/s15326942dn2802\\_2](https://doi.org/10.1207/s15326942dn2802_2).
- Samanez-Larkin GR, Robertson ER, Mikels JA (2010). Selective attention to emotion in the aging brain. *Psychol Aging* 24 (3): 519–529. <https://doi.org/10.1037/a0016952>. Selective.
- Sander D, Grafman J, Zalla T (2003). The human amygdala: an evolved system for relevance detection. *Rev Neurosci* 14 (4): 303–316.
- Sarkheil P, Zilverstand A, Kilian-Hötten N et al. (2015). fMRI feedback enhances emotion regulation as evidenced by a reduced amygdala response. *Behav Brain Res* 281: 326–332. <https://doi.org/10.1016/j.bbr.2014.11.027>.
- Satpute AB, Badre D, Ochsner KN (2014). Distinct regions of prefrontal cortex are associated with the controlled retrieval and selection of social information. *Cereb Cortex* 24: 1269–1277.
- Satpute AB, Kang J, Bickart KC et al. (2015). Involvement of sensory regions in affective experience: a meta-analysis. *Front Psycho* 16. <https://doi.org/10.3389/fpsyg.2015.01860>.
- Scheibe S, Sheppes G, Staudinger UM (2015). Distract or reappraise? Age-related differences in emotion-regulation choice. *Emotion (Washington, DC)* 15 (6): 677–681. <https://doi.org/10.1037/a0039246>.
- Schiller D, Delgado MR (2010). Overlapping neural systems mediating extinction, reversal and regulation of fear. *Trends Cogn Sci* 14 (6): 268–276. <https://doi.org/10.1016/j.tics.2010.04.002>.
- Schwarz ST, Abaei M, Gontu V et al. (2013). Diffusion tensor imaging of nigral degeneration in Parkinson's disease: a region-of-interest and voxel-based study at 3 T and systematic review with meta-analysis. *NeuroImage Clin* 3: 481–488.
- Seo D, Oltman Ca, Haut KM et al. (2014). Neural correlates of preparatory and regulatory control over positive and negative emotion. *Soc Cogn Affect Neurosci* 9 (4): 494–504. <https://doi.org/10.1093/scan/nst115>.

- Shackman AJ, Salomons TV, Slagter Ha et al. (2011). The integration of negative affect, pain and cognitive control in the cingulate cortex. *Nat Rev Neurosci* 12 (3): 154–167. <https://doi.org/10.1038/nrn2994>.
- Shafritz KM, Collins SH, Blumberg HP (2006). The interaction of emotional and cognitive neural systems in emotionally guided response inhibition. *Neuroimage* 31 (1): 468–475. <https://doi.org/10.1016/j.neuroimage.2005.11.053>.
- Shenhav A, Botvinick MM, Cohen JD (2013). The expected value of control: an integrative theory of anterior cingulate cortex function. *Neuron* 79 (2): 217–240. <https://doi.org/10.1016/j.neuron.2013.07.007>.
- Sheppes G, Scheibe S, Suri G et al. (2011). Emotion-regulation choice. *Psychol Sci* 22 (11): 1391–1396. <https://doi.org/10.1177/0956797611418350>.
- Sheppes G, Scheibe S, Suri G et al. (2014). Emotion regulation choice: a conceptual framework and supporting evidence. *J Exp Psychol Gen* 143 (1): 163–181. <https://doi.org/10.1037/a0030831>.
- Shiffman S, Stone AA, Hufford MR (2008). Ecological momentary assessment. *Annu Rev Clin Psychol* 4 (1): 1–32. <https://doi.org/10.1146/annurev.clinpsy.3.022806.091415>.
- Shiota MN, Levenson RW (2009). Effects of aging on experimentally instructed detached reappraisal, positive reappraisal, and emotional behavior suppression. *Psychol Aging* 24 (4): 890–900. <https://doi.org/10.1037/a0017896>.
- Silk JS, Stroud LR, Siegle GJ et al. (2012). Peer acceptance and rejection through the eyes of youth: pupillary, eyetracking and ecological data from the chatroom interact task. *Soc Cogn Affect Neurosci* 7 (1): 93–105. <https://doi.org/10.1093/scan/nsr044>.
- Silvers JA, Buhle JT, Ochsner KN et al. (2014a). The neuroscience of emotion regulation: basic mechanisms and their role in development, aging and psychopathology. In: KN Ochsner, SM Kosslyn (Eds.), *The handbook of cognitive neuroscience*. NY, New York.
- Silvers JA, Insel C, Powers A et al. (2014b). Curbing craving: behavioral and brain evidence that children regulate craving when instructed to do so but have higher baseline craving than adults. *Psychol Sci* 25 (10): 1932–1942. <https://doi.org/10.1177/0956797614546001>.
- Silvers JA, Insel C, Powers A et al. (2017). vPFC–vmPFC–amygdala interactions underlie age-related differences in cognitive regulation of emotion. *Cereb Cortex* 27 (7): 3502–3514. <https://doi.org/10.1093/cercor/bhw073>.
- Singer T, Seymour B, O’Doherty J et al. (2004). Empathy for pain involves the affective but not sensory components of pain. *Science (New York, NY)* 303 (5661): 1157–1162. <https://doi.org/10.1126/science.1093535>.
- Sokol-Hessner P, Camerer CF, Phelps EA (2013). Emotion regulation reduces loss aversion and decreases amygdala responses to losses. *Soc Cogn Affect Neurosci* 8 (3): 341–350. <https://doi.org/10.1093/scan/nss002>.
- Somerville LH, Casey BJ (2010). Developmental neurobiology of cognitive control and motivational systems. *Curr Opin Neurobiol* 20 (2): 236–241. <https://doi.org/10.1016/j.conb.2010.01.006>.
- Spreng RN, Stevens WD, Chamberlain JP et al. (2010). Default network activity, coupled with the frontoparietal control network, supports goal-directed cognition. *Neuroimage* 53 (1): 303–317. <https://doi.org/10.1016/j.neuroimage.2010.06.016>.
- Sripada C, Angstadt M, Kessler D et al. (2014). Volitional regulation of emotions produces distributed alterations in connectivity between visual, attention control, and default networks. *Neuroimage* 89: 110–121. <https://doi.org/10.1016/j.neuroimage.2013.11.006>.
- Staudinger MR, Erk S, Walter H (2011). Dorsolateral prefrontal cortex modulates striatal reward encoding during reappraisal of reward anticipation. *Cereb Cortex* 21 (11): 2578–2588. <https://doi.org/10.1093/cercor/bhr041>.
- Steinbeis N, Bernhardt BC, Singer T (2012). Impulse control and underlying functions of the left DLPFC mediate age-related and age-independent individual differences in strategic social behavior. *Neuron* 73 (5): 1040–1051. <https://doi.org/10.1016/j.neuron.2011.12.027>.
- Sulzer J, Haller S, Scharnowski F et al. (2013). Real-time fMRI neurofeedback: progress and challenges. *Neuroimage* 76: 386–399. <https://doi.org/10.1016/j.neuroimage.2013.03.033>.
- Swartz JR, Carrasco M, Wiggins JL et al. (2014). Age-related changes in the structure and function of prefrontal cortex-amygdala circuitry in children and adolescents: a multi-modal imaging approach. *Neuroimage* 86: 212–220. <https://doi.org/10.1016/j.neuroimage.2013.08.018>.
- Thompson-Schill SL, Bedny M, Goldberg RF (2005). The frontal lobes and the regulation of mental activity. *Curr Opin Neurobiol* 15 (2): 219–224. <https://doi.org/10.1016/j.conb.2005.03.006>.
- Timbie C, Barbas H (2015). Pathways for emotions: specializations in the amygdalar, mediodorsal thalamic, and posterior orbitofrontal network. *J Neurosci* 35 (34): 11976–11987. <https://doi.org/10.1523/JNEUROSCI.2157-15.2015>.
- Tisserand DJ, Van Boxtel MP, Pruessner JC et al. (2004). A voxel-based morphometric study to determine individual differences in gray matter density associated with age and cognitive change over time. *Cereb Cortex* 14 (9): 966–973. <https://doi.org/10.1093/cercor/bhh057>.
- Tomasi D, Volkow ND (2012). Aging and functional brain networks. *Mol Psychiatry* 17 (5): 471–558. <https://doi.org/10.1038/mp.2011.81>.
- Tottenham N, Hare TA, Quinn BT et al. (2010). Prolonged institutional rearing is associated with atypically large amygdala volume and difficulties in emotion regulation. *Dev Sci* 13 (1): 46–61.
- Tottenham N, Hare TA, Millner A et al. (2011). Elevated amygdala response to faces following early deprivation. *Dev Sci* 14 (2): 190–204. <https://doi.org/10.1111/j.1467-7687.2010.00971.x>.
- Tottenham N, Shapiro M, Telzer EH et al. (2012). Amygdala response to mother. *Dev Sci* 15: 307–319.
- Tsai JL (2007). Ideal affect: cultural causes and behavioral consequences. *Perspect Psychol Sci* 2 (3): 242–259. <https://doi.org/10.1111/j.1745-6916.2007.00043.x>.
- Tucker AM, Feuerstein R, Mende-Siedlecki P et al. (2012). Double dissociation: circadian off-peak times increase emotional reactivity; aging impairs emotion regulation via reappraisal. *Emotion (Washington, DC)* 12 (5): 869–874. <https://doi.org/10.1037/a0028207>.

- Uddin LQ, Supekar K, Menon V (2010). Typical and atypical development of functional human brain networks: insights from resting-state fMRI. *Front Syst Neurosci* 4: 21. <https://doi.org/10.3389/fnsys.2010.00021>.
- Uddin LQ, Kinnison J, Pessoa L et al. (2014). Beyond the tripartite cognition–emotion–interoception model of the human insular cortex. *J Cogn Neurosci* 26 (1): 16–27. [https://doi.org/10.1162/jocn\\_a\\_00462](https://doi.org/10.1162/jocn_a_00462).
- Uddin LQ, Nomi JS, Hébert-seropian B et al. (2017). Structure and function of the human insula. *J Clin Neurophysiol* 34 (4): 300–306. <https://doi.org/10.1097/WNP.0000000000000377>.
- Urry HL, van Reekum CM, Johnstone T et al. (2006). Amygdala and ventromedial prefrontal cortex are inversely coupled during regulation of negative affect and predict the diurnal pattern of cortisol secretion among older adults. *J Neurosci* 26 (16): 4415–4425.
- Urry HL, van Reekum CM, Johnstone T et al. (2009). Individual differences in some (but not all) medial prefrontal regions reflect cognitive demand while regulating unpleasant emotion. *Neuroimage* 47 (3): 852–863. <https://doi.org/10.1016/j.neuroimage.2009.05.069>.
- Vanderhasselt MA, Baeken C, Van Schuerbeek P et al. (2013a). Inter-individual differences in the habitual use of cognitive reappraisal and expressive suppression are associated with variations in prefrontal cognitive control for emotional information: an event related fMRI study. *Biol Psychol* 92 (3): 433–439. <https://doi.org/10.1016/j.biopsycho.2012.03.005>.
- Vanderhasselt MA, Kühn S, De Raedt R (2013b). “Put on your poker face”: neural systems supporting the anticipation for expressive suppression and cognitive reappraisal. *Soc Cogn Affect Neurosci* 8 (8): 903–910. <https://doi.org/10.1093/scan/nss090>.
- Vijayakumar N, Whittle S, Yücel M et al. (2014). Thinning of the lateral prefrontal cortex during adolescence predicts emotion regulation in females. *Soc Cogn Affect Neurosci* 9 (11): 1845–1854. <https://doi.org/10.1093/scan/nst183>.
- Vrtička P, Sander D, Vuilleumier P (2011). Effects of emotion regulation strategy on brain responses to the valence and social content of visual scenes. *Neuropsychologia* 49 (5): 1067–1082. <https://doi.org/10.1016/j.neuropsychologia.2011.02.020>.
- Wager TD, Barrett LF (2017). From affect to control: functional specialization of the insula in motivation and regulation. *BioRxiv* 102368.
- Wager TD, Sylvester CY, Lacey SC et al. (2005). Common and unique components of response inhibition revealed by fMRI. *Neuroimage* 27 (2): 323–340. <https://doi.org/10.1016/j.neuroimage.2005.01.054>.
- Wager TD, Davidson ML, Hughes BL et al. (2008). Prefrontal-subcortical pathways mediating successful emotion regulation. *Neuron* 59 (6): 1037–1050. <https://doi.org/10.1016/j.neuron.2008.09.006>.
- Wagner DD, Heatherton TF (2013). Self-regulatory depletion increases emotional reactivity in the amygdala. *Soc Cogn Affect Neurosci* 8 (4): 410–417. <https://doi.org/10.1093/scan/nss082>.
- Webb TL, Miles E, Sheeran P (2012). Dealing with feeling: a meta-analysis of the effectiveness of strategies derived from the process model of emotion regulation. *Psychol Bull* 138 (4): 775–808. <https://doi.org/10.1037/a0027600>.
- Whelock MD, Sreenivasan KR, Wood KH et al. (2014). Threat-related learning relies on distinct dorsal prefrontal cortex network connectivity. *Neuroimage* 102 (P2): 904–912. <https://doi.org/10.1016/j.neuroimage.2014.08.005>.
- Wincoff A, LaBar KS, Madden DJ et al. (2011). Cognitive and neural contributors to emotion regulation in aging. *Soc Cogn Affect Neurosci* 6 (2): 165–176. <https://doi.org/10.1093/scan/nsq030>.
- Wincoff A, Clithero JA, Carter RM et al. (2013). Ventromedial prefrontal cortex encodes emotional value. *J Neurosci* 33 (27): 11032–11039. <https://doi.org/10.1523/JNEUROSCI.4317-12.2013>.
- Zaki J, Ochsner KN (2012). The neuroscience of empathy: progress, pitfalls and promise. *Nat Neurosci* 15 (5): 675–680.
- Zaki J, Weber J, Bolger N et al. (2009). The neural bases of empathic accuracy. *Proc Natl Acad Sci* 106 (27): 11382–11387. <https://doi.org/10.1073/pnas.0902666106>.
- Zaki J, Wager TD, Singer T et al. (2016). The anatomy of suffering: understanding the relationship between nociceptive and empathic pain. *Trends Cogn Sci* 20 (4): 249–259.
- Zikopoulos B, Höistad M, John Y et al. (2017). Posterior orbitofrontal and anterior cingulate pathways to the amygdala target inhibitory and excitatory systems with opposite functions. *J Neurosci* 37 (20): 5051–5064. <https://doi.org/10.1523/JNEUROSCI.3940-16.2017>.
- Zimmermann P, Iwanski A (2014). Emotion regulation from early adolescence to emerging adulthood and middle adulthood. *Int J Behav Dev* 38 (2): 182–194. <https://doi.org/10.1177/0165025413515405>.
- Zotov V, Phillips R, Young KD et al. (2013). Prefrontal control of the amygdala during real-time fMRI neurofeedback training of emotion regulation. *PLoS ONE* 8 (11): <https://doi.org/10.1371/journal.pone.0079184>.

## FURTHER READING

- Barrett LF (2017). The theory of constructed emotion: an active inference account of interoception and categorization. *Soc Cogn Affect Neurosci* 12 (1): 1–23. <https://doi.org/10.1093/scan/nsw154>.
- Campos JJ, Walle EA, Dahl A et al. (2011). Reconceptualizing emotion regulation. *Emot Rev* 3 (1): 26–35. <https://doi.org/10.1177/1754073910380975>.
- Cutuli D (2014). Cognitive reappraisal and expressive suppression strategies role in the emotion regulation: an overview on their modulatory effects and neural correlates. *Front Syst Neurosci* 8 (September): 1–6. <https://doi.org/10.3389/fnsys.2014.00175>.
- Eisenberg N, Spinrad TL, Eggum ND (2010). Emotion-related self-regulation and its relation to children’s maladjustment. *Annu Rev Clin Psychol* 6: 495–525.
- Gross JJ, Muñoz RF (1995). Emotion regulation and mental health. *Clin Psychol Sci Pract* 2 (2): 151–164.
- McRae K, Gross JJ, Weber J et al. (2012). The development of emotion regulation: an fMRI study of cognitive reappraisal in children, adolescents and young adults. *Soc Cogn Affect Neurosci* 7 (1): 11–22. <https://doi.org/10.1093/scan/nsr093>.

- Mischel HN, Mischel W (1987). The development of children's knowledge of self-control strategies. In: *Motivation, intention, and volition*, Springer, Berlin, Heidelberg, pp. 321–336.
- Mischel W, Shoda Y, Peake PK (1988). The nature of adolescent competencies predicted by preschool delay of gratification. *J Pers Soc Psychol* 54 (4): 687–696.
- Mischel W, Shoda Y, Rodriguez ML (1989). Delay of gratification in children. *Science* 244 (4907): 933–938.
- Mischel W, Ayduk O, Berman MG et al. (2011). “Willpower” over the life span: decomposing self-regulation. *Soc Cogn Affect Neurosci* 6 (2): 252–256. <https://doi.org/10.1093/scan/nsq081>.
- Raio CM, O'rederu Ta, Palazzolo L et al. (2013). Cognitive emotion regulation fails the stress test. *Proc Natl Acad Sci* 110 (37): 15139–15144. <https://doi.org/10.1073/pnas.1305706110>.
- Todd RM, Cunningham WA, Anderson AK (2012). Affect-biased attention as emotion regulation. *Trends Cogn Sci* 16 (7): 365–372. <https://doi.org/10.1016/j.tics.2012.06.003>.
- Schlam TR, Wilson NL, Shoda Y et al. (2013). Preschoolers' delay of gratification predicts their body mass 30 years later. *J Pediatr* 162 (1): 90–93. <https://doi.org/10.1016/j.jpeds.2012.06.049>.
- Sheppes G, Gross JJ (2011). Is timing everything? Temporal considerations in emotion regulation. *Pers Soc Psychol Rev* 15 (4): 319–331. <https://doi.org/10.1177/1088868310395778>.
- Thompson Ra (2011). Emotion and emotion regulation: two sides of the developing coin. *Emot Rev* 3 (1): 53–61. <https://doi.org/10.1177/1754073910380969>.
- Troy AS, Shallcross AJ, Mauss IB (2013). A person-by-situation approach to emotion regulation. *Psychol Sci* 24 (12): 2505–2514. <https://doi.org/10.1177/0956797613496434>.
- Urry HL, Gross JJ (2010). Emotion regulation in older age. *Curr Dir Psychol Sci* 9 (6): 352–357. <https://doi.org/10.1177/0963721410388395>.
- Zaki J, Williams WC (2013). Interpersonal emotion regulation. *Emotion* 13 (5): 803–810. <https://doi.org/10.1037/a0033839>.