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Moreira, João F Guassi

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Review article

Capacity and tendency: A neuroscientific framework for the study of emotion regulation

Jennifer A. Silvers*, João F. Guassi Moreira

Department of Psychology, University of California, Los Angeles, 1285 Franz Hall, Box 951563, Los Angeles, CA, 90095, USA

A R T I C L E I N F O

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A B S T R A C T

It is widely accepted that the ability to effectively regulate one's emotions is a cornerstone of physical and mental health. As such, it should come as no surprise that the number of neuroimaging studies focused on emotion regulation and associated processes has increased exponentially in the past decade. To date, neuroimaging research on this topic has examined two distinct but complementary features of emotion regulation – the *capacity* to effectively utilize a strategy to regulate emotion and to a lesser extent, the *tendency* to choose to regulate. However, theoretical accounts of emotion regulation have only recently begun to distinguish capacity from tendency. In the present review, we provide a novel framework for conceptualizing these two intertwined, yet distinct, facets of emotion regulation. First we characterize brain regions that support emotion generation and are thus targeted by emotion regulation. Next, we synthesize findings from the dozens of neuroimaging studies that have examined emotion regulation capacity, focusing in particular on the most commonly studied emotion regulation strategy – reappraisal. Finally, we discuss emerging neuroimaging research examining state and trait regulatory tendencies. We conclude by integrating findings from neuroimaging research on emotion regulation capacity and tendency and suggest ways that this integrated model can inform basic and translational neuroscientific research on emotion regulation.

1. Introduction

Though emotions are generally adaptive, they can lead to mental and physical health problems if left unchecked [9,38,44,51,53,99]. Emotion regulation – the use of conscious or unconscious processes that change the nature, intensity or duration of one's emotions – is central to wellbeing [41,78].

Emotion regulation is driven jointly by one's *tendency* to choose a specific regulatory strategy and one's *capacity* to implement said strategy effectively [10,25,42,79]. Initial evidence suggests that regulatory tendency and capacity co-develop during childhood [71] and are related but not synonymous in adulthood [69]. While recent reviews have begun to characterize "different flavors" of emotion regulation by distinguishing between model-based and model-free or implicit and explicit forms of emotion regulation [11,32], prevailing models have not yet taken into account the complementary significance of regulatory capacity and tendency [25,78,82,93]. Here, we review existing neuroimaging findings related to the generation and regulation of emotion and then outline future directions for how regulatory capacity and tendency might be integrated in basic, developmental, and translational research.

2. Neuroimaging research on emotion regulation capacity and strategy

2.1. Emotion generation

Before considering how emotions are regulated, it is useful to consider how emotional responses are generated. For the purposes of this review, we define emotions as reasonably coherent combinations of affective experience, behavior and physiological activity that arise in response to motivationally-relevant stimuli [50,58,60,67]. Appraisal models suggest that emotions unfold in a series of steps that involve perceiving, attending to, interpreting and responding to an internal or external stimulus [6,92]. Importantly, such models also submit that emotions may be regulated at any point in the appraisal process [40,78]. In this framework, emotion generation and regulation rest on opposing ends of a continuum but rely on common psychological ingredients (e.g., controlling attention towards an emotional stimulus and interpreting its meaning) [43]. Here, we discuss neuroimaging data associated with emotion generation and emotion regulation separately for clarity's sake, but do not make strong claims about the extent to which neural circuits associated with these two processes are distinct

* Corresponding author.
E-mail address: silvers@ucla.edu (J.A. Silvers).

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versus overlapping.

Emotions emerge through top-down, cognitive processes or bottom-up, stimulus-driven processes via cortical-subcortical networks [16,55,64,81]. Importantly, no single neural circuit or set of neural computations can fully explain how emotions arise [64]. Here we focus on four brain regions that are most consistently implicated in emotion generation from a 'model-agnostic' perspective. The first of these is the amygdala, a subcortical structure whose functional significance remains a topic of ongoing debate. While many see the amygdala as being central to generating "core" affective responses [59,91], others have purported that amygdala activity flags the intensity [2], motivational salience [21] or ambiguity of affective stimuli [113]. Importantly, numerous neuroimaging meta-analyses and quantitative reviews have found that amygdala activity is attenuated by emotion regulation [12,24,68,93]. The insula, our second region, shares dense, bidirectional connections with the amygdala [3] and commonly co-activates with it in response to salient and negative stimuli [17,63], as part of a broader aversive processing network [48,88]. The insula's structural and functional characteristics endow it with a unique capacity to integrate converging affective, cognitive and motor inputs and to motivate relevant behavior [17]. In contrast to the amygdala and insula, the medial prefrontal cortex (mPFC) is strongly associated with top-down representations of emotion [81] and supports both emotion generation and regulation [33,93]. Dorsal mPFC (dmPFC) and neighboring cingulate regions have been implicated in the generation and maintenance of learned fear responses [13,33,70], as well as the generation and regulation of negative emotion [12,81] and social cognition [1,23,83] – suggesting that dorsal mPFC aggregates cognitive, social and affective cues to form high-level representations of emotion. Ventral mPFC (vmPFC) integrates contextual, cue and memorial inputs to update affective judgments [22,90]. This is crucial for evaluating the affective significance of stimuli and contexts [2,46,63,65], and for maintaining representations of safety in the face of threat [30]. Given the roles that the amygdala, insula, and mPFC play in emotion generation, they are also necessarily involved in emotion regulation – as targets, intermediaries or perhaps even instigators of regulation.

2.2. Emotion regulation capacity

Emotion regulation capacity may be defined as the extent to which one is *capable* of using emotion regulation. Because the vast majority of neuroimaging research examining regulatory capacity has focused on reappraisal – or changing the way one thinks about an emotional stimulus so as to alter its import [40] – this review will concentrate on reappraisal as a paradigm case for what is presently known about emotion regulation capacity. Reappraisal capacity is typically assessed by instructing participants to reappraise and then evaluating changes in self-reported emotion relative to a control condition.

2.2.1. Neural systems supporting the capacity to reappraise

Reappraisal recruits prefrontal and parietal regions that support non-affective cognitive control processes such as response inhibition, task switching, and working memory [12,24,57,75,89,111,112]. Theoretical accounts of reappraisal have interpreted this as evidence that prefrontal and parietal executive control processes can be used to regulate affect much as they do non-affective impulses, thoughts and behaviors [78,79,82]. Consistent with this, transcranial magnetic stimulation (TMS) of the prefrontal cortex enhances cognitive reappraisal [34].

Three cortical modules activate and communicate to implement reappraisal (Fig. 1) [62,72]. The first of these modules is comprised of the dorsolateral prefrontal cortex (dlPFC) and posterior parietal cortex (PPC). dlPFC and PPC form the "dorsal attention system", which exerts top-down, volitional control over attention and working memory processes [18,20,75,89,109]. In the context of reappraisal, dlPFC sends output to other prefrontal and PPC regions, helping to direct attention

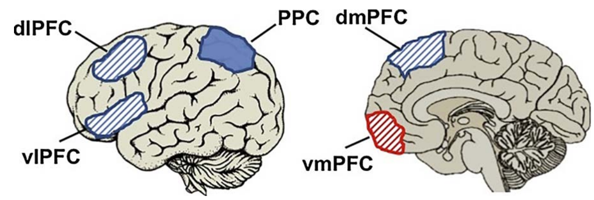

Fig. 1. Neural systems underlying emotion regulation capacity and tendency. Regions marked in blue (dlPFC; dmPFC; PPC; vlPFC) signify areas associated with the capacity to reappraise while red (vmPFC) indicates regions associated with reduced negative affect when responding to aversive stimuli. Hashed regions indicate brain areas associated with trait tendencies to self-regulate.
Note: dlPFC refers to dorsolateral prefrontal cortex; PPC refers to posterior parietal cortex; vlPFC refers to ventrolateral prefrontal cortex; dmPFC refers to dorsomedial prefrontal cortex. Depictions were created using conventional, functional anatomical knowledge and are meant to be taken as schematic.

and select reappraisals from working memory [12,24,62,99]. In addition to controlling attention [19,74], PPC supports perspective taking and spatial processing [47,104]. PPC is strongly recruited by forms of reappraisal that involve emotional distancing [79], suggesting that it regulates perceptions of an emotional stimulus's relevance or proximity [80,82]. The second module is the ventrolateral prefrontal cortex (vlPFC), which co-activates with dlPFC and PPC to coordinate complex cognitive control processes as well as reappraisal [5,12,14,24,37,57,86,87,94]. vlPFC allows one to choose and inhibit cognitions and actions in accordance with goals, and appears important for selecting and implementing reappraisals [18,75,82,99,112]. Given the linguistic nature of some reappraisal tactics (i.e., constructing an alternative narrative for an emotional stimulus), vlPFC activation might also reflect engagement of language processing during reappraisal [49,61,82]. Importantly, functional connectivity has been observed between vlPFC and the amygdala, but not other lateral prefrontal regions – suggesting that vlPFC serves as the ultimate modulatory output of prefrontal and parietal systems acting on the amygdala [73,102]. The final module implicated in reappraisal capacity is dmPFC. While anterior portions of dmPFC support mentalizing and other social cognitions, posterior dmPFC and adjacent cingulate regions are critical for monitoring goal-directed behavior [1,23,27,28,76,83]. Therefore, anterior and posterior dmPFC may respectively evaluate one's affective state and the degree to which one is staying on task during reappraisal.

Neuroimaging meta-analytic data have revealed that reappraisal recruits dlPFC, PPC, vlPFC and dmPFC, and diminishes amygdala activity [12,24]. Preliminary evidence suggests that dlPFC instigates reappraisal-related activity, which subsequently excites vlPFC and dorsomedial regions like the dorsal anterior cingulate cortex (dACC) and supplementary motor area [62,72]. By contrast, vlPFC appears to inhibit dlPFC during reappraisal in a manner that is suggestive of a self-regulating feedback loop [72]. Though such findings elucidate the nature of cortical–cortical interactions during reappraisal, it remains less clear how cortical-subcortical communication is instantiated. Prefrontal and parietal activity are inversely associated with amygdala recruitment during reappraisal [77,102,110], but it is unknown how regions like dlPFC might attenuate amygdala activity given scarce direct connections between them [36,37]. One possibility is that prefrontal and parietal "source regions" alter semantic representations of affective stimuli in posterior temporal regions, which in turn down-regulate the amygdala [12]. However, this hypothesis remains untested. A second possibility is that dlPFC and vlPFC act on vmPFC regions involved in "implicit" regulatory processes like fear extinction, which subsequently reduce amygdala activity [24,52,93,107]. This notion is appealing given that vmPFC, in particular regions close to the genu, has dense connections with the amygdala [8,15]. While little work has investigated functional connectivity during reappraisal, preliminary studies have reported vmPFC-amygdala coupling during reappraisal [4,100]. At the same time, a large meta-analysis of reappraisal studies failed to find evidence for vmPFC recruitment during reappraisal, leaving open questions about the plausibility of this pathway [12]. A final possibility is that reappraisal-related activation in lateral prefrontal and posterior parietal regions alter amygdala activation via dACC [62]. The evidence for this pathway is threefold: (1) it is supported by the sole effective connectivity study of reappraisal to date [62], (2) dACC has rich connections with the amygdala [37], and (3) dACC recruitment predicts reappraisal-related decreases in negative affect, suggesting it may target affective signals generated by the amygdala [77].

2.3. Emotion regulation tendency

While the bulk of neuroimaging research on emotion regulation has focused on capacity, it is equally important to consider an individual's *tendency* to utilize specific regulatory strategies [25,42,79]. Here, we define tendency as one's inclination to utilize particular emotion regulation strategies. As in prior sections, we will focus primarily on reappraisal but because few neuroimaging studies have looked at emotion regulation tendency of any kind, we will discuss non-reappraisal research as well. In the following section, we describe two approaches to examining regulatory tendency. The first approach involves examining stable, trait-like, person-level tendencies to use specific regulatory strategies like reappraisal. The second approach, involves examining how situational variables dynamically impact regulatory choices from one context to another. Characterizing regulatory tendency in terms of both person-level and situation-level factors enriches our emotion regulation framework and moves it beyond more traditional individual difference measures of emotion regulation.

2.3.1. Person-level variables involved in emotion regulation tendency

One approach to studying person-level *trait* regulatory tendencies is to collect self-report measures and correlate these data with brain function. For example, one study found that individuals who frequently reappraise in everyday life strongly recruit prefrontal control regions involved in reappraisal (vlPFC, dlPFC, dmPFC) and attenuate amygdala activity when presented with emotional stimuli [29]. Another study found that trait tendencies to exhibit more regulated behavior – though it was unclear what strategies participants used in order to regulate – were associated with greater decreases in negative affect, stronger attenuation of the amygdala response, and stronger amygdala connectivity with vlPFC and dmPFC during reappraisal [85]. This indicates that the tendency to self-regulate predicts recruitment in brain regions that support the capacity to reappraise [84,106]. However, additional work is needed to determine whether such activation reflects regulation-related decision making, active reappraisal, or the engagement of reappraisal-like brain networks being used in the service of alternative cognitive strategies (for example, distraction recruits similar circuits to reappraisal).

Another approach to studying emotion regulation tendencies has been to correlate brain activity or connectivity during uninstructed responding to emotional stimuli with self-reported affective *states*. The logic here is that if brain activation tracks with reduced negative affect, such activation likely reflects emotion regulation. In contrast to prior approaches discussed, this approach does not focus on specific regulatory strategies (e.g., reappraisal) or explicit endorsement of self-regulation. This approach gives unimpeded access to what neural processes give rise to more or less negative affect, but fails to tell us what participants are doing *psychologically* nor does it preclude the possibility that brain activation reflects reduced emotional reactivity rather than regulation. Broadly, this work has linked greater vmPFC recruitment and diminished amygdala activation to less negative appraisals of aversive stimuli [30,54,66,103,108]. Such results suggest that when left to their own devices, individuals tend to engage in implicit forms of emotion regulation – which are perhaps sculpted by basic feedback mechanisms – and are undergirded by vmPFC [11,32,45].

2.3.2. Situation-level variables involved in emotion regulation tendency

Behavioral research suggests that contextual factors influence regulatory tendencies [98]. For example, individuals choose to reappraise rather than self-distract when faced with low-intensity emotional stimuli and vice versa for high-intensity emotional stimuli [95,97]. This suggests that individuals compute a cost-benefit analysis to determine whether it is worth exerting the cognitive resources – for example, engaging working memory [32] – required to reappraise high-intensity affective stimuli [98]. While event-related potential data support the notion that neural computations of a stimulus's emotional intensity predict regulatory strategy choice, the limited spatial resolution associated with EEG makes it difficult to say what neural circuits support regulatory decisions and implementations [96]. As such, complementary neuroimaging methods are needed to better characterize the neural bases of situational influences on emotion regulation tendencies.

3. Synthesis and future directions

3.1. Mutual reinforcement of regulation capacity and tendency in lateral prefrontal and parietal systems

The extant literature demonstrates that reappraisal capacity is supported by interactions between dlPFC, vlPFC, dmPFC, PPC and the amygdala [12,82]. Critically, neural responses to affective stimuli in these same brain regions predicts the tendency to reappraise [26,29]. This raises the question of how closely linked individual differences associated with capacity and tendency are. One unexplored possibility is that the strength of association between capacity and tendency changes during development. Given that experience shapes neural circuits during childhood and adolescence, it is likely that neural pathways involved in emotion regulation are shaped by Hebbian-like loops of plasticity during development (i.e., the tendency to use reappraisal builds capacity and vice versa) [35]. Thus, one might predict that capacity and tendency are tightly linked during childhood and adolescence when emotion regulation abilities are changing most dramatically [101]. However, once an individual reaches adulthood and achieves regulatory proficiency, it is less clear whether tendency and capacity ought to remain coupled. For example, tendency and capacity might become uncoupled with age if one is capable of deploying multiple regulatory strategies but uses just one strategy, resulting in high capacity but low tendency for the unused strategies. Alternatively, an adult might employ a strategy that they are not skilled at using because cultural norms encourage its use, whereas a child might be less sensitive to such norms. Indeed, several studies have failed to find strong relationships between reappraisal capacity and tendency [38,69,105], and this may explain why adults with psychopathology often display normal regulation capacity while experiencing functional impairments (i.e., capacity is intact while tendency is not) [31,39,56]. Such possibilities raise intriguing questions about how emotion regulation matures and how interventions might be best implemented across development [7,71].

3.2. Conclusions

Here we have presented a preliminary framework for how regulatory capacity and tendency jointly contribute to emotion regulation. Together, these advances stand to enhance basic, developmental, and translational knowledge about how prefrontal and subcortical systems dynamically interact to support emotion regulation and associated wellbeing.

References

[1] D.M. Amodio, C.D. Frith, Meeting of minds: the medial frontal cortex and social cognition, Nat. Rev. Neurosci. 7 (2006) 268–277.

[2] A.K. Anderson, K. Christoff, I. Stappen, D. Panitz, D.G. Ghahremani, G. Glover, J.D. Gabrieli, N. Sobel, Dissociated neural representations of intensity and valence in human olfaction, Nat. Neurosci. 6 (2003) 196–202.
[3] J. Augustine, Circuitry and functional aspects of the insular lobe in primates including humans, Brain Res. Rev. 22 (1996) 229–244.
[4] S.J. Banks, K.T. Eddy, M. Angstadt, P.J. Nathan, K.L. Phan, Amygdala-frontal connectivity during emotion regulation, Soc. Cogn. Affect. Neurosci. 2 (2007) 303–312.
[5] H. Barbas, Connections underlying the synthesis of cognition, memory, and emotion in primate prefrontal cortices, Brain Res. Bull. 52 (2000) 319–330.
[6] L.F. Barret, B. Mesquita, K.N. Ochsner, J.J. Gross, The experience of emotion, Annu. Rev. Psychol. 58 (2007) 387–403.
[7] M. Beauregard, Mind does really matter: evidence from neuroimaging studies of emotional self-regulation, psychotherapy, and placebo effect, Prog. Neurobiol. 81 (2007) 218–236.
[8] M. Beckmann, H. Johansen-Berg, M.F.S. Rushworth, Connectivity-based parcellation of human cingulate cortex and its relation to functional specialization, J. Neurosci. 29 (2009) 1175–1190.
[9] M. Berking, P. Wupperman, Emotion regulation and mental health, Curr. Opin. Psychiatry 25 (2012) 128–134.
[10] E.T. Berkman, M.D. Lieberman, Using neuroscience to broaden emotion regulation: theoretical and methodological considerations, Social Pers. Psychol. Compass 3 (2009) 475–493.
[11] L.M. Braunstein, J.J. Gross, K.N. Ochsner, Explicit and implicit emotion regulation: a multi-level framework, Soc. Cogn. Affect. Neurosci. (2016).
[12] J.T. Buhle, J.A. Silvers, T.D. Wager, R. Lopez, C. Onyemekwu, H. Kober, J. Weber, K.N. Ochsner, Cognitive reappraisal of emotion: a meta-analysis of human neuroimaging studies, Cereb. Cortex 24 (2014) 2981–2990.
[13] A. Burgos-Robles, I. Vidal-Gonzalez, G.J. Quirk, Sustained conditioned responses in prelimbic prefrontal neurons are correlated with fear expression and extinction failure, J. Neurosci. 29 (2009) 8474–8482.
[14] W. Cai, T. Chen, S. Ryali, J. Kochalka, C.-S.R. Li, V. Menon, Causal interactions within a frontal-cingulate-parietal network during cognitive control: convergent evidence from a multisite–multitask investigation, Cereb. Cortex 26 (2016) 2140–2153.
[15] S.T. Carmichael, J.L. Price, Limbic connections of the orbital and medial prefrontal cortex in macaque monkeys, J. Comp. Neurol. 363 (1995) 615–641.
[16] L.J. Chang, P.J. Gianaros, S.B. Manuck, A. Krishnan, T.D. Wager, A. Sensitive, Specific neural signature for picture-induced negative affect, PLoS Biol. 13 (2015) e1002180.
[17] L.J. Chang, T. Yarkoni, M.W. Khaw, A.G. Sanfey, Decoding the role of the insula in human cognition: functional parcellation and large-scale reverse inference, Cereb. Cortex (2012).
[18] E.C. Cieslik, V.I. Mueller, C.R. Eickhoff, R. Langner, S.B. Eickhoff, Three key regions for supervisory attentional control: evidence from neuroimaging meta-analyses, Neurosci. Biobehav. Rev. 48 (2015) 22–34.
[19] M. Corbetta, G. Patel, G.L. Shulman, The reorienting system of the human brain: from environment to theory of mind, Neuron 58 (2008) 306–324.
[20] M. Corbetta, G.L. Shulman, Control of goal-directed and stimulus-driven attention in the brain, Nat. Rev. Neurosci. 3 (2002) 201–215.
[21] W.A. Cunningham, T. Brosch, Motivational salience: amygdala tuning from traits, needs, values, and goals, Curr. Direct. Psychol. Sci. 21 (2012) 54–59.
[22] M.R. Delgado, J.S. Beer, L.K. Fellows, S.A. Huettel, M.L. Platt, G.J. Quirk, D. Schiller, Viewpoints: dialogues on the functional role of the ventromedial prefrontal cortex, Nat. Neurosci. 19 (2016) 1545–1552.
[23] B.T. Denny, H. Kober, T.D. Wager, K.N. Ochsner, A meta-analysis of functional neuroimaging studies of self- and other judgments reveals a spatial gradient for mentalizing in medial prefrontal cortex, J. Cogn. Neurosci. 24 (2012) 1742–1752.
[24] E.K. Diekhof, K. Geier, P. Falkai, O. Gruber, Fear is only as deep as the mind allows: a coordinate-based meta-analysis of neuroimaging studies on the regulation of negative affect, Neuroimage 58 (2011) 275–285.
[25] B.P. Doré, J.A. Silvers, K.N. Ochsner, Toward a personalized science of emotion regulation, Social Pers. Psychol. Compass 10 (2016) 171–187.
[26] B.P. Doré, J. Weber, K.N. Ochsner, Neural predictors of decisions to cognitively control emotion, J. Neurosci. 37 (2017) 2580–2588.
[27] N.U. Dosenbach, D.A. Fair, A.L. Cohen, B.L. Schlaggar, S.E. Petersen, A dual-networks architecture of top-down control, Trends Cogn. Sci. (2008).
[28] N.U. Dosenbach, K.M. Visscher, E.D. Palmer, F.M. Miezin, K.K. Wenger, H.C. Kang, E.D. Burgund, A.L. Grimes, B.L. Schlaggar, S.E. Petersen, A core system for the implementation of task sets, Neuron 50 (2006) 799–812.
[29] E.M. Drabant, K. McRae, S.B. Manuck, A.R. Hariri, J.J. Gross, Individual differences in typical reappraisal use predict amygdala and prefrontal responses, Biol. Psychiatry 65 (2009) 367–373.
[30] N.I. Eisenberger, S.L. Master, T.K. Inagaki, S.E. Taylor, D. Shirinyan, M.D. Lieberman, B.D. Naliboff, Attachment figures activate a safety signal-related neural region and reduce pain experience, Proc. Natl. Acad. Sci. U. S. A. 108 (2011) 11721–11726.
[31] S. Erk, A. Mikschl, S. Stier, A. Ciaramidaro, V. Gapp, B. Weber, H. Walter, Acute and sustained effects of cognitive emotion regulation in major depression, J. Neurosci. 30 (2010) 15726–15734.
[32] A. Etkin, C. Büchel, J.J. Gross, The neural bases of emotion regulation, Nat. Rev. Neurosci. 16 (2015) 693–700.
[33] A. Etkin, T. Egner, R. Kalisch, Emotional processing in anterior cingulate and medial prefrontal cortex, Trends Cogn. Sci. 15 (2011) 85–93.
[34] M. Feeser, K. Prehn, P. Kazzer, A. Mungee, M. Bajbouj, Transcranial direct current stimulation enhances cognitive control during emotion regulation, Brain Stimul. 7 (2014) 105–112.
[35] L.J. Gabard-Durnam, D.G. Gee, B. Goff, J. Flannery, E. Telzer, K.L. Humphreys, D.S. Lumian, D.S. Fareri, C. Caldera, N. Tottenham, Stimulus-elicited connectivity influences resting-state connectivity years later in human development: a prospective study, J. Neurosci. 36 (2016) 4771–4784.
[36] H.T. Ghashghaei, H. Barbas, Pathways for emotion: interactions of prefrontal and anterior temporal pathways in the amygdala of the rhesus monkey, Neuroscience 115 (2002) 1261–1279.
[37] H.T. Ghashghaei, C.C. Hilgetag, H. Barbas, Sequence of information processing for emotions based on the anatomic dialogue between prefrontal cortex and amygdala, Neuroimage 34 (2007) 905–923.
[38] N.R. Giuliani, T. Mann, A.J. Tomiyama, E.T. Berkman, Neural systems underlying the reappraisal of personally craved foods, J. Cogn. Neurosci. 26 (2014) 1390–1402.
[39] P.R. Goldin, T. Manber, S. Hakimi, T. Canli, J.J. Gross, Neural bases of social anxiety disorder: emotional reactivity and cognitive regulation during social and physical threat, Arch. Gen. Psychiatry 66 (2009) 170–180.
[40] J.J. Gross, Antecedent- and response-focused emotion regulation: divergent consequences for experience, expression, and physiology, J. Pers. Soc. Psychol. 74 (1998) 224–237.
[41] J.J. Gross, The emerging field of emotion regulation: an integrative review, Rev. Gen. Psychol. 2 (1998) 271–299.
[42] J.J. Gross, Emotion regulation: current status and future prospects, Psychol. Inquiry 26 (2015) 1–26.
[43] J.J. Gross, L.F. Barrett, Emotion generation and emotion regulation one or two depends on your point of view, Emot. Rev.: J. Int. Soc. Res. Emot. 3 (2011) 8–16.
[44] J.J. Gross, R.F. Munoz, Emotion regulation and mental health, Clin. Psychol.: Sci. Pract. 2 (1995) 151–164.
[45] A. Gyurak, J.J. Gross, A. Etkin, Explicit and implicit emotion regulation: a dual-process framework, Cogn. Emot. 25 (2011) 400–412.
[46] T.A. Hare, J. O'Doherty, C.F. Camerer, W. Schultz, A. Rangel, Dissociating the role of the orbitofrontal cortex and the striatum in the computation of goal values and prediction errors, J. Neurosci. 28 (2008) 5623–5630.
[47] J.V. Haxby, C.L. Grady, B. Horwitz, L.G. Ungerleider, M. Mishkin, R.E. Carson, P. Herscovitch, M.B. Schapiro, S.I. Rapoport, Dissociation of object and spatial visual processing pathways in human extrastriate cortex, Proc. Natl. Acad. Sci. U. S. A. 88 (1991) 1621–1625.
[48] D.J. Hayes, G. Northoff, Identifying a network of brain regions involved in aversion-related processing: a cross-species translational investigation, Front. Integr. Neurosci. 5 (2011).
[49] R.M. Hinke, X. Hu, A.E. Stillman, S.G. Kim, H. Merkle, R. Salmi, K. Ugurbil, Functional magnetic resonance imaging of Broca's area during internal speech, Neuroreport 4 (1993) 675–678.
[50] C.E. Izard, Human Emotions, Plenum Press, New York, 1977.
[51] O.P. John, J.J. Gross, Healthy and unhealthy emotion regulation: personality processes, individual differences, and life span development, J. Pers. Special Issue: Emot. Pers. Health 72 (2004) 1301–1333.
[52] T. Johnstone, C.M. van Reekum, H.L. Urry, N.H. Kalin, R.J. Davidson, Failure to regulate: counterproductive recruitment of top-down prefrontal-subcortical circuitry in major depression, J. Neurosci. 27 (2007) 8877–8884.
[53] D. Keltner, J.J. Gross, Functional accounts of emotions, Cogn. Emot. 13 (1999) 467–480.
[54] H. Kim, L.H. Somerville, T. Johnstone, A.L. Alexander, P.J. Whalen, Inverse amygdala and medial prefrontal cortex responses to surprised faces, Neuroreport 14 (2003) 2317–2322.
[55] H. Kober, L.F. Barrett, J. Joseph, E. Bliss-Moreau, K. Lindquist, T.D. Wager, Functional grouping and cortical-subcortical interactions in emotion: a meta-analysis of neuroimaging studies, Neuroimage 42 (2008) 998–1031.
[56] H.W. Koenigsberg, J. Fan, K.N. Ochsner, X. Liu, K.G. Guise, S. Pizzarello, C. Dorantes, S. Guerreri, L. Tecuta, M. Goodman, A. New, L.J. Siever, Neural correlates of the use of psychological distancing to regulate responses to negative social cues: a study of patients with borderline personality disorder, Biol. Psychiatry 66 (2009) 854–863.
[57] N. Kohn, S.B. Eickhoff, M. Scheller, A.R. Laird, P.T. Fox, U. Habel, Neural network of cognitive emotion regulation—an ALE meta-analysis and MACM analysis, NeuroImage 87 (2014) 345–355.
[58] R.S. Lazarus, Emotion and Adaptation, Oxford University Press, Oxford, 1991.
[59] J.E. LeDoux, Emotion circuits in the brain, Ann. Rev. Neurosci. 23 (2000) 155–184.
[60] R.W. Levenson, Human emotions: a functional view, in: P. Ekman, R.J. Davidson (Eds.), The Nature of Emotion: Fundamental Question, Oxford University Press, New York, 1994, pp. 123–126.
[61] G. Liakakis, J. Nickel, R.J. Seitz, Diversity of the inferior frontal gyrus—a meta-analysis of neuroimaging studies, Behav. Brain Res. 225 (2011) 341–347.
[62] T.S. Ligeza, M. Wyczesany, A.D. Tymorek, M. Kamiński, Interactions between the prefrontal cortex and attentional systems during volitional affective regulation: an effective connectivity reappraisal study, Brain Topogr. 29 (2015) 253–261.
[63] K.A. Lindquist, A.B. Satpute, T.D. Wager, J. Weber, L.F. Barrett, The brain basis of positive and negative affect: evidence from a meta-analysis of the human neuroimaging literature, Cereb. Cortex 26 (2016) 1910–1922.
[64] K.A. Lindquist, T.D. Wager, H. Kober, E. Bliss-Moreau, L.F. Barrett, The brain basis of emotion: a meta-analytic review, Behav. Brain Sci. 35 (2012) 121–143.
[65] X. Liu, J. Hairston, M. Schrier, J. Fan, Common and distinct networks underlying reward valence and processing stages: a meta-analysis of functional neuroimaging studies, Neurosci. Biobehav. Rev. 35 (2011) 1219–1236.
[66] B. Martins, G. Sheppes, J.J. Gross, M. Mather, Age differences in emotion

regulation choice: older adults use distraction less than younger adults in high-intensity positive contexts, J. Gerontol. Series B: Psychol. Sci. Social Sci. (2016) gbw028.
[67] I.B. Mauss, R.W. Levenson, L. McCarter, F.H. Wilhelm, J.J. Gross, The tie that binds? Coherence among emotion experience, behavior, and physiology, Emotion 5 (2005) 175–190.
[68] K. McRae, B. Hughes, S. Chopra, J.D. Gabrieli, J.J. Gross, K.N. Ochsner, The neural bases of distraction and reappraisal, J. Cogn. Neurosci. 22 (2010) 248–262.
[69] K. McRae, S.E. Jacobs, R.D. Ray, O.P. John, J.J. Gross, Individual differences in reappraisal ability: links to reappraisal frequency, well-being, and cognitive control, J. Res. Pers. 46 (2012) 2–7.
[70] M.L. Mechias, A. Etkin, R. Kalisch, A meta-analysis of instructed fear studies: implications for conscious appraisal of threat, Neuroimage 49 (2010) 1760–1768.
[71] H.N. Mischel, W. Mischel, The development of children's knowledge of self-control strategies, Child Dev. 54 (1983) 603–619.
[72] C. Morawetz, S. Bode, J. Baudewig, E. Kirilina, H.R. Heekeren, Changes in effective connectivity between dorsal and ventral prefrontal regions moderate emotion regulation, Cereb. Cortex 26 (2016) 1923–1937.
[73] C. Morawetz, T. Kellermann, L. Kogler, S. Radke, J. Blechert, B. Derntl, Intrinsic functional connectivity underlying successful emotion regulation of angry faces, Soc. Cogn. Affect. Neurosci. (2016) nsw107.
[74] P.S. Muhle-Karbe, J. Derrfuss, M.T. Lynn, F.X. Neubert, P.T. Fox, M. Brass, S.B. Eickhoff, Co-activation-based parcellation of the lateral prefrontal cortex delineates the inferior frontal junction area, Cereb. Cortex 26 (2016) 2225–2241.
[75] D.E. Nee, J.W. Brown, M.K. Askren, M.G. Berman, E. Demiralp, A. Krawitz, J. Jonides, A meta-analysis of executive components of working memory, Cereb. Cortex 23 (2012) 264–282.
[76] G. Northoff, A. Heinzel, M. de Greck, F. Bermpohl, H. Dobrowolny, J. Panksepp, Self-referential processing in our brain-A meta-analysis of imaging studies on the self, Neuroimage (2006).
[77] K.N. Ochsner, S.A. Bunge, J.J. Gross, J.D. Gabrieli, Rethinking feelings: an FMRI study of the cognitive regulation of emotion, J. Cogn. Neurosci. 14 (2002) 1215–1229.
[78] K.N. Ochsner, J.J. Gross, The cognitive control of emotion, Trends Cogn. Sci. 9 (2005) 242–249.
[79] K.N. Ochsner, J.J. Gross, The neural bases of emotion and emotion regulation: a valuation perspective, in: J.J. Gross (Ed.), The Handbook of Emotion Regulation, The Guilford Press, New York, NY, 2014.
[80] K.N. Ochsner, R.D. Ray, J.C. Cooper, E.R. Robertson, S. Chopra, J.D.E. Gabrieli, J.J. Gross, For better or for worse: neural systems supporting the cognitive down- and up-regulation of negative emotion, Neuroimage 23 (2004) 483–499.
[81] K.N. Ochsner, R.R. Ray, B. Hughes, K. McRae, J.C. Cooper, J. Weber, J.D. Gabrieli, J.J. Gross, Bottom-up and top-down processes in emotion generation: common and distinct neural mechanisms, Psychol. Sci. (2009).
[82] K.N. Ochsner, J.A. Silvers, J.T. Buhle, Functional imaging studies of emotion regulation: a synthetic review and evolving model of the cognitive control of emotion, Ann. N. Y. Acad. Sci. 1251 (2012) E1–E24.
[83] A. Olsson, K.N. Ochsner, The role of social cognition in emotion, Trends Cogn. Sci. 12 (2008) 65–71.
[84] P.C. Opitz, J.J. Gross, H.L. Urry, Selection, optimization, and compensation in the domain of emotion regulation: applications to adolescence, older age, and major depressive disorder, Social Pers. Psychol. Compass 6 (2012) 142–155.
[85] L.M. Paschke, D. Dörfel, R. Steimke, I. Trempler, A. Magrabi, V.U. Ludwig, T. Schubert, C. Stelzel, H. Walter, Individual differences in self-reported self-control predict successful emotion regulation, Soc. Cogn. Affect. Neurosci. 11 (2016) 1193–1204.
[86] M. Petrides, D.N. Pandya, Comparative cytoarchitectonic analysis of the human and the macaque ventrolateral prefrontal cortex and corticocortical connection patterns in the monkey, Eur. J. Neurosci. 16 (2002) 291–310.
[87] M. Petrides, D.N. Pandya, Dorsolateral prefrontal cortex: comparative cytoarchitectonic analysis in the human and the macaque brain and corticocortical connection patterns, Eur. J. Neurosci. 11 (1999) 1011–1036.
[88] M.L. Phillips, W.C. Drevets, S.L. Rauch, R. Lane, Neurobiology of emotion perception I: the neural basis of normal emotion perception, Biol. Psychiatry 54 (2003) 504–514.
[89] C. Rottschy, R. Langner, I. Dogan, K. Reetz, A.R. Laird, J.B. Schulz, P.T. Fox, S.B. Eickhoff, Modelling neural correlates of working memory: a coordinate-based meta-analysis, NeuroImage 60 (2012) 830–846.
[90] M. Roy, D. Shohamy, T.D. Wager, Ventromedial prefrontal-subcortical systems and the generation of affective meaning, Trends Cogn. Sci. 16 (2012) 147–156.
[91] J.A. Russell, Core affect and the psychological construction of emotion, Psychol. Rev. 110 (2003) 145–172.
[92] K.R. Scherer, A. Schorr, T. Johnstone (Eds.), Appraisal Processes in Emotion: Theory, Methods, Research, vol. xiv, Oxford University Press, New York, NY, 2001478 pp.
[93] D. Schiller, M.R. Delgado, Overlapping neural systems mediating extinction, reversal and regulation of fear, Trends Cogn. Sci. 14 (2010) 268–276.
[94] W.W. Seeley, V. Menon, A.F. Schatzberg, J. Keller, G.H. Glover, H. Kenna, A.L. Reiss, M.D. Greicius, Dissociable intrinsic connectivity networks for salience processing and executive control, J. Neurosci. 27 (2007) 2349–2356.
[95] R. Shafir, N. Schwartz, J. Blechert, G. Sheppes, Emotional intensity influences pre-implementation and implementation of distraction and reappraisal, Soc. Cogn. Affect. Neurosci. 10 (2015) 1329–1337.
[96] R. Shafir, R. Thiruchselvam, G. Suri, J.J. Gross, G. Sheppes, Neural processing of emotional-intensity predicts emotion regulation choice, Soc. Cogn. Affect. Neurosci. (2016) nsw114.
[97] G. Sheppes, S. Scheibe, G. Suri, J.J. Gross, Emotion-regulation choice, Psychol. Sci. 22 (2011) 1391–1396.
[98] G. Sheppes, S. Scheibe, G. Suri, P. Radu, J. Blechert, J.J. Gross, Emotion regulation choice: a conceptual framework and supporting evidence, J. Exp. Psychol. Gen. 143 (2014) 163–181.
[99] J.A. Silvers, J.T. Buhle, K.N. Ochsner, The neuroscience of emotion regulation: basic mechanisms and their role in development, aging and psychopathology, in: K.N. Ochsner, S.M. Kosslyn (Eds.), The Handbook of Cognitive Neuroscience, vol. 1, Oxford University Press, New York, 2013.
[100] J.A. Silvers, C. Insel, A. Powers, P. Franz, C. Helion, R.E. Martin, J. Weber, W. Mischel, B.J. Casey, K.N. Ochsner, vlPFC–vmPFC–amygdala interactions underlie age-related differences in cognitive regulation of emotion, Cereb. Cortex (2016) hw073.
[101] J.A. Silvers, K. McRae, J.D. Gabrieli, J.J. Gross, K.A. Remy, K.N. Ochsner, Age-related differences in emotional reactivity, regulation, and rejection sensitivity in adolescence, Emotion 12 (2012) 1235–1247.
[102] J.A. Silvers, J. Shu, A.D. Hubbard, J. Weber, K.N. Ochsner, Concurrent and lasting effects of emotion regulation on amygdala response in adolescence and young adulthood, Dev. Sci. (2014).
[103] J.A. Silvers, T.D. Wager, J. Weber, K.N. Ochsner, The neural bases of uninstructed negative emotion modulation, Soc. Cogn. Affect. Neurosci. (2014).
[104] R.N. Spreng, R.A. Mar, A.S. Kim, The common neural basis of autobiographical memory, prospection, navigation, theory of mind, and the default mode: a quantitative meta-analysis, J. Cogn. Neurosci. 21 (2009) 489–510.
[105] A.S. Troy, F.H. Wilhelm, A.J. Shallcross, I.B. Mauss, Seeing the silver lining: cognitive reappraisal ability moderates the relationship between stress and depressive symptoms, Emotion 10 (2010) 783–795.
[106] H.L. Urry, J.J. Gross, Emotion regulation in older age, Curr. Direct. Psychol. Sci. 19 (2010).
[107] H.L. Urry, C.M. van Reekum, T. Johnstone, N.H. Kalin, M.E. Thurow, H.S. Schaefer, C.A. Jackson, C.J. Frye, L.L. Greischar, A.L. Alexander, R.J. Davidson, 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 (2006) 4415–4425.
[108] C.M. van Reekum, H.L. Urry, T. Johnstone, M.E. Thurow, C.J. Frye, C.A. Jackson, H.S. Schaefer, A.L. Alexander, R.J. Davidson, Individual differences in amygdala and ventromedial prefrontal cortex activity are associated with evaluation speed and psychological well-being, J. Cogn. Neurosci. 19 (2007) 237–248.
[109] S. Vossel, J.J. Geng, G.R. Fink, Dorsal and ventral attention systems: distinct neural circuits but collaborative roles, Neuroscientist 20 (2013) 150–159.
[110] T.D. Wager, M.L. Davidson, B.L. Hughes, M.A. Lindquist, K.N. Ochsner, Prefrontal-subcortical pathways mediating successful emotion regulation, Neuron 59 (2008) 1037–1050.
[111] T.D. Wager, J. Jonides, S. Reading, Neuroimaging studies of shifting attention: a meta-analysis, Neuroimage 22 (2004) 1679–1693.
[112] T.D. Wager, C.Y. Sylvester, S.C. Lacey, D.E. Nee, M. Franklin, J. Jonides, Common and unique components of response inhibition revealed by fMRI, Neuroimage 27 (2005) 323–340.
[113] P.J. Whalen, The uncertainty of it all, Trends Cogn. Sci. 11 (2007) 499–500.