



Managing fear and anxiety in development: A framework for understanding the neurodevelopment of emotion regulation capacity and tendency

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ABSTRACT

How we manage emotional responses to environmental threats is central to mental health, as difficulties regulating threat-related distress can blossom into symptoms of anxiety disorders. Given that anxiety disorders emerge early in the lifespan, it is crucial we understand the multi-level processes that support effective regulation of distress. Scholars have given increased attention to behavioral and neural development of emotion regulation abilities, particularly cognitive reappraisal *capacity* (i.e., how strongly one can down-regulate negative affect by reinterpreting a situation to change one's emotions). However, this work has not been well integrated with research on regulatory *tendency* (i.e., how often one spontaneously regulates emotion in daily life). Here, we review research on the development of both emotion regulation capacity and tendency. We then propose a framework for testing hypotheses and eventually constructing a neurodevelopmental model of both dimensions of emotion regulation. Clarifying how the brain supports both effective and frequent regulation of threat-related distress across development is crucial to identifying multi-level signs of dysregulation and developing interventions that support youth mental health.

1. Introduction

The ability to cope with threats is central to mental health and well-being across the lifespan (Aldao et al., 2010; Cole et al., 1994; Schweizer et al., 2019). Indeed, how we manage (or *regulate*) emotional responses to environmental threats has been shown to shape whether or not these responses grow into symptoms of anxiety disorders (Cisler et al., 2010; McLaughlin et al., 2009; McLaughlin and Hatzenbuehler, 2009; McLean and Foa, 2017). Given that anxiety disorders are highly likely to onset in childhood and adolescence (Costello et al., 2005; Kessler et al., 2005), it is crucial that we build an understanding of how people learn to regulate emotional responses to threats as they develop.

Scholars have dedicated substantial energy to addressing this question across multiple levels of analysis. We have consequently learned that there are tight connections between emotion regulation and both the development of psychopathology and its treatment (Aldao et al., 2010; Berking et al., 2008; Gratz and Tull, 2010; McLaughlin et al., 2011, 2009; Radkovsky et al., 2014; Sloan et al., 2017; Zorowitz et al., 2020). Although we have learned much through this research, empirical and theoretical work has so far paid little attention to a key distinction between emotion regulation *capacity* (i.e., how successfully one can

change one's emotions when instructed to do so) and emotion regulation *tendency* (i.e., how often one spontaneously deploys emotion regulation strategies in daily life) across development (though see Berkman and Lieberman, 2009; Guassi Moreira et al., 2020; McRae, 2013; Silvers and Guassi Moreira, 2019 for studies focused on adults).

In this paper, we summarize research on the neural bases of emotion regulation capacity in both adult and youth samples before offering a framework for further clarifying the neurodevelopment of emotion regulation capacity and tendency (see Table 1 for glossary). We focus this review on cognitive reappraisal (i.e., reinterpreting the meaning of a stimulus to alter its emotional impact; Gross, 1998) given that this has been a focus of most relevant research. Delineating developmental trajectories of capacity and tendency, as well as interactions between these two constructs during neurodevelopment, can advance basic understanding of emotion regulation and potentially inform translational efforts to detect and intervene on emerging maladaptive emotion regulation or even anxiety-related symptoms.

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Table 1
Glossary of terms.

Term	Definition	Relevant citations
Emotion regulation	The set of strategies people use to change the duration, intensity, or type of emotions they feel	(Gross, 2015, 1998)
Cognitive reappraisal	Changing one's thoughts or interpretation of a stimulus to alter its emotional impact	(Gross, 2015, 1998; Ochsner et al., 2002)
Regulatory capacity	How successfully one can regulate one's emotions when instructed or freely choosing to do so	(Buhle et al., 2014; Silvers and Guassi Moreira, 2019)
Regulatory tendency	How frequently one chooses to regulate one's emotions	(Gross and John, 2003; Silvers and Guassi Moreira, 2019)
Sensitive period	A period of development when the environment can have particularly strong influence on the brain and mind's development of a certain faculty (e.g., language)	(Blakemore and Mills, 2014; Fuhrmann et al., 2015; Hartley and Lee, 2015; Sisk and Gee, 2022)
Ecological momentary assessment (EMA)	A method of data collection in which people report on their psychological experiences during their daily lives (e.g., by pinging their smartphones and surveying their emotions throughout a day)	(Andrewes et al., 2017; Colombo et al., 2019)
Hierarchical Bayesian models	A statistical and conceptual approach to testing theories in which relations between variables are nested hierarchically and Bayesian statistics are used to evaluate support for a hypothesized nested model given the evidence at hand	(Glassen and Nitsch, 2016; Henderson et al., 2010)
Directed acyclic graph (DAG)	A specific type of model in which variables are proposed to causally impact each other in a directed (i.e., non-recurrent, non-circular) fashion. DAGs can be built and tested using Bayesian statistics and are a promising method for testing developmental theory.	(McNally et al., 2017; Vanderweele and Robins, 2007; Williams et al., 2018)

2. Development and neural correlates of emotion regulation capacity

2.1. Developmental trends in behavioral measures of regulatory capacity

Reappraisal capacity is often measured by comparing negative affect ratings when participants down-regulate emotional reactions to aversive or threatening stimuli to negative affect ratings when responding naturally to these stimuli (Nook et al., 2021b, 2020, 2017; Ochsner et al., 2002; Silvers et al., 2012). Several cross-sectional behavioral studies in which participants regulate their reactions to standardized emotional images show improved reappraisal capacity from childhood to young adulthood. This positive linear trend has been replicated across these reappraisal-based laboratory paradigms both in and outside of the scanner (McRae et al., 2012b; Silvers et al., 2017b). However, some studies do not show this linear increase, suggesting that there may be task- or sample-level moderators that influence when children and young adults differ in their regulatory capacity (Ahmed et al., 2018; Nook et al., 2020; Van Cauwenberge et al., 2017). Similarly, investigations into the nonlinearities of regulatory success between broad developmental stages have returned mixed results. Some studies have found quadratic trends with both peak (Silvers et al., 2012) and lowest

(McRae et al., 2012b) levels of effectiveness coinciding with mid/late adolescence (i.e., ages 14–17), whereas others have failed to find nonlinear associations (Silvers et al., 2017b). The type of stimulus used during reappraisal paradigms may in part contribute to these mixed findings. For example, young adolescents were less successful at reducing negative affect with reappraisal compared to other age groups when the stimulus was social versus nonsocial (Silvers et al., 2012). Nonetheless, the balance of evidence from these cross-sectional studies suggests increased capacity to cognitively down-regulate emotional reactions to aversive stimuli across age.

2.2. Neural correlates of emotion regulation capacity

Delineating the neurodevelopmental trajectory of regulatory effectiveness first requires identifying key brain regions within the cognitive control and salience networks that have been implicated in reappraisal of aversive stimuli (Buhle et al., 2014). A broad literature using a variety of tasks points to the dorsal and ventral lateral regions of the prefrontal cortex (IPFC) as involved in cognitive control (i.e., ventrolateral prefrontal cortex (vlPFC) and dorsolateral prefrontal cortex (dlPFC)), and this prior literature has been used to propose a model for the role of these regions in emotion regulation (Buhle et al., 2014; Ochsner et al., 2012, 2002; Ochsner and Gross, 2005). Together, the vlPFC—thought to select and inhibit appraisals depending on goals—and the dlPFC—thought to alter appraisals in working memory to align with goals—are thought to contribute to reappraisal during explicit, instructed paradigms (Badre and Wagner, 2006; Buhle et al., 2014; Thompson-Schill et al., 2005; Wager and Smith, 2003). The supplemental role of dorsal and ventral regions of the medial prefrontal cortex (mPFC) in regulatory behaviors, like reappraisal, is thought to be twofold (O'Reilly, 2010). First, the ventromedial prefrontal cortex (vmPFC) is thought to encode and represent the affective value of a stimulus in order to signal the need for regulation (Rudebeck et al., 2008). Second, the dorsomedial prefrontal cortex (dmPFC) is thought to monitor the resulting changes in affect following regulatory behaviors (e.g., cognitive control) instantiated by more lateral prefrontal regions and provide feedback to lateral prefrontal regions about whether further actions are needed (O'Reilly, 2010; Taren et al., 2011). In particular, dmPFC is thought to maintain these self-reflective processes by representing and updating the value of regulatory actions (Amodio and Frith, 2006; Binder et al., 2009; Cato et al., 2004; Crosson et al., 2002; Ochsner and Gross, 2005; Olsson and Ochsner, 2008). The dorsal anterior cingulate cortex (dACC) is thought to further support regulatory processes through its close functional and anatomical associations with the dmPFC by allocating attention as it monitors conflict between goals and current states (Cole and Schneider, 2007; O'Reilly, 2010; Shenhav et al., 2013). Thus theoretically, the dorsal and ventral regions of the mPFC work in concert to link affect and value representations with regulatory behaviors in order to guide and initiate future regulatory processes (O'Reilly, 2010; Rudebeck et al., 2008).

These lateral prefrontal regions involved in cognitive control and medial prefrontal regions involved in valuation are thought to interact with and modulate activity in subcortical regions, particularly the amygdala, which is implicated in tracking and reacting to the affective value of a stimulus, especially stimuli that may be threatening to an individual (Buhle et al., 2014; Cunningham et al., 2008; Neta and Whalen, 2011; Ochsner et al., 2002). Functional connectivity analyses during instructed reappraisal support this model: For example, inhibitory projections from the vmPFC to the amygdala reduce amygdala reactivity in response to affective stimuli (Delgado et al., 2008; Hare et al., 2008; Motzkin et al., 2015). Interactions between these cortical regions, as well as connectivity with subcortical regions, may underlie individual differences in reappraisal capacity and are often fundamental to neurodevelopmental theories of emotional development given age-related changes in these large-scale circuits (Casey et al., 2019; Heller and Casey, 2016). While this model offers an interpretation of

neural activity in reappraisal tasks, it is important to note that it is both speculative and depends largely on reverse inference (i.e., attributing functions to brain regions based on prior research associating activity in those regions with presumed cognitive functions used in certain tasks).

2.3. Changes in frontolimbic circuitry associated with emotion regulation capacity across development

Neurodevelopmental theory posits that normative developmental changes in brain circuitry play a mechanistic role in the maturing ability to regulate emotional responses to threats. The circuitry recruited during reappraisal in adulthood undergoes dynamic changes during childhood and adolescence, as we outline below. In particular, behavioral changes in emotion regulation across development correspond to maturational cascades from subcortical circuitry, to subcortical-cortical circuitry, to cortical-cortical circuitry (Casey et al., 2019, 2016) (Fig. 1).

2.3.1. Interactions between subcortical regions in childhood

Both structural and functional brain imaging highlight the relatively faster and earlier changes in the development of limbic regions compared to the prefrontal cortex (PFC) (Fig. 1A). Within the first year of life, the total volume of subcortical regions, such as the amygdala and thalamus, increase on average almost 110% (Gilmore et al., 2012). Additional studies have identified anatomical changes in other subcortical regions such as the ventral striatum (VS) in children as young as five (Raznahan et al., 2014). Functional brain imaging has shown heightened reactivity in subcortical regions, especially the amygdala, to emotional cues in children as young as six compared to adults (Gee et al., 2013; Silvers et al., 2017a; Swartz et al., 2014; Vink et al., 2014). Given the hypothesized role of the amygdala and the VS in tracking affective or

threatening cues (Hare et al., 2008; Somerville et al., 2011) and supporting reward learning processes relevant for motivated behaviors (e.g., Fiorillo, 2003), these two subcortical regions have received significant attention in the literature as regions influenced by top-down regulatory processes.

Age-dependent interactions between subcortical regions contribute to variability in affective responding and regulatory success across development. In a cross-sectional sample ranging from age 5 to young adulthood, the strength of amygdala-VS connectivity decreased with age and was associated with cognitive control when responding to emotional cues (Heller et al., 2016). Studies have also found less mature patterns of functional connectivity between the mPFC and subcortical regions (e.g., amygdala) during both naturally viewing (Gee et al., 2013) and cognitive control conditions with affective stimuli in children (Perlman and Pelphrey, 2011). Additionally, resting state fMRI reveals that interactions between neighboring subcortical regions, such as the amygdala and VS, tend to emerge earlier in development compared to connections between more distal regions (e.g., between subcortical and cortical regions; Fareri et al., 2015; Gabard-Durnam et al., 2018). These findings, coupled with age-related increases in structural connectivity from amygdala to PFC in rodents (Bouwmeester et al., 2002) and humans (Swartz et al., 2014), suggest that subcortical-subcortical and later emerging bottom-up subcortical-cortical circuitry characterize childhood neurodevelopment. A dominant subcortical circuitry may explain reduced reappraisal capacity for aversive stimuli in childhood compared to older ages. Note, however, that the studies reviewed in this section and some of the following sections do not use classic reappraisal paradigms but rather involve exerting cognitive control in the context of affective stimuli (e.g., withholding a button press to a smiling face). Some authors have argued that these tasks can assess implicit rather

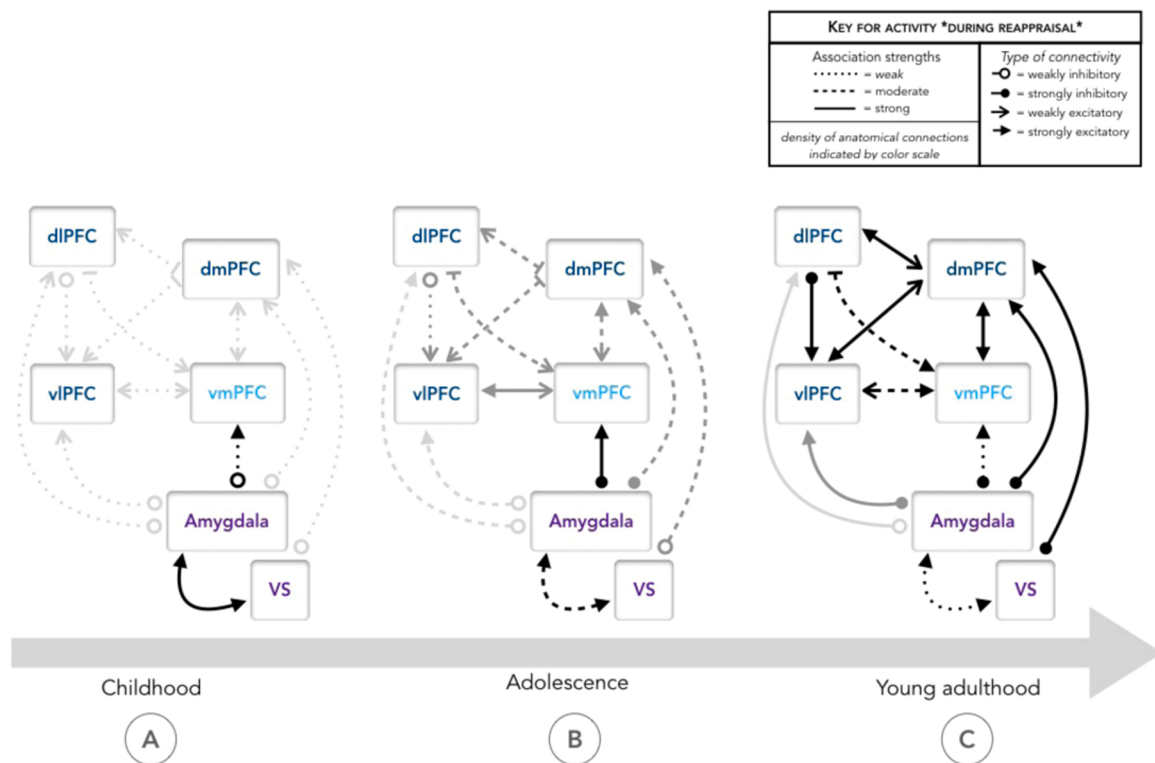


Fig. 1. Age-related changes in frontolimbic circuitry during reappraisal implicated in dimensions of emotion regulation in (A) childhood, (B) adolescence, and (C) young adulthood. The arrows represent bidirectional projections (e.g., in part A, amygdala to vmPFC is an excitatory projection, whereas vmPFC to amygdala is an inhibitory projection). This figure depicts patterns of connectivity during reappraisal; changes in functional connectivity strengths are indicative of their relative role in the active process of using reappraisal (which is related but not limited to changes in the density of anatomical connections). The schematic emphasizes developmental shifts in circuitry from dominant interactions between subcortical regions in childhood to reciprocal frontolimbic projections in adolescence and stronger cortical-cortical interactions in young adulthood. vmPFC = ventromedial prefrontal cortex, vIPFC = ventrolateral prefrontal cortex, dmPFC = dorsomedial prefrontal cortex, dIPFC = dorsolateral prefrontal cortex, VS = ventral striatum.

than explicit emotion regulation (Braunstein et al., 2017), and consequently they provide only indirect information regarding the role of these networks in the development of cognitive reappraisal.

2.3.2. Development of reciprocal frontolimbic projections and ventral-to-dorsal mPFC engagement in adolescence

Early adolescent experiences with increased emotional lability, still-maturing regulatory capacity, and sensitivity to environmental threats may arise from protracted development of connections between earlier-developing subcortical versus later-developing cortical regions (Somerville and Casey, 2014). Heightened activity of subcortical regions begets not only the increase in reactivity but also drives the maturation of bottom-up and top-down projections (Tottenham and Gabard-Durnam, 2017). Increased engagement of subcortical-cortical circuitry leads in turn to the strengthening of reciprocal projections from prefrontal regions back to subcortical regions, which is associated with increased reappraisal capacity (Silvers et al., 2017b). Structural tracing studies in rodents document this sequential cascade from earlier developing amygdala-PFC projections to later strengthening of projections from the PFC to the amygdala (Bouwmeester et al., 2002), with initial evidence of a similar directional shift in human development (Gee et al., 2022).

Molecular changes within subcortical and cortical regions coincide with this shift from excitatory bottom-up to inhibitory top-down frontolimbic projections (Hensch, 2004) with maturation of relevant gamma-aminobutyric acid (GABA) circuitry thought to underlie shifts in excitatory-inhibitory balance during adolescence (Werker and Hensch, 2015). These molecular changes often mark the onset of system-specific “sensitive periods,” during which certain brain circuits are uniquely restructuring given biological readiness and increased potency of environmental inputs to guide learning and shape behaviors (Doremus-Fitzwater et al., 2010; Kaufman, 2018; Morgan et al., 2018; Spear, 2000), relative to other developmental stages (Takesian and Hensch, 2013; Werker and Hensch, 2015). Characterized by concurrent cascades of hierarchical changes in subcortical and cortical circuitry, adolescence may be a sensitive period in brain development that supports age-dependent changes in emotion regulation capacity (Blakemore and Mills, 2014; Fuhrmann et al., 2015; Larsen et al., 2022; Sisk and Gee, 2022).

An adolescent peak in mPFC engagement during reappraisal (McRae et al., 2012a) highlights its role in scaffolding functional switches in frontolimbic circuitry underlying changes in the capacity to regulate emotional responses (Fig. 1B). Cross-sectional neuroimaging studies of frontolimbic functional connectivity during the transition into adolescence reflect these dynamic developmental processes. For example, 10 year-olds and older youth exhibited negative amygdala-mPFC functional connectivity while viewing threat-related stimuli (e.g., fearful faces), whereas younger youth had positive functional connectivity (Gee et al., 2013). This directional switch in connectivity was associated with better task performance, lower amygdala reactivity during the task, and age-related declines in anxiety. In another study, amygdala-mPFC connectivity was associated with better cognitive control while viewing emotional cues, and this regulation-related pattern of connectivity mediated the negative correlation between amygdala-VS connectivity and cognitive control (Heller et al., 2016). Further evidence shows that the valence of amygdala-vmPFC connectivity moderated the association between vlPFC activity and age-related decreases in amygdala activity, such that negative amygdala-vmPFC connectivity was associated with higher levels of vlPFC engagement (Silvers et al., 2017b). These findings suggest that age-related changes in amygdala-mPFC connectivity may act as a “rate-limiting step” for increasing IPFC engagement and modulation of subcortical reactivity during these tasks. Indeed, age-related increases in vlPFC activity, as well as decreased coupling between the vlPFC and vmPFC, are associated with higher reappraisal effectiveness (McRae et al., 2012a; Morawetz et al., 2017; Silvers et al., 2017b).

Age-related changes in reappraisal capacity may also hinge on

functional shifts within mPFC subregions. Specifically, the dmPFC and vmPFC have dissociable structural developmental trajectories (Markham et al., 2007; Shaw et al., 2008) and distinct functional contributions to emotional processes (Etkin et al., 2011). As reviewed earlier, the vmPFC is often associated with encoding and updating the affective value of stimuli, whereas the dmPFC is thought to track the effectiveness of regulatory behaviors by monitoring subsequent changes in affective states (e.g., through the dACC). Several studies have documented less robust vmPFC activity in late adolescence during the transition into young adulthood while responding to aversive stimuli (Lindquist et al., 2016; McRae et al., 2012a; Silvers et al., 2017a). Concurrently, increasing dmPFC response to aversive stimuli driving stronger dmPFC-vmPFC connectivity suggests that this ventral-to-dorsal shift within the mPFC underlies an enhanced ability to tightly couple the representation of emotional events with cognitive control regulatory behaviors (Cohen et al., 2016; Silvers et al., 2017a).

Adolescents engage the dmPFC and dACC more than adults during both cognitive control tasks and while viewing affective stimuli (Blakemore, 2008). Top-down inputs from the dmPFC to the vmPFC are additionally associated with downregulation of amygdala activity in late adolescence and adulthood (Banks et al., 2007; Hartley and Phelps, 2010; Lee et al., 2012; Roy et al., 2012), and the dmPFC and dACC have relatively more outputs to the amygdala than other prefrontal regions (Ray and Zald, 2012). This ventral-to-dorsal shift within the mPFC tracks age-related improvements in regulatory effectiveness not only by exerting modulatory effects on subcortical regions but also by acting as the conduit of affective information to and from lateral prefrontal regions that are critical in cognitive control processes (Allard and Kensing, 2014; Helion et al., 2019; Mitchell, 2011; Phillips et al., 2008). For example, stronger coupling between the dmPFC and vlPFC during reappraisal was associated with reappraisal effectiveness in adults (Morawetz et al., 2017; Wager et al., 2008). As such, the dmPFC and dACC are well poised to integrate different components of prefrontal function to support increasing regulatory capacity. In support of this idea, patterns of vlPFC-amygdala or vmPFC-amygdala connectivity do not track with individual differences in reappraisal effectiveness in adults (Morawetz et al., 2017, 2016) but do during other developmental stages (Silvers et al., 2017b). Instead, stronger dlPFC-vlPFC coupling is related to reappraisal effectiveness in adults (Morawetz et al., 2017, 2016) (Fig. 1C).

3. Development and neural correlates of emotion regulation tendency

The tendency to use cognitive reappraisal to manage one's emotions is often operationalized as a trait-like behavior and assessed using the reappraisal subscale of the well-validated Emotion Regulation Questionnaire, of which there are both adult and child versions (Gross and John, 2003). As such, the following section largely discusses studies that focus on this construct. That said, operationalizing frequency in this trait-like manner may overlook the fluctuations, or state-like variability, in strategy use that vary across development and interact with contextual factors. We return to this point in the Discussion.

3.1. Developmental trends in behavioral measures of emotion regulation tendency

Behavioral research documents a normative shift from behavioral, attention-related strategies for regulating distressing emotions (e.g., hiding under the covers) to more frequent use of effortful, cognitive strategies (i.e., reappraisal) during development, and this shift parallels improvements in effectiveness to implement these strategies (Cracco et al., 2017; Garnefski and Kraaij, 2007; Giuliani and Pfeifer, 2015; Kopp, 1989; Riediger and Klipker, 2014; Thompson, 1991). Frequency of reappraisal use is thought to stabilize in adulthood, and studies find limited within-individual variability of strategy selection and use during

adulthood (Benson et al., 2019). Similarly, analyses of age-related differences in reappraisal subtypes used within a laboratory task and cross-sectional sample show increased use of “normative” tendency to “change circumstances” of a situation across age and a peak of “denying reality” in early adolescence (Nook et al., 2020). That said, one accelerated longitudinal study found a slight linear decrease in frequency as a function of age within 1130 youth (9- to 15-year-olds) using latent growth curve modeling across three time points (Gullone et al., 2010). Measurement approaches (e.g., trait-like versus state-like self-report questionnaires) and unassessed contextual factors may explain this discrepancy. Further empirical work can guide the field in supporting or refining the notion that the tendency to use reappraisal to manage emotions increases with age.

3.2. Neural correlates of emotion regulation tendency

Compared to capacity, there is a paucity of studies on neural processes related to reappraisal tendency. In one study, greater dispositional use of reappraisal was associated with increased activation in the dlPFC, vlPFC, and dmPFC and less amygdala activation while adults viewed affective stimuli (Drabant et al., 2009). These brain regions correspond to the neural correlates of reappraisal capacity, hinting at a potential link between one’s frequency of reappraisal and spontaneous use of this strategy while viewing affective stimuli (i.e., an association between capacity and tendency). In another study, higher dispositional reappraisal use was associated with lower left basolateral amygdala-insula and right basolateral amygdala-supplementary motor cortex functional connectivity during resting state fMRI (Picó-Pérez et al., 2018). These patterns of connectivity were distinct from the connectivity pattern associated with dispositional suppression use, suggesting that individual differences in habitual emotion regulation strategy use may manifest in unique tonic brain processes. Lastly, higher self-reported trait regulatory tendency—collapsing across all strategies—correlated with decreased amygdala activity, stronger amygdala-vlPFC and amygdala-dmPFC connectivity, and less negative affect during reappraisal (Paschke et al., 2016). Together, these initial studies hint at the neural processes underlying regulatory tendency in adults.

3.3. Open questions in the neurodevelopment of tendency

Echoing the paucity of neuroimaging studies probing the neural correlates of reappraisal tendency, only one study to date has examined this topic during development. Greater cortical thinning of the dlPFC and vlPFC in a longitudinal study of female adolescents assessed at two time points (at ages 12 and 16) was prospectively related to greater dispositional use of reappraisal in late adolescence (age 19) (Vijayakumar et al., 2014). Age-related decreases in cortical thickness have also been associated with increases in cognitive control ability in cross-sectional studies (Tamnes et al., 2010a, 2010b). These structural MRI findings suggest that some of the same brain regions that support reappraisal effectiveness may also relate to reappraisal tendency. Although additional studies are needed to clarify the extent to which neural processes supporting tendency parallel those supporting capacity, this result suggests that interrelated neurodevelopmental mechanisms may drive age-related changes in capacity and tendency.

Another open question is whether the processes driving age-dependent changes in reappraisal use differ by developmental stage. That is, do changes in the frequency of reappraisal use (or lack thereof) stem from changes in the same underlying process during childhood as during adolescence? For example, more frequent use in late childhood to mid-adolescence may reflect an increasing number of potential learning opportunities to experiment with using reappraisal. By contrast, more frequent use in late adolescence may be driven by learning from prior experiences in which reappraisal was effective in managing emotions within a similar context. As an analogy from the field of education,

“learning to read versus reading to learn new concepts” captures this potential switch in the meaning behind frequency measures (i.e., “learning to reappraise versus reappraising to regulate emotions”).

Finally, a key task for future research is to develop an evidence-based neurodevelopmental model of how emotion regulation capacity and tendency *interactively* develop. We provide a preliminary framework for constructing, testing, and refining such a model in (Fig. 2). Research exploring how effectiveness and frequency relate to each other in adulthood is limited and mixed, with some studies finding that reappraisal use is related to capacity (McRae et al., 2012b) and others finding no relationship (Troy et al., 2018). Although prior studies document both more frequent use of effortful, cognitive strategies (e.g., reappraisal) from childhood to young adulthood and age-related improvements in reappraisal effectiveness (Garnefski and Kraaij, 2007; McRae et al., 2012b), we are not aware of studies directly testing relationships between tendency and capacity in developmental samples. Such an investigation is sorely needed, as it is unlikely that these dimensions of emotion regulation develop orthogonally.

Given age-related differences in factors underlying improvements in emotion regulation—such as hierarchical, dynamic changes in fronto-limbic circuitry (Casey et al., 2019) and the potential for more opportunities to practice reappraisal in novel situations during adolescence (Guyer et al., 2016)—it is likely that changes in effectiveness and frequency may be tightly linked during a period of dynamic change in brain development and social context. Here, we propose that developmental stage might moderate the relationship between capacity and tendency (Fig. 2). In particular, we hypothesize that (i) synchrony between capacity and tendency may be lower in childhood given that children still have little evidence concerning the utility of regulation and the stronger subcortical-subcortical circuitry may limit belief updating concerning the value of regulation (e.g., Sutton, 1999), (ii) adolescence is a period of heightened coupling between capacity and tendency given that this is an active stage of exploration and developing subcortical-cortical circuitry facilitates learning of responses that foster adaptive outcomes, and (iii) adulthood will be a period of reduced capacity-tendency coupling due to relative decreases in neuroplasticity and greater crystallization of one’s regulatory habits (Hartley and Lee, 2015; Morawetz et al., 2017, 2016). Thus, adolescence may be a unique developmental stage during which changes in capacity and tendency may be closely linked and iteratively shape each other given dynamic cascades of hierarchical changes in subcortical and cortical circuitry (Fig. 2). If so, adolescence is a key period in which learning cognitive skills to effectively manage emotional responses to threats and then implementing those skills may shape longer-term trajectories of resilience and mental health. Although our framework provides a sketch for how these processes may develop, these are all preliminary hypotheses built on the best available (though often indirect) evidence. As such, this framework is in need of direct empirical scrutiny and careful refinement to eventually produce a clear and well validated model of these processes.

4. Discussion

Environmental stressors and threats are extraordinarily common, and the ability to effectively manage one’s emotions is key to mental health and well-being across the lifespan (Aldao et al., 2010; Gross and Jazaieri, 2014). However, such beneficial outcomes require *both* choosing to regulate one’s emotional reactions to threats and doing so effectively. Although attention to this distinction between regulatory capacity and regulatory tendency is growing (Berkman and Lieberman, 2009; Gross et al., 2006; Guassi Moreira et al., 2020; McRae, 2013; McRae et al., 2012b; Silvers and Guassi Moreira, 2019), we lack a clear model of how these processes *develop* at the neural and behavioral levels. Here, we have summarized research on what is known about the development and neural bases of both emotion regulation capacity and tendency, sketched a framework, and generated a set of hypotheses that can guide future research on developing such a model. We now conclude

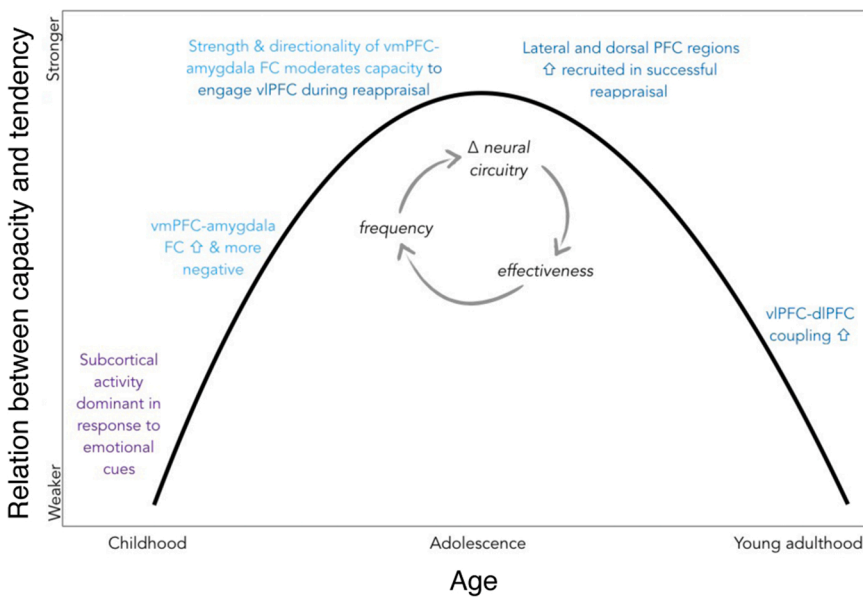


Fig. 2. Hypothesized framework for studying age-related changes in the association between regulatory capacity and tendency (specifically for cognitive reappraisal). Based on preliminary results, we propose that developmental maturation of frontolimbic circuitry facilitates changes in effectiveness, which will reinforce frequency of use, which will in turn shape functional connections with experience. We hypothesize an inverted-U relationship between emotion regulation capacity and tendency across age. In childhood, dominant subcortical circuitry may mean that fluctuations in one dimension do not lead as directly to learning or changes in the other dimension. In adolescence, increased functional connectivity (FC) between the vmPFC and amygdala and increased maturation of the prefrontal cortex (PFC) may lead to increased coupling between capacity and tendency. The adolescent brain may be better tuned to increase regulatory tendency as regulatory capacity increases. This synchrony may decrease in young adulthood, as both vIPFC-dIPFC coupling and regulatory capacity fully mature but regulatory tendencies become fixed habits. vmPFC = ventromedial prefrontal cortex, vIPFC = ventrolateral prefrontal cortex, dIPFC = dorsolateral prefrontal cortex.

with a brief discussion of the potential implications of this research and directions for future research.

The field's initial focus on regulatory capacity has offered important insight into the neural bases and development of this important skill. It is likely that part of the appeal of studying capacity over tendency is because emotion regulation capacity can be measured using a behavioral task, whereas tendency is typically measured via a self-report questionnaire. However, as we argue in this paper, there are several important reasons why future research should focus on a multidimensional approach to emotion development. First, there are theoretical reasons why we might hypothesize that capacity and tendency iteratively influence each other and that these relations vary across developmental stage (see Section 3.3). Second, evidence suggests that studies of capacity alone miss a key part of emotion regulation's benefits, as recent studies have found weak or null relations between behavioral measures of capacity and well-being but instead stronger relations with tendency (Andrews et al., 2022; Guassi Moreira et al., 2020; Wylie et al., 2022). Third, understanding the neurodevelopment of regulatory frequency (i.e., deciding to regulate emotions in a given context) is itself an interesting scientific question that offers an opportunity for synthesis across affective scientists, social psychologists, neuroscientists, cognitive scientists studying decision-making, and clinical scientists interested in facilitating mental health. What experiences or contexts cue individuals to choose to regulate their emotions, how does an individual's learned value of regulation unfold over time, and what emerging brain systems support these developments? These are key open questions that we hope our framework highlights and organizes research around. Given the early age of onset for anxiety disorders and their potential for long-term negative impacts (Compton et al., 2004; Costello et al., 2005; Kessler et al., 2005), addressing these questions is particularly important for supporting youths' ability to adaptively manage emotional responses to threatening experiences that generate distress, fear, and anxiety. Although several successful interventions for youth fear and anxiety are established and in development, clarifying the multi-level processes that support effective emotion regulation across development can further inform how to treat or even prevent anxiety disorders in youth.

There are several exciting next steps for research in this area. Ongoing developments in and widespread use of sophisticated data collection methods (e.g., ecological momentary assessment; EMA), technology (e.g., neuroimaging; Berkman and Falk, 2013), and analytical methods (e.g., Bayesian network models) offer new opportunities to

investigate how capacity and tendency develop. As mentioned, relying on trait-level self-report questionnaires has likely dampened interest in tendency research, as these questionnaires can be prone to bias, rely on accurate recall (which may differ across development), and require reporting on averages that may not reflect important contextual variation. As such, examining these processes as they occur in ecologically-valid contexts with EMA study designs presents an exciting complement to retrospective self-report questionnaires. Leveraging the real-time data collection of emotion regulation strategy use and effectiveness through EMA offers the potential to provide meaningful insight into real-world, multidimensional processes of emotion regulation across the lifespan. Given the dynamic nature of developmental processes underlying multidimensional phenomena, these multimodal and naturalistic approaches are critical.

Initial evidence supports enthusiasm for an EMA approach, as one study found that adolescents who experienced prolonged periods of negative affect—suggesting lower emotion regulation effectiveness—following a real-world stressor also reported greater depression severity (Silk et al., 2003). Another study examined the co-occurrence of regulatory strategies in daily life and their association with internalizing symptoms in adults with and without a clinical diagnosis (McMahon & Naragon-Gainey, 2019). Finally, a set of studies has examined how adolescents' level of internalizing symptomatology is related to their daily "repertoire" of emotion regulation strategies (i.e., the strategies they tend to use, including reappraisal; de France and Hollenstein, 2017; Grommisch et al., 2019; Lennarz et al., 2018; Loughheed and Hollenstein, 2012). Leveraging the real-time data collection of emotion regulation strategy use and efficacy through EMA study designs offers the potential to provide meaningful insight into the real-world, multidimensional processes of emotion regulation. Novel use of analytical approaches such as Bayesian network models can further support empirical efforts to address this gap in the literature. Given the hierarchical relationship between the variables of interest (e.g., frontolimbic functional connectivity, effectiveness, frequency) across development, Bayesian network models, or directed acyclic graphs (Henderson et al., 2010), provide one example of a suitable analytical tool to account for the structure of these age-dependent associations. Additionally, more naturalistic laboratory methods that expose participants to threats using panels of dour judges, virtual reality goggles, or video game devices can balance the naturalism of real-world threatening situations with the tight control of in-lab designs (Kitt et al., 2022; Parrish et al., 2016; Seddon et al., 2020). Another methodological concern that the field must address is that common

paradigms of emotion regulation capacity suffer from suboptimal psychometric reliability and ongoing concerns regarding construct validity (Braunstein et al., 2017; Guassi Moreira et al., 2020). We must continue to innovate to ensure our tasks measure what we think they measure and do so reliably.

When reviewing how the field approaches the neuroscience of emotion and emotion regulation, it appears that most studies focus broadly on several negative emotions, for example by using standardized emotional images that tend to induce sadness, anxiety, fear, disgust, and anger (Mikels et al., 2005). Consequently, the current review focuses on how reappraisal functions *generally* across these affective experiences. However, there are potentially interesting distinctions between how anxiety and fear are regulated compared to other emotional experiences. Theoretically, *avoidance* is seen as a key strategy people use to regulate fear and anxiety, although this only serves to promote symptomatic reactions to threatening stimuli, and reducing avoidance is a central target in both youth and adult anxiety treatment (Arnaudova et al., 2017; Berman et al., 2010; Craske et al., 2014; Foa and Goldstein, 1978; Lebowitz et al., 2013; Zorowitz et al., 2020). Distinctions between emotion regulation in anxious versus other populations have been empirically documented, including differences in maladaptive regulatory strategies like worry and rumination (Desrosiers et al., 2013; Kashdan et al., 2013; Kircanski et al., 2015). These lines of research offer interesting future directions for extending the general framework provided here to specifically understand the role of fear and anxiety regulation in the development of anxiety disorders. Another limitation of the current framework is that it is based largely on cross-sectional rather than longitudinal studies. This leaves open the possibility that relations we propose based on prior work are due to third variables or cohort effects. Additionally, without longitudinal studies, we have little insight into potential bidirectional relations between variables (e.g., regulatory tendency and capacity could influence each other cyclically). As such, longitudinal designs will be crucial in gathering additional evidence regarding the ideas proposed here.

In addition to applying novel research tools to validate our hypothesized relations and address limitations of the proposed framework, we encourage researchers to further expand it. We have purposefully constrained the set of factors relevant to emotional development in our framework. However, after validating it, attention should be paid to incorporating additional factors such as emotion regulation repertoire (i.e., how many strategies an individual has at their disposal; Grommisch et al., 2019), social context (i.e., how the presence or influence of others shapes capacity and frequency; Gee et al., 2014; Guyer et al., 2016; Nelson et al., 2016; Rodman et al., 2017), the interplay of biological and environmental inputs (Hensch, 2004), stress or situational demands (Troy et al., 2013), temporal dynamics (Heller and Casey, 2016), and other aspects of emotion expertise like the ability to specifically identify one's emotions (Hoemann et al., 2021; Nook, 2021; Nook et al., 2021a, 2018). Another important line of extension is to push our understanding of neural processes beyond mere blood-oxygen-level-dependent (BOLD) responses in fMRI contexts and down into finer neuron-level and molecular-level processes. Finally, we encourage researchers to work towards creating formal models of these phenomena to provide precise mathematical tests of key relations (Robinaugh et al., 2021). We hope the framework we offer here can become a center point of a fuller model that leads to a rich understanding of emotion regulation and its neurodevelopment. Even more so, this model may connect to developmental cascade theories (Thelen, 2005) of clinical change that can help hone interventions to the precise strengths and challenges individuals have managing fear, anxiety, distress, or other negative emotions given their neurodevelopmental stage.

Competing Interests

The authors declare no competing interests.

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Camila Caballero, the first author of this paper, was a beloved Ph.D. student in the Clinical Affective Neuroscience & Development Lab at Yale who died in December 2021. She was a brilliant researcher, talented clinician, gifted leader, and a cherished mentor and friend to so many. Camila's research broadly focused on the development of emotion regulation among youth experiencing highly stressful environments. Motivated by her experiences working in the classroom as a special education math teacher, Camila was especially interested in understanding heterogeneity in emotion regulation at the behavioral and neural levels to inform how interventions can be better tailored for specific children based on their strengths and areas for growth. Camila brought incredible depth of thought to these questions, approaching her studies with great nuance and consideration for the multifaceted nature of emotion and the environments in which children develop. She was highly creative, both in her scientific approach to designing clever studies to tackle challenging questions that the field has long struggled to answer, and in her design of research materials that are engaging, effective with children and adolescents, and specifically suited for use with youth who have experienced adversity. During her four years in the CANDLab, Camila made invaluable contributions to the lab's line of research on emotion regulation, using fMRI and EMA to better understand how specific dimensions of emotion regulation develop as a function of changes in corticolimbic circuitry. Camila's approach to her research was beautifully human-centered, and was often inspired by the experiences of particular children she had worked with as a teacher or therapist. Camila often referenced Tupac Shakur's famous quote in her work: "You see you wouldn't ask why the rose that grew from the concrete had damaged petals. On the contrary we would all celebrate its tenacity." She recognized and honored the humanity and immense potential and strengths in every child. Camila's contributions to psychology will continue to reverberate through the many contributions she made to children's mental health, her lasting influence on the CANDLab's research, and the immeasurable impact that she had on her labmates in the CANDLab, the Yale Psychology community, and colleagues across the field.

From D.G.G. and E.C.N.: As we have grieved and spent time in community together over the past year, our lab community has felt strongly about helping bring Camila's work to the world. Camila was brilliant and thoughtful and cared deeply about the research she was pursuing. This paper originated as Camila's theme essay in her Ph.D. program and formed the basis of a framework she had proposed to begin to empirically test in her dissertation prospectus. Camila wrote the paper in its original form and revised it with feedback from D.G.G. and her theme essay committee (BJ Casey and Jutta Joormann) over the course of a year, with the goal to ultimately submit it for publication following the completion of her theme essay requirement. In preparing the paper for publication over the past year, E.C.N. condensed it from the longer theme essay format, updated the literature review with newly published studies, and incorporated thoughtful feedback from two reviewers with support from D.G.G. We know Camila would have been very proud and excited to see this work out in the field and are grateful for the opportunity to share it. We thank Alex Shackman and Miquel Fullana for their

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