

UCLA

UCLA Previously Published Works

Title

Extinction Learning and Cognitive Reappraisal: Windows Into the Neurodevelopment of Emotion Regulation

Permalink

<https://escholarship.org/uc/item/5514j0kp>

Journal

Child Development Perspectives, 14(3)

ISSN

1750-8592

Author

Silvers, Jennifer A

Publication Date

2020-09-01

DOI

10.1111/cdep.12372

Peer reviewed

Neurodevelopment of Emotion Regulation

Extinction learning and cognitive reappraisal: Windows into the
neurodevelopment of emotion regulation

For consideration at *Child Development Perspectives*

Jennifer A. Silvers

Word count: 3,243

Figures: 2

Keywords: Emotion regulation, neurodevelopment, prefrontal cortex,
amygdala

Department of Psychology, University of California, Los Angeles

1285 Franz Hall, Box 951563, Los Angeles, California, 90095, USA

Email: silvers@ucla.edu

Phone: 310-206-9024

Neurodevelopment of Emotion Regulation

Abstract

Over the past two decades, interest in the development of emotion regulation (ER) has surged. In this review, I argue for the utility of contrasting the neurodevelopment of two distinct and powerful forms of ER: extinction learning and cognitive reappraisal. Using extinction learning and cognitive reappraisal as illustrative examples of implicit and explicit ER, respectively, I propose that these two forms of ER develop on different timelines and utilize partially overlapping and partially distinct neural circuits in the brain. I then use this extinction/reappraisal framework to consider how experiences like early life stress may differentially shape distinct aspects of ER neurodevelopment. I conclude by describing open questions for the field and prescribing key future directions to advance neurodevelopmental accounts of ER.

Neurodevelopment of Emotion Regulation

Emotion regulation (ER) is a collection of processes that allows one to change the valence, intensity or duration of one's emotions (Thompson, 1994). ER is a cornerstone of positive development and delayed, diminished or maladaptive use of ER strategies constitutes a transdiagnostic risk factor for psychopathology (McLaughlin, Garrad, & Somerville, 2015). Researchers frequently distinguish between implicit (automatic) and explicit (deliberate, effortful) forms of ER (Braunstein, Gross, & Ochsner, 2017; Calkins & Hill, 2007). Developmental theories of ER stipulate that infants and young children regulate emotion automatically (e.g., gaze aversion) or when scaffolded by caregivers, whereas adolescents often self-regulate using explicit, top-down strategies (Calkins & Hill, 2007; Morris, Criss, Silk, & Houlberg, 2017). While several neuroscientific frameworks distinguish between implicit and explicit ER in adults (Braunstein et al., 2017), this is rarer in developmental neuroscience. Characterizing the neurodevelopment of implicit and explicit forms of ER has important implications for our understanding of what types of ER are most effective at different developmental stages, whether different forms of ER co-develop, and how experience shapes the development of ER.

In this review, I draw from animal research and human neuroimaging studies to compare the neurodevelopment of two respectively implicit and explicit forms of ER, fear extinction and cognitive reappraisal. Contrasting extinction and reappraisal marks a

Neurodevelopment of Emotion Regulation

first step towards creating a formalized neuroscientific framework for implicit and explicit ER neurodevelopment. Extinction learning, which involves learning through repeated experience that a stimulus once paired with an aversive outcome (e.g., shock or an unpleasant noise) is no longer predictive of this outcome, is implicit because it does not require a goal of reducing fear and may not even require conscious awareness – though this latter point has been debated (Baeuchi, Hoppstädter, Meyer, & Flor, 2018). By contrast, cognitive reappraisal, involves intentionally thinking about a stimulus differently so as to alter its emotional import, requires a conscious goal to self-regulate and deployment of effortful cognitive processes. The focus on these two regulatory subtypes is motivated by the facts that (1) they are relatively extreme in their respective implicitness/explicitness which makes it easier to contrast them, and (2) they represent two components of cognitive behavioral therapy, cognitive restructuring and gradual exposure, which is commonly used to treat pediatric mood and anxiety disorders. While extinction and reappraisal are characterized as implicit and explicit here because that is consistent with their canonical implementation, this is not always the case – for example, reappraisal becomes increasingly automatic with practice and extinction is facilitated by explicit contingency knowledge (Baeuchi et al., 2018; Denny, Inhoff, Zerubavel, Davachi, & Ochsner, 2015). Moreover, extinction and reappraisal differ not only in terms of their

implicit/explicitness, but also in terms of the types of emotional stimuli they act upon and the conditions of their implementation (for example, extinction is only effective if a conditioned stimulus no longer predicts threat whereas reappraisal can regulate responses to current and retrospective threats).

In the latter portion of this review, I will examine links between early life stress (ELS) and ER neurodevelopment, and suggest that ELS exerts differential effects on extinction and reappraisal because they mature on different timescales and are differentially responsive to environmental inputs in childhood. Considering ELS facilitates a broader discussion of how experiences shape ER, and how brain development explains ER in everyday life – for example, by linking neural and behavioral markers of emotion regulation in ELS-exposed youth.

Neurodevelopment of implicit and explicit forms of ER

Neurodevelopment of extinction learning

Extinction learning is a powerful means of regulating fear. Theoretical and experimental accounts have tied atypical extinction learning to the emergence of anxiety in development (Baker, Den, Graham, & Richardson, 2014; Casey, Glatt, & Lee, 2015; Morriss, Christakou, & van Reekum, 2019). Extinction learning is dependent on communication between subcortical and cortical brain systems that develop in childhood and adolescence. This is true in both rodents and

Neurodevelopment of Emotion Regulation

humans – though extinction engages a broader suite of prefrontal regions in humans than in rodents (Knight, Waters, King, & Bandettini, 2010) – in spite of the fact that the species differ in terms of prefrontal structure, developmental timescale and cognitive abilities (Casey et al., 2015).

During extinction, a conditioned stimulus is repeatedly presented without the aversive outcome with which it was previously paired, so that one learns that the conditioned stimulus no longer poses a threat. Interactions between the amygdala, a subcortical structure involved in detecting and coordinating behavioral responses to motivationally salient stimuli, and the ventromedial prefrontal cortex (vmPFC), which integrates information from prior and present experiences to update stimulus representations, undergird this learning processes (Quirk, Garcia, & Gonzalez-Lima, 2006). Extinction does not erase the initial conditioned stimulus-threat association, but instead forms a new safety association with the stimulus (Quirk et al., 2006). The vmPFC retains extinction memories and regulates fear by allowing organisms to re-evaluate a CS's meaning (i.e., “this no longer poses a threat”) (Phelps, Delgado, Nearing, & LeDoux, 2004; Quirk et al., 2006).

Children show physiological (Michalska et al., 2016) and behavioral evidence of extinction learning (Waters, Theresiana, Neumann, & Craske, 2017) (Figure 1), suggesting it is an early-emerging form of ER. The efficacy of extinction learning in

adolescence, however, is more debated. While some behavioral data indicates that adolescents extinguish fears similarly to children and adults (Den, Graham, Newall, & Richardson, 2015; Waters et al., 2017), other physiological data research suggests that adolescents exhibit attenuated extinction learning (Pattwell et al., 2012). One possible explanation, supported by research examining extinction at multiple timepoints, is that adolescents initially extinguish fears but fail to recall extinction memories over time (Baker et al., 2014).

The amygdala and vmPFC support extinction learning to varying degrees across development (Figure 2). Rodent models suggest that fear conditioning and extinction learning are amygdala-dependent in juveniles, whereas in adult rodents and humans conditioning is supported by the amygdala and extinction is coordinated by vmPFC-amygdala interactions (J. H. Kim & Richardson, 2008; Phelps et al., 2004; Quirk et al., 2006). That the amygdala underlies both conditioning and extinction in early development may explain why extinction literally erases conditioned fears in juvenile, but not adult rodents (J. H. Kim & Richardson, 2008) – though it is unknown whether this is also true in human children. Human adolescents recruit vmPFC during extinction learning, but relative to adults, this recruitment is weak or sluggish – especially during extinction recall – a finding that is explained by immature vmPFC-amygdala connectivity (Ganella, Drummond, Ganella, Whittle, & Kim, 2018; Morriss et al., 2019).

Neurodevelopment of Emotion Regulation

Importantly, vmPFC-amygdala functional connectivity during extinction also correlates with adolescent anxiety symptomology, underscoring amygdala-vmPFC circuitry's role in establishing mental health (Gold et al., 2016). In sum, extinction learning is present, but immature, during adolescence and neuromaturational changes in vmPFC-amygdala circuitry make adolescence a time of opportunity and risk for mental health (Baker et al., 2014; Casey et al., 2015).

Neurodevelopment of cognitive reappraisal

While extinction works via *implicit* learning, cognitive reappraisal uses *explicit* cognitive control processes to regulate emotion.

Canonical reappraisal paradigms require participants to change their appraisals of affective stimuli (e.g., upsetting photographic images) – for example, by telling themselves that a person who appears sick is likely to get better soon.

Reappraisal requires maintaining a regulatory goal, generating and holding reappraisals in working memory, selecting and implementing a chosen reappraisal, and monitoring one's regulatory efficacy. The cognitive complexities of reappraisal make it difficult to study in animal models and thus, what is known about the neural bases of reappraisal comes largely from human neuroimaging and patient studies (Figure 1). Like extinction, reappraisal attenuates amygdala responses to emotional stimuli (Buhle et al., 2014), highlighting this structure's central role in the generation and

Neurodevelopment of Emotion Regulation

regulation of affective experiences. In contrast to extinction, adults do not recruit vmPFC during reappraisal, but instead engage dorsal and lateral prefrontal and parietal regions implicated in cognitive control (Buhle et al., 2014). During reappraisal, the lateral prefrontal cortices choose reappraisals from working memory, similarly to how they select cognitions and actions in non-affective cognitive tasks (Miller, 2000). The dorsomedial prefrontal and dorsal anterior cingulate cortices, brain regions crucial for self-reflection and error monitoring, work to introspect and monitor reappraisal performance (Amodio & Frith, 2006).

Behavioral data suggest that reappraisal ability is poor in childhood – but may be bolstered by parental scaffolding (Myruski et al., 2019) – and improves during adolescence (Silvers et al., 2017; Silvers et al., 2012; Silvers, Shu, Hubbard, Weber, & Ochsner, 2015). Reappraisal ability develops rapidly around 10 years of age and steadily improves before plateauing in the late teens (Silvers et al., 2017; Silvers et al., 2012). These age-related changes in reappraisal ability mirror results from non-affective cognitive control tasks (Luna, 2009), and are borne out by fMRI data (Figure 2). In contrast to adults, young children paradoxically increase amygdala activity and fail to attenuate electroencephalogram markers of sustained attention and emotional arousal during reappraisal – perhaps reflecting increased focus on aversive stimuli or cognitive effort (DeCicco, O’Toole, &

Neurodevelopment of Emotion Regulation

Dennis, 2014; Dougherty, Blankenship, Spechler, Padmala, & Pessoa, 2015; Silvers et al., 2017). Reappraisal begins to effectively reduce amygdala responses during late childhood and adolescence, with linear age-related decreases occurring throughout the teen years (Silvers et al., 2017; Silvers et al., 2015). Relative to adults, however, adolescents show weaker reappraisal-related regulation of the amygdala and amygdala responses to previously reappraised stimuli rebound when re-presented with them at a later time (Silvers et al., 2015). This is similar to what is observed in extinction paradigms, where adolescents are capable of initially extinguishing fears but display diminished extinction recall. Crucially, age-related declines in the amygdala response during reappraisal as well as during re-presentation of previously reappraised stimuli are mediated by recruitment of the ventrolateral prefrontal cortex - underscoring the role of cognitive control processes in the development of reappraisal (Silvers et al., 2017; Silvers et al., 2015).

Comparing the neurodevelopment of extinction learning and cognitive reappraisal

Partially overlapping and partially distinct cortical networks support extinction learning and reappraisal in adults and both extinction learning and reappraisal attenuate amygdala activity (Buhle et al., 2014; Phelps et al., 2004; Picó-Pérez et al., 2019). The dorsal anterior cingulate cortex is recruited during extinction learning and

Neurodevelopment of Emotion Regulation

reappraisal, suggesting that it supports appraisal and introspective processes important for multiple forms of ER (Buhle et al., 2014; Picó-Pérez et al., 2019). Given this and neuroanatomical projections (Amodio & Frith, 2006), dorsal anterior cingulate-amygdala connectivity may serve as a point of convergence for both implicit and explicit forms of regulation. However, this is speculative given that no neuroimaging studies have compared extinction and reappraisal within the same individuals.

Age-related changes in extinction learning and reappraisal show both convergence and divergence. Extinction learning emerges prior to reappraisal, but children show distinct patterns of neural recruitment from adults on both forms of regulation because of immature prefrontal-amygdala connections. Adolescents, by contrast, appear capable of both extinction learning and cognitive reappraisal, but these regulatory efforts are not as robust or enduring over time as they are in adults (Baker et al., 2014; Silvers et al., 2015). In sum, extinction emerges prior to reappraisal in childhood and both are present, but immature, in adolescence.

While neural circuitry involved in implicit and explicit regulatory processes are relatively distinct in adults, two pieces of evidence indicate that they are less segregated during development. First, youth with “mature” vmPFC-amygdala connectivity (circuitry involved in extinction learning) show a stronger relationship between ventrolateral

Neurodevelopment of Emotion Regulation

prefrontal activation and amygdala attenuation during reappraisal (Silvers et al., 2017). This is intriguing, given that vmPFC is not typically observed in adult studies of reappraisal (Buhle et al., 2014), and imply that implicit regulation supports explicit regulation development. Within-individual longitudinal studies are needed to formally test this hypothesis. Second, reappraisal training potentiates extinction learning in adolescents (Shore, Cohen Kadosh, Lommen, Cooper, & Lau, 2016). This suggests that while prefrontal-amygdala circuits are still maturing, explicit and implicit ER may be successfully combined. From a basic science perspective, this raises questions about how ER effectiveness differs by neurodevelopmental stage (Casey et al., 2015). For example, reappraisal training may facilitate extinction learning in adolescence when the lateral prefrontal cortices are developing, but not in childhood when they are immature. From a translational perspective, this opens up exciting possibilities for the treatment of developmental psychopathology. Reappraisal might be taught as a compensatory strategy for individuals with anxiety disorders who show deficits in extinction learning (Blechert et al., 2015) - particularly in adolescence, when anxiety disorders peak and the lateral prefrontal cortices are highly plastic. If anxious youth can learn to reappraise despite having impaired extinction learning, this would suggest that while implicit regulation scaffolds explicit

regulation in typical development, this order of operations could be circumvented with intervention for clinical populations.

ELS as a model for understanding the role of experience in ER neurodevelopment

Exposure to ELS in the form of abuse, neglect or institutionalization has been linked to psychopathology characterized by emotion dysregulation (Kessler et al., 2010). While this suggests that ELS alters ER processes, little work has tested whether ELS may exert differential effects on different forms of ER. Here, I suggest that ELS accelerates extinction learning neurodevelopment and behavior and delays or impedes brain development relevant for reappraisal – while acknowledging that different forms of ELS are likely to have heterogeneous effects on ER development. Although the focus here is on ELS, this discussion has implications for how a broader array of childhood experiences likely shape the neurodevelopment of ER.

Effects of ELS on extinction learning and cognitive reappraisal

ELS may differentially alter the development of extinction learning and reappraisal because these two forms of ER have distinct neurodevelopmental timescales. As described above, extinction learning emerges relatively early in childhood, though its neural bases change during adolescence. Prior work suggests that because the amygdala is an early-developing structure that is highly sensitive to environmental demands, ELS can accelerate amygdala development

Neurodevelopment of Emotion Regulation

and associated fear learning behavior (Callaghan, Sullivan, Howell, & Tottenham, 2014). This adaptation may promote self-preservation in dangerous or stressful environments, a possibility supported by the fact that accelerated fear learning is stronger in youth with a history of threat exposure (e.g., abuse) than youth who have experienced deprivation (e.g., poverty) (Machlin, Miller, Snyder, McLaughlin, & Sheridan, 2019). Given how ELS influences fear learning, it is likely to accelerate development of fear extinction processes as well. Indeed, there are several lines of cross-species evidence suggesting that ELS exposure accelerates development of vmPFC-amygdala functional connectivity and adult-like conditioning and extinction behavior (Callaghan & Richardson, 2011; Gee et al., 2013; Silvers et al., 2016). Such neural adaptations may be protective in the short run, given research linking precocious vmPFC-amygdala development in ELS youth to reduced anxiety symptoms (Gee et al., 2013; Silvers et al., 2016). However, much remains unknown with regards to how ELS shapes implicit emotion regulation development, including how accelerated vmPFC-amygdala neurodevelopment impacts long-term mental health as well as how a broader variety of early experiences (different forms of ELS as well as normative variations in caregiving) may differentially shape vmPFC-amygdala development.

A second reason for why ELS may induce different effects on extinction learning and cognitive reappraisal is because childhood

Neurodevelopment of Emotion Regulation

experience likely shapes these two forms of ER in highly divergent ways. While far less research has examined the effects of ELS on reappraisal than extinction learning, initial findings suggest that ELS alters reappraisal processes. While no neuroscientific studies to date have compared how different forms of ELS exposure impact the brain bases of reappraisal, other data suggest that exposure to deprivation may be particularly detrimental to the development of the lateral prefrontal cortex and associated cognitive control skills, which support reappraisal (Lambert, King, Monahan, & McLaughlin, 2016; Mueller et al., 2010). Moreover, multiple forms of ELS predict atypical brain activity during reappraisal, with abuse exposure predicting less efficient lateral prefrontal recruitment in adolescence and childhood poverty predicting weaker lateral prefrontal recruitment in adulthood (P. Kim et al., 2013; McLaughlin, Peverill, Gold, Alves, & Sheridan, 2015). That ELS appears to accelerate development of extinction, but not reappraisal, implies that the developing brain can shift its maturational strategy for acquiring ER in accordance with environmental demands (Callaghan et al., 2014).

Reappraisal develops readily in the presence of complex interpersonal inputs such as regulatory coaching and modeling (Morris et al., 2011; Myruski et al., 2019). Thus, it stands to reason that reappraisal abilities flourish in safe and enriching environments but perhaps less so in threatening or deprived ones (P. Kim et al., 2013;

Neurodevelopment of Emotion Regulation

McLaughlin, Peverill, et al., 2015), while extinction learning is simple enough to develop in a variety of social climates. It is likely more difficult for ELS-exposed youth to acquire reappraisal because of altered lateral prefrontal development and because their contexts might not scaffold reappraisal skills – for example, if caregivers model maladaptive regulatory strategies (i.e., in threatening contexts) or if children fail to receive the stimulation required to scaffold cognitive skills (i.e., in deprived contexts). That is not to say that ELS exposure makes learning to reappraise impossible. Indeed, recent findings suggest that reappraisal use can buffer ELS-exposed individuals against internalizing symptoms – pointing to the potential utility of reappraisal training regimens for promoting resilience (Johnson & Tottenham, 2015). Future work will need to carefully examine when, how and under what conditions reappraisal skills can be cultivated in ELS-exposed youth. For example, it is possible that while reappraisal builds upon implicit regulatory skills in typical development, it may develop through different neurocognitive mechanisms in ELS-exposed youth given the effects of ELS on extinction learning and related processes. It is also possible that ELS-exposed individuals are more likely to develop effective reappraisal skills if they did not experience significant stressors during late childhood and early adolescence, when reappraisal abilities typically develop most rapidly (Silvers et al., 2012). However, these two possibilities remain untested at present.

Conclusion and future directions

ER promotes resilience and wellbeing across the lifespan. Here, I have argued for the utility of delineating the neurodevelopment of implicit and explicit forms of ER, with extinction learning and cognitive reappraisal serving as respective exemplars. Supporting this logic are the facts that extinction and reappraisal rely upon distinct prefrontal-amygdala circuitry, develop on different timescales and are differentially impacted by early experiences like ELS.

Several outstanding questions warrant attention in future research. First, no published neuroscientific work has examined fear extinction or reappraisal longitudinally – thus, most of the conclusions in this paper hinge on the assumption that cross-sectional analyses approximate within-individual development. Second, no studies have examined extinction learning and reappraisal within the same individual over time. Such studies will be needed to test the hypothesis put forward here that implicit regulation scaffolds the development of explicit regulation. Third, while the present review focused on extinction learning and cognitive reappraisal, other forms of ER are worthy of neurodevelopmental interrogation and discussion, including strategies that blur implicit/explicit boundary conditions (e.g., emotional go/nogo paradigms) and strategies that are socially instantiated (e.g., parental buffering). Fourth, given that the prefrontal-

Neurodevelopment of Emotion Regulation

subcortical networks described here are not only important for extinction and reappraisal but also other consequential behaviors – future work must examine how experiences like ELS differentially shape network engagement in affective (e.g., reappraisal) and non-affective (e.g., cognitive control) contexts within the same individuals. Fifth, it will be essential for future work to carefully examine how severity and type of ELS exposure (e.g., poverty versus abuse) differentially impacts various forms of ER development. Finally, it will be crucial moving forward to link real-world ER behavior with neurodevelopmental assessments of ER. Doing so in the context of ELS is one particularly powerful way to unpack how experience shapes affective neurodevelopment, which in turn predicts behavior and symptomology in everyday life.

References

- Amodio, D. M., & Frith, C. D. (2006). Meeting of minds: the medial frontal cortex and social cognition. *Nat Rev Neurosci*, *7*(4), 268-277.
- Baeuchl, C., Hoppstädter, M., Meyer, P., & Flor, H. (2018). Contingency awareness as a prerequisite for differential contextual fear conditioning. *Cognitive, Affective, & Behavioral Neuroscience*, *19*(4), 811-828. doi:10.3758/s13415-018-00666-z
- Baker, K. D., Den, M. L., Graham, B. M., & Richardson, R. (2014). A window of vulnerability: Impaired fear extinction in adolescence. *Neurobiology of Learning and Memory*, *113*, 90-100. doi:10.1016/j.nlm.2013.10.009
- Blechert, J., Wilhelm, F. H., Williams, H., Braams, B. R., Jou, J., & Gross, J. J. (2015). Reappraisal facilitates extinction in healthy and socially anxious individuals. *Journal of Behavior Therapy and Experimental Psychiatry*, *46*, 141-150. doi:10.1016/j.jbtep.2014.10.001
- Braunstein, L. M., Gross, J. J., & Ochsner, K. N. (2017). Explicit and implicit emotion regulation: a multi-level framework. *Social Cognitive and Affective Neuroscience*, *12*(10), 1545-1557. doi:10.1093/scan/nsx096
- Buhle, J. T., Silvers, J. A., Wager, T. D., Lopez, R., Onyemekwu, C., Kober, H., . . . Ochsner, K. N. (2014). Cognitive reappraisal of emotion: A meta-analysis of human neuroimaging studies. *Cereb Cortex*, *24*(11), 2981-2990. doi:10.1093/cercor/bht154
- Calkins, S. D., & Hill, A. (2007). Caregiver Influences on Emerging Emotion Regulation: Biological and Environmental Transactions in Early Development. In J. J. Gross (Ed.), *Handbook of emotion regulation* The Guilford Press.
- Callaghan, B. L., & Richardson, R. (2011). Maternal separation results in early emergence of adult-like fear and extinction learning in infant rats. *Behav Neurosci*, *125*(1), 20-28. doi:10.1037/a0022008
- Callaghan, B. L., Sullivan, R. M., Howell, B., & Tottenham, N. (2014). The international society for developmental psychobiology Sackler symposium: early adversity and the maturation of emotion circuits--a cross-species analysis. *Dev Psychobiol*, *56*(8), 1635-1650. doi:10.1002/dev.21260
- Casey, B. J., Glatt, Charles E., & Lee, Francis S. (2015). Treating the Developing versus Developed Brain: Translating Preclinical Mouse and Human Studies. *Neuron*, *86*(6), 1358-1368. doi:10.1016/j.neuron.2015.05.020
- DeCicco, J. M., O'Toole, L. J., & Dennis, T. A. (2014). The Late Positive Potential as a Neural Signature for Cognitive Reappraisal in

- Children. *Developmental Neuropsychology*, 39(7), 497-515.
doi:10.1080/87565641.2014.959171
- Den, M. L., Graham, B. M., Newall, C., & Richardson, R. (2015). Teens that fear screams: A comparison of fear conditioning, extinction, and reinstatement in adolescents and adults. *Developmental Psychobiology*, 57(7), 818-832. doi:10.1002/dev.21330
- Denny, B. T., Inhoff, M. C., Zerubavel, N., Davachi, L., & Ochsner, K. N. (2015). Getting Over It: Long-Lasting Effects of Emotion Regulation on Amygdala Response. *Psychological Science*, 26(9), 1377-1388. doi:10.1177/0956797615578863
- Dougherty, L. R., Blankenship, S. L., Spechler, P. A., Padmala, S., & Pessoa, L. (2015). An fMRI Pilot Study of Cognitive Reappraisal in Children: Divergent Effects on Brain and Behavior. *Journal of Psychopathology and Behavioral Assessment*, 37(4), 634-644. doi:10.1007/s10862-015-9492-z
- Ganella, D. E., Drummond, K. D., Ganella, E. P., Whittle, S., & Kim, J. H. (2018). Extinction of Conditioned Fear in Adolescents and Adults: A Human fMRI Study. *Frontiers in Human Neuroscience*, 11. doi:10.3389/fnhum.2017.00647
- Gee, D. G., Gabard-Durnam, L. J., Flannery, J., Goff, B., Humphreys, K. L., Telzer, E. H., . . . Tottenham, N. (2013). Early developmental emergence of human amygdala-prefrontal connectivity after maternal deprivation. *Proc Natl Acad Sci U S A*, 110(39), 15638-15643. doi:10.1073/pnas.1307893110
- Gold, A. L., Shechner, T., Farber, M. J., Spiro, C. N., Leibenluft, E., Pine, D. S., & Britton, J. C. (2016). Amygdala-Cortical Connectivity: Associations with Anxiety, Development, and Threat. *Depression and Anxiety*, 33(10), 917-926. doi:10.1002/da.22470
- Johnson, A. J., & Tottenham, N. (2015). Regulatory skill as a resilience factor for adults with a history of foster care: A pilot study. *Developmental Psychobiology*, 57(1), 1-16. doi:10.1002/dev.21227
- Kessler, R. C., McLaughlin, K. A., Green, J. G., Gruber, M. J., Sampson, N. A., Zaslavsky, A. M., . . . Williams, D. R. (2010). Childhood adversities and adult psychopathology in the WHO World Mental Health Surveys. *Br J Psychiatry*, 197(5), 378-385. doi:10.1192/bjp.bp.110.080499
- Kim, J. H., & Richardson, R. (2008). The Effect of Temporary Amygdala Inactivation on Extinction and Reextinction of Fear in the Developing Rat: Unlearning as a Potential Mechanism for Extinction Early in Development. *Journal of Neuroscience*, 28(6), 1282-1290. doi:10.1523/jneurosci.4736-07.2008
- Kim, P., Evans, G. W., Angstadt, M., Ho, S. S., Sripada, C. S., Swain, J. E., . . . Phan, K. L. (2013). Effects of childhood poverty and chronic stress on emotion regulatory brain function in adulthood.

Neurodevelopment of Emotion Regulation

- Proceedings of the National Academy of Sciences*, 110(46), 18442-18447. doi:10.1073/pnas.1308240110
- Knight, D. C., Waters, N. S., King, M. K., & Bandettini, P. A. (2010). Learning-related diminution of unconditioned SCR and fMRI signal responses. *NeuroImage*, 49(1), 843-848. doi:10.1016/j.neuroimage.2009.07.012
- Lambert, H. K., King, K. M., Monahan, K. C., & McLaughlin, K. A. (2016). Differential associations of threat and deprivation with emotion regulation and cognitive control in adolescence. *Development and Psychopathology*, 29(03), 929-940. doi:10.1017/s0954579416000584
- Luna, B. (2009). Developmental changes in cognitive control through adolescence. *Adv Child Dev Behav*, 37, 233-278.
- Machlin, L., Miller, A. B., Snyder, J., McLaughlin, K. A., & Sheridan, M. A. (2019). Differential Associations of Deprivation and Threat With Cognitive Control and Fear Conditioning in Early Childhood. *Frontiers in Behavioral Neuroscience*, 13. doi:10.3389/fnbeh.2019.00080
- McLaughlin, K. A., Garrad, M. C., & Somerville, L. H. (2015). What develops during emotional development? A component process approach to identifying sources of psychopathology risk in adolescence. *Dialogues Clin Neurosci*, 17(4), 403-410.
- McLaughlin, K. A., Peverill, M., Gold, A. L., Alves, S., & Sheridan, M. A. (2015). Child Maltreatment and Neural Systems Underlying Emotion Regulation. *J Am Acad Child Adolesc Psychiatry*, 54(9), 753-762. doi:10.1016/j.jaac.2015.06.010
- Michalska, K. J., Shechner, T., Hong, M., Britton, J. C., Leibenluft, E., Pine, D. S., & Fox, N. A. (2016). A developmental analysis of threat/safety learning and extinction recall during middle childhood. *Journal of Experimental Child Psychology*, 146, 95-105. doi:10.1016/j.jecp.2016.01.008
- Miller, E. K. (2000). The prefrontal cortex and cognitive control. *Nat Rev Neurosci*, 1(1), 59-65.
- Morris, A. S., Criss, M. M., Silk, J. S., & Houlberg, B. J. (2017). The Impact of Parenting on Emotion Regulation During Childhood and Adolescence. *Child Development Perspectives*, 11(4), 233-238. doi:10.1111/cdep.12238
- Morris, A. S., Silk, J. S., Morris, M. D. S., Steinberg, L., Aucoin, K. J., & Keyes, A. W. (2011). The influence of mother-child emotion regulation strategies on children's expression of anger and sadness. *Developmental Psychology*, 47(1), 213-225. doi:10.1037/a0021021
- Morriss, J., Christakou, A., & van Reekum, C. M. (2019). Multimodal evidence for delayed threat extinction learning in adolescence and young adulthood. *Scientific Reports*, 9(1). doi:10.1038/s41598-019-44150-1

Neurodevelopment of Emotion Regulation

- Mueller, S. C., Maheu, F. S., Dozier, M., Peloso, E., Mandell, D., Leibenluft, E., . . . Ernst, M. (2010). Early-life stress is associated with impairment in cognitive control in adolescence: An fMRI study. *Neuropsychologia*, *48*(10), 3037-3044. doi:10.1016/j.neuropsychologia.2010.06.013
- Myruski, S., Birk, S., Karasawa, M., Kamikubo, A., Kazama, M., Hirabayashi, H., & Dennis-Tiway, T. (2019). Neural signatures of child cognitive emotion regulation are bolstered by parental social regulation in two cultures. *Social Cognitive and Affective Neuroscience*, *14*(9), 947-956. doi:10.1093/scan/nsz070
- Pattwell, S. S., Duhoux, S., Hartley, C. A., Johnson, D. C., Jing, D., Elliott, M. D., . . . Lee, F. S. (2012). Altered fear learning across development in both mouse and human. *Proc Natl Acad Sci U S A*, *109*(40), 16318-16323. doi:10.1073/pnas.1206834109
- Phelps, E. A., Delgado, M. R., Nearing, K. I., & LeDoux, J. E. (2004). Extinction learning in humans: role of the amygdala and vmPFC. *Neuron*, *43*(6), 897-905.
- Picó-Pérez, M., Alemany-Navarro, M., Dunsmoor, J. E., Radua, J., Albajes-Eizagirre, A., Vervliet, B., . . . Fullana, M. A. (2019). Common and distinct neural correlates of fear extinction and cognitive reappraisal: A meta-analysis of fMRI studies. *Neuroscience & Biobehavioral Reviews*, *104*, 102-115. doi:10.1016/j.neubiorev.2019.06.029
- Quirk, G. J., Garcia, R., & Gonzalez-Lima, F. (2006). Prefrontal mechanisms in extinction of conditioned fear. *Biol Psychiatry*, *60*(4), 337-343.
- Shore, T., Cohen Kadosh, K., Lommen, M., Cooper, M., & Lau, J. Y. F. (2016). Investigating the effectiveness of brief cognitive reappraisal training to reduce fear in adolescents. *Cognition and Emotion*, *31*(4), 806-815. doi:10.1080/02699931.2016.1159542
- Silvers, J. A., Insel, C., Powers, A., Franz, P., Helion, C., Martin, R. E., . . . Ochsner, K. N. (2017). vIPFC-vmPFC-Amygdala Interactions Underlie Age-Related Differences in Cognitive Regulation of Emotion. *Cerebral Cortex*, *27*(7), 3502-3514. doi:10.1093/cercor/bhw073
- Silvers, J. A., Lumian, D. S., Gabard-Durnam, L., Gee, D. G., Goff, B., Fareri, D. S., . . . Tottenham, N. (2016). Previous Institutionalization Is Followed by Broader Amygdala-Hippocampal-PFC Network Connectivity during Aversive Learning in Human Development. *J Neurosci*, *36*(24), 6420-6430. doi:10.1523/JNEUROSCI.0038-16.2016
- Silvers, J. A., McRae, K., Gabrieli, J. D., Gross, J. J., Remy, K. A., & Ochsner, K. N. (2012). Age-related differences in emotional reactivity, regulation, and rejection sensitivity in adolescence. *Emotion*, *12*(6), 1235-1247. doi:10.1037/a0028297

Neurodevelopment of Emotion Regulation

- Silvers, J. A., Shu, J., Hubbard, A. D., Weber, J., & Ochsner, K. N. (2015). Concurrent and lasting effects of emotion regulation on amygdala response in adolescence and young adulthood. *Developmental Science, 18*(5), 771-784.
- Thompson, R. A. (1994). Emotion Regulation: A Theme in Search of Definition. *Monographs of the Society for Research in Child Development, 59*(2-3), 25-52.
- Waters, A. M., Theresiana, C., Neumann, D. L., & Craske, M. G. (2017). Developmental differences in aversive conditioning, extinction, and reinstatement: A study with children, adolescents, and adults. *Journal of Experimental Child Psychology, 159*, 263-278. doi:10.1016/j.jecp.2017.02.012

Neurodevelopment of Emotion Regulation

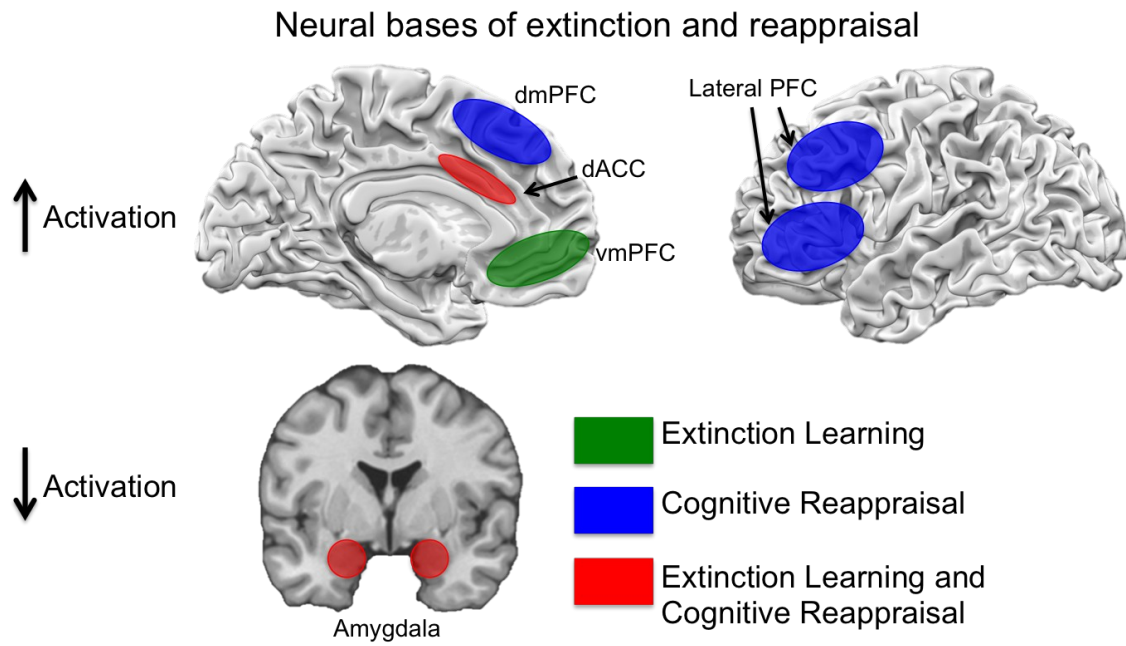


Figure 1. Neural systems involved in extinction learning and cognitive reappraisal.

Neurodevelopment of Emotion Regulation

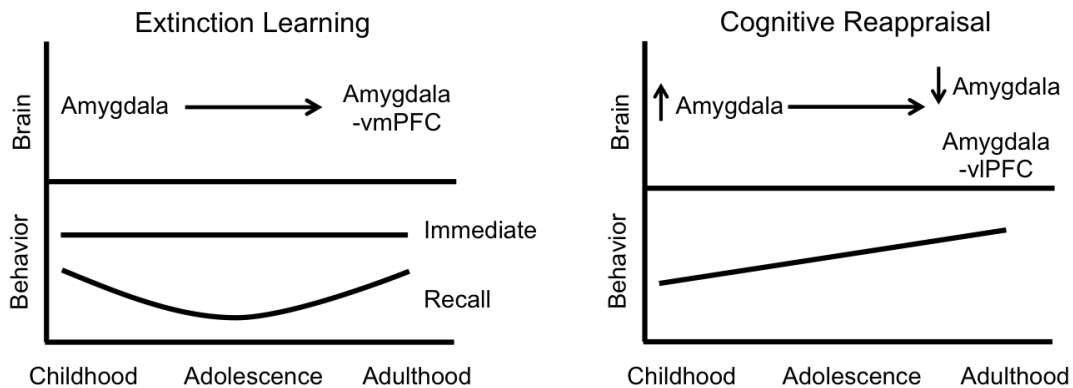


Figure 2. Age-related changes in extinction learning and cognitive reappraisal. Top: The left panel depicts a shift across development from amygdala-mediated extinction learning to one that is governed by amygdala-vmPFC interactions. The right panel depicts a shift from reappraisal causing increased amygdala reactivity in childhood to reductions in amygdala activity in adulthood due to increased ventrolateral prefrontal cortex (vIPFC) recruitment. Bottom: The left panel illustrates minimal age-related differences in extinction learning immediately after learning and curvilinear age differences in extinction recall. The right panel illustrates linear increases in reappraisal ability.