

UC Davis

UC Davis Previously Published Works

Title

The neurobiology of the emotional adolescent: From the inside out

Permalink

<https://escholarship.org/uc/item/35n9g0vx>

Authors

Guyer, Amanda E

Silk, Jennifer S

Nelson, Eric E

Publication Date

2016-11-01

DOI

10.1016/j.neubiorev.2016.07.037

Peer reviewed



Published in final edited form as:

Neurosci Biobehav Rev. 2016 November ; 70: 74–85. doi:10.1016/j.neubiorev.2016.07.037.

The neurobiology of the emotional adolescent: From the inside out

Amanda E. Guyer^{a,*}, Jennifer S. Silk^b, and Eric E. Nelson^c

^aDepartment of Human Ecology and Center for Mind and Brain, University of California, Davis, Davis, CA 95618, United States

^bDepartment of Psychology, University of Pittsburgh, Pittsburgh, PA 15260, United States

^cSection on Developmental Affective Neuroscience, National Institute of Mental Health, Bethesda, MD 20892, United States

Abstract

Adolescents are commonly portrayed as highly emotional, with their behaviors often hijacked by their emotions. Research on the neural substrates of adolescent affective behavior is beginning to paint a more nuanced picture of how neurodevelopmental changes in brain function influence affective behavior, and how these influences are modulated by external factors in the environment. Recent neurodevelopmental models suggest that the brain is designed to promote emotion regulation, learning, and affiliation across development, and that affective behavior reciprocally interacts with age-specific social demands and different social contexts. In this review, we discuss current findings on neurobiological mechanisms of adolescents' affective behavior and highlight individual differences in and social-contextual influences on adolescents' emotionality. Neurobiological mechanisms of affective processes related to anxiety and depression are also discussed as examples. As the field progresses, it will be critical to test new hypotheses generated from the foundational empirical and conceptual work and to focus on identifying more precisely how and when neural networks change in ways that promote or thwart adaptive affective behavior during adolescence.

Keywords

Affect; Brain; fMRI; Puberty; Physiology; Individual differences; Social context

1. Introduction

The emotional life of an adolescent is complex both inside and out. From the “inside”, adolescents experience vast hormonal changes and fine tuning of the neural networks that both produce and manage emotions. From the “outside”, they experience dramatic and dynamic shifts in the structure and significance of key social relationships, such as those with parents, peers, and romantic partners as well as a variety of novel experiences and

*Corresponding author at: Department of Human Ecology, Center for Mind and Brain, University of California, Davis, 267 Cousteau Place, Davis, CA 95618; Tel.: 530-297-4445; Fax: 530-297-4440. aeguyer@ucdavis.edu (A. E. Guyer).

increasing societal demands. The convergence of these internal and external changes can result in affective experiences and behaviors that are sometimes overwhelming, confusing, and difficult to manage.

Although adolescence has long been hailed as a period of emotional challenge (for both adolescents and their parents) (Hall, 1931), it is only in the past 15 years that we have really begun to understand the “inside” of the adolescent from the perspective of the brain. Tapping into the emotional lives of adolescents is not a straightforward endeavor because adolescents can be reluctant to share their emotions, and, particularly during adolescence, emotional reactions vary tremendously by context. Fortunately, recent methodological advances in neuroscience with particular applications for developmental and clinical populations has led to considerable improvement in our understanding of neurobiological mechanisms of adolescents’ emotional lives. Moreover, recent conceptual models of neurodevelopment in adolescence (Crone and Dahl, 2012) suggest that we can use what has been learned about brain growth and plasticity in adolescence to leverage adolescents’ heightened emotionality in productive ways (e.g., civic engagement) and to discover new strategies to ameliorate forms of emotional dysregulation (e.g., anxiety and depression) that often emerge during adolescence.

In this review, we discuss evidence of three primary connections between neurobiological and affective development in adolescence. First, adolescence is marked by a high level of emotionality and a substantial increase in psychopathological levels of dysfunctional affect. Although individual differences exist in levels of adolescent emotionality, they also correspond broadly with the ordering of changes instantiated by pubertal and brain development. Second, learning to manage one’s emotional reactions is a principal task of adolescence that relates to social-cognitive development. These social-cognitive processes are supported by changes in the connections among brain structures implicated in functions such as mentalizing, self-appraisal, social learning, and emotion regulation. Third, in addition to the influence of brain maturation, adolescents’ affective behavior is intertwined with a number of other psychological factors that modify emotional experience. The valence and novelty of certain contexts (particularly in the social domain) and the latent effects of past social experiences interact with neural bases of cognition and emotion to further modify the salience of current experiences. We conclude our review by describing implications of the findings reviewed and recommending future directions for research on the brain’s role in affective behavior during adolescence.

Of note, we orient this review on research that emphasizes social context and social affect; uses neuroimaging; and focuses on a set of specific brain regions for three main reasons. First, we have argued that social interactions and relationships are among the most critical contexts to interact with neurobiological development in adolescence (Nelson and Guyer, 2011; Nelson et al., 2016, 2014, 2005). Given the importance of social relationships to well-being and optimal functioning, the human brain must be designed to promote social learning and affiliation with others across development. However, adolescence is a particularly dynamic, context-dependent phase of development for social-affiliative behavior. While most individuals experience an increase in the intensity and frequency of emotions during adolescence, heightened emotionality is mostly and most strongly experienced in social

settings. Affective behavior and social demands interact and, with experience and time, typically facilitate adaptive behavior. Nonetheless, although we focus on social affect and social context, we do recognize that several constructs including emotional intensity, emotion regulation, and context dependence may have broader application than just the social domain.

Second, we concentrate on functional magnetic resonance imaging (fMRI) because it is a widely used, powerful tool with which to link specific neural substrates with cognitive and behavioral responses to representations of emotional information. fMRI can reveal brain-based responses underlying emotion processing that may lack a behavioral corollary or may be undetectable through other methods of analysis (e.g., observation) or informants (e.g., parents). Furthermore, fMRI can help index inter-individual variance in the neural inputs that are recruited to achieve common behavioral outputs and delineate neural circuits that contribute to different affective phenotypes (e.g., irritability, euphoria). Although fMRI has low temporal resolution relative to electroencephalography, another commonly used assessment of the neural bases of emotion, it offers high spatial resolution for measuring neural processing within both the subcortical structures believed to be at the core of emotional responses, as well as the cortical structures implicated in behavioral integration. Finally, fMRI research has expanded recently to include tasks with high ecological validity designed to show cues or situations that represent more realistic aspects of adolescents' experiences. This shift has been significant because it has revealed nuances about the neurobiology of affective behavior that relate to social context.

Lastly, both conceptual frameworks of adolescent neurodevelopment and empirical work conducted in adult, clinical, and animal samples (Blakemore and Mills, 2014; Bruhl et al., 2014; Casey et al., 2005; Ernst and Fudge, 2009; Jarcho et al., 2013; Nelson et al., 2005; Scherf et al., 2013; Smith et al., 2014; Somerville et al., 2010; Steinberg, 2005) have guided a large number of neuroimaging studies of adolescent affective behavior to focus on the role of a relatively small number of brain regions in mediating social-affective behavior. Specifically, much attention has been given to the amygdala, striatum, insula, and anterior cingulate cortex (ACC), and a number of regions within the prefrontal cortex (PFC). These regions work together to assign salience, promote learning, monitor conflict, compute relative valence of social stimuli, and integrate this information to generate and guide affective behaviors toward wider goals and within the contexts in which they occur. Although early fMRI studies emphasized localized patterns of regional activation, a recent trend is to delineate patterns of functional interconnection both among these regions, and between these regions and brain areas that sub-serve different functional processes (Ernst et al., 2015; Spear, 2013).

2. Heightened emotionality in adolescence: form and function

Behaviorally, adolescents show high levels of emotionality, with emotions that are more frequent, intense, and volatile, particularly compared with adults and in ways that differ from emotionality in early childhood (Arnett, 1999; Casey et al., 2010; Larson et al., 2002; Steinberg, 2008). For example, systematic sampling of adolescents' and adults' moods over the course of a week has shown that adolescents are more euphoric and more depressed in

response to events (e.g., talking to friends, being in class), their positive feelings do not last as long as adults', and they are generally more emotionally responsive to events than are adults (Larson et al., 1980; Weinstein and Mermelstein, 2007). Adolescence is also a time of thrill-seeking where emotional experiences - even if they are potentially threatening - are actively sought out. This push-pull of affective stimuli bears out in reactivity of both threat-avoidance and reward-pursuit brain regions in relation to pubertal maturation (Baker et al., this issue; Spielberg et al., 2014).

From a functional perspective, human emotions have been preserved throughout our evolutionary history to promote adaptive responses to salient events (Davidson, 2003; Lazarus, 1991). Across the myriad classes of information that we encounter at any given moment, stimuli with emotional salience have a high probability of attracting our attention, despite, at times, even our best intentions to block them out (Luo et al., 2010; Pessoa, 2005; Vuilleumier et al., 2001). The affective characteristics of stimuli then serve to direct our attention to critical information, generate a behavioral response, facilitate learning, and help generate adaptive response patterns. Adolescent hyper-emotionality is well-documented particularly in association with behaviors that involve social interaction such as with peers and parents (Steinberg and Morris, 2001). Other behaviors in which hyper-emotionality is clearly displayed during adolescence include risk taking and reward seeking, although these behaviors are strongly moderated by the social context in which they occur (Lougheed et al., 2015; Somerville et al., 2010; Steinberg, 2008).

Another important and often overlooked aspect of adolescence is that many of the affective experiences occur in a completely novel context – particularly those related to social interaction. For example, emotional experiences related to intimacy, romantic love, jealousy, targeted rejection and acceptance by both partners and peers are often experienced for the first time during adolescence, and the novelty of these experiences may well enhance the impact of the associated emotions (Siegel and Shaughnessy, 1995; Suleiman and Harden, 2016). The important moderating role of the social group in adolescents' emotional experience is likely to result in behaviors more conducive to norms of a novel peer group than of the natal family unit from which they are preparing to exit (Hostinar et al., 2015; Nelson et al., 2016; Spear, 2000; Steinberg, 2008). Heightened impulsivity, sensation-seeking, and reward sensitivity may help to push adolescents toward seeking novel experiences and social interactions at a time when they are leaving the natal group, establishing their identity, and developing routines in a new setting.

2.1. Long-term impact of heightened emotionality

A prominent feature of affective behavior in adolescence relative to childhood or adulthood is the striking change that occurs in terms of increased psychopathology that involves dysregulated affect (Monahan et al., 2016). Emotional reactions can become maladaptive when the type, strength, or coordination across neurophysiological systems is not optimal for a particular context. Indeed, the onset of psychiatric disorders during the adolescent years is high, particularly for mood, anxiety, and substance use disorders (Kessler et al., 2012; Paus et al., 2008). This feature has led to a historical view of adolescence as a time of “storm and stress” and of extreme volatility, discussed at great length in the popular press

and scientific community (Arnett, 1999; Casey et al., 2010; Hall, 1931; Spear, 2000; Steinberg, 2005).

Although many now consider the “storm and stress” concept misleading because it is not universally experienced (Hollenstein and Lougheed, 2013; Steinberg and Silk, 2002), evidence generally supports adolescence as a time of hypersensitivity to both appetitive and aversive emotional experiences, particularly when salient events occur in a social context. Epidemiological data indicates that adolescence is when individuals are the most susceptible to mortality and morbidity due to behaviors that directly relate to emotional experiences (Casey, 2015). These include accidents, excessive drug and alcohol use, suicide, and sexual promiscuity. However, this dynamic of emotionality and risk taking may also lead to beneficial outcomes as adolescents may be prone to emotional forces facilitating prosocial behaviors, such as academic, artistic, and family-oriented activities (Crone and Dahl, 2012; Telzer et al., 2013). Thus, adolescence has been construed more recently as a period of both vulnerability and opportunity (Dahl, 2004; Haller et al., 2015), hinged on the power of affective systems to influence behavior.

The function of adolescent hyper-emotionality may also relate in part to the outsized influence emotions have on shaping short- and long-term behavior. A particularly important function of emotions is that they serve to orient, engage, and teach. An increased desire to try new things, a need to ramp up one’s emotional state, and/or heightened worry over fitting in socially may tip adolescents into long-term maladaptive patterns. As an example, substance experimentation for some adolescents may alter neural circuitry underlying affective and cognitive processing and create reinforcing habits over time that lead to long term substance use disorders (Goodman and Packard, 2016). These mechanisms may be further enhanced by stressful experiences that are commonly encountered in adolescence (Goodman and Packard, 2016; Romeo, 2010; Spear, 2009).

Likewise, increased interaction with peers and the emergence of sexual behaviors brought on by changes in social emotions establishes behavioral patterns and perspectives of the self that may continue well into adulthood. For example, patterns of peer interaction and sexual behavior during early adolescence tend to persist into adulthood (Dishion et al., 2012; Sisk, 2016) and adoption of group social norms and group culture tends to be much more profound during childhood and adolescence than during adulthood (Cheung et al., 2011). Furthermore, at a mechanistic level, many of the processes that underlie brain maturation can also mediate learning across the lifespan. These include synaptic pruning, myelination, and use-dependent synaptic stabilization (Fields, 2015; Petanjek et al., 2011; Takesian and Hensch, 2013; Werker and Hensch, 2015). Thus, the brain may be in a state of localized hyper-plasticity as circuits mature during adolescence. Because many of the brain circuits involved in social information processing continue to develop throughout the teenage years, adolescence may represent a sensitive period for the long-term organization of social behavior (Blakemore and Mills, 2014; Sisk, 2016; see reviews by Gur and Gur, this issue; Schulz and Sisk, this issue).

2.2. Mechanisms of heightened emotionality

Large-scale neuroimaging studies conducted over the last decade have shown that brain structures continue to develop into the third decade of life (Giedd et al., 2012; Gogtay et al., 2004), reinforcing the idea that there is a prolonged post-childhood period of brain and behavior change. In addition to brain development, adolescent-specific changes in pubertal maturation and social relationships also influence neural mechanisms of affective behavior. These fundamental changes typically follow a predictable ordering, yet the variability seen in their onset, rate of change, and/or interaction with each other may help us understand why heightened emotionality characterizes adolescence. As examples of this variability, earlier work showed that harsh and controlling parenting relates to early pubertal timing specifically among girls (Belsky et al., 2007b) and new evidence shows that extreme environmental factors (e.g., early life separation from biological parents) may shift the timing of neurodevelopment (Gee et al., 2013).

With regard to puberty itself, the so-called ‘organizational effects’ of gonadal hormones on brain function had previously been thought to occur primarily during perinatal and late gestation periods of development, which was then followed by behavioral activation of previously-organized behaviors with the re-emergence of gonadal hormones at puberty. However, more recent conceptualizations point to a second organizational wave that occurs during puberty (see Gur and Gur, this issue and Schulz and Sisk, this issue; Sisk, 2016). Animal models have demonstrated that both specific reproductive behaviors and non-sexual social behaviors such as dominance and play with conspecifics and parental behavior in adulthood are critically dependent on presence of gonadal hormones during the developmental period that comprises adolescence. Replacing steroids in adulthood that were absent during the typical pubertal window does not restore normative patterns of these behaviors (see Schulz and Sisk, this issue; Sisk, 2016). These animal models have further revealed organizational effects in brain regions such as the lateral septum and medial amygdala that depend critically on presence of gonadal steroids during puberty (see Schulz and Sisk, this issue; Sisk, 2016). In addition to the organizational effects of pubertal hormones, a number of acute or excitatory effects of hormones on brain function have been observed, many of which relate to an increase in emotionality (Patton and Viner, 2007; Sisk and Zehr, 2005).

In humans, the surge in gonadal hormones during adolescence has also been linked to changes in behavior although in a highly context-specific manner. For boys, increased testosterone levels have been associated with deviant behaviors and social dominance in those who are enmeshed with other deviant peers, whereas increased leadership and social status have been found in those without a deviant peer group (Rowe et al., 2004). Among girls, increased estradiol levels have been linked to heightened emotionality and internalizing psychopathology in many studies (Balzer et al., 2015), as well as with increased risk-taking and substance use behaviors during adolescence (Balzer et al., 2015).

The changes seen in emotionality, social interactions, and risk-taking during adolescence are at least partly mediated by changes in neural reactivity in regions including the striatum, amygdala, and PFC that is generated by the surge in gonadal hormones (Peper and Dahl, 2013; Scherf et al., 2013; Tyborowska et al., 2016). Pubertal maturation alters not only focal

areas of activation, but also network dynamics, as the patterns of functional connectivity between subcortical regions and regions within the PFC are found to change significantly in adolescence (Scherf et al., 2013; Spielberg et al., 2015a). Some of these network changes have been directly linked to changes in circulating hormone levels at puberty (Tyborowska et al., 2016). For example, testosterone levels have been positively associated with an adolescent-limited peak in ventral striatum activity during reward processing tasks that then declines in adulthood (Braams et al., 2015; Op de Macks et al., 2011). Interestingly, low striatal reactivity when anticipating and receiving rewards has been associated with decreased sleep, a factor that, when combined with gonadal hormonal surges, may jointly contribute to risky behavior and emotional problems (Holm et al., 2009). Overall, individual differences in pubertal development relate to neural responses to reward cues, which in turn may contribute to affective behavior in adolescents.

Variation in neural responsivity to socially-oriented tasks has also been found in relation to markers of pubertal maturation. Adolescents in middle or late versus early stages of puberty show reduced amygdala reactivity to faces versus non-social stimuli and reduced ventrolateral PFC reactivity to fearful faces in particular, patterns that were also linked with negative affect and depression (Forbes et al., 2011). Consistent with this developmental trend, longitudinal work has shown that pubertal stage and reactivity of the amygdala, hippocampus, and temporal pole to emotional faces were more strongly associated in early adolescence than in late childhood (Moore et al., 2012). When faced with more complex social-emotional information (i.e., processing social (e.g., embarrassment) versus basic (e.g., fear) emotional vignettes), increased hormone levels in adolescent girls were related to greater activity in the anterior temporal cortex (ATC) but more advanced age was related to reduced dorsomedial PFC activity (Goddings et al., 2012). An extension of Goddings et al.,'s (2012) study reported that, independent of age, girls with more advanced puberty (based on self-report and hormonal levels) have greater connectivity between the dorsomedial PFC and the ATC and temporal parietal junction (TPJ), two regions involved in mentalizing (Klapwijk et al., 2013). The findings from these latter two studies highlight a divergent effect of age and pubertal maturation on the brain's processing of another's mental state in the context of social emotions, consistent with Gur and Gur, this issue.

3. Control and regulation of affective behavior: Form and function

One of the primary tasks of adolescence is to refine one's cognitive control over behavior and emotional reactions. Virtually all contemporary models of emotional changes during adolescence contain some aspect of a gradually emerging modulatory control neural system. A peak of emotionality in early adolescence is followed by a slowly emerging ability to exert greater self-directed control over behaviors and emotions. This is most evident in the dual systems and imbalance conceptual models of adolescent neurodevelopment, which both characterize neocortical systems as developing increasing inhibitory control over striatal and limbic regions as adolescence progresses (Casey et al., 2016; Shulman et al., 2016). Even within models that argue for a more complex relationship between top-down and bottom-up neural input across development (Nelson et al., 2016, 2005; Pfeifer and Allen, 2012), the influence of high emotionality on guiding behavior is thought to diminish in part due to maturation of neocortical modulatory inputs. There are many examples where cortically-

mediated cognitive processes modulate emotionality in the social domain. Below, we discuss behavioral and neural evidence related to mentalizing, self-appraisal, social learning, and emotion regulation as processes that underscore the interface of cognitive and affective maturation in adolescence.

3.1. Mentalizing and perspective-taking

A particularly important form of social cognitive development relates to mentalizing and perspective-taking – the ability to understand the mental and emotional state and the perspective of other individuals, respectively. Understanding others' mental states allows us to figure out their goals and behaviors, and to adjust our own behavior accordingly. Although some basic aspects of mentalizing are functional from a relatively early age, more nuanced capabilities linked to changes in the PFC continue to develop through the adolescent years (Blakemore, 2008). For example, the ability to alter behavior as a consequence of the emotional experience of others, such as viewing others in the distressing situation of being socially excluded, is an aspect of mentalizing that continues to mature through late adolescence (Will et al., 2013). Evidence of this type of social-affective perspective taking has been indexed by increased involvement of the TPJ and dorsolateral PFC in older adolescents in contrast to recruitment of self-processing regions such as the anterior medial PFC (mPFC) in younger adolescents (van den Bos et al., 2011). Additionally, relative to children, adolescents are better at incorporating social context into making decisions that impact others. Specifically, older adolescents show more prosocial behavior towards friends than anonymous peers, neutral peers, and antagonists (categorized as such based on classroom sociometrics), an effect also mediated by greater perspective-taking ability (Guroglu et al., 2014). Consistent with social information processing models, these results suggest that taking another's perspective is a mechanism in the development of prosocial behavior (Nelson and Crick, 1999). Even further, these results underscore the impact of *who* one interacts with has on eliciting different emotions, which in turn can differentially direct behavior.

3.2. Self-appraisal

Another social-cognitive mechanism that becomes greatly enhanced and influential for affective behavior in adolescence is self-appraisal. Self-appraisal ties into one of the more important developmental tasks of adolescence – exploring and establishing one's sense of individual identity (Meeus, 2011; Meeus et al., 1999). Adolescence is a time when individuals deepen and expand the values, interests, and capabilities that uniquely define themselves as an individual and consider how their self-definition compares to others around them. There is a marked increase in the degree to which individuals engage in these kinds of self-cognitions at the beginning of adolescence, precisely when integrating with other peer groups and individuating the self from parents becomes more frequent and salient (Meeus et al., 1999). Greater engagement in self-appraisal relates in part to cognitive and brain development and in part to affective and motivational changes (Casey et al., 2011; Crone and Dahl, 2012; Nelson et al., 2016; Pfeifer and Peake, 2012; Steinberg, 2008). The capacity to cognitively represent a more nuanced understanding of the perspectives of others (e.g., mentalizing) goes hand in hand with the tendency to engage in self-appraisals or to view the self from the perspective of other individuals. Interestingly, adolescents exhibit greater

activity than adults in brain regions that sub-serve social-cognition during self-reflection, suggesting that adolescents rely heavily on how they believe others in the social context perceive them as they construct their own self-perceptions (Pfeifer et al., 2009). Thus, self-referential processing appears to be modulated by social-contextual and affective factors during adolescence.

3.3. Social-emotional learning

Neural networks underlying adolescents' emotions play a key role in social and appetitive learning, which are critical for shaping subsequent behavior during adolescence. Learning occurs when an outcome differs from what was expected. With repeated experience, we learn to improve predictions about outcomes. Understanding the neural mechanisms related to learning may help us better understand how adolescents' affective behavior is swayed by rewarding social experiences. The striatum has been implicated in appetitive learning – particularly in the prediction error learning framework (Schultz, 2006), and in adolescent social reinforcement learning (Jones et al., 2011). In the prediction error framework, a novel and unexpected reward elicits strong activity within the striatum and PFC, and this activity then transfers from the reward itself to cues which reliably predict the onset of the reward.

Functional connections between the striatum and mPFC during an appetitive prediction error task have been shown to strengthen across development (van den Bos et al., 2012) and relate to the ability to integrate positive feedback into expectations. Recent data suggest that reward-based prediction error signals in the striatum peak during adolescence, perhaps contributing to hypersensitivity to reward in adolescence (Cohen et al., 2010). Investigators have developed tasks to examine prediction error in response to social rather than monetary rewards (Poore et al., 2012). In one social prediction error task, we found dysfunctional connectivity between striatum and mPFC in socially anxious adolescents, a pattern related to a specific memory deficit for social reward (Jarcho et al., 2015). Specially, social prediction errors were related to heightened striatal activity and negative fronto-striatal functional connectivity when socially anxious adolescents received unexpected positive feedback from peers that they had judged positively (i.e., the peers participants most wanted to chat with). These findings suggest that forming functional connections between the striatum and PFC may be an important aspect of social learning in adolescence.

3.4. Regulating emotions

Another process expected to strengthen in adolescence in association with the maturation of cognitive-control brain regions is the regulation of one's emotions, and particularly within social contexts. Emotion regulation is the ability to engage in processes that alter how one experiences or expresses emotions (Gross, 2014; Thompson, 1994). This is a process that begins in infancy but becomes increasingly independent and sophisticated throughout middle childhood and adolescence as meta-cognitive skills are refined and strategies shift with age from involving behavioral (e.g., looking away) to cognitive (e.g., thinking about the situation from another perspective) regulation (Kopp, 1982; Zeman et al., 2006). Emotion regulation is critical in navigating and managing one's interactions with other individuals, and thus reflects an important task for adolescents in their newly expanded social landscapes and roles.

One emotion regulation strategy that becomes more refined during adolescence is cognitive reappraisal. Reappraisal involves altering emotions by changing one's thoughts and requires cognitive effort to reframe the stimulus or experience (McRae et al., 2012; Ochsner and Gross, 2005). Reappraisal has been examined in several ways such as reappraising aversive stimuli with the goal of diminishing negative responses to them. This regulatory strategy occurs early in the emotion generation process and, as a whole, findings from questionnaire, behavioral task, and neuroimaging data indicate that reappraisal is effective at reducing negative affect (Gross, 2014). Behavioral work has demonstrated that, from early adolescence to young adulthood, increased age relates to greater success with emotion regulation attempts but not to emotional reactivity (Silvers et al., 2012). In addition, younger adolescents who were very sensitive to social rejection were less successful at emotion regulation when responding to social vs. nonsocial contexts (Silvers et al., 2012).

Neuroimaging work has shown that structural development of the PFC is implicated in the use of emotion regulation strategies (Vijayakumar et al., 2014). Specifically, greater cortical thinning of dorsolateral and ventrolateral PFC in early adolescence was associated with greater use of cognitive reappraisal strategies in late adolescence. While the fMRI literature on the development of emotion regulation and its relation to neurodevelopment in adolescence is relatively nascent, some initial studies have examined brain activity in adolescents and young adults during directed cognitive reappraisal while viewing emotional images (McRae et al., 2012; Stephanou et al., 2016). McRae et al., (2012) found linear age-related increases in activation in the left ventrolateral prefrontal cortex during cognitive reappraisal, a region previously implicated in appraisal among adults, across 10–22 year olds. These results suggest an increase in the recruitment of cognitive control structures to accomplish cognitive reappraisal from early adolescence into early adulthood. Another study compared adolescents and adults to examine the neural correlates of emotional reactivity and reappraisal in response to aversive social imagery (Stephanou et al., 2016). Younger participants showed greater activation of temporal-occipital brain regions during reappraisal and weaker suppression of amygdala reactivity, with the latter considered to be a general correlate of successful reappraisal. Overall, neuroimaging-based evidence suggests that emotional regulatory efficiency increases with age and in sync with PFC maturation. However, little is known about how social contexts influence successful engagement of cognitive strategies used to regulate emotions as experienced in naturalistic settings. This is an important area for future focus given its potential for translation into interventions to help those vulnerable to emotional dysregulation (Ahmed et al., 2015).

4. The emotional adolescent brain in context

Affective behavior during adolescence does not occur in a vacuum. In fact, evidence suggests that the neural circuits that support affective responding are highly sensitive to contextual influences, especially during adolescence. Crone and Dahl (2012), for example, argue that the adolescent brain is highly attuned to social inputs, which facilitates flexible responding among a highly salient and changing social context. This is consistent with Nelson et al.'s (2005) conceptualization of adolescence as a period of neurodevelopment that corresponds with social reorientation, in which peer social interactions take on increasing salience, and Nelson and Guyer's (2011) hypothesis that protracted ventral PFC

development is in place to accommodate the need for children and adolescents to develop social flexibility. In this section, we describe work showing various short- and long-term social-contextual influences on brain function, affective processing, and behavior in adolescence.

4.1. Short-term social-contextual influences on social-affective neural circuitry

Social influences on the brain's processing of affective stimuli and situations can operate within relatively short time frames or within discrete situations or exchanges with others. For adolescents, this might include hanging out with friends at a party where there are drugs, learning that a peer likes you or not, being excluded from a game at school, or having a conflict with a parent. Although adolescents spend more time with their peers than do adults (Brown and Larson, 2009), it has been hypothesized that shorter-term peer influences are not related to more peer exposure per se but to processes specific to where adolescents are developmentally such as limited self-reliance, reduced ability to act independently, or decision-making that is easily swayed by emotional and social factors (Albert and Steinberg, 2011; Blakemore and Robbins, 2012; Cauffman and Steinberg, 2000; Steinberg and Cauffman, 1996). Additionally, it has been proposed that adolescents assign elevated reward value to peers, which sensitizes incentive-processing brain regions to respond to the potential rewards of risk taking (Blakemore and Robbins, 2012; Spear, 2009) as well as social brain processing regions to react strongly to valenced social events such as peer evaluation or exclusion (Nelson and Guyer, 2011; Somerville, 2013). Although greater attention has been paid to peer influences, some recent work has also considered the influence of discrete parent-child interactions on these processes.

4.1.1. Peer presence—Some of the strongest support for the idea that the adolescent brain's response to affective stimuli is modulated by the social context comes from work demonstrating that the presence of peers increases risk-taking behavior and heightens the responsivity of the brain's reward circuit in adolescents but not adults (Chein et al., 2011; Gardner and Steinberg, 2005). Gardner and Steinberg (2005) demonstrated that adolescents took more risks on a simulated driving task when they were observed by two peers, compared to when they performed the task alone. These adolescents were more likely to risk crashing the car in order to earn a potential reward when they were observed by peers, while they made safer driving decisions when they were alone. The influence of peers on risky driving was stronger in adolescents than adults, suggesting that the influence of peers on affective behavior is uniquely heightened during adolescence. A subsequent neuroimaging study showed that increased risky driving in the peer observation condition (relative to alone) was associated with increased activity in the ventral striatum and orbitofrontal cortex (OFC) among adolescents but not adults (Chein et al., 2011).

In contrast to focusing on peers' influence on the neural correlates of risk-taking and reward processing, recent work has examined peer effects on prosocial behavior and associated neural activity (Van Hoorn et al., 2016). In the presence of peers, adolescents engaged in greater prosocial behavior, indexed as ostensibly donating more money to others, especially when peers provided prosocial feedback. Adolescents also demonstrated greater activity in the mPFC, TPJ, precuneus, and superior temporal sulcus when choosing to donate in the

presence of their peers. These regions fall within the social detection and cognitive regulatory circuits outlined in the social brain network (Blakemore and Mills, 2014) and social-reorientation neurodevelopmental framework (Nelson et al., 2005), with mPFC activated during mentalizing and in response to social influence (Welborn et al., 2015) and increased TPJ involvement associated with more advanced types of perspective-taking (van den Bos et al., 2011) in adolescence.

4.1.2. Peer feedback—Being evaluated by one’s peers is a common experience for adolescents, and one that has a high level of emotional investment. Adolescents derive a sense of belonging and identity from their peers’ judgments and acceptance or rejection of them. Using a ball toss game to deliver social exclusion, a type of peer rejection, adolescents showed increased activity in the subgenual ACC (sgACC), in reaction to being excluded versus included from the game (Masten et al., 2009; Sebastian et al., 2010). Results from this study highlighted the relation of sgACC activity during social exclusion to feeling distress in response and the potential role of the striatum and ventrolateral PFC in moderating this response.

To tap into another type of salient aspect of adolescents’ daily emotional lives, several ecologically-valid tasks (e.g., Chatroom Task, Social Judgment Task, Chatroom Interact Task) have been used to assess neural and behavioral responses to socially evaluative feedback experiences (Gunther Moor et al., 2010; Guyer et al., 2008; Silk et al., 2013). In line with expectations from ecological momentary assessment (EMA) work (Larson et al., 1980; Weinstein and Mermelstein, 2007), typically developing adolescents report more positive affect after being accepted versus rejected by peers they like when engaged in the Chatroom Task (Guyer et al., 2014b, 2012). Of interest, being accepted vs. rejected by peers generated greater activity in the caudate and putamen, striatal regions that support approach behaviors and social-reward processing (Guyer et al., 2014a, 2012). Additional work suggests that adolescents, especially girls, exhibit age-related increases in neural response to peer evaluation in several affective and self-evaluative networks including striatum, insula, and ventromedial prefrontal cortex (Gunther Moor et al., 2010; Guyer et al., 2009) and that increased neural response to peer rejection may be a function of pubertal development (Silk et al., 2013).

In a study that used a version of the Social Judgment Task, Gunther Moor et al., (2010) reported age-variant effects of social expectations and the context-dependency of social feedback on the brain among 8–25 year olds. An age-related increase was found in striatal and ventral mPFC response when participants expected to be liked by peers. Striatal and ventral mPFC activation also occurred in response to being accepted when positive social feedback was expected, but this pattern was similar across all ages. Finally, adults, but not younger participants, showed increased activity in a regulatory network (including the striatum, ventral mPFC, OFC, and lateral PFC) when their expectations for social rejection matched the experience of social rejection. This latter finding suggests that adults are better at regulating their emotional responses to salient experiences when they are expected versus unexpected. Overall, these results provide further support that the brain regions involved in reward-processing, mentalizing, and self-processing respond to social evaluation differently

as a function of development and are modulated by expectations about social feedback and its valence.

4.1.3. Parent-child interaction—Researchers have begun to investigate the effects of the parent-child relationship on neural response to social-affective information in adolescence. Despite the amplified focus on peer relationships during adolescence, adolescents continue to care what their parents think about them (Steinberg and Morris, 2001; Steinberg and Silk, 2002). This was demonstrated in a recent neuroimaging study that probed the neural response to negative feedback from mothers (Lee et al., 2015). In this study, adolescents listened to audio clips of their mothers criticizing them as well as discussing neutral topics such as the weather. When listening to critical comments, adolescents showed increased brain activity (relative to neutral comments) in subcortical-limbic regions, such as the lentiform nucleus and posterior insula, but decreased activity in regions of the brain that subserve cognitive control of emotion, such as the dorsolateral PFC and the caudal ACC. These findings suggest that maternal criticism is processed as emotionally salient during adolescence, and that typically developing adolescents fail to recruit cognitive control networks to help them regulate emotion when passively listening to critical comments from their mothers.

4.2. Long-term social-contextual influences on social-affective neural circuitry

Neural circuits that support affective behavior are not only influenced by the current social context, but are also shaped by earlier social experience. As discussed in this issue, there is evidence that extreme stress and adverse experiences early in life influence the functioning of the adolescent brain within circuits that support affective behavior. However, emerging research suggests that variations in social context within the more typical range of experience and in the years more proximal to adolescence can also influence adolescent brain function.

4.2.1. Exposure to peer victimization—Casement et al., (2014) found that peer victimization in early adolescence was associated with decreased mPFC response to potential rewards at age 16. Other evidence suggests that the experience of peer victimization during middle childhood sensitizes the adolescent brain to social exclusion later in adolescence (Will et al., 2016). Specifically, adolescents who were repeatedly victimized from the 6 to 12 years of age showed greater dorsal anterior cingulate cortex activation to social exclusion on the Cyberball task in mid-adolescence. These results indicate that earlier experiences with peers have long-standing effects on subsequent neural correlates of affective behavior.

4.2.2. Quality of peer relationships—The quality of peer relationships has been found to influence neural response to appetitive stimuli. Evidence shows that risk-taking in mid-adolescence is modulated by the quality of peer relationships in the preceding two years (Telzer et al., 2015). Specifically, adolescents who reported greater conflict with peers in their daily life took more risks on a computerized risk-taking task, and showed greater activation in reward processing regions, such as the striatum and insula, when completing the task. Furthermore, the association between peer conflict and increased risk-taking, as

well as insula and striatal responsivity while engaging in risk-taking, were both attenuated for adolescents who also reported high levels of peer support. Collectively, these findings provide some of the first evidence demonstrating that the quality of peer relationships has the potential to modulate the sensitivity of reward and threat circuits to future affective cues. These results may also lend support to the concept of a functional role for adolescent hyper-emotionality. Risk taking may serve to integrate individuals within new social networks in adolescence; for those with already-established, stable peer networks, the rewards associated with risk taking may be diminished.

4.2.3. Quality of parental relationships—The adolescent brain is also responsive to social inputs from the family environment. For example, Morgan et al., (2014) found that higher levels of observed maternal warmth during early adolescence were associated with greater striatal activation during reward anticipation during late adolescence for a subset of boys at familial risk for depression. Whittle et al., (2014) have further shown that warm parenting in early adolescence (age 12) is associated with a pattern of presumably adaptive structural changes in limbic-striatal brain regions over the next four years. In addition, parental warmth has been associated with reduced self-referential processing of maternal criticism in healthy adolescents (Lee et al., 2015). These findings suggest that warm and supportive parenting earlier in adolescence may have neuroprotective effects on adolescent brain development. Furthermore, two recent studies showed that the quality of parenting can influence how adolescents respond to peer feedback, with negative parenting attenuating striatal responsiveness to peer acceptance (Tan et al., 2014) and positive parenting attenuating striatal reactivity to peer rejection (Guyer et al., 2015). These findings demonstrate that, given continued plasticity in the neural circuitry that supports affective behavior during adolescence, relationships with parents remain influential on how adolescents process and manage both positive and negative emotional experiences.

4.3. Individual differences in brain function and affective behavior

Individuals vary in their ability to modulate or canalize their emotional experiences, and for some, compromised emotion regulation abilities can lead to increased dysfunction (Gross and Jazaieri, 2014). Emotions such as fear, anxiety, or sadness, for example, can become dysfunctional or psychopathological when they bubble up in inappropriate social contexts, or when their valence or arousal is unpredictable or extreme and are incongruent within the situational demands. The outsized role that social-emotional experiences play in shaping behavior is evident in the high onset of psychiatric disorders during the adolescent years, such as anxiety and depressive disorders (Kessler et al., 2012; Paus et al., 2008). Researchers have suggested that increased rates of both anxiety (especially social anxiety) and depression during adolescence may be at least partially driven by these increases in neural sensitivity to socially threatening stimuli (see Baker et al., this issue; Caouette and Guyer, 2014; Davey et al., 2008; Haller et al., 2015; Silk et al., 2012a). Thus, although increased sensitivity to peer feedback is normative during adolescence, this process appears to be particularly enhanced among youth with anxiety and depression.

Paradigms that probe neural response to simulated peer evaluation have generated new findings that are consistent with these models. For example, two studies have demonstrated

heightened activation in the amygdala in socially anxious versus healthy adolescents when reflecting on how interested they expected virtual peers to be in chatting with them during the Chatroom task (Guyer et al., 2008; Spielberg et al., 2015b). This pattern was specific to peers whom the participants had previously judged negatively, potentially reflecting a fear of impending negative outcomes such as social retaliation. Socially anxious adolescents also demonstrated a stronger pattern of co-activation between the amygdala and vIPFC during anticipation of peer evaluation compared to healthy adolescents (Guyer et al., 2008). The amygdala facilitates attention toward salient emotion stimuli, signaling the need to avoid a potentially threatening stimulus. In contrast, the vIPFC inhibits such responses by shifting attention or overriding basic emotional response, presumably via its strong anatomical connections with the amygdala (Etkin et al., 2015). The role of vIPFC in modulating amygdala response to a potential social threat suggests that socially anxious adolescents are attempting to redirect their attention away from and/or regulate their emotional reaction during the anticipation of rejection. Spielberg et al., (2015b) similarly found that socially anxious compared to healthy youth exhibited a stronger pattern of co-activation between the amygdala and the rostral ACC when anticipating feedback from negatively judged peers, especially for older adolescents. While most studies of anxious youth have focused on the anticipation of peer feedback, Lau et al., (2012) showed that, after the receipt of peer rejection, amygdala-hippocampal activation decreased for healthy adolescents but remained heightened for socially anxious adolescents, which may again relate to a compromised ability to downregulate emotional responses.

Silk et al., (2013) reported a similar pattern of increased neural response to simulated peer rejection in adolescents with depression compared to healthy adolescents in regions of the brain involved in processing affective salience. Depression was associated with increased reactivity to receipt of peer rejection in the amygdala, as well as the sgACC, anterior insula, and striatum. The finding of heightened sgACC activity to social rejection in adolescents with depression converges with other work demonstrating that sgACC activity to social exclusion predicted increases in depressive symptoms over one year (Masten et al., 2011). These studies suggest that sgACC response to social evaluation could be a unique biomarker of risk for adolescent depression. In contrast, potentiated amygdala response to social threat could be a shared risk factor for both anxiety and depression. Silk et al., (2013) also found that participants further along in pubertal maturation showed enhanced activation to peer rejection in the bilateral amygdala/parahippocampal gyrus, caudate, and sgACC. Thus, increased neural sensitivity to peer rejection naturally increases across pubertal development, but is exacerbated among adolescents with depression.

Collectively, this new cadre of peer interaction studies demonstrates that individual differences in neural responses to socially-relevant affective stimuli are increasingly thought to play a role in the emergence of anxiety and depression in adolescence. Although we focused on anxiety and depressive disorders, which have been the focus of most of the research using peer evaluation paradigms, it is likely that individual differences in neural responses to socially-relevant stimuli play a key role in altered affective behaviors implicated in other forms of psychopathology that often emerge in adolescence, such as substance use disorders, bipolar spectrum disorders, and eating disorders. Understanding how individual differences in the development and function of neural circuits underlying

affective behavior interact with other biological factors (i.e., epigenetic changes, hormones) and social experiences to amplify or attenuate risk for psychopathology remains a critical target for future adolescent research.

5. Future directions and conclusions

In our review of the literature, we have highlighted recent work illustrative of the substantial progress that has been made in our understanding of the neurobiology of adolescent affective behavior, particularly with regard to the role of social context and social experiences. As the field moves forward, we suggest extending the existing knowledge-base on the emotional adolescent brain by applying new methodological advances, integrating multiple units of analysis sampled in multiple contexts, and testing hypotheses from theoretical conceptualizations of neurobiological development.

With regard to methodology, researchers will need to continue pairing neuroimaging methods with new task paradigms that have a high level of ecological validity and capability of capturing real-time cognitions and behaviors. This approach will allow us to probe adolescent emotional behavior more deeply and in novel ways by simulating social experiences encountered in daily life. One of the limitations of using neuroimaging is that the scanning environment is constrained in its ability to capture how the brain represents information in a contextually-sensitive way, demonstrating the need to add real-world experience as much as possible. For example, new fMRI paradigms could be designed to assess adolescent affective behavior in response to peer interactions delivered in a simulated social media context or, as done in recent work, a virtual classroom environment (Jarcho et al., 2016, 2013). For the study of adolescent emotional and brain development, this is particularly important given that daily fluctuations in affective behavior relate to the types of activities in which adolescents are engaged (Larson and Richards, 1998; Larson and Asmussen, 1991).

Because the relation between neural function and sources of daily changes in adolescents' mood are not well understood, it will also be important to increasingly link fMRI and EMA measures to real-world affective behavior (Forbes et al., 2009; Price et al., 2016). For example, Price et al., (2016) recently showed that PFC-amygdalar connectivity during threat processing was associated with the use of emotion regulation strategies in the real-world as assessed via EMA in anxious adolescents. The use of wearable, mobile technologies to assess ambulatory psychophysiology may be another way to capture nuances in adolescents' daily emotional experiences that can be integrated with measures of brain function to provide a more complete picture of adolescent affective behavior. In addition to EMA, methods such as eye-tracking and fNIRS are promising new techniques that may integrate well with neuroimaging data, but also offer more flexible usage (Perlman et al., 2015; Silk et al., 2012b). A challenge here is to account for differing time scales across these measurements. Modeling of their unique time courses will need to be addressed through analytical advancements and careful experimental design with respect to onset and duration of task stimuli or emotional challenges used to elicit responses across systems. Nonetheless, affective behavior is generated from multiple systems at different levels, and capturing these facets should elucidate target points for intervention.

Recent advances in the ability to conduct real-time fMRI may also help to reveal the neural substrates of dynamic changes in affect as they unfold. For example, fMRI-based neurofeedback has been used to teach adolescents to up-regulate activity in the insula, a key region in emotion regulation neural circuitry (Cohen Kadosh et al., 2016). Based on a Granger causality analysis, Cohen Kadosh et al., (2016) found that the flow of information increased from the amygdala to the insula and from the insula to the mid-cingulate cortex, supplementary motor area and inferior parietal lobe specifically when youth engaged in up-regulation. This work highlights the potential for future interventions with adolescents that target the use of emotional regulation to change brain response and vice versa.

The application of advanced statistical modeling and patterning techniques will be important for characterizing adolescent development from an individual differences perspective. Incorporating methods such as pattern-classification algorithms to multi-voxel pattern analysis of fMRI data will help elucidate how social-emotional information is represented in the adolescent brain for different cognitive states and at different stages of processing (Norman et al., 2006). For example, time course changes in how peer feedback or emotionally-laden stimuli are represented and processed in the brain during adolescence may increase the precision of our interpretations of brain activity. Graph theory is another statistical method for classifying patterns of interconnectivity between brain regions that has generated important insights into neurodevelopmental processes and could increase our understanding of the interface between cognitive-control and affective neural circuits during social-emotional information processing (Fair et al., 2009, 2008).

Deeper characterization of the neural coding and processing of social-emotional information will also inform both typical neurobiological profiles of adolescent emotional development and dimensions of dysregulation that characterize adolescents with affect system difficulties such as depression and anxiety. For example, a recent study reported the development of a brain maturation index using structural MRI images (Cao et al., 2015). This index was derived from a regression-based algorithm ‘trained’ to integrate changes in brain anatomy across age to enhance prediction accuracy and differentiation of individual brain maturity. Results of this study provided a validated, accurate metric of brain maturation, which is significant in its potential application to reliably identify those who may deviate from a normative trajectory of brain development. Functional changes (e.g., peak or extent of activation) in regions with documented reactivity to social-affective cues could be similarly integrated across chronological age or pubertal stage to predict an adolescent’s affective brain maturation index, which could be useful in a diagnostic or clinical intervention setting.

From a conceptualization standpoint, neuroimaging research has been limited in its integration of developmental theory into either design or interpretation of experimental results. A number of biologically-based developmental theories such as developmental systems theory (Smith and Thelen, 2003), differential susceptibility (Belsky et al., 2007a), interactive specialization (Johnson, 2011), and critical periods of development (Takesian and Hensch, 2013) have been articulated in the developmental literature, but not necessarily used to guide neuroimaging research as suggested in a recent paper using differential susceptibility as an example (Schriber and Guyer, 2015). Relevant hypotheses from these theories could be tested in a neuroimaging environment and, in turn, these theories could be

further refined. We believe the field of adolescent developmental neuroscience would benefit from a greater integration of the theoretical and methodological approaches discussed in this section.

Finally, conceptual understanding of affective neurobiology would be deepened by capturing other aspects of adolescents' emotional lives. This might include further consideration of more complex emotions like contempt, pride, and disgust, as done in the study by Goddings et al., (2012). Similarly, more focus on the neural underpinnings of experiences related to intimacy and sexual relationships is needed (Suleiman and Harden, 2016). Indeed, recent work has examined the neural correlates of sexual decision-making in adolescent girls and found greater ACC activity during high-risk sexual decisions, along with sexual decision ratings that aligned with sexual emotions and behaviors (Hensel et al., 2015).

A common theme of the work reviewed in this paper is the importance of both representing what happens externally in adolescents' emotional lives and upholding methodological control to test how those experiences are represented internally by the brain. By using techniques such as fMRI, we are beginning to identify more precisely in the brain how adolescents' affective behavior differs from adults or with age, varies with individual differences such as pubertal maturation and affective forms of psychopathology, and differs in response to specific social experiences. We expect future neuroscientific investigations that integrate multiple methods will advance knowledge of the brain-based opportunities and vulnerabilities of adolescent affective behavior.

Acknowledgments

Financial support for the writing of the article was provided by the National Institutes of Health awards R01MH8370 (A. E. G.), R01MH3605 (A. E. G.), R01MH103241 (J.S.), R01 MH091327 (J.S.), and the National Institute of Mental Health, Intramural Research Program (E. E. N.). These sponsors played no role in the preparation or publication of this report.

References

- Ahmed SP, Bittencourt-Hewitt A, Sebastian CL. Neurocognitive bases of emotion regulation development in adolescence. *Dev Cogn Neurosci*. 2015; 15:11–25. DOI: 10.1016/j.dcn.2015.07.006 [PubMed: 26340451]
- Albert D, Steinberg L. Judgment and decision making in adolescence. *J Res Adolesc*. 2011; 21:211–224. DOI: 10.1111/j.1532-7795.2010.00724.x
- Arnett JJ. Adolescent storm and stress, reconsidered. *Am Psychol*. 1999; 54:317–326. [PubMed: 10354802]
- Baker KD, Bisby MA, Richardson R. Impaired fear extinction in adolescent rodents: Behavioural and neural analyses. *Neurosci Biobehav Rev*. 2016
- Balzer BWR, Duke S-A, Hawke CI, Steinbeck KS. The effects of estradiol on mood and behavior in human female adolescents: a systematic review. *Eur J Pediatr*. 2015; 174:289–298. DOI: 10.1007/s00431-014-2475-3 [PubMed: 25567794]
- Belsky J, Bakermans-Kranenburg MJ, Van Ijzendoorn MH. For better and for worse: Differential susceptibility to environmental influences. *Curr Dir Psychol Sci*. 2007a; 16:300–304. DOI: 10.1111/j.1467-8721.2007.00525.x
- Belsky J, Steinberg LD, Houts RM, Friedman SL, Dehart G, Cauffman E, Roisman GI, Halpern-Felsher BL, Susman E. Family rearing antecedents of pubertal timing. *Child Dev*. 2007b; 78:1302–1321. DOI: 10.1111/j.1467-8624.2007.01067.x [PubMed: 17650140]

- Blakemore SJ. The social brain in adolescence. *Nat Rev Neurosci*. 2008; 9:267–277. DOI: 10.1038/nrn2353 [PubMed: 18354399]
- Blakemore SJ, Mills KL. Is adolescence a sensitive period for sociocultural processing? *Annu Rev Psychol*. 2014; 65:187–207. DOI: 10.1146/annurev-psych-010213-115202 [PubMed: 24016274]
- Blakemore S-J, Robbins TW. Decision-making in the adolescent brain. *Nat Neurosci*. 2012; 15:1184–1191. DOI: 10.1038/nn.3177 [PubMed: 22929913]
- Braams BR, van Duijvenvoorde AC, Peper JS, Crone EA. Longitudinal changes in adolescent risk-taking: a comprehensive study of neural responses to rewards, pubertal development, and risk-taking behavior. *J Neurosci*. 2015; 35:7226–7238. DOI: 10.1523/JNEUROSCI.4764-14.2015 [PubMed: 25948271]
- Brown, BB.; Larson, J. Peer relationships in adolescence. In: Lerner, RM.; Steinberg, L., editors. *Handbook of Adolescent Psychology: Vol. 2: Contextual Influences on Adolescent Development*. John Wiley & Sons; Hoboken, NJ: 2009. p. 74–103.
- Bruhl AB, Delsignore A, Komossa K, Weidt S. Neuroimaging in social anxiety disorder—a meta-analytic review resulting in a new neurofunctional model. *Neurosci Biobehav Rev*. 2014; 47:260–280. DOI: 10.1016/j.neubiorev.2014.08.003 [PubMed: 25124509]
- Cao B, Mwangi B, Hasan KM, Selvaraj S, Zeni CP, Zunta-Soares GB, Soares JC. Development and validation of a brain maturation index using longitudinal neuroanatomical scans. *Neuroimage*. 2015; 117:311–318. DOI: 10.1016/j.neuroimage.2015.05.071 [PubMed: 26037051]
- Caouette JD, Guyer AE. Gaining insight into adolescent vulnerability for social anxiety from developmental cognitive neuroscience. *Dev Cogn Neurosci*. 2014; 8:65–76. DOI: 10.1016/j.dcn.2013.10.003 [PubMed: 24239049]
- Casement MD, Guyer AE, Hipwell AE, McAloon RL, Hoffmann AM, Keenan KE, Forbes EE. Girls’ challenging social experiences in early adolescence predict neural response to rewards and depressive symptoms. *Dev Cogn Neurosci*. 2014; 8:18–27. DOI: 10.1016/j.dcn.2013.12.003 [PubMed: 24397999]
- Casey B, Jones RM, Somerville LH. Braking and accelerating of the adolescent brain. *J Res Adolesc*. 2011; 21:21–33. DOI: 10.1111/j.1532-7795.2010.00712.x [PubMed: 21475613]
- Casey BJ. Beyond simple models of self-control to circuit-based accounts of adolescent behavior. *Annu Rev Psychol*. 2015; 66:295–319. DOI: 10.1146/annurev-psych-010814-015156 [PubMed: 25089362]
- Casey BJ, Galvan A, Hare TA. Changes in cerebral functional organization during cognitive development. *Curr Opin Neurobiol*. 2005; 15:239–244. S0959-4388(05)00044-9 [pii]. DOI: 10.1016/j.conb.2005.03.012 [PubMed: 15831409]
- Casey BJ, Galvan A, Somerville LH. Beyond simple models of adolescence to an integrated circuit-based account: A commentary. *Dev Cogn Neurosci*. 2016; 17:128–130. DOI: 10.1016/j.dcn.2015.12.006 [PubMed: 26739434]
- Casey BJ, Jones RM, Levita L, Libby V, Pattwell SS, Ruberry EJ, Soliman F, Somerville LH. The storm and stress of adolescence: insights from human imaging and mouse genetics. *Dev Psychobiol*. 2010; 52:225–235. DOI: 10.1002/dev.20447 [PubMed: 20222060]
- Cauffman E, Steinberg L. (Im)maturity of judgment in adolescence: Why adolescents may be less culpable than adults. *Behav Sci Law*. 2000; 18:741–760. DOI: 10.1002/bsl.416 [PubMed: 11180420]
- Chen J, Albert D, O’Brien L, Uckert K, Steinberg L. Peers increase adolescent risk taking by enhancing activity in the brain’s reward circuitry. *Dev Sci*. 2011; 14:F1–10. DOI: 10.1111/j.1467-7687.2010.01035.x [PubMed: 21499511]
- Cheung BY, Chudek M, Heine SJ. Evidence for a sensitive period for acculturation: younger immigrants report acculturating at a faster rate. *Psychol Sci*. 2011; 22:147–152. DOI: 10.1177/0956797610394661 [PubMed: 21189354]
- Cohen Kadosh K, Luo Q, de Burca C, Sokunbi MO, Feng J, Linden DE, Lau JY. Using real-time fMRI to influence effective connectivity in the developing emotion regulation network. *Neuroimage*. 2016; 125:616–626. DOI: 10.1016/j.neuroimage.2015.09.070 [PubMed: 26475487]

- Cohen JR, Asarnow RF, Sabb FW, Bilder RM, Bookheimer SY, Knowlton BJ, Poldrack RA. A unique adolescent response to reward prediction errors. *Nat Neurosci.* 2010; 13:669–671. DOI: 10.1038/nn.2558 [PubMed: 20473290]
- Crone EA, Dahl RE. Understanding adolescence as a period of social-affective engagement and goal flexibility. *Nat Rev Neurosci.* 2012; 13:636–650. DOI: 10.1038/nrn3313 [PubMed: 22903221]
- Dahl RE. Adolescent brain development: a period of vulnerabilities and opportunities. Keynote address. *Ann New York Acad Sci.* 2004; 1021:1–22. [PubMed: 15251869]
- Davey CG, Yucel M, Allen NB. The emergence of depression in adolescence: development of the prefrontal cortex and the representation of reward. *Neurosci Biobehav Rev.* 2008; 32:1–19. DOI: 10.1016/j.neubiorev.2007.04.016 [PubMed: 17570526]
- Davidson RJ. Darwin and the neural bases of emotion and affective style. *Ann N Y Acad Sci.* 2003; 1000:316–336. [PubMed: 14766646]
- Dishion TJ, Ha T, Veronneau MH. An ecological analysis of the effects of deviant peer clustering on sexual promiscuity, problem behavior, and childbearing from early adolescence to adulthood: an enhancement of the life history framework. *Dev Psychol.* 2012; 48:703–717. DOI: 10.1037/a0027304 [PubMed: 22409765]
- Ernst M, Fudge JL. A developmental neurobiological model of motivated behavior: anatomy, connectivity and ontogeny of the triadic nodes. *Neurosci Biobehav Rev.* 2009; 33:367–382. DOI: 10.1016/j.neubiorev.2008.10.009 [PubMed: 19028521]
- Ernst M, Torrisi S, Balderston N, Grillon C, Hale EA. fMRI Functional Connectivity Applied to Adolescent Neurodevelopment. *Annu Rev Clin Psychol.* 2015; 11:361–377. DOI: 10.1146/annurev-clinpsy-032814-112753 [PubMed: 25581237]
- Etkin A, Buchel C, Gross JJ. The neural bases of emotion regulation. *Nat Rev Neurosci.* 2015; 16:693–700. DOI: 10.1038/nrn4044 [PubMed: 26481098]
- Fair DA, Cohen AL, Dosenbach NU, Church JA, Miezin FM, Barch DM, Raichle ME, Petersen SE, Schlaggar BL. The maturing architecture of the brain's default network. *Proc Natl Acad Sci U S A.* 2008; 105:4028–4032. DOI: 10.1073/pnas.0800376105 [PubMed: 18322013]
- Fair DA, Cohen AL, Power JD, Dosenbach NU, Church JA, Miezin FM, Schlaggar BL, Petersen SE. Functional brain networks develop from a “local to distributed” organization. *PLoS Comput Biol.* 2009; 5:e1000381.doi: 10.1371/journal.pcbi.1000381 [PubMed: 19412534]
- Fields RD. A new mechanism of nervous system plasticity: activity-dependent myelination. *Nat Rev Neurosci.* 2015; 16:756–767. DOI: 10.1038/nrn4023 [PubMed: 26585800]
- Forbes EE, Hariri AR, Martin SL, Silk JS, Moyles DL, Fisher PM, Brown SM, Ryan ND, Birmaher B, Axelson DA, Dahl RE. Altered striatal activation predicting real-world positive affect in adolescent major depressive disorder. *Am J Psychiatry.* 2009; 166:64–73. [PubMed: 19047324]
- Forbes EE, Phillips ML, Silk JS, Ryan ND, Dahl RE. Neural systems of threat processing in adolescents: role of pubertal maturation and relation to measures of negative affect. *Dev Neuropsychol.* 2011; 36:429–452. DOI: 10.1080/87565641.2010.550178 [PubMed: 21516542]
- Gardner M, Steinberg L. Peer influence on risk taking, risk preference, and risky decision making in adolescence and adulthood: an experimental study. *Dev Psychol.* 2005; 41:625–635. 2005-08221-004 [pii]. DOI: 10.1037/0012-1649.41.4.625 [PubMed: 16060809]
- Gee DG, Gabard-Durnam LJ, Flannery J, Goff B, Humphreys KL, Telzer EH. Early developmental emergence of human amygdala – prefrontal connectivity after maternal deprivation. *Proc Natl Acad Sci U S A.* 2013; 110:15638–15643. www.pnas.org/cgi/doi/10.1073/pnas.1307893110. DOI: 10.1073/pnas.1307893110/-/DCSupplemental [PubMed: 24019460]
- Giedd JN, Raznahan A, Mills KL, Lenroot RK. Review: magnetic resonance imaging of male/female differences in human adolescent brain anatomy. *Biol Sex Differ.* 2012; 3:19.doi: 10.1186/2042-6410-3-19 [PubMed: 22908911]
- Goddings AL, Burnett Heyes S, Bird G, Viner RM, Blakemore SJ. The relationship between puberty and social emotion processing. *Dev Sci.* 2012; 15:801–811. DOI: 10.1111/j.1467-7687.2012.01174.x [PubMed: 23106734]
- Gogtay N, Giedd JN, Lusk L, Hayashi KM, Greenstein D, Vaituzis AC, Nugent TF 3rd, Herman DH, Clasen LS, Toga AW, Rapoport JL, Thompson PM. Dynamic mapping of human cortical

- development during childhood through early adulthood. *Proc Natl Acad Sci U S A*. 2004; 101:8174–8179. DOI: 10.1073/pnas.0402680101 [PubMed: 15148381]
- Goodman J, Packard MG. Memory Systems and the Addicted Brain. *Front Psychiatry*. 2016; 7:24.doi: 10.3389/fpsy.2016.00024 [PubMed: 26941660]
- Gross, JJ. Emotion regulation: conceptual and empirical foundations. In: Gross, JJ., editor. *Handbook of Emotion Regulation*. The Guilford Press; New York: 2014. p. 3-20.
- Gross JJ, Jazaieri H. Emotion, Emotion Regulation, and Psychopathology: An Affective Science Perspective. *Clin Psychol Sci*. 2014; 2:387–401. DOI: 10.1177/2167702614536164
- Gunther Moor B, van Leijenhorst L, Rombouts SA, Crone EA, Van der Molen MW. Do you like me? Neural correlates of social evaluation and developmental trajectories. *Soc Neurosci*. 2010; 5:461–482. DOI: 10.1080/17470910903526155 [PubMed: 20721813]
- Gur RE, Gur RC. Puberty, sex differences and the adolescent brain. *Neurosci Biobehav Rev*. 2016
- Guroglu B, van den Bos W, Crone EA. Sharing and giving across adolescence: an experimental study examining the development of prosocial behavior. *Front Psychol*. 2014; 5:291.doi: 10.3389/fpsyg.2014.00291 [PubMed: 24782796]
- Guyer AE, Benson B, Choate VR, Bar-Haim Y, Perez-Edgar K, Jarcho JM, Pine DS, Ernst M, Fox NA, Nelson EE. Lasting associations between early-childhood temperament and late-adolescent reward-circuitry response to peer feedback. *Dev Psychopathol*. 2014a; 26:229–243. DOI: 10.1017/S0954579413000941 [PubMed: 24444176]
- Guyer AE, Caouette JD, Lee CC, Ruiz SK. Will they like me? Adolescents' emotional responses to peer evaluation. *Int J Behav Dev*. 2014b; 38:155–163. DOI: 10.1177/0165025413515627 [PubMed: 25076803]
- Guyer AE, Choate VR, Pine DS, Nelson EE. Neural circuitry underlying affective response to peer feedback in adolescence. *Soc Cogn Affect Neurosci*. 2012; 7:81–92. DOI: 10.1093/scan/nsr043 [PubMed: 21828112]
- Guyer AE, Jarcho JM, Pérez-Edgar K, Degnan KA, Pine DS, Fox NA, Nelson EE. Temperament and parenting styles in early childhood differentially influence neural response to peer evaluation in adolescence. *J Abnorm Child Psychol*. 2015; 43:863–874. DOI: 10.1007/s10802-015-9973-2 [PubMed: 25588884]
- Guyer AE, Lau JYF, McClure-Tone EB, Parrish J, Shiffrin ND, Reynolds RC, Chen G, Blair RJR, Leibenluft E, Fox NA, Ernst M, Pine DS, Nelson EE. Amygdala and ventrolateral prefrontal cortex function during anticipated peer evaluation in pediatric social anxiety. *Arch Gen Psychiatry*. 2008; 65:1303–1312. DOI: 10.1001/archpsyc.65.11.1303 [PubMed: 18981342]
- Guyer AE, McClure-Tone EB, Shiffrin ND, Pine DS, Nelson EE. Probing the neural correlates of anticipated peer evaluation in adolescence. *Child Dev*. 2009; 80:1000–1015. DOI: 10.1111/j.1467-8624.2009.01313.x [PubMed: 19630890]
- Hall, GS. *Adolescence: Its psychology and its relations to physiology, anthropology, sociology, sex, crime, religion, and education*. D. Appleton and Company; New York, NY: 1931.
- Haller SP, Cohen Kadosh K, Scerif G, Lau JY. Social anxiety disorder in adolescence: How developmental cognitive neuroscience findings may shape understanding and interventions for psychopathology. *Dev Cogn Neurosci*. 2015; 13:11–20. DOI: 10.1016/j.dcn.2015.02.002 [PubMed: 25818181]
- Hensel DJ, Hummer TA, Acurcio LR, James TW, Fortenberry JD. Feasibility of functional neuroimaging to understand adolescent women's sexual decision making. *J Adolesc Heal*. 2015; 56:389–395. DOI: 10.1016/j.jadohealth.2014.11.004
- Hollenstein T, Loughheed JP. Beyond storm and stress: Typicality, transactions, timing, and temperament to account for adolescent change. *Am Psychol*. 2013; 68:444–454. DOI: 10.1037/a0033586 [PubMed: 23915399]
- Holm SM, Forbes EE, Ryan ND, Phillips ML, Tarr JA, Dahl RE. Reward-Related Brain Function and Sleep in Pre/Early Pubertal and Mid/Late Pubertal Adolescents. *J Adolesc Heal*. 2009; 45:326–334. DOI: 10.1016/j.jadohealth.2009.04.001
- Hostinar CE, Johnson AE, Gunnar MR. Parent support is less effective in buffering cortisol stress reactivity for adolescents compared to children. *Dev Sci*. 2015; 18:281–297. DOI: 10.1111/desc.12195 [PubMed: 24942038]

- Jarcho JM, Davis MM, Shechner T, Henderson HA, Stoddard J, Fox NA, Leibenluft E, Pine DS, Nelson EE. Early-Childhood Social Reticence Predicts Brain Function in Preadolescent Youths During Distinct Forms of Peer Evaluation. *Psychol Sci.* 2016; 27:821–835. DOI: 10.1177/0956797616638319 [PubMed: 27150109]
- Jarcho JM, Leibenluft E, Walker OL, Fox Na, Pine DS, Nelson EE. Neuroimaging studies of pediatric social anxiety: paradigms, pitfalls and a new direction for investigating the neural mechanisms. *Biol Mood Anxiety Disord.* 2013; 3:14.doi: 10.1186/2045-5380-3-14 [PubMed: 23849682]
- Jarcho JM, Romer AL, Shechner T, Galvan A, Guyer AE, Leibenluft E, Pine DS, Nelson EE. Forgetting the best when predicting the worst: Preliminary observations on neural circuit function in adolescent social anxiety. *Dev Cogn Neurosci.* 2015; 13:21–31. DOI: 10.1016/j.dcn.2015.03.002 [PubMed: 25933410]
- Johnson MH. Interactive Specialization: A domain-general framework for human functional brain development? *Dev. Cogn Neurosci.* 2011; doi: 10.1016/j.dcn.2010.07.003
- Jones RM, Somerville LH, Li J, Ruberry EJ, Libby V, Glover G, Voss HU, Ballon DJ, Casey BJ. Behavioral and neural properties of social reinforcement learning. *J Neurosci.* 2011; 31:13039–13045. DOI: 10.1523/JNEUROSCI.2972-11.2011 [PubMed: 21917787]
- Kessler RC, Avenevoli S, Costello J, Green JG, Gruber MJ, McLaughlin KA, Petukhova M, Sampson NA, Zaslavsky AM, Merikangas KR. Severity of 12-month DSM-IV disorders in the National Comorbidity Survey Replication Adolescent Supplement. *Arch Gen Psychiatry.* 2012; 69:381–389. DOI: 10.1001/archgenpsychiatry.2011.1603 [PubMed: 22474106]
- Klapwijk ET, Goddings AL, Burnett Heyes S, Bird G, Viner RM, Blakemore SJ. Increased functional connectivity with puberty in the mentalising network involved in social emotion processing. *Horm Behav.* 2013; 64:3140322.doi: 10.1016/j.yhbeh.2013.03.012
- Kopp CB. Antecedents of self-regulation: A developmental perspective. *Dev Psychol.* 1982; 18:199–214.
- Larson R, Csikszentmihalyi M, Graef R. Mood variability and the psychosocial adjustment of adolescents. *J Youth Adolesc.* 1980; 9:469–490. DOI: 10.1007/BF02089885 [PubMed: 24318310]
- Larson, R.; Richards, M. A.C.C. *Temporal Rhythms in Adolescence: Clocks, Calendars, and the Coordination of Daily Life.* Jossey-Bass Inc, Publishers; San Francisco, CA: 1998. Waiting for the weekend: Friday and Saturday nights as the emotional climax of the week; p. 37-51.
- Larson, RW.; Asmussen, L. Anger, worry, and hurt in early adolescence: An enlarging world of negative emotions. In: Colten, ME.; Gore, S., editors. *Adolescent Stress: Causes and Consequences.* Aldine de Gruyter; Hawthorne, NY: 1991. p. 21-41.
- Larson RW, Moneta G, Richards MH, Wilson S. Continuity, stability, and change in daily emotional experience across adolescence. *Child Dev.* 2002; 73:1151–1165. [PubMed: 12146740]
- Lau JYF, Guyer AE, Tone EB, Jenness J, Parrish JM, Pine DS, Nelson EE. Neural responses to peer rejection in anxious adolescents: Contributions from the amygdala-hippocampal complex. *Int J Behav Dev.* 2012; 36:36–44. DOI: 10.1177/0165025411406854
- Lazarus, RS. *Emotion and adaptation.* Oxford University Press; New York: 1991.
- Lee KH, Siegle GJ, Dahl RE, Hooley JM, Silk JS. Neural responses to maternal criticism in healthy youth. *Soc Cogn Affect Neurosci.* 2015; 10:902–912. nsu133 [pii]. DOI: 10.1093/scan/nsu133 [PubMed: 25338632]
- Lougheed JP, Craig WM, Pepler D, Connolly J, O'Hara A, Granic I, Hollenstein T. Maternal and Peer Regulation of Adolescent Emotion: Associations with Depressive Symptoms. *J Abnorm Child Psychol.* 2015; doi: 10.1007/s10802-015-0084-x
- Luo Q, Holroyd T, Majestic C, Cheng X, Schechter J, Blair RJ. Emotional automaticity is a matter of timing. *J Neurosci.* 2010; 30:5825–5829. DOI: 10.1523/JNEUROSCI.BC-5668-09.2010 [PubMed: 20427643]
- Masten CL, Eisenberger NI, Borofsky LA, McNealy K, Pfeifer JH, Dapretto M. Subgenual anterior cingulate responses to peer rejection: A marker of adolescents' risk for depression. *Dev Psychopathol.* 2011; 23:283–292. DOI: 10.1017/S0954579410000799 [PubMed: 21262054]
- Masten CL, Eisenberger NI, Borofsky LA, Pfeifer JH, McNealy K, Mazziotta JC, Dapretto M. Neural correlates of social exclusion during adolescence: understanding the distress of peer rejection. *Soc Cogn Affect Neurosci.* 2009; 4:143–157. DOI: 10.1093/scan/nsp007 [PubMed: 19470528]

- McRae K, Gross JJ, Weber J, Robertson ER, Sokol-Hessner P, Ray RD, Gabrieli JD, Ochsner KN. The development of emotion regulation: an fMRI study of cognitive reappraisal in children, adolescents and young adults. *Soc Cogn Affect Neurosci*. 2012; 7:11–22. DOI: 10.1093/scan/nsr093 [PubMed: 22228751]
- Meeus W. The study of adolescent identity formation 2000–2010: A review of longitudinal research. *J Res Adolesc*. 2011; 21:75–94. DOI: 10.1111/j.1532-7795.2010.00716.x
- Meeus W, Iedema J, Helsen M, Vollebergh W. Patterns of Adolescent Identity Development: Review of Literature and Longitudinal Analysis. *Dev Rev*. 1999; 19:419–461. DOI: 10.1006/drev.1999.0483
- Monahan, K.; Guyer, AE.; Silk, JS.; Fitzwater, T.; Steinberg, L. Integration of developmental neuroscience and contextual approaches to the study of adolescent psychopathology. In: Cicchetti, D., editor. *Developmental Psychopathology*. Wiley; Hoboken, NJ: 2016.
- Moore WE, Pfeifer JH, Masten CL, Mazziotta JC, Iacoboni M, Dapretto M. Facing puberty: associations between pubertal development and neural responses to affective facial displays. *Soc Cogn Affect Neurosci*. 2012; 7:35–43. DOI: 10.1093/scan/nsr066 [PubMed: 22228752]
- Morgan JK, Shaw DS, Forbes EE. Maternal depression and warmth during childhood predict age 20 neural response to reward. *J Am Acad Child Adolesc Psychiatry*. 2014; 53doi: 10.1016/j.jaac.2013.10.003
- Nelson, Da; Crick, NR. Rose-Colored Glasses:: Examining the Social Information-Processing of Prosocial Young Adolescents. *J Early Adolesc*. 1999; 19:17–38. DOI: 10.1177/0272431699019001002
- Nelson EE, Guyer AE. The development of the ventral prefrontal cortex and social flexibility. *Dev Cogn Neurosci*. 2011; 1:233–245. DOI: 10.1016/j.dcn.2011.01.002 [PubMed: 21804907]
- Nelson EE, Jarcho JM, Guyer AE. Social re-orientation and brain development: An expanded and updated view. *Dev Cogn Neurosci*. 2016; 17:118–127. DOI: 10.1016/j.dcn.2015.12.008 [PubMed: 26777136]
- Nelson EE, Lau JY, Jarcho JM. Growing pains and pleasures: How emotional learning guides development. *Trends Cogn Sci*. 2014; 18:99–108. DOI: 10.1016/j.tics.2013.11.003 [PubMed: 24405846]
- Nelson EE, Leibenluft E, McClure EB, Pine DS. The social re-orientation of adolescence: a neuroscience perspective on the process and its relation to psychopathology. *Psychol Med*. 2005; 35:163–174. [PubMed: 15841674]
- Norman KA, Polyn SM, Detre GJ, Haxby JV. Beyond mind-reading: multi-voxel pattern analysis of fMRI data. *Trends Cogn Sci*. 2006; 10:424–430. DOI: 10.1016/j.tics.2006.07.005 [PubMed: 16899397]
- Ochsner KN, Gross JJ. The cognitive control of emotion. *Trends Cogn Sci*. 2005; 9:242–249. DOI: 10.1016/j.tics.2005.03.010 [PubMed: 15866151]
- Op de Macks ZA, Gunther Moor B, Overgaauw S, Guroglu B, Dahl RE, Crone EA. Testosterone levels correspond with increased ventral striatum activation in response to monetary rewards in adolescents. *Dev Cogn Neurosci*. 2011; 1:506–516. DOI: 10.1016/j.dcn.2011.06.003 [PubMed: 22436568]
- Patton GC, Viner R. Pubertal transitions in health. *Lancet*. 2007; 369:1130–1139. DOI: 10.1016/S0140-6736(07)60366-3 [PubMed: 17398312]
- Paus T, Keshavan M, Giedd JN. Why do many psychiatric disorders emerge during adolescence? *Nat Rev Neurosci*. 2008; 9:947–957. DOI: 10.1038/nrn2513 [PubMed: 19002191]
- Peper JS, Dahl RE. The Teenage Brain: Surging Hormones--Brain-Behavior Interactions During Puberty. *Curr Dir Psychol Sci*. 2013; 22:134–139. DOI: 10.1177/0963721412473755 [PubMed: 26290625]
- Perlman SB, Huppert TJ, Luna B. Functional Near-Infrared Spectroscopy Evidence for Development of Prefrontal Engagement in Working Memory in Early Through Middle Childhood. *Cereb Cortex*. 2015; doi: 10.1093/cercor/bhv139
- Pessoa L. To what extent are emotional visual stimuli processed without attention and awareness? *Curr Opin Neurobiol*. 2005; 15:188–196. DOI: 10.1016/j.conb.2005.03.002 [PubMed: 15831401]

- Petanjek Z, Judas M, Simic G, Rasin MR, Uylings HB, Rakic P, Kostovic I. Extraordinary neoteny of synaptic spines in the human prefrontal cortex. *Proc Natl Acad Sci U S A*. 2011; 108:13281–13286. DOI: 10.1073/pnas.1105108108 [PubMed: 21788513]
- Pfeifer JH, Allen NB. Arrested development? Reconsidering dual-systems models of brain function in adolescence and disorders. *Trends Cogn Sci*. 2012; 16:322–329. DOI: 10.1016/j.tics.2012.04.011 [PubMed: 22613872]
- Pfeifer JH, Masten CL, Borofsky LA, Dapretto M, Fuligni AJ, Lieberman MD. Neural correlates of direct and reflected self-appraisals in adolescents and adults: when social perspective-taking informs self-perception. *Child Dev*. 2009; 80:1016–1038. DOI: 10.1111/j.1467-8624.2009.01314.x [PubMed: 19630891]
- Pfeifer JH, Peake SJ. Self-development: integrating cognitive, socioemotional, and neuroimaging perspectives. *Dev Cogn Neurosci*. 2012; 2:55–69. DOI: 10.1016/j.dcn.2011.07.012 [PubMed: 22682728]
- Poore JC, Pfeifer JH, Berkman ET, Inagaki TK, Welborn BL, Lieberman MD. Prediction-error in the context of real social relationships modulates reward system activity. *Front Hum Neurosci*. 2012; 6:218.doi: 10.3389/fnhum.2012.00218 [PubMed: 22891055]
- Price RB, Allen KB, Silk JS, Ladouceur CD, Ryan ND, Siegle GJ. Vigilance in the Laboratory Predicts Avoidance in the Real World: A Dimensional Analysis of Neural, Behavioral, and Ecological Momentary Data in Anxious Youth. *Dev Cogn Neurosci*. 2016; 19:128–136. DOI: 10.1016/j.dcn.2016.03.001 [PubMed: 27010577]
- Romeo RD. Adolescence: A central event in shaping stress reactivity. *Dev Psychobiol*. 2010; 52:244–253. DOI: 10.1002/dev.20437 [PubMed: 20175102]
- Rowe R, Maughan B, Worthman CM, Costello EJ, Angold A. Testosterone, antisocial behavior, and social dominance in boys: Pubertal development and biosocial interaction. *Biol Psychiatry*. 2004; 55:546–552. DOI: 10.1016/j.biopsych.2003.10.010 [PubMed: 15023584]
- Scherf KS, Smyth JM, Delgado MR. The amygdala: an agent of change in adolescent neural networks. *Horm Behav*. 2013; 64:298–313. DOI: 10.1016/j.yhbeh.2013.05.011 [PubMed: 23756154]
- Schriber RAA, Guyer AEE. Adolescent neurobiological susceptibility to social context. *Dev Cogn Neurosci*. 2015; 19:1–18. DOI: 10.1016/j.dcn.2015.12.009 [PubMed: 26773514]
- Schultz W. Behavioral theories and the neurophysiology of reward. *Annu Rev Psychol*. 2006; 57:87–115. DOI: 10.1146/annurev.psych.56.091103.070229 [PubMed: 16318590]
- Schulz KM, Sisk CL. Organizing actions of adolescent gonadal steroid hormones on brain and behavioral development. *Neurosci Biobehav Rev*. 2016
- Sebastian C, Viding E, Williams KD, Blakemore SJ. Social brain development and the affective consequences of ostracism in adolescence. *Brain Cogn*. 2010; 72:134–145. DOI: 10.1016/j.bandc.2009.06.008 [PubMed: 19628323]
- Shulman EP, Smith AR, Silva K, Icenogle G, Duell N, Chein J, Steinberg L. The dual systems model: Review, reappraisal, and reaffirmation. *Dev Cogn Neurosci*. 2016; 17:103–117. DOI: 10.1016/j.dcn.2015.12.010 [PubMed: 26774291]
- Siegel J, Shaughnessy MF. There's a first time for everything: understanding adolescence. *Adolescence*. 1995; 30:217–221. [PubMed: 7625260]
- Silk JS, Davis S, McMakin DL, Dahl RE, Forbes EE. Why do anxious children become depressed teenagers? The role of social evaluative threat and reward processing. *Psychol Med*. 2012a; 42:2095–2107. DOI: 10.1017/S0033291712000207 [PubMed: 22340187]
- Silk JS, Siegle GJ, Lee KH, Nelson EE, Stroud LR, Dahl RE. Increased neural response to peer rejection associated with adolescent depression and pubertal development. *Soc Cogn Affect Neurosci*. 2013; 9:1798–1807. DOI: 10.1093/scan/nst175 [PubMed: 24273075]
- Silk JS, Stroud LR, Siegle GJ, Dahl RE, Lee KH, Nelson EE. Peer acceptance and rejection through the eyes of youth: pupillary, eyetracking and ecological data from the Chatroom Interact task. *Soc Cogn Affect Neurosci*. 2012b; 7:93–105. DOI: 10.1093/scan/nsr044 [PubMed: 21775386]
- Silvers JA, McRae K, Gabrieli JD, Gross JJ, Remy KA, Ochsner KN. Age-related differences in emotional reactivity, regulation, and rejection sensitivity in adolescence. *Emotion*. 2012; 12:1235–1247. DOI: 10.1037/a0028297 [PubMed: 22642356]

- Sisk CL. Hormone-dependent adolescent organization of socio-sexual behaviors in mammals. *Curr Opin Neurobiol.* 2016; 38:63–68. DOI: 10.1016/j.conb.2016.02.004 [PubMed: 26963894]
- Sisk CL, Zehr JL. Pubertal hormones organize the adolescent brain and behavior. *Front Neuroendocr.* 2005; 26:163–174. DOI: 10.1016/j.yfrne.2005.10.003
- Smith AR, Steinberg L, Chein J. The role of the anterior insula in adolescent decision making. *Dev Neurosci.* 2014; 36:196–209. DOI: 10.1159/000358918 [PubMed: 24853135]
- Smith LB, Thelen E. Development as a dynamic system. *Trends Cogn Sci.* 2003; doi: 10.1016/S1364-6613(03)00156-6
- Somerville LH. The teenage brain: Sensitivity to social evaluation. *Curr Dir Psychol Sci.* 2013; 22:121–127. DOI: 10.1177/0963721413476512 [PubMed: 24761055]
- Somerville LH, Jones RM, Casey BJ. A time of change: behavioral and neural correlates of adolescent sensitivity to appetitive and aversive environmental cues. *Brain Cogn.* 2010; 72:124–133. DOI: 10.1016/j.bandc.2009.07.003 [PubMed: 19695759]
- Spear LP. Adolescent neurodevelopment. *J Adolesc Heal.* 2013; doi: 10.1016/j.jadohealth.2012.05.006
- Spear LP. Heightened stress responsivity and emotional reactivity during pubertal maturation: Implications for psychopathology. *Dev Psychopathol.* 2009; 21:87–97. DOI: 10.1017/S0954579409000066 [PubMed: 19144224]
- Spear LP. The adolescent brain and age-related behavioral manifestations. *Neurosci Biobehav Rev.* 2000; 24:417–463. [PubMed: 10817843]
- Spielberg JM, Forbes EE, Ladouceur CD, Worthman CM, Olinio TM, Ryan ND, Dahl RE. Pubertal testosterone influences threat-related amygdala-orbitofrontal cortex coupling. *Soc Cogn Affect Neurosci.* 2015a; 10:408–415. DOI: 10.1093/scan/nsu062 [PubMed: 24795438]
- Spielberg JM, Jarcho JM, Dahl RE, Pine DS, Ernst M, Nelson EE. Anticipation of peer evaluation in anxious adolescents: Divergence in neural activation and maturation. *Soc Cogn Affect Neurosci.* 2015b; 10:1084–1091. DOI: 10.1093/scan/nsu165 [PubMed: 25552568]
- Spielberg JM, Olinio TM, Forbes EE, Dahl RE. Exciting fear in adolescence: does pubertal development alter threat processing? *Dev Cogn Neurosci.* 2014; 8:86–95. DOI: 10.1016/j.dcn.2014.01.004 [PubMed: 24548554]
- Steinberg L. A social neuroscience perspective on adolescent risk-taking. *Dev Rev.* 2008; 28:78–106. DOI: 10.1016/j.dr.2007.08.002 [PubMed: 18509515]
- Steinberg L. Cognitive and affective development in adolescence. *Trends Cogn Sci.* 2005; 9:69–74. DOI: 10.1016/j.tics.2004.12.005 [PubMed: 15668099]
- Steinberg L, Cauffman E. Maturity of judgment in adolescence: Psychosocial factors in adolescent decision making. *Law Hum Behav.* 1996; doi: 10.1007/BF01499023
- Steinberg L, Morris AS. Adolescent development. *Annu Rev Psychol.* 2001; 52:83–110. [PubMed: 11148300]
- Steinberg, L.; Silk, JS. Parenting adolescents. In: Bornstein, MH., editor. *Handbook of Parenting: Vol. 1: Children and Parenting.* Lawrence Erlbaum Associates; Mahwah, NJ: 2002. p. 103-133.
- Stephanou K, Davey CG, Kerestes R, Whittle S, Pujol J, Yucel M, Fornito A, Lopez-Sola M, Harrison BJ. Brain functional correlates of emotion regulation across adolescence and young adulthood. *Hum Brain Mapp.* 2016; 37:7–19. DOI: 10.1002/hbm.22905 [PubMed: 26596970]
- Suleiman AB, Harden KP. The importance of sexual and romantic development in understanding the developmental neuroscience of adolescence. *Dev Cogn Neurosci.* 2016; 17:145–147. DOI: 10.1016/j.dcn.2015.12.007 [PubMed: 26778337]
- Takesian AE, Hensch TK. Balancing plasticity/stability across brain development. *Prog Brain Res.* 2013; 207:3–34. DOI: 10.1016/B978-0-444-63327-9.00001-1 [PubMed: 24309249]
- Tan PZ, Lee KH, Dahl RE, Nelson EE, Stroud LJ, Siegle GJ, Morgan JK, Silk JS. Associations between maternal negative affect and adolescent's neural response to peer evaluation. *Dev Cogn Neurosci.* 2014; 8:28–39. S1878-9293(14)00008-5 [pii]. DOI: 10.1016/j.dcn.2014.01.006 [PubMed: 24613174]
- Telzer EH, Fuligni AJ, Lieberman MD, Galvan A. Meaningful family relationships: neurocognitive buffers of adolescent risk taking. *J Cogn Neurosci.* 2013; 25:374–387. DOI: 10.1162/jocn_a_00331 [PubMed: 23163412]

- Telzer EH, Fuligni AJ, Lieberman MD, Miernicki ME, Galván A. The quality of adolescents' peer relationships modulates neural sensitivity to risk taking. *Soc Cogn Affect Neurosci*. 2015; 10:389–398. DOI: 10.1093/scan/nsu064 [PubMed: 24795443]
- Thompson, RA. Emotion regulation: A theme in search of definition. In: Fox, NA., editor. *The Development of Emotion Regulation: Biological and Behavioral Considerations*. The University of Chicago Press; Chicago: 1994. p. 25-52.
- Tyborowska A, Volman I, Smeekens S, Toni I, Roelofs K. Testosterone during Puberty Shifts Emotional Control from Pulvinar to Anterior Prefrontal Cortex. *J Neurosci*. 2016; 36:6156–6164. DOI: 10.1523/JNEUROSCI.3874-15.2016 [PubMed: 27277794]
- van den Bos W, Cohen MX, Kahnt T, Crone EA. Striatum-medial prefrontal cortex connectivity predicts developmental changes in reinforcement learning. *Cereb Cortex*. 2012; 22:1247–1255. DOI: 10.1093/cercor/bhr198 [PubMed: 21817091]
- van den Bos W, van Dijk E, Westenberg M, Rombouts SA, Crone EA. Changing brains, changing perspectives: the neurocognitive development of reciprocity. *Psychol Sci*. 2011; 22:60–70. DOI: 10.1177/0956797610391102 [PubMed: 21164174]
- Van Hoorn J, Van Dijk E, Güro lu B, Crone EA. Neural correlates of prosocial peer influence on public goods game donations during adolescence. *Soc Cogn Affect Neurosci* nsw013. 2016; doi: 10.1093/scan/nsw013
- Vijayakumar N, Whittle S, Yucel M, Dennison M, Simmons J, Allen NB. Thinning of the lateral prefrontal cortex during adolescence predicts emotion regulation in females. *Soc Cogn Affect Neurosci*. 2014; 9:1845–1854. DOI: 10.1093/scan/nst183 [PubMed: 24532701]
- Vuilleumier P, Armony JL, Driver J, Dolan RJ. Effects of attention and emotion on face processing in the human brain: an event-related fMRI study. *Neuron*. 2001; 30:829–841. [PubMed: 11430815]
- Weinstein SM, Mermelstein R. Relations between daily activities and adolescent mood: the role of autonomy. *J Clin Child Adolesc Psychol*. 2007; 36:182–194. DOI: 10.1080/15374410701274967 [PubMed: 17484691]
- Welborn BL, Lieberman MD, Goldenberg D, Fuligni AJ, Galván A, Telzer EH. Neural mechanisms of social influence in adolescence. *Soc Cogn Affect Neurosci*. 2015; 11:100–109. DOI: 10.1093/scan/nsv095 [PubMed: 26203050]
- Werker JF, Hensch TK. Critical periods in speech perception: new directions. *Annu Rev Psychol*. 2015; 66:173–196. DOI: 10.1146/annurev-psych-010814-015104 [PubMed: 25251488]
- Whittle S, Simmons JG, Dennison M, Vijayakumar N, Schwartz O, Yap MBH, Sheeber L, Allen NB. Positive parenting predicts the development of adolescent brain structure: A longitudinal study. *Dev Cogn Neurosci*. 2014; 8:7–17. doi:<http://dx.doi.org/10.1016/j.dcn.2013.10.006>. [PubMed: 24269113]
- Will GJ, Crone EA, van den Bos W, Guroglu B. Acting on observed social exclusion: Developmental perspectives on punishment of excluders and compensation of victims. *Dev Psychol*. 2013; 49:2236–2244. DOI: 10.1037/a0032299 [PubMed: 23544860]
- Will GJ, van Lier PAC, Crone EA, Güro lu B. Chronic Childhood Peer Rejection is Associated with Heightened Neural Responses to Social Exclusion During Adolescence. *J Abnorm Child Psychol*. 2016; 44:43–55. DOI: 10.1007/s10802-015-9983-0 [PubMed: 25758671]
- Zeman J, Cassano M, Perry-Parrish C, Stegall S. Emotion regulation in children and adolescents. *J Dev Behav Pediatr*. 2006; 27:155–168. [PubMed: 16682883]