

**Neurobiological Development in Adolescence and Young Adulthood: Implications for
Positive Youth Adjustment**

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Since the advent of magnetic resonance imaging (MRI), and the first MRI scans of children in the 1990s, the study of the developing brain has increased exponentially, contributing to our understanding of both typical and atypical brain development. Prior to MRI, much of our understanding of brain development came from studies of people who suffered brain damage to particular parts of the brain, or from postmortem studies of youth who had died prematurely. The ability to study the developing brain *in vivo* has provided unprecedented opportunities to further our understanding of changes in the brain across the lifespan. Based on functional and structural MRI research over the past two decades, we now know that the brain is rapidly changing and adapting to its environment across the first three decades of life and beyond. Indeed, adolescence is marked by dramatic changes in brain development, second only to infancy, with continued neural development well into the 20s and 30s. Such developmental changes in the brain promote learning, skill acquisition, empathy, and prosocial behaviors, which contribute to positive youth development (Crone & Fuligni, 2020; Telzer, 2016).

At the same time, the adolescent brain has been portrayed as defective and viewed as the cause of suboptimal behaviors. Media depictions of the adolescent brain are fraught with images of teens' brains with regions dedicated to sex, sleep, and emotional liability. For example, an article in the Wall Street Journal, "*What's wrong with the teenage mind?*" includes a graphic of a teen's brain with regions for "angst," "self-control under construction," and "L8R" (Gopnik, 2012). Although well-intentioned and meant to be humorous, such media depictions of adolescent brain development paint an overwhelmingly negative picture of adolescence. Although portrayed less, there are many positive and adaptive behaviors highlighted by the media as well, including adolescents engaging in youth-led demonstrations, such as demonstrations to promote antigun violence or address climate change. In fact, the activists of

the youth movement “March for Our Lives” were short-listed for person of the year by Time Magazine in 2018, and Greta Thunberg, an adolescent activist for climate change, was the 2019 person of the year. Nonetheless, these examples of adolescents engaging in positive behaviors are often overlooked or attributed to a select few, which may reinforce the stereotype of negative behaviors of adolescence.

Characterizing the adolescent brain as immature and broken may contribute to negative stereotypes of adolescents. Indeed, public perceptions of the teenage brain are largely negative. For example, when asked to generate free associations with the word “teenage brain,” adolescents and adults describe undesirable behaviors (e.g., “irresponsible,” “lazy,” “irritating”) more often than desirable behaviors (e.g., “independent,” “kind,” “creative”; Altikulaç, Lee, van der Veen, Benneker, Krabbendam, & van Atteveldt, 2019). Such stereotypes can impact adolescents’ self-concept and behaviors, becoming self-fulfilling prophecies (Buchanan & Hughes, 2009). Youth’s ideas about adolescence reflect what they see as normative during this phase of development, which they may use as a standard for their own behavior. If they believe adolescence is a time of irresponsibility, laziness, or heightened risk taking, they may engage more in that behavior, especially if they consider it inevitable due to their “immature brain”. Indeed, correlational, longitudinal, and experimental research has shown that when adolescents hold more negative stereotypes of adolescence, they are more likely to engage in risk taking, have more conflictual family relationships, and show poorer academic performance (Altikulaç et al., 2019; Buchanan & Hughes, 2009; Qu, Pomerantz, McCormick, & Telzer, 2018; Qu, Pomerantz, & Wu, 2020). Interestingly, such negative stereotypes even become instantiated in the developing brain. For instance, adolescents who believe that adolescence is characterized by decreasing responsibility to the family show longitudinal increases in risk-taking behavior as

well as longitudinal increases in prefrontal cortex (PFC) activation when engaging in cognitive control tasks (Qu et al., 2018). Thus, some of the negative behaviors that emerge during adolescence are likely byproducts of stereotypes that become self-fulfilling prophecies and exacerbate or even create problems that might not otherwise exist.

Rather than contributing to problem behaviors, the developing brain is evolutionarily programmed to adapt and learn, to promote social connection and competence, and to set the stage for lifelong flourishing. Adolescence is a sensitive period during which the brain is especially tuned to the social context and youth are building social connections, learning to care and engage in other-oriented tendencies, and developing competence, confidence and character. This chapter seeks to unpack the many ways that the developing brain contributes to positive youth development during the adolescent years.

Theoretical Contributions of Brain Development to Positive Youth Adjustment

Many theoretical models have been proposed to link neural changes to adolescent behavior. Most models to date (e.g., dual systems model (Steinberg, 2008), imbalance model (Casey, 2015) have focused primarily on the vulnerabilities and deficits of adolescence, with specific reference to rapid development of reward sensitivity coupled with slower development of cognitive control, which is proposed to bias adolescents towards socioemotionally rewarding contexts during a developmental period when they are unable to effectively regulate their behavior, resulting in suboptimal decision making (e.g., risk taking). Here, we focus on several recent models that highlight the opportunities of adolescent brain development. Specifically, these theories address brain regions that facilitate motivation and goal flexibility, susceptibility to positive environmental contexts, and integration of past experiences into decision-making. Importantly, though these models acknowledge and explain negative aspects of adolescence,

they also hold promise for describing how the developing brain contributes to positive youth development.

Models of motivation and goal flexibility. Teens often face unpredictable, complex, and rapidly changing social challenges. Dual-process theories (e.g., dual systems model, imbalance model), pit cognitive control systems against valuation systems, and assume that adolescent behaviors occur because of an internal failure of cognitive control. In contrast, models of motivation and goal flexibility underscore the adaptive function of the adolescent brain for promoting positive developmental outcomes. The natural remodeling of the brain (e.g., synaptic pruning) around the time of puberty introduces plasticity in brain regions, particularly in networks involved in motivation and goal flexibility (e.g., PFC; Crone & Dahl, 2012). This helps teens adapt quickly to their ever-changing environment and can help focus their motivation toward the things they value. Of course, this could lead to negative trajectories for teens who value unhealthy incentives, but a strength of this model is that it also recognizes that many teens have positive goals, and the PFC helps them successfully explore and take adaptive risks. Thus, rather than a one-size fits all model of the PFC as deficient, the PFC is proposed to be flexible, coming online in the moment to respond to shifting priorities according to social incentives (Do, Sharp, & Telzer, 2020). The capacity of the PFC to be flexibly recruited according to goal priorities may enable adolescents to effectively engage cognitive control systems in situations in which they are motivated to do so, which may confer advantages for promoting social motivation to explore, take risks, and try new behaviors, but may also result in negative trajectories, particularly in response to unhealthy incentives (e.g., motivation towards negative goals such as substance use; Crone & Dahl, 2012). Of course, substance use can also serve positive functions such as building peer relationships, so the positive and negative goals may be intertwined for

particular behaviors. Although not explicitly described in this framework, whether youth demonstrate positive or negative developmental outcomes may depend on the sociocultural context.

Neurobiological susceptibility to social context framework. Other models of adolescent brain development explicitly underscore the importance of the sociocultural context for determining positive or negative trajectories by focusing on person-environment interactions. The Neurobiological Susceptibility to Social Context Framework (Do, Prinstein, & Telzer, in press; Schriber & Guyer, 2016), proposes that individuals vary in their sensitivity to the social environment as a function of neurobiological factors. Adolescents with high neurobiological susceptibility will show adjustment outcomes in a for-better or for-worse fashion depending on their social environment. Adolescents with high neurobiological susceptibility will be both more vulnerable to aversive contexts (e.g., harsh parenting), but also more responsive to positive contexts (e.g., supportive parenting; Rudolph et al., 2020). This model is particularly promising for understanding positive youth development, as it explicitly focuses on the opportunities afforded by high neurobiological sensitivity; youth will thrive in positive contexts, *especially* if they are neurobiologically sensitive. Thus, rather than serving a monolithically negative role, neurobiological sensitivity can be highly adaptive when youth are in positive sociocultural contexts.

Experience-driven models. Finally, other models take into account how prior experience interacts with the developing brain to inform adolescent behavior. Experience-dependent plasticity involves neural changes in response to the environment, whereby neural circuits adapt to an ever-changing constellation of internal and external inputs. The Experience-Driven Adaptive Cognitive Model of adolescence proposes that the ability to incorporate prior

experiences into task-relevant responses promotes more adaptive executive function during adolescence (Murty, FeldmanHall, Hunter, Phelps, & Davachi, 2016). In particular, the neural systems underlying basic memory processing (e.g., hippocampus) and executive functions (e.g., PFC) reach critical maturation around adolescence, and strengthening of PFC-hippocampus integration allows individuals to reliably probe prior experiences in order to select behaviors that are most adaptive to facilitate task-relevant goals. Thus, refinement in executive function emerges in adolescence, not only from maturation of cognitive control-related neural processing, but also from the accumulation of experience and the ability to engage the hippocampus in order to develop heuristics that reduce the need for trial and error, and promotes learning by relying on prior knowledge and experience (Murty et al., 2016).

Empirical Contributions of Brain Development to Positive Youth Adjustment

In this section we will review how changes in the brain undergird four key changes that take place during adolescence: becoming more oriented toward others, establishing a clearer sense of identity, making adaptive decisions, and learning via cognitive flexibility. It is important to note that each of these domains of growth carries certain vulnerabilities that are often thought of negatively, such as hypersensitivity to peer influence, identity insecurity, impulsivity and risk-taking behavior. Despite these possibilities, we highlight the positive aspects of these changes and show how they help adolescents flourish in the present and prepare for the future decisions, roles, and responsibilities of adulthood. We also introduce how emerging cross-cultural research is extending our understanding of brain development and its association with positive youth development.

Mentalizing and other-oriented behaviors. One of the primary changes that occurs in adolescence is a shift from self-oriented behavior to other-oriented behavior. As their social

interactions become more complex, adolescents increasingly model their own behavior on those of their peers and learn how their own actions affect others (Burnett & Blakemore, 2009).

Although basic forms of theory of mind are in place by early childhood, more complex social-cognitive skills develop throughout adolescence. Mentalizing – the ability to take the perspective of others and to understand others’ emotions, intentions and beliefs – is supported by neurobiological changes in the putative “social brain” (Blakemore, 2008). When thinking about the intentions of others, adolescents recruit the medial PFC (mPFC) more than adults do, whereas adults recruit the posterior superior temporal sulcus (pSTS) more than adolescents do (Blakemore, den Ouden, Choudhury, & Frith, 2007). Moreover, from childhood (i.e., age 9 years) to adolescence (i.e., age 16 years), there is an increase in activation of the dorsal portion of the mPFC and a decrease in activation in the ventral portion when engaging in theory of mind tasks (Moriguchi, Ohnishi, Mori, Matsuda, & Komachi, 2007). Other studies have also shown that younger adolescents recruit the ventral portion of the mPFC more strongly than older adolescents when mentalizing about the thoughts of others (Gunther Moor et al., 2012). Together, these studies suggest a potential developmental shift in the neural regions supporting mentalizing, which might reflect a change in the strategies used to engage in theory of mind and more advanced social cognition across adolescence.

Mentalizing may be the initial building block that contributes to other-oriented behaviors. Indeed, better perspective-taking abilities mediate age-related increases in prosocial behavior in children and adolescents (Güroglu, van des Bos, & Crone, 2014). Furthermore, neural activation and structural development of brain regions involved in mentalizing support engagement in prosocial behaviors. For example, higher prosociality is related to faster cortical thinning during adolescence followed by attenuation of this thinning during the transition to early adulthood in

regions involved in mentalizing and social cognition (e.g., mPFC, temporoparietal junction (TPJ), pSTS; Ferschmann et al., 2019). Moreover, late adolescents who show greater mPFC activation when observing a peer in distress subsequently engage in more spontaneous prosocial behavior towards the peer (Masten, Morelli, & Eisenberger, 2011), and adolescents who show greater TPJ activation when viewing prosocial scenes donate more money to charities (Tashjian, Weissman, Guyer, & Galván, 2018). Additionally, relative to older adolescents, younger adolescents show greater dorsomedial PFC (dmPFC) and pSTS activation when making prosocial decisions in the presence of peers (van Hoorn et al., 2016), and early adolescents show peaks in activation in the pSTS relative to children and mid-adolescents when making costly decisions that benefit their peers (Do, McCormick, & Telzer, 2019), suggesting that neural regions involved in mentalizing are critical for prosocial behavior, particularly during early adolescence when youth also show peaks in self-conscious emotions and sensitivity to peers (Somerville et al., 2013). Together these results underscore early adolescence as a potential sensitive period during which social-cognitive neural regions come online to promote other-oriented behaviors.

The ability to take the perspective of others may facilitate vicarious reward processing (i.e., feeling good when others benefit), thereby promoting engagement in behaviors that benefit others (e.g., sharing, prosocial and altruistic behaviors). Also referred to as the “warm glow”, this perspective underscores that it feels good to help others (Moll, Zahn, De Oliveira-Souza, Krueger, & Grafman, 2005), perhaps by providing a sense of meaning and happiness to the giver (Dunn, Aknin, & Norton, 2008). Indeed, adolescents show heightened activation in the ventral striatum (VS) not only when gaining rewards for themselves but also when gaining rewards for others, including their family and close friends (e.g., Braams & Crone, 2017; Braams, Peters,

Peper, Güroglu, & Crone, 2014; Telzer, Masten, Berkman, Lieberman, & Fuligni, 2010; Telzer, Fuligni, & Galván, 2016). This heightened VS response is elevated in mid adolescence relative to childhood and adulthood when winning for their family (Braams & Crone, 2017), providing further evidence that adolescence may be a sensitive period for other-oriented behaviors, perhaps because such behaviors provide a sense of self-worth and meaning. Indeed, adolescents who show greater VS activation when making prosocial decisions for their family, even when it comes at a cost to the self, report a greater sense of happiness and role fulfillment when they help their family in daily life (Telzer et al., 2010).

Interestingly, there are adolescent-specific peaks in VS activation for both self-oriented (Braams et al., 2014) and vicarious (Braams & Crone, 2017) rewards. This heightened VS activation has potentially different psychological implications. Whereas adolescents with greater VS activation when making costly prosocial decisions for their family show improvements in positive adjustment over the high school years, including declines in risk-taking behaviors and depressive symptoms, adolescents with heightened VS activation to risky rewards or self-oriented rewards show increases in risk taking and depressive symptoms (Telzer, Fuligni, Lieberman, & Galván, 2013, 2014; Qu, Galván, Fuligni, Lieberman, & Telzer, 2015). Vicarious reward-related activation in the VS may represent a motivational orientation toward engaging in inherently meaningful activities that increase feelings of value and meaning, thereby leading to positive adjustment over time, whereas self-oriented reward-related activation in the VS may represent a motivational orientation to negative or maladaptive rewards in one's environment. Together, these findings suggest that reward-related neural responses pose both opportunities for positive development, but also potential vulnerabilities, underscoring adolescence as a potential inflection point during which neurobiological development can set the stage for long-term

positive or negative trajectories. The cultural context, quality of youths' social relationships, and their environment may play a role in guiding and shaping such developmental pathways.

Identity and self-concept development. The development of mentalizing and perspective taking abilities also heavily influences adolescents' sense of identity and self-concept. Children's self-concepts tend to be simple, unrealistic, and primarily based in the child's own experience and perspective (Harter, 2012). As perspective taking abilities increase, other people are incorporated into self-concepts. Thus, in addition to direct self-appraisals (i.e., "What do I think of myself"), adolescent self-concepts become more based in reflected self-appraisals (i.e., "What do others think of me") and social comparisons (i.e., "How am I compared to others"; Callan, Kim, & Matthews, 2015; Harter, 2012). Though this time of flux often brings about dips in overall self-perceptions, in normative development these are temporary and an important part of establishing stable, realistic, and multifaceted self-concepts (Harter, 2012).

An increasing body of research has shown that the mPFC is particularly important in thinking about the self (e.g., self-evaluation, social comparison; Crone & Fuligni, 2020; Denny, Kober, Wager, & Ochsner, 2012). From a developmental perspective, the mPFC is one of the last brain structures to fully develop, undergoing gray matter volume reduction (i.e., synaptic pruning) into the early twenties (Mills et al., 2014). Furthermore, though the mPFC is related to self-processing across developmental periods, research shows that activation is greater for adolescents relative to both children and adults (Crone & Fuligni, 2020; Pfeifer et al., 2009) and that this increase is associated with the onset of puberty (Pfeifer et al., 2013). This pattern, along with similar activation in other "social brain" regions (i.e., TPJ, pSTS), suggests that neural changes during adolescence support the shifting of self-concepts toward becoming more social

(Pfeifer et al., 2009). Thus, the inclusion of others into the self helps foster self-concepts that prepare adolescents for adulthood.

Several changes occur in self-concept across adolescents. First, self-concepts become more diverse, meaning that adolescents differentiate self-evaluations across domains and can also recognize and appreciate both positive and negative traits within themselves (Harter, 2012). In this vein, researchers have tested neural responses to evaluating the self in different domains, such as social, academic, and physical (Pfeifer et al., 2013; van der Cruijssen, Peters, van der Aar, & Crone, 2018). Across different age groups, the mPFC shows heightened activation during self-evaluations regardless of domain (van der Cruijssen et al., 2018). However, age-related increases in mPFC activation are found to be domain-specific, such that mPFC activation increases from childhood to adolescence in the physical and social (compared to academic) domains (Pfeifer et al., 2013; van der Cruijssen et al., 2018). As the mPFC is important for social cognition, these results suggest that greater inclusion of others in self-concepts may differ by domain, showing that adolescents are more likely to think of others when evaluating their physical appearance and their social interactions.

A second change in self-concepts during adolescence is the ability to comprehend and accept both positive and negative traits in oneself. Compared to children and young adults, mid and late adolescents show less differentiation between positive and negative statements in terms of striatal activation (van der Cruijssen et al., 2018). In other words, children and adults show greater striatal activation toward positive statements, suggesting that positive statements are more salient for their self-evaluations. Adolescents, on the other hand, show nearly equal striatal activation to both positive and negative statements, suggesting that the two are equally salient for self-evaluations. As teens become more aware of negative traits, it appears that the brain more

equally weighs positive and negative aspects of the self. This increased sensitivity to negative traits may contribute to positive outcomes. For example, adolescents with higher evaluations of their academic self are more likely to have thought about their future educational choices, and this is mediated by precuneus activation for negative self-statements (van der Aar, Peters, van der Crujisen, & Crone, 2019). Greater precuneus activity toward negative statements may reflect greater social comparison, indicating that social comparison when evaluating negative self-statements may be linked to greater motivation to prepare for the future. Thus, the increased recognition of negative traits about the self may help adolescents better prepare for adulthood.

Third, heightened social awareness helps bring about greater clarity and stability in adolescents' self-concepts. One study compared direct (i.e., what people think of themselves) and reflected (i.e., what they think others think about them) self-appraisals across 11- to 21-year-olds (van der Crujisen, Peters, Zoetendaal, Pfeifer, & Crone, 2019). Findings revealed that with age, not only did self-appraisals become more positive overall, but direct and reflected self-appraisals become more similar at both the behavioral and neural level. In other words, what older adolescents think about themselves and what they perceive others to think about themselves converges, suggesting greater stability in self-concept. Furthermore, with age, mPFC activity during both types of appraisals also converged, showing that the brain is processing direct and reflected appraisals more and more similarly across adolescence. Thus, stability in self-concept is aided by the ability to mentalize/incorporate others' minds into the self, and evidence suggests that the mPFC is closely related to these changes (see Crone & Fuligni, 2020). Taken together, an increasing body of neuroscience research suggests that the developing brain, particularly the mPFC, plays an important role in the development of adolescent self-concepts.

Developments in social cognition contribute to more diverse and stable self-concepts that prepare adolescents for their future as adults.

Adaptive risk-taking behaviors. One of the hallmarks of the adolescent period is a rise in sensation-seeking and risk taking. The focus of much research, funding mechanisms, popular media, and parental worries has centered on how adolescence is a time of vulnerability when youths engage in health-compromising behavior such as drug experimentation, excessive drinking, risky sex, and reckless behaviors. Indeed, statistics such as those showing that morbidity and mortality rates increase 300% from childhood to adolescence (CDC, 2014) contribute to these sentiments, and thus render adolescent risk taking a public health concern. But what is often overlooked is that the survival rate of US high-school students is at 99.96% (Willoughby, Good, Adachi, Hamza, & Tavernier, 2013), and most adolescents navigate the teenage years with few problems. In fact, extreme problem behaviors are concentrated in a small proportion of the adolescent population yet they are often used to describe adolescents as a whole.

A popular misconception about adolescents is that their heightened risky behavior is maladaptive. There is an evolutionary basis as to why risk taking during adolescence is essential for survival (e.g., Ellis et al., 2012). For instance, adolescents' risk taking may serve a social goal to establish a social hierarchy within their peer network and to navigate their social world (Ellis et al., 2012). Risk taking may also enable youth to adapt to new situations by adjusting their risky or explorative behaviors to meet the unpredictable demands of the new environment. Thus, there are times and situations when risk taking is in fact advantageous and adaptive. Indeed, enhanced exploration and tolerance of ambiguity during adolescence may facilitate learning and the acquisition of experience (e.g., Tymula et al., 2012). Over time, experience gained during

risk taking can be integrated into future decision-making, which is deemed necessary for preparing adolescents for adult roles and responsibilities.

One form of adaptive risk taking relies on the expected value (EV) of one's decision: in situations where the EV of the risky decision is higher than the EV of the known or safe decision, it is better to make the risky decision. The opposite also holds true, in which case it is smarter to avoid the risky decision. The tracking and utilization of EV information in decision-making develops during adolescence (e.g., Barkley-Levenson & Galván, 2014).

Developmentally, children show a deficit or weakness in using EV information when making risky decisions whereas adults make more risky decisions as EV increases (Levin, Weller, Pederson, & Harshman, 2007; van Duijvenvoorde et al., 2015). Compared to adults, adolescents are more sensitive to EV information such that they are more likely to take risks in a gambling task as EV increases (Barkley-Levenson & Galván, 2014; van Duijvenvoorde et al., 2015). This parallels neural differences in the VS, such that adolescents recruit greater VS activation as EV increases, whereas this pattern is not observed in adults (Barkley-Levenson & Galván, 2014).

This VS hyperactivation to EV information in adolescents – a neural phenotype often paired with poor, risky decisions (e.g., Chein, Albert, O'Brien, Uckert, & Steinberg, 2011) – suggests that adolescents' heightened sensitivity to rewards may be the driving force behind their rational and adaptive decisions as well. Therefore, adolescents' VS hyperactivation may be re-directed towards promoting and engaging in adaptive risks. In addition, adolescents and adults similarly recruit mPFC and dorsolateral PFC (dlPFC) as EV increases (Barkley-Levenson & Galván, 2014), which indicates that adolescents display mature, adult-like neural patterns in value computation.

Moreover, not all risk taking is negative (e.g., substance use), and adolescents may engage in risky behaviors that are positive (e.g., trying out for a new sports team; Duell & Steinberg, 2018) or even prosocial (e.g., standing up against a school bully; Do, Guassi Moreira, & Telzer, 2017). Positive risk taking is socially acceptable and constructive and is ultimately aimed to benefit the individual (Duell & Steinberg, 2018). One example of positive risk taking that may be particularly salient to adolescents is disclosure of intimate information – an opportunity to connect with others that also harbors the possibility of rejection or embarrassment (Omarzu, 2000). In addition to recruiting reward processing regions as observed in adults (Tamir & Mitchell, 2012), self-disclosure in youth further recruits the dmPFC and TPJ (Vijayakumar & Pfeifer, 2020), which suggests that taking the risk to share personal information involves mentalizing processes.

Prosocial risk taking refers to other-oriented risk taking where an individual's risky decisions are sought to benefit others (Do et al., 2017) such as acts of volunteerism that highlight adolescents' moral reasonings and other-oriented respondings. The intersection of prosocial and risk-taking behaviors challenges the widely supported model of adolescence as a period of heightened vulnerability by suggesting that traditionally negative behaviors, like risk taking, could foster positive development if those risks are taken to help others. Interestingly, recent work illustrates that risk-taking behaviors and positive, prosocial behaviors are linked. For example, prosocial and rebellious behaviors both show quadratic age effects, peaking in late adolescence, with parallel trajectories of structural and functional brain development in the VS and mPFC (Braams et al., 2014; Blankenstein, Telzer, Do, van Duijvenvoorde, & Crone, in press; Wierenga et al., 2018). Importantly, prosocial and rebellious behaviors are positively correlated, and each are predicted by a similar behavioral trait – fun seeking – suggesting that the

tendency to approach rewards may lead adolescents to develop prosocial behaviors in some instances, but risk taking and rebellious behaviors in other instances (Blakenstein et al., in press). Interestingly, faster structural development (i.e., greater reductions in volume) in the mPFC but not VS is linked to reduced rebellious behavior (Blakenstein et al., in press), indicating that structural maturation in social cognitive regions modulates adolescent risky behavior and may have implications for prosocial risk-taking behavior. Though there is limited research on positive and prosocial risk taking, current findings elucidate the importance of the brain in contributing to positive youth behavior.

Risk-taking behaviors that are geared towards positive and meaningful outcomes, whether they are aimed to benefit oneself or others (e.g., teen-led demonstrations), challenge a popular belief that adolescent risk taking is largely maladaptive. Instead, the public's attention and attitudes toward adolescent risk taking should be reoriented in order to support these positive risks that not only facilitate positive development, but also contribute to the larger community and society (e.g., fighting for justice). Further, the same neural patterns that underlie negative risks also underlie these adaptive risks, thereby highlighting the importance of the developing brain in promoting adaptive risk-taking behaviors.

Learning and cognitive flexibility. An important feature of adolescents is their ability to anticipate and respond appropriately to their increasingly complex social world. This capacity relies on cognitive flexibility which supports learning and adapting their behavior to the ever more challenging environments they face, both in school and in social relationships. Network integration between the PFC, striatum, and hippocampus contributes to learning in the face of potential threats and rewards and determining how to respond appropriately to such environmental challenges. While traditionally viewed as a vulnerability, adolescent-specific

peaks in reward-related neural responses in the striatum can serve an adaptive role, orienting adolescents toward motivationally positive behaviors (e.g., striving for academic success, working toward a goal), thereby promoting learning and exploration (Telzer, 2016). Similarly, flexibility in the recruitment of the PFC to exert cognitive control is essential for learning. While the still developing PFC was originally proposed to be a vulnerability, slower maturation of the PFC may promote adolescents' ability to flexibly adapt to new contexts which fosters learning, problem solving, and creativity (Crone & Dahl, 2012).

Adolescents show optimal learning, outperforming children and adults across various contexts (Davidow, Foerde, Galván, & Shohamy, 2016; Peters & Crone, 2017; van der Schaaf, Warmerdam, Crone, & Cools, 2011). At the neural level, activation in the striatum during learning (Peters & Crone, 2017), and functional connectivity between the striatum and hippocampus during learning (Davidow et al., 2016) peak in adolescence. Importantly, heightened striatal activity and stronger functional connectivity between the striatum and hippocampus predict better memory and learning performance (Davidow et al., 2016, Peters & Crone, 2017). This suggests that functional development of reward systems in adolescence uniquely affects the strengthening of reward-guided actions that promote learning and memory. Interestingly, adolescent mice also show increased flexibility and learning when pursuing rewards (Johnson & Wilbrecht, 2011), suggesting adolescence might be a sensitive developmental period for promoting skill acquisition across species.

Adolescents also outperform children and adults in learning across risk-taking contexts. For instance, adolescents show higher learning (i.e., improvements in performance across the task) compared to children and adults, but only in a particularly high-risk relative to low-risk environment (Humphreys et al., 2016). Moreover, compared to children, adolescents explore

more and adaptively change their behavior in response to feedback during risk taking, which facilitates task-relevant goals, suggesting that risk taking may emerge, in part, from an increased ability of adolescents to flexibly learn from the environment (McCormick & Telzer, 2017). Improvements in learning in a risky context during adolescence is supported by age-related increases in both motivational (e.g., VS, orbitofrontal cortex (OFC)) and regulatory (mPFC) neural activation as well as connectivity between these regions, which may help adolescents track the motivational salience of risk as well as integrate reward and punishment feedback from the task in order to flexibly learn and adapt behavior in the service of attaining rewards (McCormick & Telzer, 2017).

Motivational signals – both intrinsic and extrinsic – can also promote cognitive control and persistence. Extrinsic motivation is driven by the outcome or external factors, such as being explicitly rewarded for performing well. For instance, adolescents show better cognitive control when rewarded to do so, showing adult-like levels of cognitive performance when provided with an incentive (e.g., money), but showing compromised cognitive control relative to adults under neutral conditions (Padmanabhan, Geier, Ordaz, Teslovich, & Luna, 2011). Such improvements in cognitive control in the presence of rewards are paralleled by increased activation in the VS in adolescents compared to children and adults (Padmanabhan et al., 2011), suggesting that the heightened reward-related peaks we see in adolescence can be directed towards adaptive behaviors through the use of incentives.

Intrinsic motivation is driven by internal processes, such as engaging in a challenging task because it is inherently interesting or enjoyable irrespective of the outcome. For instance, during a challenging working memory task without explicit incentives, VS activation scales with task difficulty, such that the VS is more activated following more difficult working memory

tasks in youth (Satterthwaite et al., 2012). Moreover, across a difficult cognitive control task, VS activation and functional coupling between the VS and inferior frontal gyrus (IFG) increase across time to support cognitive persistence in late adolescents (Telzer, Qu, & Lin, 2017).

Together, these studies suggest that the VS may reflect intrinsic reinforcement signals that serve an adaptive function. Importantly, intrinsic reinforcement signals in the VS peak in adolescence, and promote task engagement and performance (Satterthwaite et al., 2012), underscoring adolescence as an important developmental period when reward-related neural signals may be optimized for cognitive engagement and learning in school.

Culture, brain development, and positive youth development. Though culture has been largely absent in developmental neuroscience research, recent efforts are beginning to call attention to the great need of incorporating a cultural lens into such research (Qu, Jorgensen, & Telzer, in press). Research has already shown cultural variation in several areas covered in this chapter. In terms of other-oriented behavior, though adolescents generally show greater mesolimbic reward activation when earning rewards for other people (Braams & Crone, 2017) this is even greater for youth who endorse cultural values of family obligation. Indeed, Latin American adolescents with stronger family obligation values and who gain more happiness on a daily basis from helping their family show greater mesolimbic activation when making decisions to contribute to their family (Telzer et al., 2010). In terms of self-concept development, self-appraisals recruit activation in social cognition brain regions during adolescence compared to both childhood and young adulthood (Pfeifer et al., 2009). However, one study of young adults showed that self-appraisals elicited more activation in social brain regions for Chinese compared to American participants (Pfeifer et al., 2017). Thus, in adulthood, people from a culture that encourages a more interdependent sense of self show greater neural overlap between self and

other. Though preliminary, the findings raise important developmental questions – if cultural differences exist in adulthood, when and how does culture get embedded in the brain? Does the shift toward a more social self occur earlier in interdependent cultures, or are there different trajectories altogether?

In terms of decision making, the dual systems model posits that the adolescent brain emphasizes reward-seeking over cognitive control, making adolescents more susceptible to negative risk-taking decisions (Steinberg, 2008). However, holding certain cultural values appears to reverse this trend. Indeed, Latin American adolescents with greater family obligation values actually show less reward-related activation in the VS during risk taking and greater cognitive control-related activation in the PFC during behavioral inhibition (Telzer, Fuligni et al., 2013a). Furthermore, those youth who show greater reward activation in the VS when contributing to their family exhibit less risk-taking behavior over time (Telzer, Fuligni et al., 2013b). These findings suggest that cultural values such as family obligation call into question common conceptions of the adolescent brain, showing that culture can promote positive decision making. Again, more research is needed to uncover the timing and mechanisms involved in these processes.

Lastly, related to motivation and learning, one study found that Chinese and American late-adolescents displayed different patterns of neural activation during a cognitive persistence task, such that Chinese youth showed increases in cognitive performance across time, whereas American youth showed declines. These behavioral patterns were paralleled by increasing activation and functional coupling between the IFG and VS across the task among Chinese participants, compared to neural activation and coupling that remained low in American participants (Telzer, Qu, & Lin, 2017). These findings may, in part, help explain cultural

differences in academic achievement. Taken together, research on developmental cultural neuroscience is still young, but has already provided promising evidence of cross-cultural variation and can guide future research in understanding how brain development can promote positive youth development.

Summary. Significant neuroimaging research is still emerging, highlighting the adolescent years as a time of opportunity during which changes in the developing brain support positive adjustment and behaviors. As reviewed here, neural regions implicated in theory of mind and reward processing undergo restructuring in adolescence, supporting the development of other-oriented behaviors such as mentalizing and prosociality. Moreover, self-concepts become more stable, realistic, and diverse in adolescence, which is largely undergirded by changes in mPFC activation, suggesting, in part, that greater consideration of the self in relation to others fosters healthier self-concepts. Finally, motivational signals including sensitivity to rewards, peak in sensitivity in adolescence, which supports adaptive and positive risk taking in addition to exploration and learning. Together, this research suggests that adolescence is indeed a sensitive period in which the brain and behavior are in transition. Despite frequent negative interpretations of this time of flux, neuroimaging research is furthering our understanding of these changes as crucial for positive youth development. Furthermore, cross-cultural neuroimaging research is extending our understanding of what constitutes normative brain development during adolescence, as well as how it relates to positive youth development.

Future Directions

Longitudinal studies to identify sensitive periods. Development is a continuous trajectory, which begs the need for the field of developmental cognitive neuroscience to transition towards using more longitudinal methods. Utilizing longitudinal neuroimaging

methods better captures within-person changes in behavior and brain across time and individual differences in developmental trajectories. Longitudinal models are also better suited for testing causal factors in development (Crone & Elzinga, 2015) that may be particularly important for investigating positive youth development. For instance, this method will better identify neural predictors of positive self-development, neural patterns that link age and enhanced adaptive decision-making over time, and sensitive periods (e.g., adolescent-specific peaks or inflection points in development with heightened neural activation) that serve as a time of opportunity for promoting positive behaviors. Conducting longitudinal neuroimaging will be imperative for advancing neurodevelopmental research to examine and understand patterns of positive youth development.

Brain development beyond adolescence and into early adulthood. To date, both cross-sectional and longitudinal studies differ in the ages selected to examine developmental differences/changes, with large discrepancies in how adolescence and adulthood are defined (van Duijvenvoorde, Peters, Braams, & Crone, 2016). As a result, there is sometimes inconsistencies in what is considered adolescence versus adulthood across studies (e.g., 18 year olds being considered adolescents in one paper but adults in another) or a cap on the ages studied (e.g., most samples range from ages 7 to 22) which results in our understanding of the “end-point” of development being very limited. Indeed, the study of brain development past adolescence is much less common, so our understanding of the young adult brain is a major lacuna.

Developmental research often compares children to adolescents or adolescents to young adults, and adults across diverse ages (e.g., 22 to 35) are often clumped together. Development of the brain from early adulthood to adulthood is lacking. Understanding whether brain development in early adulthood is fundamentally different than in adolescence or adulthood is currently limited

by a lack of attention to longitudinal research that carefully tracks brain maturation from ages 22-35. Future research that carefully studies the developing brain in early adulthood is needed.

Countering negative stereotypes of adolescent brain development. For developmental neuroscience research to have the largest impact on scientific discourse and real-world implications for youth, it is essential that the developing brain be framed in more positive and balanced ways (Altikulaç et al., 2018). Indeed, reframing efforts show great promise. For instance, in a counter stereotyping intervention, stereotypes of teens as irresponsible were described as inaccurate portrayals, and youth provided their own observations of teens acting responsibly (Qu, Pomerantz, & Wu, 2020). Youth in this counter stereotyping intervention reported higher academic engagement, a higher sense of family responsibility, and lower intentions to engage in risk taking compared to youth in a control group, an effect that largely persisted days after the intervention. These findings support the importance of changing the current framing of adolescent brain development away from vulnerabilities and redirecting youth to see teens as responsible. As we reviewed here, many domains of neurobiological growth may carry some vulnerabilities that are often thought of negatively, but such changes are also positive and help adolescents flourish. Perhaps with our efforts to counter the negative stereotypes of adolescent brain development, we can provide more opportunities for positive youth development.

References

- Altıkulaç, S., Lee, N. C., van der Veen, C., Benneker, I., Krabbendam, L., & van Atteveldt, N. (2018). The teenage brain: Public perceptions of neurocognitive development during adolescence. *Journal of Cognitive Neuroscience, 31*(3), 339–359. https://doi.org/10.1162/jocn_a_01332
- Barkley-Levenson, E., & Galván, A. (2014). Neural representation of expected value in the adolescent brain. *Proceedings of the National Academy of Sciences of the United States of America, 111*(4), 1646–1651. <https://doi.org/10.1073/pnas.1319762111>
- Blakemore, S. J. (2008). The social brain in adolescence. *Nature Reviews Neuroscience, 9*(4), 267–277. <https://doi.org/10.1038/nrn2353>
- Blakemore, S. J., den Ouden, H., Choudhury, S., & Frith, C. (2007). Adolescent development of the neural circuitry for thinking about intentions. *Social Cognitive and Affective Neuroscience, 2*(2), 130–139. <https://doi.org/10.1093/scan/nsm009>
- Blankenstein, N. E., Telzer, E. H., Do, K. T., van Duijvenvoorde, A. C. K., & Crone, E. A. (2019). Behavioral and neural pathways supporting the development of prosocial and risk-taking behavior across adolescence. *Child Development, 91*, e665-e681. <https://doi.org/10.1111/cdev.13292>
- Braams, B. R., & Crone, E. A. (2017). Peers and parents: A comparison between neural activation when winning for friends and mothers in adolescence. *Social Cognitive and Affective Neuroscience, 12*(3), 417–426. <https://doi.org/10.1093/scan/nsw136>
- Braams, B. R., Peters, S., Peper, J. S., Güroğlu, B., & Crone, E. A. (2014). Gambling for self, friends, and antagonists: Differential contributions of affective and social brain regions on

adolescent reward processing. *NeuroImage*, *100*, 281–289.

<https://doi.org/10.1016/j.neuroimage.2014.06.020>

Buchanan, C. M., & Hughes, J. L. (2009). Construction of social reality during early adolescence: Can expecting storm and stress increase real or perceived storm and stress? *Journal of Research on Adolescence*, *19*(2), 261–285. <https://doi.org/10.1111/j.1532-7795.2009.00596.x>

Burnett, S., & Blakemore, S. J. (2009). Functional connectivity during a social emotion task in adolescents and in adults. *European Journal of Neuroscience*, *29*(6), 1294–1301.

<https://doi.org/10.1111/j.1460-9568.2009.06674.x>

Callan, M. J., Kim, H., & Matthews, W. J. (2015). Age differences in social comparison tendency and personal relative deprivation. *Personality and Individual Differences*, *87*, 196–199. <https://doi.org/10.1016/j.paid.2015.08.003>

Casey, B. J. (2015). Beyond simple models of self-control to circuit-based accounts of adolescent behavior. *Annual Review of Psychology*, *66*, 295–319.

CDC, (2014). Centers for Disease Control and Prevention National Vital Statistics Reports, vol. 64(2), Centers for Disease Control and Prevention, Hyattsville, MD (2014). Available from: <http://www.cdc.gov/nchs/data/hus/2014/021.pdf>

Chein, J. M., Albert, D., O’Brien, L., Uckert, K., & Steinberg, L. (2011). Peers increase adolescent risk taking by enhancing activity in the brain’s reward circuitry. *Developmental Science*, *14*(2), F1–10. <https://doi.org/10.1111/j.1467-7687.2010.01035.x>

Crone, E. A., & Dahl, R. E. (2012). Understanding adolescence as a period of social-affective engagement and goal flexibility. *Nature Reviews Neuroscience*, *13*(9), 636–650.

<https://doi.org/10.1038/nrn3313>

- Crone, E. A., & Elzinga, B. M. (2015). Changing brains: How longitudinal functional magnetic resonance imaging studies can inform us about cognitive and social-affective growth trajectories. *Wiley Interdisciplinary Reviews: Cognitive Science*, *6*(1), 53–63.
<https://doi.org/10.1002/wcs.1327>
- Crone, E. A., & Fuligni, A. J. (2020). Self and others in adolescence. *Annual Review of Psychology*, *71*(1), 447–469. <https://doi.org/10.1146/annurev-psych-010419-050937>
- Davidow, J. Y., Foerde, K., Galván, A., & Shohamy, D. (2016). An upside to reward sensitivity: The hippocampus supports enhanced reinforcement learning in adolescence. *Neuron*, *92*(1), 93–99. <https://doi.org/10.1016/j.neuron.2016.08.031>
- Denny, B. T., Kober, H., Wager, T. D., & Ochsner, K. N. (2012). A meta-analysis of functional neuroimaging studies of self- and other judgments reveals a spatial gradient for mentalizing in medial prefrontal cortex. *Journal of Cognitive Neuroscience*, *24*, 1742–1752.
https://doi.org/10.1162/jocn_a_00233
- Do, K. T., Guassi Moreira, J. F., & Telzer, E. H. (2017). But is helping you worth the risk? Defining prosocial risk taking in adolescence. *Developmental Cognitive Neuroscience*, *25*, 260–271. <https://doi.org/10.1016/j.dcn.2016.11.008>
- Do, K. T., McCormick, E. M., & Telzer, E. H. (2019). The neural development of prosocial behavior from childhood to adolescence. *Social Cognitive and Affective Neuroscience*, *14*(2), 129–139. <https://doi.org/10.1093/scan/nsy117>
- Do, K. T., Sharp, P. B., & Telzer, E. H. (2020). Modernizing conceptions of valuation and cognitive-control deployment in adolescent risk taking. *Current Directions in Psychological Science*, *29*(1), 102–109. <https://doi.org/10.1177/0963721419887361>

- Do, K.T., Prinstein, M.J., & Telzer, E.H. (in press). *Neurobiological susceptibility to peer influence in adolescence*. In K.C. Kadosh (Ed). *The Handbook of Developmental Cognitive Neuroscience*. New York, NY: Oxford University Press.
- Duell, N., & Steinberg, L. (2019). Positive risk taking in adolescence. *Child Development Perspectives*, 13(1), 48–52. <https://doi.org/10.1111/cdep.12310>
- Dunn, E. W., Aknin, L. B., & Norton, M. I. (2008). Spending money on others promotes happiness. *Science*, 319(5870), 1687–1688. <https://doi.org/10.1126/science.1150952>
- Ellis, B. J., Del Giudice, M., Dishion, T. J., Figueredo, A. J., Gray, P., Griskevicius, V., ... Wilson, D. S. (2012). The evolutionary basis of risky adolescent behavior: Implications for science, policy, and practice. *Developmental Psychology*, 48(3), 598–623. <https://doi.org/10.1037/a0026220>
- Ferschmann, L., Vijayakumar, N., Grydeland, H., Overbye, K., Sederevicius, D., Due-Tønnessen, P., ... Tamnes, C. K. (2019). Prosocial behavior relates to the rate and timing of cortical thinning from adolescence to young adulthood. *Developmental Cognitive Neuroscience*, 40, 100734. <https://doi.org/10.1016/j.dcn.2019.100734>
- Gopnik, A. (2012, January 28). What's Wrong With the Teenage Mind? *Wall Street Journal*. <https://www.wsj.com/articles/SB10001424052970203806504577181351486558984>
- Gunther Moor, B., Macks, Z. A., Güroglu, B., Rombouts, S. A., Molen, M. W., & Crone, E. A. (2012). Neurodevelopmental changes of reading the mind in the eyes. *Social Cognitive and Affective Neuroscience*, 7(1), 44–52. <https://doi.org/10.1093/scan/nsr020>
- Güroglu, B., van den Bos, W., & Crone, E. A. (2014). Sharing and giving across adolescence: An experimental study examining the development of prosocial behavior. *Frontiers in Psychology*, 5, 291. <https://doi.org/10.3389/fpsyg.2014.00291>

- Harter, S. (2012). *The construction of the self: Developmental and sociocultural foundations* (2nd ed.). New York, NY: The Guilford Press.
- Humphreys, K. L., Telzer, E. H., Flannery, J., Goff, B., Gabard-Durnam, L., Gee, D. G., ... Tottenham, N. (2016). Risky decision making from childhood through adulthood: Contributions of learning and sensitivity to negative feedback. *Emotion, 16*(1), 101–109. <https://doi.org/10.1037/emo0000116>
- Johnson, C., & Wilbrecht, L. (2011). Juvenile mice show greater flexibility in multiple choice reversal learning than adults. *Developmental Cognitive Neuroscience, 1*(4), 540–551. <https://doi.org/10.1016/j.dcn.2011.05.008>
- Levin, I. P., Weller, J. A., Pederson, A. A., & Harshman, L. A. (2007). Age-related differences in adaptive decision making: Sensitivity to expected value in risky choice. *Judgment and Decision Making, 2*(4), 225–233.
- Masten, C. L., Morelli, S. A., & Eisenberger, N. I. (2011). An fMRI investigation of empathy for “social pain” and subsequent prosocial behavior. *NeuroImage, 55*(1), 381–388. <https://doi.org/10.1016/j.neuroimage.2010.11.060>
- McCormick, E. M., & Telzer, E. H. (2017). Adaptive adolescent flexibility: Neurodevelopment of decision-making and learning in a risky context. *Journal of Cognitive Neuroscience, 29*(3), 413–423. https://doi.org/10.1162/jocn_a_01061
- Mills, K. L., Lalonde, F., Clasen, L. S., Giedd, J. N., & Blakemore, S.-J. (2014). Developmental changes in the structure of the social brain in late childhood and adolescence. *Social Cognitive and Affective Neuroscience, 9*(1), 123–131. <https://doi.org/10.1093/scan/nss113>

- Moll, J., Zahn, R., De Oliveira-Souza, R., Krueger, F., & Grafman, J. (2005). Opinion: The neural basis of human moral cognition. *Nature Reviews Neuroscience*, *6*, 799–809.
<https://doi.org/10.1038/nrn1768>
- Moriguchi, Y., Ohnishi, T., Mori, T., Matsuda, H., & Komaki, G. (2007). Changes of brain activity in the neural substrates for theory of mind during childhood and adolescence. *Psychiatry and Clinical Neurosciences*, *61*(4), 355–363. <https://doi.org/10.1111/j.1440-1819.2007.01687.x>
- Murty, V. P., FeldmanHall, O., Hunter, L. E., Phelps, E. A., & Davachi, L. (2016). Episodic memories predict adaptive value-based decision-making. *Journal of Experimental Psychology: General*, *145*(5), 1–11. <https://doi.org/10.1037/xge0000158>
- Omarzu, J. (2000). A disclosure decision model: determining how and when individuals will self-disclose. *Personality and Social Psychology Review*, *4*(2), 174–185.
https://doi.org/10.1207/S15327957PSPR0402_05
- Padmanabhan, A., Geier, C. F., Ordaz, S. J., Teslovich, T., & Luna, B. (2011). Developmental changes in brain function underlying the influence of reward processing on inhibitory control. *Developmental Cognitive Neuroscience*, *1*(4), 517–529.
<https://doi.org/10.1016/j.dcn.2011.06.004>
- Peters, S., & Crone, E. A. (2017). Increased striatal activity in adolescence benefits learning. *Nature Communications*, *8*(1), 1–9. <https://doi.org/10.1038/s41467-017-02174-z>
- Pfeifer, J. H., Kahn, L. E., Merchant, J. S., Peake, S. J., Veroude, K., Masten, C. L., ... Dapretto, M. (2013). Longitudinal change in the neural bases of adolescent social self-evaluations: Effects of age and pubertal development. *The Journal of Neuroscience*, *33*, 7415-7419.
<https://doi.org/10.1523/JNEUROSCI.4074-12.2013>

- Pfeifer, J. H., Masten, C. L., Borofsky, L. A., Dapretto, M., Fuligni, A. J., & Lieberman, M. D. (2009). Neural correlates of direct and reflected self-appraisals in adolescents and adults: When social perspective-taking informs self-perception. *Child Development, 80*, 1016–1038. <https://doi.org/10.1111/j.1467-8624.2009.01314.x>.
- Pfeifer, J. H., Mahy, C. E. V., Merchant, J. S., Chen, C., Masten, C. L., Fuligni, A. J., Lieberman, M. D., Lessard, J., Dong, Q., & Chen, C. (2017). Neural systems for reflected and direct self-appraisals in Chinese young adults: Exploring the role of the temporal-parietal junction. *Cultural Diversity and Ethnic Minority Psychology, 23*(1), 45–58. <https://doi.org/10.1037/cdp0000122>
- Qu, Y., Galván, A., Fuligni, A. J., Lieberman, M. D., & Telzer, E. H. (2015). Longitudinal changes in prefrontal cortex activation underlie declines in adolescent risk taking. *Journal of Neuroscience, 35*(32), 11308–11314. <https://doi.org/10.1523/JNEUROSCI.1553-15.2015>
- Qu, Y., Jorgensen, N. A., & Telzer, E. H. (in press). A call for greater attention to culture in the study of brain and development. *Perspectives on Psychological Science*. <https://doi.org/10.1177/1745691620931461>
- Qu, Y., Pomerantz, E. M., & Wu, G. (2020). Countering youth's negative stereotypes of teens fosters constructive behavior. *Child Development, 91*(1), 197–213. <https://doi.org/10.1111/cdev.13156>
- Qu, Y., Pomerantz, E. M., McCormick, E., & Telzer, E. H. (2018). Youth's conceptions of adolescence predict longitudinal changes in prefrontal cortex activation and risk taking during adolescence. *Child Development, 89*(3), 773–783. <https://doi.org/10.1111/cdev.13017>

- Rudolph, K. D., Davis, M. M., Modi, H. H., Fowler, C., Kim, Y., & Telzer, E. H. (2020). Differential susceptibility to parenting in adolescent girls: Moderation by neural sensitivity to social cues. *Journal of Research on Adolescence*, *30*(S1), 177–191. <https://doi.org/10.1111/jora.12458>
- Satterthwaite, T. D., Ruparel, K., Loughhead, J., Elliott, M. A., Gerraty, R. T., Calkins, M. E., ... Wolf, D. H. (2012). Being right is its own reward: Load and performance related ventral striatum activation to correct responses during a working memory task in youth. *NeuroImage*, *61*(3), 723–729. <https://doi.org/10.1016/j.neuroimage.2012.03.060>
- Schriber, R. A., & Guyer, A. E. (2016). Adolescent neurobiological susceptibility to social context. *Developmental Cognitive Neuroscience*, *19*, 1–18. <https://doi.org/10.1016/j.dcn.2015.12.009>.
- Somerville, L. H., Jones, R. M., Ruberry, E. J., Dyke, J. P., Glover, G., & Casey, B. J. (2013). The medial prefrontal cortex and the emergence of self-conscious emotion in adolescence. *Psychological Science*, *24*(8), 1554–1562. <https://doi.org/10.1177/0956797613475633>
- Steinberg, L. (2008). A social neuroscience perspective on adolescent risk-taking. *Developmental Review*, *28*(1), 78–106. <https://doi.org/10.1016/j.dr.2007.08.002>
- Tashjian, S. M., Weissman, D. G., Guyer, A. E., & Galván, A. (2018). Neural response to prosocial scenes relates to subsequent giving behavior in adolescents: A pilot study. *Cognitive, Affective and Behavioral Neuroscience*, *18*(2), 342–352. <https://doi.org/10.3758/s13415-018-0573-9>
- Tamir, D. I., & Mitchell, J. P. (2012). Disclosing information about the self is intrinsically rewarding. *Proceedings of the National Academy of Sciences of the United States of America*, *109*(21), 8038–8043. <https://doi.org/10.1073/pnas.1202129109>

- Telzer, E. H. (2016). Dopaminergic reward sensitivity can promote adolescent health: A new perspective on the mechanism of ventral striatum activation. *Developmental Cognitive Neuroscience, 17*, 57–67. <https://doi.org/10.1016/j.dcn.2015.10.010>.
- Telzer, E. H., Fuligni, A. J., Lieberman, M. D., & Galván, A. (2014). Neural sensitivity to eudaimonic and hedonic rewards differentially predict adolescent depressive symptoms over time. *Proceedings of the National Academy of Sciences of the United States of America, 111*(18), 6600–6605. <https://doi.org/10.1073/pnas.1323014111>
- Telzer, E. H., Fuligni, A. J., Lieberman, M. D., & Galván, A. (2013a). Meaningful family relationships: Neurocognitive buffers of adolescent risk taking. *Journal of Cognitive Neuroscience, 25*(3), 374–387. https://doi.org/10.1162/jocn_a_00331
- Telzer, E. H., Fuligni, A. J., Lieberman, M. D., & Galván, A. (2013b). Ventral striatum activation to prosocial rewards predicts longitudinal declines in adolescent risk taking. *Developmental Cognitive Neuroscience, 3*, 45-52. doi:10.1016/j.dcn.2012.08.004
- Telzer, E. H., Masten, C. L., Berkman, E. T., Lieberman, M. D., & Fuligni, A. J. (2010). Gaining while giving: An fMRI study of the rewards of family assistance among white and latino youth. *Social Neuroscience, 5*(5), 508–518. <https://doi.org/10.1080/17470911003687913>
- Telzer, E. H., Qu, Y., & Lin, L. C. (2017). Neural processes underlying cultural differences in cognitive persistence. *NeuroImage, 156*, 224–231. <https://doi.org/10.1016/j.neuroimage.2017.05.034>
- Telzer, E.H., Fuligni, A.J., & Galván, A. (2016). *Identifying a cultural resource: Neural correlates of familial influence on risk taking among Mexican-origin adolescents*. In J.Y. Chiao, S-C Li, R. Seligman, & R. Turner (Eds). *The Oxford Handbook of Cultural Neuroscience*. New York, NY: Oxford University Press.

- Tymula, A., Rosenberg Belmaker, L. A., Roy, A. K., Ruderman, L., Manson, K., Glimcher, P. W., & Levy, I. (2012). Adolescents' risk-taking behavior is driven by tolerance to ambiguity. *Proceedings of the National Academy of Sciences of the United States of America*, *109*(42), 17135–17140. <https://doi.org/10.1073/pnas.1207144109>
- van der Aar, L. P. E., Peters, S., van der Cruijssen, R., & Crone, E. A. (2019). The neural correlates of academic self-concept in adolescence and the relation to making future-oriented academic choices. *Trends in Neuroscience and Education*, *15*, 10–17. <https://doi.org/10.1016/j.tine.2019.02.003>
- van der Cruijssen, R., Peters, S., van der Aar, L. P. E., & Crone, E. A. (2018). The neural signature of self-concept development in adolescence: The role of domain and valence distinctions. *Developmental Cognitive Neuroscience*, *30*, 1–12. <https://doi.org/10.1016/j.dcn.2017.11.005>
- van der Cruijssen, R., Peters, S., Zoetendaal, K. P. M., Pfeifer, J. H., & Crone E. A. (2019). Direct and reflected self-concept show increasing similarity across adolescence: A functional neuroimaging study. *Neuropsychologia*, *129*, 407-417. <https://doi.org/10.1016/j.neuropsychologia.2019.05.001>
- van der Schaaf, M. E., Warmerdam, E., Crone, E. A., & Cools, R. (2011). Distinct linear and non-linear trajectories of reward and punishment reversal learning during development: Relevance for dopamine's role in adolescent decision making. *Developmental Cognitive Neuroscience*, *1*(4), 578–590. <https://doi.org/10.1016/j.dcn.2011.06.007>
- van Duijvenvoorde, A. C. K., Huizenga, H. M., Somerville, L. H., Delgado, M. R., Powers, A., Casey, B. J., ... Figner, B. (2015). Neural correlates of expected risks and returns in risky

choice across development. *Journal of Neuroscience*, 35(4), 1549–1560.

<https://doi.org/10.1523/JNEUROSCI.1924-14.2015>

van Duijvenvoorde, A. C. K., Peters, S., Braams, B. R., & Crone, E. A. (2016). What motivates adolescents? Neural responses to rewards and their influence on adolescents' risk taking, learning, and cognitive control. *Neuroscience and Biobehavioral Reviews*, 70, 135–147. <https://doi.org/10.1016/j.neubiorev.2016.06.037>

van Hoorn, J., van Dijk, E., Güroğlu, B., & Crone, E. A. (2016). Neural correlates of prosocial peer influence on public goods game donations during adolescence. *Social Cognitive and Affective Neuroscience*, 11(6), 923–933. <https://doi.org/10.1093/scan/nsw013>

Vijayakumar, N., & Pfeifer, J. H. (2020). Self-disclosure during adolescence: exploring the means, targets, and types of personal exchanges. *Current Opinion in Psychology*, 33, 135–140. <https://doi.org/10.1016/j.copsyc.2019.08.005>

Wierenga, L. M., Bos, M. G. N., Schreuders, E., vd Kamp, F., Peper, J. S., Tamnes, C. K., & Crone, E. A. (2018). Unraveling age, puberty and testosterone effects on subcortical brain development across adolescence. *Psychoneuroendocrinology*, 91, 105–114. <https://doi.org/10.1016/j.psyneuen.2018.02.034>

Willoughby, T., Good, M., Adachi, P. J. C., Hamza, C., & Tavernier, R. (2013). Examining the link between adolescent brain development and risk taking from a social-developmental perspective. *Brain and Cognition*, 83(3), 315–323. <https://doi.org/10.1016/j.bandc.2013.09.008>