

NEUROBIOLOGICAL DEVELOPMENT IN ADOLESCENCE AND EARLY 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 2 decades, we now know that the brain is rapidly changing and adapting to its environment across the first 3 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 titled "What's Wrong With the Teenage Mind?" included 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, many positive and adaptive behaviors are 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, 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 described undesirable behaviors (e.g., "irresponsible," "lazy," "irritating") more often than desirable behaviors (e.g., "independent," "kind," "creative"; Altikulaç et al., 2019). Such stereotypes can affect

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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 et al., 2018, 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 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 toward 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, although 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 toward 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, 2020; 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 et al., 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, which 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 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, risk-taking behavior, and impulsivity. 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 et al., 2007). Moreover, from childhood (i.e., 9 years old) to adolescence (i.e., 16 years old), 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 et al., 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 (Güroğlu et al., 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 toward the peer (Masten et al., 2011), and adolescents who show greater TPJ activation when viewing prosocial scenes donate more money to charities (Tashjian et al., 2018). Additionally, relative to older adolescents, younger adolescents show greater dorso-medial 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 midadolescents when making costly decisions that benefit their peers (Do et al., 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 et al., 2005), perhaps by providing a sense of meaning and happiness to the helper (Dunn et al., 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 et al., 2014; Telzer et al., 2010, 2016). This heightened VS response is elevated in midadolescence 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 rewards (Braams & Crone, 2017). 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 et al., 2013b, 2014; Qu et al., 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 as well as 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 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 with others?"; Callan et al., 2015; Harter, 2012). Although 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 et al., 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 20s (Mills et al., 2014). Furthermore, although 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 Crujisen et al., 2018). Across different age groups, the mPFC shows heightened activation during

self-evaluations regardless of domain (van der Cruisen 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 with academic) domains (Pfeifer et al., 2013; van der Cruisen 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-concept during adolescence is the ability to comprehend and accept both positive and negative traits in oneself. Compared with children and young adults, mid- and late adolescents show less differentiation between positive and negative statements in terms of striatal activation (van der Cruisen 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 et al., 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 Cruisen et al., 2019). Findings revealed that with age, not only did self-appraisals become more positive overall but direct and reflected self-appraisals became 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 processes 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 (Centers for Disease Control and Prevention, 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 U.S. high school students is at 99.96% (Willoughby et al., 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 et al., 2007; van Duijvenvoorde et al., 2015). Compared with 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 et al., 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 redirected toward 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, adultlike 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, 2019) or even prosocial (e.g., standing up against a school bully; Do et al., 2017). Positive risk taking is socially acceptable and constructive and is ultimately aimed to benefit the individual (Duell & Steinberg, 2019). 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 seek 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 (Blankenstein et al., 2020; Braams et al., 2014; 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 to develop risk-taking and rebellious behaviors in other instances (Blankenstein et al., 2020). Interestingly, faster structural development (i.e., greater reductions in volume) in the mPFC but not VS is linked to reduced rebellious behavior (Blankenstein et al., 2020), indicating that structural maturation in social cognitive regions modulates adolescents' risky behavior and may have implications for prosocial risk-taking behavior. Although 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 toward 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 behavior to the ever more challenging environments adolescents 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 et al., 2016; Peters & Crone, 2017; van der Schaaf et al., 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 with children and adults, but only in a particularly high-risk relative to low-risk environment (Humphreys et al., 2016). Moreover, compared with 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 (e.g., 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 adultlike levels of cognitive performance when provided with an incentive (e.g., money) but showing compromised cognitive control relative to adults under neutral conditions (Padmanabhan et al., 2011). Such improvements in cognitive control in the presence of rewards are paralleled by increased activation in the VS in adolescents compared with children and adults (Padmanabhan et al., 2011), suggesting that the heightened reward-related peaks seen in adolescence can be directed toward 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 in youth following more difficult working memory tasks (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 et al., 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

Although culture has been largely absent from developmental neuroscience research, recent efforts

are beginning to call attention to the great need of incorporating a cultural lens into such research (Qu et al., 2021). Research has already shown cultural variation in several areas covered in this chapter. In terms of other-oriented behavior, although 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 with 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 with American participants (Pfeifer et al., 2017). Thus, in adulthood, people from cultures that encourage a more interdependent sense of self show greater neural overlap between self and other. Although 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 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 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 with neural activation and coupling that remained low in American participants (Telzer et al., 2017). These findings may, in part, help explain cultural differences in academic achievement. Taken together, research on developmental cultural neuroscience is still young, but it has already provided promising evidence of cross-cultural variation and can guide future research in understanding how brain development promotes positive youth development.

SUMMARY AND FUTURE DIRECTIONS

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. Below we briefly review several areas of future research that will contribute to this growing field.

Longitudinal Studies to Identify Sensitive Periods

Development is a continuous trajectory, which begs the need for the field of developmental cognitive neuroscience to transition toward 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 et al., 2016). As a result, there are 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, 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 with adolescents or adolescents with young adults, and adults across diverse ages (e.g., 22–35) 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 to 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 (Altıkulaç et al., 2019). 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 et al., 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 with 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 can also be 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.

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