Is Adolescence a Sensitive Period for Sociocultural Processing?

Sarah-Jayne Blakemore[1] and Kathryn L. Mills[1,2]

[1]Institute of Cognitive Neuroscience, University College London, London, WC1N 3HT United Kingdom; email: s.blakemore@ucl.ac.uk

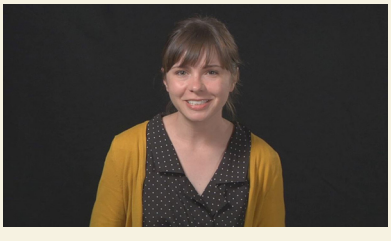
[2]Child Psychiatry Branch, National Institute of Mental Health, Bethesda, Maryland 20892

Annu. Rev. Psychol. 2014. 65:187–207

First published online as a Review in Advance on September 6, 2013

The *Annual Review of Psychology* is online at http://psych.annualreviews.org

This article's doi: 10.1146/annurev-psych-010213-115202



Watch a video lecture online

Keywords

social cognition, mentalizing, adolescent brain development, risk taking, plasticity, sensitive period

Abstract

Adolescence is a period of formative biological and social transition. Social cognitive processes involved in navigating increasingly complex and intimate relationships continue to develop throughout adolescence. Here, we describe the functional and structural changes occurring in the brain during this period of life and how they relate to navigating the social environment. Areas of the social brain undergo both structural changes and functional reorganization during the second decade of life, possibly reflecting a sensitive period for adapting to one's social environment. The changes in social environment that occur during adolescence might interact with increasing executive functions and heightened social sensitivity to influence a number of adolescent behaviors. We discuss the importance of considering the social environment and social rewards in research on adolescent cognition and behavior. Finally, we speculate about the potential implications of this research for society.

Contents

OVERVIEW

Adolescence is often defined as the period between the onset of puberty and the achievement of relative self-sufficiency. Therefore the beginning of adolescence is largely defined by a biological event, whereas the end of adolescence is often defined socially. Adolescence is particularly protracted in humans compared with other species (Bogin & Smith 1996). Behavioral changes and improvements in cognitive skills in adolescence have been reported for millennia, including by Aristotle (Ross 1925). Recently, with the advent of brain imaging technologies, we have begun to understand changes occurring in the brain during this period of life (Casey et al. 2008). This review highlights research on adolescent social cognitive development, which paints a picture of adolescence as a period of heightened sensitivity to sociocultural signals in the environment. This framework addresses the social contextual factors and motivations that might influence behavior during adolescence. We propose that social context and social acceptance play a pivotal role in adolescence because they influence the majority of adolescent-typical behaviors. This review integrates research across neuroscience and psychology within the framework that adolescents' health and well-being are influenced through interacting with their environment (Call et al. 2002). We also discuss potential implications of basic research on adolescence for society.

DEFINING ADOLESCENCE AS A SENSITIVE PERIOD FOR SOCIAL PROCESSING

The period of adolescence begins with the physical, cognitive, and social changes occurring with the onset of puberty. The adults that emerge from adolescence must be equipped to navigate the

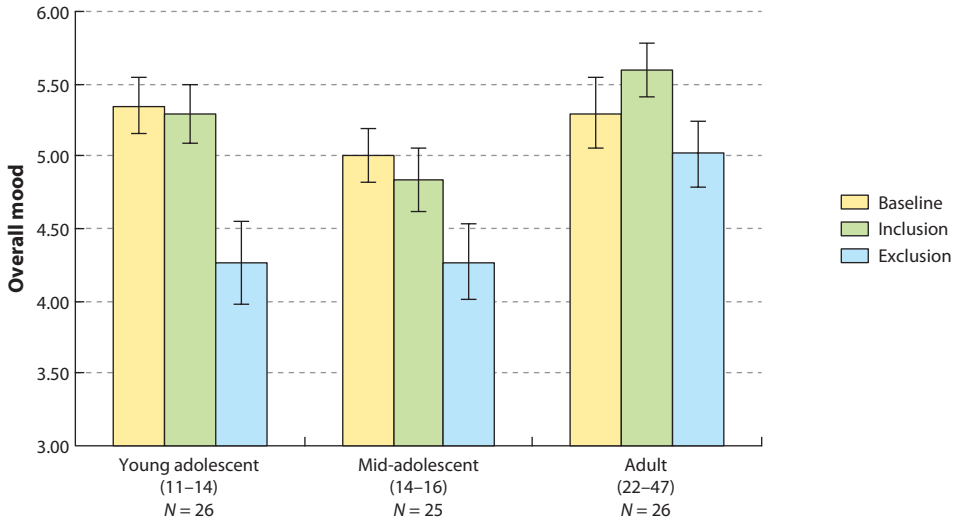


Figure 1

Adolescents are hypersensitive to the negative consequences of social exclusion. In this study, young adolescents (11–14 years), mid-adolescents (14–16 years), and adults (22–47 years) first completed baseline measures of mood. They then played the *Cyberball* online ball game and were either included or excluded by the other players in the game. After each run (inclusion and exclusion), participants completed measures of mood again. The graph shows overall mood ratings for each group under each condition. Mood was lowered by the social exclusion condition, compared with baseline and inclusion, particularly strongly in the two adolescent groups. Adapted from Sebastian et al. (2010).

social complexities of their community. It has been proposed that adolescence is a time of particular cultural susceptibility (Choudhury 2010, Fiske 2009) and that the impact of puberty on the brain makes adolescents particularly sensitive to their social environments (Crone & Dahl 2012, Peper & Dahl 2013). Adolescents go through a period of social reorienting where the opinions of peers become more important than those of family members (Larson & Richards 1991, Larson et al. 1996). Adolescents aged 13 to 17 years reported that peer evaluations affect their feelings of social or personal worth and that peer rejection indicates their unworthiness as an individual (O'Brien & Bierman 1988). Although the adolescents and children aged 10 to 13 years similarly felt that peers provided companionship, stimulation, and support, the younger group did not indicate that peer acceptance impacted self-evaluation. The authors suggest that increasing abilities to form abstract representations, as well as increasing motivation for peer acceptance, might account for the influence of peers on self-evaluations in adolescence. These self-reported accounts of the importance of peer acceptance are supported by the results of a behavioral study investigating the effects of social exclusion in the lab. After being excluded by other players in an online game called *Cyberball*, young and mid-adolescents (11–16 years) reported lowered overall mood, and young adolescents (11–14 years) reported higher state anxiety, compared with adults (Sebastian et al. 2010). Thus, it appears that the desire to be accepted by one's peers, and avoidance of social rejection, is particularly acute in adolescence and might drive adolescent behavior (**Figure 1**).

Mental health disorders often have an onset in adolescence (Kessler et al. 2005) (**Figure 2**). The heightened vulnerability to psychiatric conditions during adolescence has been proposed to relate to genetically preprogrammed neural development at the same time as new stresses and challenges emerge in the environment (Andersen & Teicher 2008, Leussis & Andersen 2008). Stress exposure, including social stress, during adolescence may be longer lasting and qualitatively

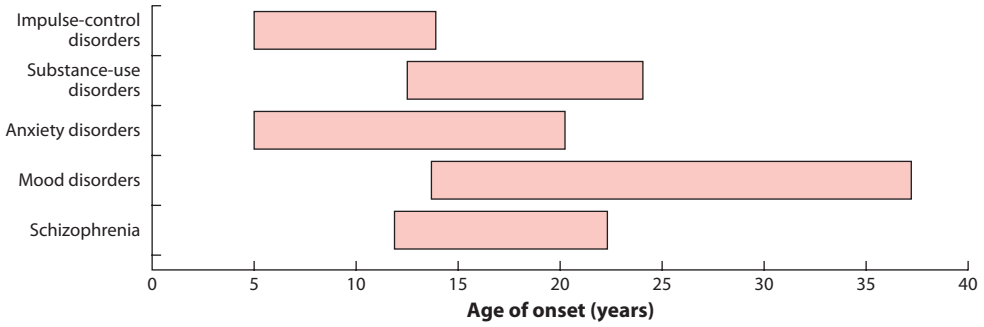


Figure 2

The ranges of onset age for common psychiatric disorders. The graph is based on the results of a nationally representative epidemiological survey of mental disorders and demonstrates that most individuals diagnosed with a mental disorder show the beginnings of the illness in late childhood or in adolescence. Adapted from Paus et al. (2008) with data from Kessler et al. (2005).

Hypothalamic-pituitary-adrenal (HPA) axis: major part of the neuroendocrine system that controls reactions to stress and regulates many body processes

Glucocorticoid: a steroid hormone that is produced by the adrenal cortex of animals

different from stress exposure at other periods of life, possibly due to the interaction between the developing hypothalamic-pituitary-adrenal (HPA) axis and glucocorticoids (for review, see McCormick et al. 2010). One reason why adolescents show increased sensitivity to stress-induced levels of glucocorticoids is the increase in glucocorticoid regulation in the human prefrontal cortex (Perlman et al. 2007). This neural change, which increases from infancy through childhood and adolescence, might make adolescents more vulnerable to psychiatric illnesses (Perlman et al. 2007). Rodent studies indicate that social stress induced by isolation can have long-lasting impacts (see sidebar Possible Consequences of Social Isolation in Adolescence). Exposure to social isolation during adolescence increases the likelihood of depressive-like behaviors as well as alterations in the structure of the prefrontal cortex (Leussis & Andersen 2008). The long-lasting effects of stress in adolescence include disrupted social and reproductive behavior. For example, male rats exposed to chronic social instability stress during adolescence were, in adulthood, more anxious and less socially interactive (Green et al. 2012), showed deficits across many sexual behaviors (McCormick et al. 2013), and had lower plasma testosterone concentrations than rats not exposed to social stressors during adolescence (McCormick et al. 2013). There is also evidence from studies on hamsters that adolescence is a period of increased sensitivity to the organizational

POSSIBLE CONSEQUENCES OF SOCIAL ISOLATION IN ADOLESCENCE

A recent study found that rats socially isolated during early adolescence were faster at remembering drug-associated contextual stimuli than rats that were not socially isolated during early adolescence or rats that were socially isolated during late adolescence (Whitaker et al. 2013). The socially isolated rats showed enhanced synaptic plasticity in an area of the brain involved in reward-based learning and addictive behaviors, and their drug-associated memories were harder to extinguish (Whitaker et al. 2013). Importantly, later resocialization of the rats isolated during early adolescence did not reverse the neural changes. This study suggests that early adolescence is a sensitive period for social signals and that social isolation during this time can change neural mechanisms involved in acquiring and maintaining drug-associated cues, possibly increasing vulnerability to addictive behaviors (Whitaker et al. 2013). Although the study involved rodents, the impact of social isolation on adolescent health and life trajectories likely applies to humans. If so, the consequences of social exclusion can be so great that mechanisms and behaviors promoting peer acceptance are considered adaptive.

effects of testosterone, which in turn affects adult reproductive behavior (Schulz et al. 2009). These and many other animal studies (reviewed in Toledo-Rodriguez & Sandi 2011) show that stress exposure during adolescence has a significant impact on the adult. Mild stress exposure during the pubertal transition in rats (postnatal days 28–42) increases risk-taking and novelty-seeking behavior and decreases anxious behavior in later adolescence (postnatal days 45–51), suggesting that stress experienced during puberty motivates the rats to hasten independence-building behaviors (Toledo-Rodriguez & Sandi 2011).

Although much evidence for adolescence as a sensitive period for social processing comes from rodent studies, there is evidence that socioenvironmental conditions experienced during human adolescence can impact attitudes toward health and reproduction in young adulthood (Brumbach et al. 2009). Adolescents within socially unpredictable environments not only experienced decreased physical and mental health in the short term but also adopted faster life history strategies in young adulthood, such as decreased health, less sexual restrictedness, and less resource-accruing potential (Brumbach et al. 2009). Further human studies are needed to investigate whether the adolescent brain is particularly sensitive to cues from the social environment or lack thereof.

SOCIAL COGNITIVE DEVELOPMENT

Social cognition refers to the ability to make sense of the world through processing signals generated by members of the same species (Frith 2008). Social cognitive processes include basic perceptual processes such as face processing (Farroni et al. 2005), biological motion detection (Pelphrey & Carter 2008), and joint attention (Carpenter et al. 1998)—all of which rapidly develop from birth (see Baillargeon et al. 2010). Other social cognitive processes are more complex, such as understanding others' mental states (Blakemore et al. 2007), social emotional processing (Burnett et al. 2009), and negotiating complex interpersonal decisions (Crone 2013). Recent neuroimaging and behavioral studies have shown that these skills continue to develop past childhood and throughout adolescence (reviewed in Apperly 2010, Blakemore 2012).

Social Cognitive Development in Adolescence

Until recently, there was a shortage of studies looking into social cognitive abilities after childhood, as it was generally assumed that these abilities were already mature by mid-childhood in typically developing children. Most paradigms have been designed to investigate social cognition (in particular, theory of mind) in young children and result in ceiling effects after mid-childhood (Apperly 2010).

One of the first studies to investigate neurotypical changes in social cognitive behavior in adolescence showed the ability to integrate the perspectives and intentions of others when making fairness considerations continues to improve (Güroğlu et al. 2009). The authors of this study suggested that the rewarding nature of peer relationships during adolescence could affect social decision-making processes. Another study demonstrated that online social cognitive skills improve across adolescence (Dumontheil et al. 2010a). Participants aged 7 to 27 years were tested on their ability to take the perspective of another person when making decisions. Their paradigm adapted a referential communication task in which participants are instructed to move objects around a set of shelves by a director, who cannot see some of the objects that the participant can see. Adults frequently make mistakes in this type of trial, in which the participant needs to take account of the director's perspective in order to guide decisions (Keysar et al. 2000, 2003). As an added control, Dumontheil et al. (2010a) included a condition in which the director is gone and participants have to follow a nonsocial rule ("ignore objects with a grey background") when following the (otherwise)

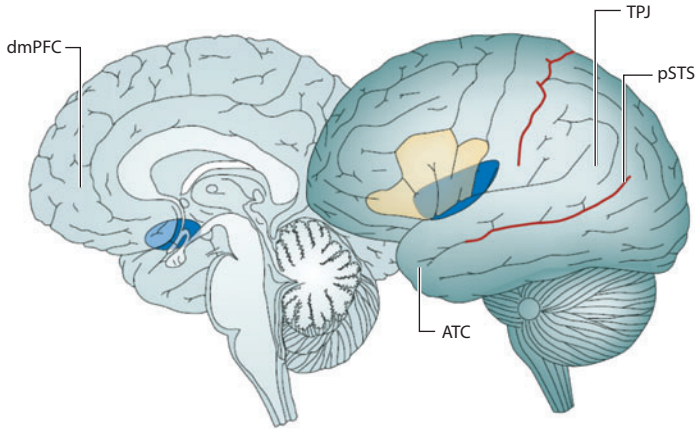


Figure 3

Mentalizing network: areas of the brain that may be sensitive to social cognitive processes necessary to navigate the adolescent social environment. Regions on the lateral surface of the brain that are involved in social cognition include the dorsal medial prefrontal cortex (dmPFC) and temporoparietal junction (TPJ), which are involved in thinking about mental states; the posterior superior temporal sulcus (pSTS), which is involved in observing faces and biological motion; and anterior temporal cortex (ATC), which is involved in applying social knowledge. Adapted from Blakemore (2008).

same instructions as in the director condition. Although accuracy improved until mid-adolescence in both conditions, accuracy in the director condition continued to improve after mid-adolescence. This suggests that the ability to use another's perspective to guide decisions continues to develop beyond the establishment of abilities recruited in the control condition (e.g., working memory, response inhibition). This improvement may be due to increased motivation to take account of another's perspective as well as improved integration of social cognition and cognitive control systems (Dumontheil et al. 2010a). Introspective awareness of one's performance on a perceptual task also improves across adolescence, following a trajectory similar to mentalizing (Weil et al. 2013). This finding that self-awareness increases during adolescence might have implications for how adolescents integrate their own self-judgments with peer evaluations.

SOCIAL BRAIN NETWORK

It has been proposed that social cognition has been so fundamental to the survival and reproductive fitness of various primate species that primate brains include regions specialized for social cognitive processes (Brothers 2002, Rushworth et al. 2013). Although this idea remains contentious, there exists a network of brain regions consistently involved in social cognitive processes (Adolphs 2009, Frith 2007). Mentalizing (theory of mind), the process of mental state attribution, has been associated with a network of brain regions including the dorsal medial prefrontal cortex (dmPFC), temporoparietal junction (TPJ), posterior superior temporal sulcus (pSTS), and anterior temporal cortex (ATC) (**Figure 3**). Together, this set of regions is sometimes called the social brain network. The mentalizing tasks that recruit these regions use stimuli such as animated shapes (Castelli et al. 2000), cartoon stories (Brunet et al. 2000, Gallagher et al. 2000), and written stories (Fletcher et al. 1995) designed to elicit the representation of mental states. Although the coactivation of these regions has been demonstrated in many social cognitive neuroimaging experiments, the individual contributions of these anatomically distinct regions to social cognitive processes are debated.

Mentalizing: the ability to understand other people's behavior and actions in terms of underlying mental states

Electrophysiological and functional magnetic resonance imaging (fMRI) studies consistently report the involvement of the pSTS in the perception of biological motion and eye gaze (Puce & Perrett 2003) and in grasping the intentionality and appropriateness of biological motion (Pelphrey et al. 2004). It may be that the pSTS is involved in decoding complex social gestures conveyed through eye gaze and body movement. The TPJ, while in close anatomical proximity to the pSTS, is involved in different aspects of social cognition. It is suggested that the TPJ is activated specifically in situations when one is inferring the mental states of others rather than just information known about another (Saxe & Kanwisher 2003, Saxe et al. 2009). In contrast, dmPFC is activated in multiple conditions: when inferring the mental states of others, when reflecting on knowledge of another's traits, and when reflecting on the traits of oneself (Frith 2007). Frith (2007) has proposed that the underlying similarity between tasks that activate the dmPFC is their involvement in handling communicative intentions, which requires a second-order representation of mental state, whether our own or another's. A combination of lesion, nonhuman primate, and fMRI studies has prompted researchers to theorize the involvement of the ATC in applying social knowledge (Olson et al. 2013) and processing social scripts (Frith 2007, Frith & Frith 2003).

Some of the strongest evidence linking areas of the mentalizing brain network to adaptations to the social environment comes from primate studies. In macaques, the size of an individual's social group is associated with both the structure and function of homologous brain areas involved in social cognition (Sallet et al. 2011). Macaques housed in more complex social environments had greater gray matter volume in the temporal cortex and rostral prefrontal cortex, and higher-ranking male macaques had greater gray matter volume in similar regions after controlling for network size, weight, and age (Sallet et al. 2011). These studies support the idea of the existence of a mentalizing brain network as well as the idea that this network exists in nonhuman primates (Rushworth et al. 2013).

Structural Development

The cerebral cortex in humans is formed during a well-defined developmental period. Anatomical studies of postmortem human brain tissue provided some of the first evidence that the brain undergoes profound changes in anatomy across the first decades of life (Petanjek et al. 2011, Webb et al. 2001, Yakovlev & Lecours 1967). However, MRI studies over the past 20 years have illuminated how and when the human brain develops. Neuroimaging methods, such as structural MRI, have enabled the investigation of these anatomical changes in the living human brain across development. Structural MRI studies have consistently shown continuing neuroanatomical development in gray matter and white matter (Brain Dev. Coop. Group 2012, Giedd et al. 1999, Sowell et al. 2003, Tamnes et al. 2013), with association cortices reducing in gray matter volume across adolescence and white matter increasing into adulthood. Until recently, most structural MRI studies of the developing brain have examined gray and white matter volumes in relatively large regions. Gray matter volume itself is the product of cortical thickness and surface area, which are influenced by distinct genetic (Panizzon et al. 2009, Winkler et al. 2010), evolutionary (Rakic 1995), and cellular (Chenn & Walsh 2002) processes, in addition to being phenotypically distinct (Winkler et al. 2010). Gray matter volume is more highly correlated with, and genetically and environmentally related to, surface area than with cortical thickness (Winkler et al. 2010). Differences in surface area are pronounced across species, whereas cortical thickness is highly conserved in comparison (Hill et al. 2010, Rakic 1995).

Areas within the mentalizing network continue to develop in gray matter volume, cortical thickness, and surface area across adolescence before relatively stabilizing in the early twenties (Mills et al. 2013). In a study using a large sample of individuals with at least two brain scans between

ages 7 and 30 years, we examined the structural developmental trajectories of the mentalizing brain network. Gray matter volume and cortical thickness in medial Brodmann area 10 (a proxy for dmPFC), TPJ, and pSTS decreased from childhood into the early twenties, whereas the ATC increased in gray matter volume until adolescence and in cortical thickness until early adulthood. Surface area for each region followed a cubic trajectory, reaching a peak in late childhood or early adolescence before decreasing into the early twenties (Mills et al. 2013). This protracted development demonstrates that areas of the brain involved in deciphering the mental states of others are still maturing from late childhood into early adulthood.

The underlying mechanisms associated with a reduction in gray matter volume are still debated (Paus et al. 2008, Poldrack 2010), and to date no studies have tested the relationship between developmental changes in underlying cellular or synaptic anatomy and structural MRI measures. Despite these limitations, it is thought that reductions in gray matter volume might reflect synaptic reorganization and/or increases in white matter integrity (Paus et al. 2008). Histological studies of postmortem human brain tissue support the idea that the prefrontal cortex continues to undergo synaptic pruning across adolescence (Huttenlocher & Dabholkar 1997, Petanjek et al. 2011). White matter generally increases in volume and integrity across adolescence and into young adulthood (Lebel et al. 2008, Lenroot et al. 2007). The developmental changes in white matter are thought to provide evidence for an extended period of myelination of connections between association cortices, which has been found in histological studies (Yakovlev & Lecours 1967).

Functional Development of the Social Brain Network in Adolescence

A number of fMRI studies show functional changes across adolescence in the brain networks associated with social cognition, including face processing, mentalizing, peer evaluation, and peer influence. We discuss these studies below.

Face processing. Understanding the mental states of others by processing facial expressions is a crucial skill and is one that continues to develop across adolescence (McGivern et al. 2002). Recruitment of the prefrontal cortex during face-processing tasks increases between childhood and adolescence and then decreases between adolescence and adulthood (reviewed in Blakemore 2008). Brain systems supporting detection and interpretation of communicative signals from face processing also show age-related changes from childhood to adulthood, perhaps due to changing cognitive strategies (Cohen Kadosh et al. 2013a,b).

Recent longitudinal neuroimaging studies are beginning to provide evidence of changes in neural responses to social stimuli such as faces between childhood and adolescence. As participants transitioned from late childhood (~10 years) to adolescence (~13 years), they showed greater neural activity in the ventral striatum and ventromedial PFC while looking at facial displays (Pfeifer et al. 2011). The ATC was the only area to show a longitudinal change in preference for emotional facial displays. This study correlated longitudinal changes in ventral striatal activity with decreasing susceptibility (i.e., increasing resistance) to peer influence, demonstrating that heightened subcortical reactivity in socioemotional situations might indicate better emotion-regulation capacities (Pfeifer et al. 2011). In addition, pubertal status during early adolescence was related to increased neural recruitment of the amygdala, hippocampus, and ATC when participants looked at affective facial stimuli (i.e., happy, sad, angry faces) (Moore et al. 2012).

Mentalizing. Many fMRI studies that use mentalizing report decreases in dmPFC recruitment between adolescence and adulthood (reviewed in Blakemore 2008, 2012). These studies have used a variety of tasks that require mental state attribution, such as understanding irony (Wang et al.

2006), thinking about social emotions such as guilt (Burnett et al. 2009), understanding intentions (Blakemore et al. 2007), understanding emotions from photographs of eyes (Moor et al. 2012), and thinking about the preferences and dispositions of oneself or a fictitious story character (Pfeifer et al. 2009). In some studies, higher activity in more posterior regions, such as the pSTS/TPJ (Blakemore et al. 2007), and in the ATC (Burnett et al. 2009), was observed in adults as compared to adolescents. These changes in functional recruitment have been hypothesized to reflect changes in neurocognitive strategy and/or neuroanatomy (Blakemore 2008).

In an adapted version of the Director task (Apperly et al. 2010, Dumontheil et al. 2010a), areas of the mentalizing brain network were engaged when participants had to use social cues to select an appropriate action in a communicative context (Dumontheil et al. 2012). Although both adults and adolescents recruited the dmPFC when the social cues were needed to accurately perform the task, adolescents also recruited the dmPFC when social cues were not needed. The authors suggest that this engagement of the dmPFC in social conditions, even when social signals are irrelevant, may reflect the use of brain regions involved in mentalizing even when they are not necessary during adolescence.

Adolescents also show developmental changes in sensitivity to the perspectives of others. In an fMRI study, young adolescents (12 to 14 years), older adolescents (15 to 17 years), and emerging adults (18 to 22 years) completed a social exchange game in which participants were the second player in an investment game (van den Bos et al. 2011). These participants were first given an amount of money by an anonymous first player, which they could divide equally between themselves and the first player (reciprocate) or keep most for themselves (defect). Participants' ability to understand the intentions of the first player was also measured by comparing trials on which the first player stood to lose a large amount of money by trusting the second player with trials where the first player stood to lose a relatively small amount of money. Older adolescents and emerging adults were more likely to reciprocate when the first player stood to lose more money, whereas the younger adolescents did not differentiate, supporting the idea that the ability to understand the intentions of others increases into adulthood. The recruitment of the left TPJ when participants were shown that the first player trusted them increased with age, and this level of activation correlated with participants' sensitivity to the first player's intentions. All participants showed greater recruitment in the dmPFC when making self-oriented choices (defecting), but only young adolescents engaged this region when making reciprocal choices. This heightened activation in the dmPFC for reciprocal choices decreased between early and late adolescence and remained stable into early adulthood, possibly reflecting a shift away from engaging in social interactions from an egocentric perspective (van den Bos et al. 2011).

Social emotion. Social emotions—such as guilt, embarrassment, shame, and pride—require representing another's mental state, whereas basic emotions such as fear and disgust do not. Because adolescence is a period of increased sensitivity to peer evaluation, there may be changes in how social emotions are processed. One fMRI study investigated changes in neural recruitment during a social emotional task between adolescence (11 to 18 years) and adulthood (23 to 32 years) (Burnett et al. 2009). Participants were instructed to read sentences describing social or basic emotion scenarios. Adolescents recruited the dmPFC more than adults when reading social emotional sentences relative to basic emotion sentences. In contrast, adults recruited the left ATC more than did adolescents when reading social emotional sentences relative to basic emotion sentences (Burnett et al. 2009).

A more recent study investigated the influence of puberty on social emotion processing in adolescence (Goddings et al. 2012). In a sample of 42 female adolescents (11 to 13 years), levels of pubertal hormones (testosterone, estradiol, and dehydroepiandrosterone) were related to ATC

Conformity: changes in valuation to match the group

recruitment during social emotional processing. Whereas activity in the left ATC was positively correlated with hormone levels (irrespective of age), activity in the dmPFC was negatively correlated with chronological age (irrespective of hormone levels), providing evidence for a dissociation between puberty- and age-related changes in neural function during adolescence (Goddings et al. 2012).

Peer evaluation. There are a number of fMRI investigations of experimentally manipulated social exclusion using the *Cyberball* task. This task involves participants playing a game of "catch" with two other players under the guise that they are playing with real peers over the Internet. However, the other players are actually preprogrammed to include or exclude the participant. In one study, recruitment of the mPFC during exclusion relative to inclusion was associated with greater self-reported susceptibility to peer influence in adolescents but not in adults (Sebastian et al. 2011). This study also found age-related differences in right ventrolateral PFC (vlPFC) recruitment during exclusion conditions, with adults recruiting right vlPFC more than adolescents. Another fMRI study using the *Cyberball* task specifically in a group of adolescents aged 12 to 13 years found recruitment of the right vlPFC during exclusion conditions was negatively correlated with self-reported measures of distress following exclusion (Masten et al. 2009). Together, these studies suggest the vlPFC plays a role in regulating distress following social exclusion and that this region is still developing functionally between adolescence and adulthood. Healthy adolescents who display heightened activity in an area of the brain called the subgenual anterior cingulate cortex while being excluded from peers in *Cyberball* were more likely to show an increase in depressive symptoms during the following year (Masten et al. 2011).

Prompted by research linking good peer relationships to well-being, Masten and colleagues examined how 12- to 13-year-olds respond to witnessing peer rejection in an online game (Masten et al. 2010). Participants first completed a self-reported measure of trait empathy before participating in an fMRI task where they witnessed peer exclusion in a game of *Cyberball*. Afterward, they were asked to write a letter to the rejected player as a measure of prosocial behavior. Activity in the mentalizing network was related to observed exclusion compared to observed inclusion. Although recruitment of the dmPFC and ATC appeared to be related to self-reported trait empathy, only the anterior insula showed a positive correlation with prosocial behavior. Together, these findings suggest that young adolescents recruit the mentalizing network more while witnessing peer rejection than in a situation where peers are being treated equally.

Peer influence. Peer influence on conformity shows a curvilinear pattern between middle childhood and late adolescence, reaching a peak in early adolescence (Berndt 1979). The popularity rankings of a given song influence how much adolescents like it (Berns et al. 2010). In an fMRI task, adolescents aged 12 to 17 years listened to and rated the likeability of short music clips, first without knowing the popularity of the song and then after receiving its popularity ranking. Adolescents' change in song evaluation correlated with increased recruitment of the anterior insula and ACC, which the authors suggest may reflect the anxiety of having preferences that are dissimilar to those of others.

The presence of peers affects how likely adolescents are to take risks in a driving game. Adolescents (13 to 16 years), young adults (18 to 22 years), and adults (24+ years) took around the same number of driving risks when alone, whereas the adolescents took significantly more in the presence of their friends (Gardner & Steinberg 2005). In contrast, peers had no impact on risk taking in adults and had an intermediate effect on risk taking in youths (Gardner & Steinberg 2005) (see **Figure 4**). In an fMRI version of this task, in the peers-present condition two friends communicated with the participant (who was in the MRI scanner) over an intercom (Chein et al.

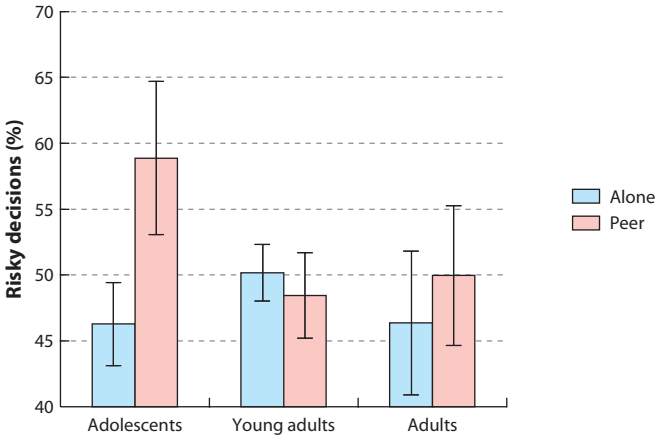


Figure 4

Risky behavior in adolescents, young adults, and adults when alone or when being watched by peers. This graph illustrates the average percentage of risky decisions for adolescent, young adult, and adult participants when playing the Stoplight task alone and with a peer audience. Adapted from Chein et al. (2011).

2011). Adults aged 24 to 29 years showed higher activity in lateral PFC than did adolescents aged 14 to 18 years or younger adults aged 19 to 22 years when they had to make critical decisions in the driving game, both when alone and when peers were present. Relative to both groups of adults, adolescents showed increased recruitment of the ventral striatum and orbitofrontal cortex during the driving decisions with peers compared to when alone.

Social context modulates risk attitudes adopted by adolescents (Engelmann et al. 2012). Relative to adults, adolescents showed greater risk-adverse behavior after receiving expert advice, and this effect is modulated by increased engagement of the dorsolateral PFC by adolescents during valuation in the presence of advice (Engelmann et al. 2012). The authors suggest enhanced inhibitory and cognitive control processes may underlie the effect of social context on risky decision making in adolescents.

THE SOCIAL ENVIRONMENT DURING ADOLESCENCE AND EMERGING BEHAVIORS AND COGNITIONS

Characteristic behaviors of adolescence, such as heightened self-consciousness, mood variability, novelty seeking, risk taking, and peer orientation, are fundamental to the successful transition into a stable adult role. Here we discuss changes in the social environment during adolescence as well as how emerging behaviors and cognitions are involved in the successful navigation of these environments.

Changes in Social Environment

The adolescent social environment is different from the child and adult social environments in many ways. In many school systems, the transition from primary to secondary school occurs around the onset of puberty, which may place children into new environments without the same peers, in a different structure of learning, and at the bottom of the age hierarchy. Adolescents are also exposed to novel situations that they were unlikely to encounter as children, which might play a role in the increased risky decision making seen in the transition from childhood to adolescence.

Risky Decision Making

Adolescents are stereotypically known for their engagement in risky behaviors. There is experimental evidence supporting the idea that, while in laboratory settings, adolescents are more likely than children and adults to make risky decisions in "hot" contexts (Blakemore & Robbins 2012). Experimental evidence from risky decision making and probabilistic reward paradigms mostly supports the hypothesis that adolescents are biased to taking risks due to overactive reward-related circuitry (i.e., ventral striatum) (Ernst et al. 2006, Van Leijenhorst et al. 2010). Probabilistic reward paradigms in laboratory experiments on risk taking often involve gambling tasks. Children and adolescents show adult levels of probability estimation and reward evaluation during one such gambling task, suggesting that heightened risky decision making in adolescents is probably not related to a change in risk perception (Van Leijenhorst et al. 2008). When asked in a laboratory setting to estimate the risks of negative outcomes to some risky behaviors, adolescents actually overestimate risks (Reyna & Farley 2006). Adolescents also rate the potential reward to be gained as very high, which may make the perceived benefits outweigh the perceived risk (Reyna & Farley 2006). Social and contextual cues can bias the way adolescents perceive the risk involved in certain behaviors (Reyna 2008, Reyna & Adam 2003, Reyna & Farley 2006). Although risky decision making during adolescence is often framed as maladaptive and unavoidable, this perspective leaves out many key features of risky decision making, including the fact that the outcome can be positive and that some risky decision making is necessary in development and throughout life. A recent report highlights the benefits of asking "What's in it for the adolescent?" when studying risky behavior and risky decision making in adolescence (Ellis et al. 2012). We propose that some rewards gained by risky behaviors are social in nature, such as peer acceptance or the avoidance of social exclusion, and that this is a potential major driver of risky behavior, in particular in adolescence, when social acceptance is especially important. (see **Figure 5**).

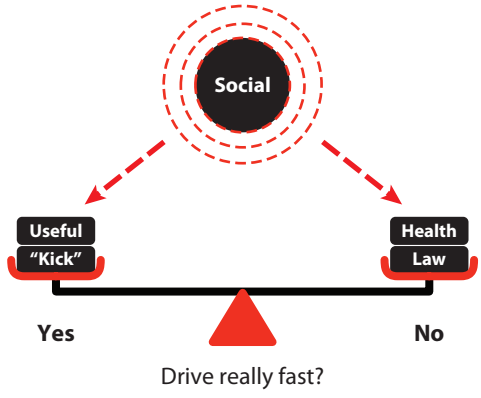


Figure 5

Illustration of some of the factors that influence certain risky decisions. In a scenario in which the individual is making a choice whether or not to drive very fast, multiple factors might weigh in, such as the potential outcome of injury (health), being arrested (law), arriving somewhere in less time (useful), and getting a subjective feeling of pleasure from the experience ("kick"). Above this "seesaw" is another potential factor that could weigh on either side of the decision process, which is made up of social factors (e.g., family, teachers, peers). The potential of peer acceptance/rejection could weigh on either side of the seesaw depending on the peers, and the weight of the factor (indicated by dashed lines) could vary on the basis of the individual and the developmental stage.

Executive Functions

Cognitive abilities such as processing speed, voluntary response suppression, delay discounting, future planning, and working memory all mature into adolescence (Luna et al. 2004, Steinberg et al. 2009). Developmental improvements in executive functions likely influence—and are influenced by—social cognitive processing during adolescence. Developmental neuroimaging studies show correlations between the protracted development of the prefrontal cortex and maturing cognitive and behavioral abilities during adolescence, such as manipulating multiple items in mind (Crone et al. 2006b), suppressing reflexive behavior (Luna et al. 2001), relational reasoning (Dumontheil et al. 2010b), future planning (Kaller et al. 2012), and delay discounting (Costa Dias et al. 2013). Successful emotion regulation in early adolescence (10 to 13 years) is impacted by the adolescent's sensitivity to rejection as well as situational factors of the emotional stimuli. Compared with older adolescents and adults (14 to 23 years), young adolescents found it harder to regulate their emotions when presented with social affective stimuli compared to nonsocial affective stimuli (Silvers et al. 2012).

Executive functions: a set of cognitive processes that regulate, control, and manage other cognitive processes

Acculturation: adaptation to the mainstream culture of where one has immigrated

The ability to consider future consequences of actions continues to improve across adolescence (Crone & van der Molen 2004), which might impact how adolescents interact in social situations. Both young adolescents (12 to 14 years) and older adolescents (16 to 18 years) showed heart rate slowing after erring on a task-switching task, which might indicate an increasing ability to monitor performance (Crone et al. 2006a). The ability to monitor one's performance in social situations likely affects the overall success of the interaction. Developmental fMRI studies suggest that distinct neural systems develop at different rates across childhood and adolescence and that these age-related changes in regions involved in feedback processing may underlie behavioral differences in flexible performance adjustment (Crone et al. 2008). A qualitative shift in neural recruitment during feedback-based learning is seen in early adolescence, possibly reflecting the increasing influence of negative feedback on behavioral adjustment (van Duijvenvoorde et al. 2008). The changes in the processing of feedback in adolescence have implications for successful social communication; however, further studies are needed to use integrative tasks to test directly the influence of gradually improving executive functions on social cognition.

IMPLICATIONS FOR SOCIETY

Is the Human Brain Particularly Sensitive to Social Signals During Adolescence?

This review has focused on evidence from the psychology and neuroscience literatures to support the view of adolescence as a period particularly sensitive to social environmental cues. However, two further lines of evidence need to be acquired to support this theory: (*a*) the brain during adolescence (more than in childhood and adulthood) is particularly susceptible to social environmental cues, and (*b*) changes in the brain during adolescence reflect particular susceptibility to social environmental cues (more than other types of stimuli). That is, are our brains organized in such a manner that reflects our ancestors navigating increasingly complex social environments, or foraging in increasingly unstable climates? Similarly, is the protracted development of the mentalizing brain network reflective of the need for later acculturation into one's society and culture? Acculturation, or adaptation to the mainstream culture of where one has immigrated, occurs more rapidly at younger ages (1 to 15 years) (Cheung et al. 2011), suggesting that the sensitive period for cultural learning is not adolescent specific but instead that cultural sensitivity may begin to close during adolescence. Perhaps the cognitive and behavioral abilities that emerge during adolescence enhance social signals or allow them to be more easily integrated.

Educational Implications

Adolescence represents a period of brain development during which environmental experiences—including teaching—can and do profoundly shape the developing brain. If early childhood is seen as a major opportunity—or a sensitive period—for teaching, so too might adolescence. It is only recently that teenagers have been routinely educated in the West. In many countries a large proportion of teenagers have no access to secondary school education. And yet the adolescent brain is malleable and adaptable—this is an excellent opportunity for learning and creativity. Risk taking in an educational context is a vital skill that enables progress and creativity. Although some adolescents use risk taking to achieve great things, many are worried about taking risks in the context of learning. The heightened risk taking in this age group should be harnessed for learning and creativity.

A prevailing view in adolescent research is that certain behaviors are desirable (e.g., long-term planning), and certain behaviors are undesirable (e.g., risk taking). Although long-term planning can help many individuals attain high-quality and stable adult lives, other external factors may prevent individuals from attaining this goal despite their using long-term planning (Ellis et al. 2012). In certain situations, taking a risk might actually be more likely to give the individual a chance to obtain the preferred outcome. The research described above emphasizes the role of contextual cues in influencing adolescent behaviors. A shift from treating adolescent behaviors, especially risk-taking behaviors, in isolation to a model that integrates social environmental cues might enhance our understanding of adolescent behaviors and improve interventions. What is sometimes seen as the problem with adolescents—risk taking, poor impulse control, self-consciousness, and so forth—is actually reflective of brain changes that provide an excellent opportunity for education and social development.

Adolescence is a time of opportunity for learning new skills and forging an adult identity. Research on brain development suggests that adolescence might represent a period of relatively high neural plasticity, in particular in brain regions involved in executive function and social cognition. The research on the brain basis of social development in adolescence might have implications for "when to teach what" and could inform both curriculum design and teaching practice with the aim of ensuring that classroom activities exploit periods of neural plasticity that facilitate maximal learning.

Legal Implications

Developmental neuroscience has already affected legal proceedings in United States by calling into question the sentencing procedures applied to adolescents (see Steinberg 2013), and many developmental scientists are still struggling with questions of culpability during an age of relative brain immaturity (Cauffman & Steinberg 2000, Steinberg 2009, Steinberg & Scott 2003). Although the discussion on culpability and the brain is ongoing, evidence from multiple fields supports the need for special consideration in prosecuting and punishing adolescents. Twenty years ago, Terrie Moffitt presented evidence supporting the idea that the majority of adolescents who engage in criminal behavior will do so during adolescence and at no other period of their life (Moffitt 1993). Such problem behaviors have also been shown to decrease without formal training (Chamberlain & Moore 1998). Further, interventions that segregate adolescents engaging in problem behaviors into groups can actually be harmful (Dishion & Tipsord 2011, Dishion et al. 2012, Ellis et al. 2012). The social augmentation hypothesis suggests that peer exclusion in adolescence can lead to neuroanatomical shifts in reward sensitivity, therefore making the adolescent more susceptible to peer influence (Dishion et al. 2012). The research reviewed in this article would support this

speculative hypothesis, and future work will need to integrate measures of social exclusion and peer influence with neuroimaging paradigms, as some have already begun to do (Peake et al. 2013).

Psychology and intervention research provide a strong argument for reducing situations in which high-risk behaviors such as gang affiliation and crime are rewarded through positive peer responses (Dishion & Tipsord 2011). The capacity for change is reflected in the extended neuroanatomical and functional development of the human brain. By understanding and harnessing the plasticity of the brain during adolescence, legal interventions might better prevent reoffending and promote prosocial behavior. It is important that these interventions take into account not only the adolescent but also the influences of the social and physical environments in which the adolescent finds him or herself. Evidence from neuroscience and psychology studies shows that the social environment during adolescence has a profound impact on life course trajectories, and it is necessary to attempt to change the adolescent engaging in criminal behaviors as well as the social environment that may promote such behaviors.

Social Implications

A consequence of research on adolescence might be a change in how adolescents are perceived, including how adolescents perceive themselves, the period of adolescence and what can be expected, and how adolescents interpret their experiences in the world. Research on adolescent brains and behaviors has penetrated multiple media outlets and is a perennial topic that receives much attention. One study has investigated how adolescents understand and feel about research on the adolescent brain (Choudhury et al. 2012). The participating adolescents in this study felt that although research on the adolescent brain is necessary and important, the model of the adolescent brain as an explanation for adolescent behavior is insufficient (Choudhury et al. 2012). Interestingly, participants were less interested in how neuroscience could influence how they understand themselves and more interested in how research on the adolescent brain could influence the perspectives of adults (Choudhury et al. 2012). They pointed out the potential for neuroscience research to perpetuate stereotypes or combat stereotypes, depending on how adults incorporate research in their understanding of adolescence (Choudhury et al. 2012).

Adolescents are sensitive to the signals within their social environment, and these signals can impact how likely they are to invest in the future. A recent report suggested that adolescents perceive their risk of dying soon as higher than it actually is (Fischhoff et al. 2010). This perception may impact the likelihood of engaging in behaviors reflecting a faster life history strategy, although this has not been directly tested. Indeed, the authors voice similar concerns in the first sentence of the report: "Adolescents' willingness to prepare for the future depends, in part, on their confidence in living long enough to get a return on that investment" (Fischhoff et al. 2010). Perceived threats and crime expectations in the environment, but not actual experience with violence, correlated with mortality judgments (Fischhoff et al. 2010). Larger social structures have consequences for the health of adolescents, with factors such as inequality and poverty reducing adolescent health (Viner et al. 2012).

CONCLUSION

In the present review, we have discussed research that describes adolescence as a period of biological and social transition. Neuroimaging and behavioral studies in humans, and neuroanatomical and behavioral studies in animals, have demonstrated that the social brain and social cognition undergo a profound period of development in adolescence. As such, adolescence might represent a sensitive period for the processing and acquisition of sociocultural knowledge.

SUMMARY POINTS

1. Areas of the brain involved in understanding the mental states of others continue to develop structurally and functionally across adolescence.
2. Adolescence might represent a period of enhanced sensitivity to social signals in the environment, and these signals might influence an adolescent's life course trajectory by motivating certain behaviors.
3. Studies of adolescent behaviors would benefit from measuring social influences.
4. Adults can have a large impact on the social cognitive development and life course trajectories of adolescents by creating and maintaining the structures of social environments.

FUTURE ISSUES

1. How can we better define the transition period between adolescence and adulthood? What factors influence this transition, and are there differential outcomes in health, reproduction, and quality of life between those who transition at different ages?
2. Do heritability studies support the theory that areas of the mentalizing brain network are particularly sensitive to social environmental cues during adolescence?
3. How does research on adolescent brain development influence adolescents' self-perception and health?
4. How many abilities that develop during adolescence are related to navigating the social environment?
5. How does risk taking in adolescence relate to social status and the social context?
6. How do individual differences, such as gender, personality, and resistance to peer influence, affect the developing adolescent brain?

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

The authors thank A.L. Goddings, R.M. Walford, and S. Burnett Heyes for their help with this review. Support for K.L.M. came from the National Institutes of Mental Health Graduate Partnership Program. Support for S.J.B. came from the Royal Society and the Leverhulme Trust. S.J.B. is funded by a Royal Society University Research Fellowship.

LITERATURE CITED

Adolphs R. 2009. The social brain: neural basis of social knowledge. *Annu. Rev. Psychol.* 60:693–716

Andersen SL, Teicher MH. 2008. Stress, sensitive periods and maturational events in adolescent depression. *Trends Neurosci.* 31:183–91

Apperly IA. 2010. *Mindreaders: The Cognitive Basis of "Theory of Mind."* New York: Psychol. Press

Apperly IA, Carroll DJ, Samson D, Humphreys GW, Qureshi A, Moffitt G. 2010. Why are there limits on theory of mind use? Evidence from adults' ability to follow instructions from an ignorant speaker. *Q. J. Exp. Psychol.* 63:1201–17

Baillargeon R, Scott RM, He Z. 2010. False-belief understanding in infants. *Trends Cogn. Sci.* 14(3):110–18

Berndt TJ. 1979. Developmental changes in conformity to peers and parents. *Dev. Psychol.* 15:608–16

Berns GS, Capra CM, Moore S, Noussair C. 2010. Neural mechanisms of the influence of popularity on adolescent ratings of music. *NeuroImage* 49:2687–96

Blakemore S-J. 2008. The social brain in adolescence. *Nat. Rev. Neurosci.* 9:267–77

Blakemore S-J. 2012. Development of the social brain in adolescence. *J. R. Soc. Med.* 105:111–16

Blakemore S-J, Den Ouden H, Choudhury S, Frith C. 2007. Adolescent development of the neural circuitry for thinking about intentions. *Soc. Cogn. Affect. Neurosci.* 2:130–39

Blakemore S-J, Robbins TW. 2012. Decision-making in the adolescent brain. *Nat. Neurosci.* 15:1184–91

Bogin B, Smith BH. 1996. Evolution of the human life cycle. *Am. J. Human Biol.* 8:703–16

Brain Dev. Coop. Group. 2012. Total and regional brain volumes in a population-based normative sample from 4 to 18 years: the NIH MRI Study of Normal Brain Development. *Cereb. Cortex* 22:1–12

Brothers L. 2002. The social brain: a project for integrating primate behavior and neurophysiology in a new domain. In *Foundations in Social Neuroscience*, ed. JT Cacioppo, GG Berntson, R Adolphs, CS Carter, RJ Davidson, MK McClintock, BS McEwen, MJ Meaney, DL Schacter, EM Sternberg, SS Suomi, SE Taylor, pp. 367–85. Cambridge, MA: MIT Press

Brumbach BH, Figueredo AJ, Ellis BJ. 2009. Effects of harsh and unpredictable environments in adolescence on development of life history strategies: a longitudinal test of an evolutionary model. *Hum. Nat.* 20:25–51

Brunet E, Sarfati Y, Hardy-Baylé MC, Decety J. 2000. A PET investigation of the attribution of intentions with a nonverbal task. *NeuroImage* 11:157–66

Burnett S, Bird G, Moll J, Frith C, Blakemore S-J. 2009. Development during adolescence of the neural processing of social emotion. *J. Cogn. Neurosci.* 21:1736–50

Call KT, Riedel AA, Hein K, McLoyd V, Petersen A, Kipke M. 2002. Adolescent health and well-being in the twenty-first century: a global perspective. *J. Res. Adolesc.* 12:69–98

Carpenter M, Nagell K, Tomasello M. 1998. Social cognition, joint attention, and communicative competence from 9 to 15 months of age. *Monogr. Soc. Res. Child Dev.* 63:i–vi, 1–143

Casey BJ, Getz S, Galvan A. 2008. The adolescent brain. *Dev. Rev.* 28:62–77

Castelli F, Happé F, Frith U, Frith C. 2000. Movement and mind: a functional imaging study of perception and interpretation of complex intentional movement patterns. *NeuroImage* 12:314–25

Cauffman E, Steinberg L. 2000. (Im)maturity of judgment in adolescence: why adolescents may be less culpable than adults. *Behav. Sci. Law* 18:741–60

Chamberlain P, Moore KJ. 1998. Models of community treatment for serious offenders. In *Social Programs That Work*, ed. J Crane, pp. 258–76. Princeton, NJ: Sage Found.

Chein J, Albert D, O'Brien L, Uckert K, Steinberg L. 2011. Peers increase adolescent risk taking by enhancing activity in the brain's reward circuitry. *Dev. Sci.* 14:F1–10

Chenn A, Walsh CA. 2002. Regulation of cerebral cortical size by control of cell cycle exit in neural precursors. *Science* 297:365–69

Cheung BY, Chudek M, Heine SJ. 2011. Evidence for a sensitive period for acculturation: younger immigrants report acculturating at a faster rate. *Psychol. Sci.* 22:147–52

Choudhury S. 2010. Culturing the adolescent brain: What can neuroscience learn from anthropology? *Soc. Cogn. Affect. Neurosci.* 5:159–67

Choudhury S, McKinney KA, Merten M. 2012. Rebelling against the brain: public engagement with the "neurological adolescent." *Soc. Sci. Med.* 74:565–73

Cohen Kadosh K, Johnson MH, Dick F, Cohen Kadosh R, Blakemore S-J. 2013a. Effects of age, task performance, and structural brain development on face processing. *Cereb. Cortex* 23:1630–42

Cohen Kadosh K, Johnson MH, Henson RN, Dick F, Blakemore S-J. 2013b. Differential face-network adaptation in children, adolescents and adults. *NeuroImage* 69:11–20

Costa Dias TG, Wilson VB, Bathula DR, Iyer SP, Mills KL, et al. 2013. Reward circuit connectivity relates to delay discounting in children with attention-deficit/hyperactivity disorder. *Eur. Neuropsychopharmacol.* 23:33–45

Crone EA. 2013. Considerations of fairness in the adolescent brain. *Child Dev. Perspect.* 7:97–103

Crone EA, Dahl RE. 2012. Understanding adolescence as a period of social-affective engagement and goal flexibility. *Nat. Rev. Neurosci.* 13:636–50

Crone EA, Somsen RJM, Zanolie K, Van der Molen MW. 2006a. A heart rate analysis of developmental change in feedback processing and rule shifting from childhood to early adulthood. *J. Exp. Child Psychol.* 95:99–116

Crone EA, Van der Molen MW. 2004. Developmental changes in real life decision making: performance on a gambling task previously shown to depend on the ventromedial prefrontal cortex. *Dev. Neuropsychol.* 25:251–79

Crone EA, Wendelken C, Donohue S, Van Leijenhorst L, Bunge SA. 2006b. Neurocognitive development of the ability to manipulate information in working memory. *Proc. Natl. Acad. Sci. USA* 103:9315–20

Crone EA, Zanolie K, Van Leijenhorst L, Westenberg PM, Rombouts SA. 2008. Neural mechanisms supporting flexible performance adjustment during development. *Cogn. Affect. Behav. Neurosci.* 8:165–77

Dishion TJ, Ha T, Véronneau M-H. 2012. An ecological analysis of the effects of deviant peer clustering on sexual promiscuity, problem behavior, and childbearing from early adolescence to adulthood: an enhancement of the life history framework. *Dev. Psychol.* 48:703–17

Dishion TJ, Tipsord JM. 2011. Peer contagion in child and adolescent social and emotional development. *Annu. Rev. Psychol.* 62:189–214

Dumontheil I, Apperly IA, Blakemore S-J. 2010a. Online usage of theory of mind continues to develop in late adolescence. *Dev. Sci.* 13:331–38

Dumontheil I, Hillebrandt H, Apperly IA, Blakemore S-J. 2012. Developmental differences in the control of action selection by social information. *J. Cogn. Neurosci.* 24:2080–95

Dumontheil I, Houlton R, Christoff K, Blakemore S-J. 2010b. Development of relational reasoning during adolescence. *Dev. Sci.* 13:F15–24

Ellis BJ, Del Giudice M, Dishion TJ, Figueredo AJ, Gray P, et al. 2012. The evolutionary basis of risky adolescent behavior: implications for science, policy, and practice. *Dev. Psychol.* 48:598–623

Engelmann JB, Moore S, Monica Capra C, Berns GS. 2012. Differential neurobiological effects of expert advice on risky choice in adolescents and adults. *Soc. Cogn. Affect. Neurosci.* 7:557–67

Ernst M, Pine DS, Hardin M. 2006. Triadic model of the neurobiology of motivated behavior in adolescence. *Psychol. Med.* 36:299–312

Farroni T, Johnson MH, Menon E, Zulian L, Faraguna D, Csibra G. 2005. Newborns' preference for face-relevant stimuli: effects of contrast polarity. *Proc. Natl. Acad. Sci. USA* 102:17245–50

Fischhoff B, Bruine de Bruin W, Parker AM, Millstein SG, Halpern-Felsher BL. 2010. Adolescents' perceived risk of dying. *J. Adolesc. Health* 46:265–69

Fiske ST. 2009. *Handbook of Neuroscience for the Behavioral Sciences*. New York: Wiley

Fletcher PC, Happé F, Frith U, Baker SC, Dolan RJ, et al. 1995. Other minds in the brain: a functional imaging study of "theory of mind" in story comprehension. *Cognition* 57:109–28

Frith CD. 2007. The social brain? *Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci.* 362:671–78

Frith CD. 2008. Social cognition. *Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci.* 363:2033–39

Frith U, Frith CD. 2003. Development and neurophysiology of mentalizing. *Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci.* 358:459–73

Gallagher HL, Happé F, Brunswick N, Fletcher PC, Frith U, Frith CD. 2000. Reading the mind in cartoons and stories: an fMRI study of "theory of mind" in verbal and nonverbal tasks. *Neuropsychologia* 38:11–21

Gardner M, Steinberg L. 2005. Peer influence on risk taking, risk preference, and risky decision making in adolescence and adulthood: an experimental study. *Dev. Psychol.* 41:625–35

Giedd JN, Blumenthal J, Jeffries NO, Castellanos FX, Liu H, et al. 1999. Brain development during childhood and adolescence: a longitudinal MRI study. *Nat. Neurosci.* 2:861–63

Goddings A-L, Burnett Heyes S, Bird G, Viner RM, Blakemore S-J. 2012. The relationship between puberty and social emotion processing. *Dev. Sci.* 15:801–11

Green MR, Barnes B, McCormick CM. 2012. Social instability stress in adolescence increases anxiety and reduces social interactions in adulthood in male Long-Evans rats. *Dev. Psychobiol.* doi: 10.1002/dev.21077

Güroğlu B, van den Bos W, Crone EA. 2009. Fairness considerations: increasing understanding of intentionality during adolescence. *J. Exp. Child Psychol.* 104:398–409

Hill J, Inder T, Neil J, Dierker D, Harwell J, Van Essen D. 2010. Similar patterns of cortical expansion during human development and evolution. *Proc. Natl. Acad. Sci. USA* 107:13135–40

Huttenlocher PR, Dabholkar AS. 1997. Regional differences in synaptogenesis in human cerebral cortex. *J. Comp. Neurol.* 387:167–78

Kaller CP, Heinze K, Mader I, Unterrainer JM, Rahm B, et al. 2012. Linking planning performance and gray matter density in mid-dorsolateral prefrontal cortex: moderating effects of age and sex. *NeuroImage* 63:1454–63

Kessler RC, Berglund P, Demler O, Jin R, Merikangas KR, Walters EE. 2005. Lifetime prevalence and age-of-onset distributions of DSM-IV disorders in the National Comorbidity Survey Replication. *Arch. Gen. Psychiatry* 62:593–602

Keysar B, Barr DJ, Balin JA, Brauner JS. 2000. Taking perspective in conversation: the role of mutual knowledge in comprehension. *Psychol. Sci.* 11:32–38

Keysar B, Lin S, Barr DJ. 2003. Limits on theory of mind use in adults. *Cognition* 89:25–41

Larson R, Richards MH. 1991. Daily companionship in late childhood and early adolescence: changing developmental contexts. *Child Dev.* 62:284–300

Larson RW, Richards MH, Moneta G, Holmbeck G, Duckett E. 1996. Changes in adolescents' daily interactions with their families from ages 10 to 18: disengagement and transformation. *Dev. Psychol.* 32:744–54

Lebel C, Walker L, Leemans A, Phillips L, Beaulieu C. 2008. Microstructural maturation of the human brain from childhood to adulthood. *NeuroImage* 40:1044–55

Lenroot RK, Gogtay N, Greenstein DK, Wells EM, Wallace GL, et al. 2007. Sexual dimorphism of brain developmental trajectories during childhood and adolescence. *NeuroImage* 36:1065–73

Leussis MP, Andersen SL. 2008. Is adolescence a sensitive period for depression? Behavioral and neuroanatomical findings from a social stress model. *Synapse* 62:22–30

Luna B, Garver KE, Urban TA, Lazar NA, Sweeney JA. 2004. Maturation of cognitive processes from late childhood to adulthood. *Child Dev.* 75:1357–72

Luna B, Thulborn KR, Munoz DP, Merriam EP, Garver KE, et al. 2001. Maturation of widely distributed brain function subserves cognitive development. *NeuroImage* 13:786–93

Masten CL, Eisenberger NI, Borofsky LA, McNealy K, Pfeifer JH, Dapretto M. 2011. Subgenual anterior cingulate responses to peer rejection: a marker of adolescents' risk for depression. *Dev. Psychopathol.* 23:283–92

Masten CL, Eisenberger NI, Borofsky LA, Pfeifer JH, McNealy K, et al. 2009. Neural correlates of social exclusion during adolescence: understanding the distress of peer rejection. *Soc. Cogn. Affect. Neurosci.* 4:143–57

Masten CL, Eisenberger NI, Pfeifer JH, Dapretto M. 2010. Witnessing peer rejection during early adolescence: neural correlates of empathy for experiences of social exclusion. *Soc. Neurosci.* 5:496–507

McCormick CM, Green MR, Cameron NM, Nixon F, Levy MJ, Clark RA. 2013. Deficits in male sexual behavior in adulthood after social instability stress in adolescence in rats. *Horm. Behav.* 63:5–12

McCormick CM, Mathews IZ, Thomas C, Waters P. 2010. Investigations of HPA function and the enduring consequences of stressors in adolescence in animal models. *Brain Cogn.* 72:73–85

McGivern RF, Andersen J, Byrd D, Mutter KL, Reilly J. 2002. Cognitive efficiency on a match to sample task decreases at the onset of puberty in children. *Brain Cogn.* 50:73–89

Mills KL, Lalonde F, Clasen LS, Giedd JN, Blakemore S-J. 2013. Developmental changes in the structure of the social brain in late childhood and adolescence. *Soc. Cogn. Affect. Neurosci.* In press

Moffitt TE. 1993. Adolescence-limited and life-course-persistent antisocial behavior: a developmental taxonomy. *Psychol. Rev.* 100:674–701

Moor BG, Macks ZA, Güroglu B, Rombouts SA, Molen MW, Crone EA. 2012. Neurodevelopmental changes of reading the mind in the eyes. *Soc. Cogn. Affect. Neurosci.* 7:44–52

Moore WE 3rd, Pfeifer JH, Masten CL, Mazziotta JC, Iacoboni M, Dapretto M. 2012. Facing puberty: associations between pubertal development and neural responses to affective facial displays. *Soc. Cogn. Affect. Neurosci.* 7:35–43

O'Brien SF, Bierman KL. 1988. Conceptions and perceived influence of peer groups: interviews with preadolescents and adolescents. *Child Dev.* 59:1360–65

Olson IR, McCoy D, Klobusicky E, Ross LA. 2013. Social cognition and the anterior temporal lobes: a review and theoretical framework. *Soc. Cogn. Affect. Neurosci.* 8:123–33

Panizzon MS, Fennema-Notestine C, Eyler LT, Jernigan TL, Prom-Wormley E, et al. 2009. Distinct genetic influences on cortical surface area and cortical thickness. *Cereb. Cortex* 19:2728–35

Paus T, Keshavan M, Giedd JN. 2008. Why do many psychiatric disorders emerge during adolescence? *Nat. Rev. Neurosci.* 9:947–57

Pelphrey KA, Carter EJ. 2008. Charting the typical and atypical development of the social brain. *Dev. Psychopathol.* 20:1081–102

Pelphrey KA, Morris JP, McCarthy G. 2004. Grasping the intentions of others: the perceived intentionality of an action influences activity in the superior temporal sulcus during social perception. *J. Cogn. Neurosci.* 16:1706–16

Peper JS, Dahl RE. 2013. Surging hormones—brain-behavior interactions during puberty. *Curr. Dir. Psychol. Sci.* 22:134–39

Perlman WR, Webster MJ, Herman MM, Kleinman JE, Weickert CS. 2007. Age-related differences in glucocorticoid receptor mRNA levels in the human brain. *Neurobiol. Aging* 28:447–58

Petanjek Z, Judaš M, Šimic G, Rasin MR, Uylings HBM, et al. 2011. Extraordinary neoteny of synaptic spines in the human prefrontal cortex. *Proc. Natl. Acad. Sci. USA* 108:13281–86

Pfeifer JH, Masten CL, Borofsky LA, Dapretto M, Fuligni AJ, Lieberman MD. 2009. Neural correlates of direct and reflected self-appraisals in adolescents and adults: when social perspective-taking informs self-perception. *Child Dev.* 80:1016–38

Pfeifer JH, Masten CL, Moore WE 3rd, Oswald TM, Mazziotta JC, et al. 2011. Entering adolescence: resistance to peer influence, risky behavior, and neural changes in emotion reactivity. *Neuron* 69:1029–36

Poldrack RA. 2010. Interpreting developmental changes in neuroimaging signals. *Hum. Brain Mapp.* 31:872–78

Puce A, Perrett D. 2003. Electrophysiology and brain imaging of biological motion. *Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci.* 358:435–45

Rakic P. 1995. A small step for the cell, a giant leap for mankind: a hypothesis of neocortical expansion during evolution. *Trends Neurosci.* 18:383–88

Reyna VF. 2008. A theory of medical decision making and health: fuzzy trace theory. *Med. Decis. Making* 28:850–65

Reyna VF, Adam MB. 2003. Fuzzy-trace theory, risk communication, and product labeling in sexually transmitted diseases. *Risk Anal.* 23:325–42

Reyna VF, Farley F. 2006. Risk and rationality in adolescent decision making: implications for theory, practice, and public policy. *Psychol. Sci. Public Interest* 7:1–44

Ross WD. 1925. *Ethica Nicomachea.* Transl. WD Ross. London: Oxford Univ. Press

Rushworth MF, Mars RB, Sallet J. 2013. Are there specialized circuits for social cognition and are they unique to humans? *Curr. Opin. Neurobiol.* 23:1–7

Sallet J, Mars RB, Noonan MP, Andersson JL, O'Reilly JX, et al. 2011. Social network size affects neural circuits in macaques. *Science* 334:697–700

Saxe R, Kanwisher N. 2003. People thinking about thinking people. The role of the temporo-parietal junction in "theory of mind." *NeuroImage* 19:1835–42

Saxe RR, Whitfield-Gabrieli S, Scholz J, Pelphrey KA. 2009. Brain regions for perceiving and reasoning about other people in school-aged children. *Child Dev.* 80:1197–209

Schulz KM, Zehr JL, Salas-Ramirez KY, Sisk CL. 2009. Testosterone programs adult social behavior before and during, but not after, adolescence. *Endocrinology* 150:3690–98

Sebastian C, Viding E, Williams KD, Blakemore S-J. 2010. Social brain development and the affective consequences of ostracism in adolescence. *Brain Cogn.* 72:134–45

Sebastian CL, Tan GC, Roiser JP, Viding E, Dumontheil I, Blakemore S-J. 2011. Developmental influences on the neural bases of responses to social rejection: implications of social neuroscience for education. *NeuroImage* 57:686–94

Silvers JA, McRae K, Gabrieli JD, Gross JJ, Remy KA, Ochsner KN. 2012. Age-related differences in emotional reactivity, regulation, and rejection sensitivity in adolescence. *Emotion* 12:1235–47

Sowell ER, Peterson BS, Thompson PM, Welcome SE, Henkenius AL, Toga AW. 2003. Mapping cortical change across the human life span. *Nat. Neurosci.* 6:309–15

Steinberg L. 2009. Adolescent development and juvenile justice. *Annu. Rev. Clin. Psychol.* 5:459–85

Steinberg L. 2013. The influence of neuroscience on US Supreme Court decisions about adolescents' criminal culpability. *Nat. Rev. Neurosci.* 14:513–18

Steinberg L, Graham S, O'Brien L, Woolard J, Cauffman E, Banich M. 2009. Age differences in future orientation and delay discounting. *Child Dev.* 80:28–44

Steinberg L, Scott ES. 2003. Less guilty by reason of adolescence: developmental immaturity, diminished responsibility, and the juvenile death penalty. *Am. Psychol.* 58:1009–18

Tamnes CK, Walhovd KB, Dale AM, Ostby Y, Grydeland H, et al. 2013. Brain development and aging: overlapping and unique patterns of change. *NeuroImage* 68C:63–74

Toledo-Rodriguez M, Sandi C. 2011. Stress during adolescence increases novelty seeking and risk taking behavior in male and female rats. *Front. Behav. Neurosci.* 5:17

van den Bos W, Van Dijk E, Westenberg M, Rombouts SA, Crone EA. 2011. Changing brains, changing perspectives: the neurocognitive development of reciprocity. *Psychol. Sci.* 22:60–70

van Duijvenvoorde ACK, Zanolie K, Rombouts SARB, Raijmakers MEJ, Crone EA. 2008. Evaluating the negative or valuing the positive? Neural mechanisms supporting feedback-based learning across development. *J. Neurosci.* 28:9495–503

Van Leijenhorst L, Westenberg PM, Crone EA. 2008. A developmental study of risky decisions on the cake gambling task: age and gender analyses of probability estimation and reward evaluation. *Dev. Neuropsychol.* 33:179–96

Van Leijenhorst L, Zanolie K, Van Meel CS, Westenberg PM, Rombouts SARB, Crone EA. 2010. What motivates the adolescent? Brain regions mediating reward sensitivity across adolescence. *Cereb. Cortex* 20:61–69

Viner RM, Ozer EM, Denny S, Marmot M, Resnick M, et al. 2012. Adolescence and the social determinants of health. *Lancet* 379:1641–52

Wang AT, Lee SS, Sigman M, Dapretto M. 2006. Developmental changes in the neural basis of interpreting communicative intent. *Soc. Cogn. Affect. Neurosci.* 1:107–21

Webb SJ, Monk CS, Nelson CA. 2001. Mechanisms of postnatal neurobiological development: implications for human development. *Dev. Neuropsychol.* 19:147–71

Weil LG, Fleming SM, Dumontheil I, Kilford EJ, Weil RS, et al. 2013. The development of metacognitive ability in adolescence. *Conscious. Cogn.* 22:264–71

Whitaker LR, Degoulet M, Morikawa H. 2013. Social deprivation enhances VTA synaptic plasticity and drug-induced contextual learning. *Neuron* 77:335–45

Winkler AM, Kochunov P, Blangero J, Almasy L, Zilles K, et al. 2010. Cortical thickness or grey matter volume? The importance of selecting the phenotype for imaging genetics studies. *NeuroImage* 53:1135–46

Yakovlev PA, Lecours IR. 1967. The myelogenetic cycles of regional maturation of the brain. In *Regional Development of the Brain in Early Life*, ed. A Minkowski, pp. 3–70. Oxford, UK: Blackwell