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# What Factors Determine Changes in the Adolescent Brain?

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## Abstract

Over the past two decades there has been an explosion of research on the human adolescent brain. This research has demonstrated that the brain continues to mature during the second decade of life, due to ontogeny and experience. The majority of this work has focused on changes that occur in regulation and affective circuitry; in particular, on how these neurobiological changes relate to characteristic adolescent behavior. This chapter summarizes existing understanding and speculates about agents of change that impact neurobiological development in the adolescent brain. It begins with a discussion of what adolescence refers to and reviews the prevailing neurobiological models of adolescent brain development. Factors are considered that contribute to adolescent brain development (e.g., puberty, sleep, social relationships, adolescent risk-taking). Open questions are posed to aid further consideration and research.


## What Is Adolescence?

Across the world and across different species, adolescence refers to an important function in development: it is the time when individuals move from a state of dependence on caregivers to one of relative independence. This transitional period lends itself to many changes in physical growth and biological development, as well as cognitive sophistication and psychosocial skills. These changes, in turn, drive ongoing development of the brain.

### The Beginning and End of Adolescence

The determination of when adolescence "begins" and "ends" is currently a question of intense debate. Most scientists pinpoint adolescence as "the gradual

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period of transition from childhood to adulthood" (Spear 2000) that begins at the onset of puberty and ends as individuals attain adult roles, responsibilities, and rights. The range of age at which this occurs, however, varies according to cultural and historical circumstances. In the United States, for example, adolescence begins at approximately 10–12 years of age and ends in the late teenage years (approximately 18–19 years of age). In this chapter, the work that I review and the speculative comments that result refer to these age boundaries.

### Adolescence across the Globe and across Species

Adolescent-related behaviors are observable worldwide, across different cultures (Schlegel 2001) and species (Spear 2000). A recent study of sensation-seeking and self-regulation in more than 5,000 individuals from 11 countries in Africa, Asia, Europe, and the Americas found that sensation-seeking peaked in late adolescence and that self-regulation increased linearly until the midtwenties (Steinberg et al. 2018). One explanation for this global phenomenon is that regardless of cultural experience, there are particular neurobiological and hormonal changes that arise during adolescence that are common to typically developing young people. Yet despite these observed general trends, there are vast individual differences in the extent and manner in which adolescent risk-taking manifests itself in different areas of the world. Nonetheless, these findings lend support for current working models (reviewed below) of neurobiological development in brain regions that underlie these behaviors. Juvenile rodents, immediately prior to and following sexual maturation, exhibit behavioral changes that are similar to those commonly observed in human adolescents: increased peer-directed social interactions; occasional increases in fighting with parents; increases in novelty-seeking, sensation-seeking, and risk-taking; increased consummatory behavior; and greater per occasion alcohol use. The increased proclivity toward drug use observed in human adolescents is also observed in adolescent rats (Brenhouse and Andersen 2008; Torres et al. 2008) and nonhuman primates. These data suggest that some of the characteristic adolescent behaviors observed in humans may be embedded in our evolutionary past, and that they emerge to facilitate behaviors important to the developing organism. Indeed, rapid progress is being achieved across laboratories (Crone and Dahl 2012; Varlinskaya and Spear 2008), from studies involving both animals and human adolescents, which show that neural changes in systems that underlie motivational, affective, and behavioral regulation influence the processing of and response to events in the environment in ways that bias behavior.

## Theoretical Models of Adolescent Brain Development

Currently, research is guided by four neurobiological models of adolescence: the dual systems model, the triadic model, the imbalance model, and the fuzzy

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trace theory. These models reflect the differences in maturation rates of brain systems implicated in emotion, social, and reward processing from those that are important for regulation of behavior.

In the domains of sensation-seeking and risky decisions, Steinberg (2010) described adolescent behavior in terms of a *dual systems model*. According to the model, risky decision making in adolescence is the product of an interaction between two neurobiological systems: (a) the socioemotional system, comprised of limbic regions including the amygdala, ventral striatum, orbitofrontal cortex, and medial prefrontal cortex (PFC), and (b) the cognitive control system, comprised of the lateral prefrontal and parietal cortices. Around the time of puberty, the surge in dopaminergic activity within the socioemotional system leads to increases in sensation-seeking and risky decision making, outpacing the development (and engagement) of the cognitive control system. This temporal gap leads to heightened vulnerability to these behaviors during adolescence.

To explain motivated behavior in adolescent decision making, Ernst et al. (2006) proposed the *triadic model*. This model attributes the determinants of motivated behavior to three functional neural systems (the PFC, the striatum, and the amygdala) and focuses on how the maturational timing of each region contributes to age-related differences in motivated behavior as people mature. The PFC is implicated in the regulation aspect of motivated behavior, the striatum in motivational aspects of the model, and the amygdala in the emotional components of behavior. Together, these three nodes and their associated constructs serve (a) to coordinate the calculation of whether to approach (engage in) or avoid a particular behavior and (b) to regulate the resulting calculation. This model has been used to describe typical adolescent behaviors, including cognitive impulsivity, risk-seeking, emotional intensity, and social orientation.

The *imbalance model*, developed by Casey et al. (2008), emerged from empirical studies that examined the developmental transition in humans—from childhood through adolescence and into adulthood—and translated the results across species (nonhuman primate and rodent). According to the model, developmental changes in the neurochemical, structural, and functional composition of the brain proceed on distinct time lines: some brain regions exhibit changes earlier in development than other brain regions. This leads to an imbalance in how these regions bias behavior due to differential engagement across different stages of development (see also Uhlhaas, this volume). For instance, the model has been used to explain nonlinear changes in behavior during adolescence because regions implicated in reward (e.g., striatum) exhibit greater engagement—in terms of striatal activation and behavioral bias toward reward—relative to regions critical for behavioral regulation (e.g., PFC). Importantly, unlike models that focus on specific brain regions, the imbalance model aims to attribute adolescent behavior to the coordinated integration of multiple brain circuits.

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Reyna and Farley (2006) have applied *fuzzy trace theory* as an explanatory framework for adolescent risk behavior. This model posits that sophisticated judgment and decision making are based on simple mental representations of choice ("fuzzy" memory traces) as opposed to more detailed, quantitative representations (verbatim memory traces). Accordingly, decision making becomes less computational and more intuitive as development proceeds. Specifically, risky decision making involves a focus on precise calculations (e.g., determining whether the exact amount of fun or money gained will outweigh the exact amount of risk involved in achieving the fun or money) earlier in development as compared to a "fuzzier" calculation that simply ranks the options (e.g., ranking the potential rewards against the risk involved to get the reward) as individuals get older.

## Factors that Determine Change in the Adolescent Brain

Human brain development is a prolonged process compared to nonhuman animals. The developmental periods of early childhood and adolescence, in particular, exhibit protracted development in humans as compared with most other species. Although the majority of changes and growth in the brain occur postnatally during the first few years of life, the brain undergoes another period of major development during adolescence.

The past two decades has witnessed an explosion of research on the adolescent brain aimed at examining adolescent brain development (Galván 2014). What triggers changes in the brain during adolescence? Similar to many other developmental milestones, these changes are a product of ontogeny as well as environmental or experiential input. In this regard, the adolescent brain is not unique. What distinguishes development in the brain during adolescence, however, is the sensitivity of particular circuitry, namely regions in frontostriatal circuitry, to the changing social and cognitive landscape.

### Physiological Changes

#### *Puberty*

Much has been written about the role of pubertal hormones in inciting neurobiological change in the adolescent brain (see, e.g., Sisk, this volume), so in the interest of brevity, discussion here will be brief.

Puberty is the result of a series of hormonal events during which young adolescents undergo the physical and neuroendocrine changes required to reach sexual maturity. Three characteristics describe puberty:

1. It is controlled and sustained by hormones.
2. It involves changes in body height, weight and shape.
3. It is associated with changes in behavior and mood.

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What is perhaps most fascinating about puberty is that although the physical manifestations occur at a discrete point in development, puberty is actually a long process that is influenced by many factors, some of which occur much earlier in life. This has implications for the various roles and influences pubertal hormones have on the developing brain.

The beginning of puberty is marked by the activation of the hypothalamic-pituitary-gondal (HPG) axis, when the brain starts to communicate with the gonads (sex glands). One brain region, the hypothalamus, plays a central role in this process. Generally the hypothalamus is responsible for monitoring basic human needs (e.g., eating, drinking, sex), but at the onset of puberty, it plays a special role in governing the pituitary gland through gonadotropin-releasing hormone (GnRH) neurons. The pituitary gland produces the hormones, called gonadotropins, necessary to stimulate the release of sex hormones from gonads. The level of sex hormones that need to be released from the gonads is regulated by two hormones secreted from the pituitary gland: the follicle-stimulating hormone stimulates sperm production in males and follicle development in females, whereas the luteinizing hormone regulates testosterone production in males and estrogen secretion and ovum development in females.

Adrenarche, an early stage of sexual maturation, typically begins in humans around 6 to 8 years of age. During adrenarche, the adrenal glands secrete adrenal androgens, such as dehydroepiandrosterone and dehydroepiandrosterone sulfate. Their secretion leads to androgen effects, including the emergence of pubic hair and body odor due to changes in sweat composition, and appears to play a role in changes in the oiliness of the skin that lead to acne.

Gonadarche begins typically around 8 to 10 years of age, but there is considerable variability among individuals as to its onset. Gonadarche is the period most commonly recognized as puberty because it involves the maturation of observable sexual characteristics. In females, menarche (the first menstrual period) occurs in the middle to late stages of gonadarche whereas in males, spermarche (the first ejaculation of semen) occurs in the early to middle stages.

What triggers puberty? Decades of research in animals and humans have not identified any one hormone, event, age, or environmental experience that induces puberty. Instead, all of these factors converge to signal that the organism is healthy and physically mature enough to permit sexual reproduction. These factors have been called "permissive signals" because they permit (or stop inhibiting) pubertal onset (Sisk and Foster 2004). These signals include changing levels of melatonin, body fat, and leptin, all of which are related to weight and energy balance. It is generally held that individuals do not go through puberty until they are energetically and metabolically capable of doing so.

### *Sleep*

Sleep is essential for survival and plays an important role in supporting healthy development. Growing public and scientific concern have raised

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awareness of adolescent sleep patterns and led to what is called a "sleep deprivation epidemic" among human adolescents (National Sleep Foundation 2014). Adolescent sleep deficiencies are rooted in biological and psychosocial changes that occur during this developmental period (Carskadon 2011).

Biological alterations during puberty, including brain coordination in hormonal circuitry, contribute to delay the sleep phase—the body's internal clock shifts—making it more difficult for adolescents to go to sleep earlier (Hagenauer and Lee 2012). This delay (a biological factor) pushes adolescent bed times later while school starting times (an environmental factor) force early waking times (Hagenauer and Lee 2012). Figure 14.1 shows that as children transition from grade school to high school, they go to bed at increasingly later times yet rise at roughly the same time in the morning to attend school. As a result, adolescents regularly experience insufficient sleep. Some studies report that *only 15% of adolescents sleep the recommended 8–10 hours on weekdays* (National Sleep Foundation 2014). Additional environmental factors, such as socializing and studying, contribute to sleep loss among adolescents.

Sleep is integral for various functions, ranging from restorative purposes and memory consolidation to removal of neurotoxic waste. Persistent sleep deficiency and subsequent sleepiness negatively impact adolescent health and safety, including increased risk of suicide and substance use (Owens 2014). Many studies indicate that insufficient sleep is associated with poor emotional functioning in adolescents. Less sleep in adolescents is associated with more depressive symptoms, feelings of hopelessness, and greater anxiety (Fredriksen et al. 2004). Emerging research suggests that insufficient sleep is also detrimental to brain function: poor sleep is associated with less dorsolateral PFC activation during cognitive control (Telzer et al. 2013a) and lower white matter integrity longitudinally (Telzer et al. 2015).

Despite the dwindling time spent asleep, studies suggest that the sleep "need" per se does not undergo dramatic changes during adolescence. An early longitudinal study, which followed adolescents yearly from age 10–12 until age 15–18, found that when given the opportunity to sleep ten hours, adolescents slept an average of approximately 9.25 hours, irrespective of age or maturational stage (Carskadon 2011). Wahlstrohm et al. (2014) noted that early morning school schedules contribute significantly to lower the sleep times of adolescents. When school start times are delayed, sleep is increased, enrollment rates and attendance improve, students fall asleep in class less, symptoms of depressed mood are reduced, and automobile crash rates in teen drivers are lower (Wahlstrohm et al. 2014).

Observing brain activity during sleep may provide a unique window into adolescent cortical maturation and complement waking measures (Tarokh et al. 2016). Recent studies suggest that sleep not only offers an opportunity to measure otherwise unperturbed brain activity, it may also play an active role in sculpting the adolescent brain. Using two-photon microscopy in adolescent mice, for example, Maret et al. (2012) found that synaptic spine elimination

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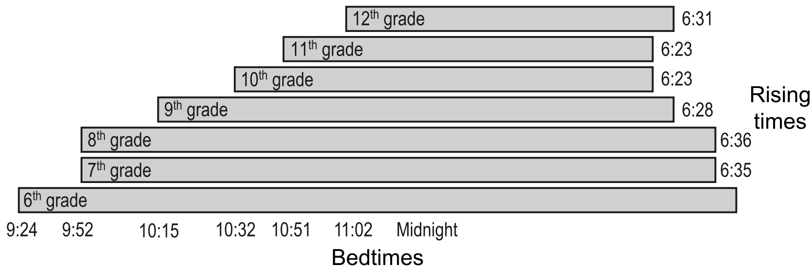


**Figure 14.1** Bedtimes (p.m.) and rising times (a.m.) for youth between sixth and twelfth grade in the United States. This figure, adapted from Carskadon (2011), illustrates the increasingly late bedtime in youth as they transition from grade school to high school.

was higher during sleep than during waking in adolescent but not adult mice, suggesting a distinctive role for sleep in the adolescent brain. Correlational studies in humans have also found associations between sleep behavior and brain development. One study examined structural magnetic resonance imaging (MRI) scans in 290 children and adolescents between the ages of 5 and 18 years and found that self-reported sleep duration was positively correlated with bilateral hippocampal gray matter volume (Taki et al. 2012). Another study found an association in adolescents between variability in sleep duration across fourteen days and white matter integrity, as measured with diffusion tensor MRI a year later (Telzer et al. 2015). Although this line of research is in its nascent stage, evidence for a role of sleep in brain development is emerging.

Uy and Galván (2017) recently published research showing that the relationship between insula response and risky behavior was exacerbated in individuals who reported that they regularly slept less than the 7 hours per night (currently recommended by the National Sleep Foundation). In a separate study from the same group, Tashijian et al. (2017) found that variability in sleep quality, not sleep duration, was predictive of immature development of neural connectivity in the default mode network. Furthermore, their data suggest that stronger neural connectivity buffers the relation between sleep variability and impulsive behavior.

## Social Relationships

Adolescence is a period of social reorientation during which young people begin to develop the identities that will define their adult relationships, interests, and social roles. As a part of the process of social identity formation, adolescents must integrate the perspectives of others with their own to create a unique, coherent sense of self, independent from others. This task can be challenging because while adolescents continue to value input from those they admire, they are also generating their own ideas, values, and behaviors, particularly as they become increasingly aware of the identity bestowed upon

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them by society (e.g., in terms of gender or ethnicity). Parents remain a crucial source of feedback and authority, but sensitivity to peer attitudes becomes increasingly essential to the adolescent. The plasticity and flexibility of the adolescent brain may render it particularly sensitive to social input because all of the brain regions that populate the "social brain network" undergo significant maturation during the adolescent period (Blakemore and Mills 2014). The relative importance of parental and peer perspectives seems to shift over the course of adolescence, at least in some domains. Parental influence is not likely to be replaced by peer influence during adolescence (Brown et al. 1993), as is commonly believed.

In one recent study, Welborn et al. (2016) used fMRI to investigate the neural basis of peer and parental influence on adolescents' subjective evaluations of artwork. We reasoned that works of art would provide a neutral domain, with potentially flexible attitudes that are not already saturated with influence from either group. While undergoing scanning, participants received information regarding their own peers' or parents' actual attitudes (i.e., there was no deception) and immediately provided their own evaluation of the artwork stimulus. Shifts in participants' attitudes toward those of their peers (i.e., peer influence) or those of their parents (i.e., parental influence) were assessed based on participant ratings of each stimulus acquired prior to the scanning session. Adolescent participants shifted their attitudes to indicate significant influence by both peers and parents. As shown in Figure 14.2, there was a significant relation between the level of social influence from both peers (left bottom)

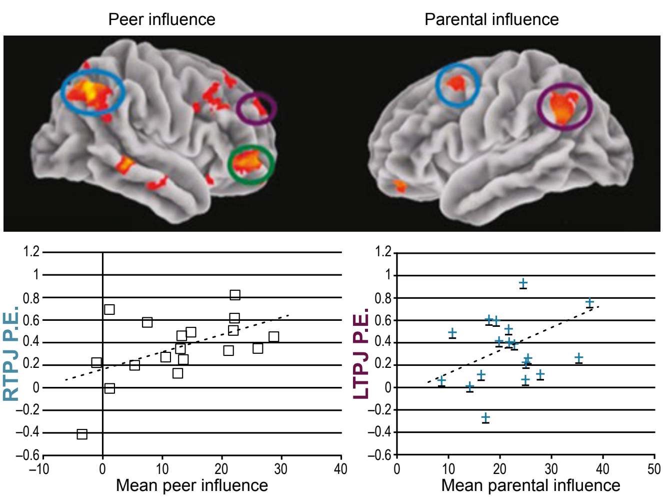


**Figure 14.2** Relation between brain activation and social influence. Brain activation in the temporoparietal junction correlates with peer (left) and parental (right) influence: right temporo-parietal junction parameter estimates (RTPJ P.E.) and left temporo-parietal junction parameter estimates (LTPJ P.E.). From Welborn et al. (2016) with permission of Oxford University Press.

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and parents (right bottom) and the extent of activation in regions typically associated with "mentalizing," including the temporoparietal junction as well as precuneus and ventrolateral PFC during both peer (left top) and parental (right top) influence. This suggests that peers and parents often play distinct roles in adolescence, but that parents continue to exert an important influence.

## Adolescence: A Sensitive Period for Romantic and Sexual Development

Neurodevelopmental models have identified the onset of adolescence, marked by the biological transition into puberty, as a period in which profound changes occur in motivation, cognition, behavior, and social relationships. However, despite the emergence of many excellent models which highlight the importance of puberty for neural development and new, adaptive learning (e.g., reviewed above), these models give limited consideration to the importance of adolescence as a sensitive period for romantic and sexual development. In the few developmental models that did consider romance and sexuality, sexual development was characterized as negative risk behavior (i.e., a risk framework of sexual behavior) (Victor and Hariri 2015). It is equally important to consider normative, healthy aspects of sexual and romantic development and the neurodevelopmental underpinnings of learning about romantic and sexual behavior. As young people enter adolescence, one of their primary tasks is to gain the knowledge and experience that will allow them to take on the social roles of adults, including engagement in romantic and sexual relationships. As such, my coauthors and I argue that the psychological, social, and hormonal changes associated with becoming a sexual being help trigger neurobiological changes in the adolescent brain (Suleiman et al. 2017).

Young people's romantic relationships—from primary school crushes (where two people might interact to a limited extent) to relationships that involve significant investment of emotion, time, and energy—are often dismissed as insignificant. In fact, these relationships serve important developmental purposes and form the primary context for young people to explore their sexual identity and gain sexual experience (Furman and Shaffer 2003). In hopes of gaining social status and winning the companionship of desirable partners, adolescents are highly motivated to learn how to navigate the complex social interactions involved with establishing and maintaining romantic relationships. A person's ability to engage in behaviors that will facilitate intimate relationships and create opportunities for sex and reproduction is the normative developmental outcome of puberty.

Although puberty motivates mating and sexual behavior, only limited research has explored the emergence of sexual behavior in adolescent humans. In contrast, pubertal research on other species has included in-depth exploration of the onset of sexual and mating behavior associated with puberty, acknowledging that the emergence of these novel behaviors requires immense coordination of developmental transitions in the brain, endocrine system, and

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nervous system. As such, animal researchers perceive early sexual experiences not only as behavioral outputs, but also as physiologic inputs that shape neural and hormonal function and development (e.g., Nutsch et al. 2014). The dearth of knowledge about the learning and the reciprocal feedback loops involved in the onset of human mating and sexual experiences highlights important oversights in existing models of human adolescent development. At the same time, while animal models offer important insights into understanding sexual developmental trajectories, they do not expand our understanding of romantic relationships and experiences in humans, nor do they identify developmental changes relevant to these important social milestones. Moreover, the mating framework of animal models offers solely a heterosexual framework for sexual development, thus limiting our understanding of the diversity and fluidity of attraction, behavior, and identity in human sexuality.

The animal literature serves as a critical reminder of the biological purpose of puberty and the reciprocal feedback loops involved in romantic and sexual experiences, which have been largely ignored in models of human adolescent development. Unfortunately, animal models and the limited human research on this topic have done little to explore how puberty shapes the opportunities for learning about the *meaning* of romantic and sexual behaviors (Fortenberry 2014). On one hand, a basic capacity for procreative behavior can be achieved with relatively little skill, knowledge, or experience; on the other, from an evolutionary perspective, social competition in attracting a mate and success in coupling relies heavily on mastery of a complex set of social and emotional skills and behaviors. The learning relevant to acquiring these skills and knowledge necessary to navigate the intertwined social and sexual motivations that emerge with puberty is central to the normative trajectory of social, affective, and cognitive development in humans. Therefore, pubertal maturation (and the natural increase in social motivation, including interest in sexual and romantic behavior) is likely to represent a normative window of learning—not simply about the mechanical aspects of sexual behavior, but also about the complex emotional and social cognitive processes that are part of navigating the charged, high-intensity emotions involved in developing an identity as a sexual being.

In our research (Suleiman et al. 2017), we explored how cognitive and socioaffective development that occurs at puberty creates a unique window of opportunity for adolescents to engage in developmentally appropriate learning opportunities relevant to navigating romantic and sexual experiences. We propose that changes in underlying neural circuitry associated with social and emotional processing may open a second developmental window (after the one in early childhood) for learning about love and attachment relationships. Further, we hypothesize that these learning processes begin with the pubertal physical and neurobiological transitions that influence motivation, yet are highly dependent on context and interpersonal relationships during this time (Suleiman et al. 2017).

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The onset of puberty seems to reorient greater attention and salience toward social and emotional information-processing streams. More specifically, puberty leads to the development of novel social behaviors and responses to newly emerging social contexts (Brown et al. 1993). Young people begin to spend increasingly more time with their peers and, at the same, experience new, sexualized feelings of attraction that motivate relationship-facilitating behaviors. Given that the biological purpose of puberty is to achieve reproductive maturity, it makes sense that the balance between plasticity and stability in this unique peripubertal neural system would create a window of opportunity for learning and motivation relevant to romantic and sexual behavior. Consider the skills that an adolescent must learn in this domain: coping with emotions related to finding someone attractive, building the communication skills required to ask someone out on a date, experiencing sexual arousal with a stranger, navigating the social consequences of dating someone more or less popular, coping with rejection or break up, and balancing the biological desire to have sexual experiences with the complex emotions associated with maintaining a romantic relationship.

Although it has been established that many of the neural systems involved in romantic love and sex undergo significant structural, connectivity, and functional transformation during puberty, little is known about how this intersects with a normative romantic and sexual developmental trajectory. Integrating what is known about the neural underpinnings of romantic love and sexual desire/arousal in adults with the literature on pubertal neurodevelopment points to some intriguing questions. While it is beyond the scope of this paper to summarize this body of literature, adolescent neurodevelopmental models have clearly demonstrated significant sex-specific restructuring of the brain during puberty (Dennison et al. 2013). Beginning with puberty, the developmental transitions in brain networks involved in motivation, reward, and social-emotional processing likely create a unique inflection point for romantic love and sexual arousal to be experienced as positive rewards.

Both love and sexual desire are dopaminergically mediated motivation states that can globally affect cognition (Diamond and Dickenson 2012). Given the developmental transitions that occur during adolescence related to emotional processing and cognitive control, it has been proposed that adolescence is an opportune time to explore the cognitions and emotions associated with romantic relationships (Collins 2003). These new motivational states significantly increase in salience at the same time that youth develop an increased capacity for self-regulation of other appetitive behaviors (Fortenberry 2014). Therefore, it makes sense that physical maturation is accompanied by increased neural plasticity and a heightened motivation to seek out a range of highly arousing, slightly scary, highly rewarding, novel experiences, and that increases in sensation-seeking make adolescents more likely to find these high-intensity experiences, such as having a first crush, enjoyable. The co-release of dopamine and oxytocin associated with repeated interactions with a specific partner

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contributes to additional reward-driven learning about romantic behaviors. Once a young person has a crush and begins to build a relationship with someone, they develop a conditioned partner response in which the dopaminergic reward that is expected and experienced is greatest with that specific bonded partner (Ortigue et al. 2010). Because of the neural development that occurs in puberty, a partner-specific response in early romantic relationships, when both the emotional and physical intimacies are novel, makes them particularly exciting, rewarding, and satisfying.

## Risk-Taking

Risk-taking behavior—for instance, elevated rates of experimentation with alcohol, cigarettes, and illicit drugs; higher rates of risky sexual activity, petty and violent crime, and reckless driving—increases in adolescence. Parents, educators, and policy makers have long wondered why this occurs and before the advent of neuroimaging, this phenomenon was primarily attributed to shifts in pubertal hormones. Although such behavior can result in negative consequences, I argue that "healthy" risk-taking, or *exploration*, serves an adaptive developmental process. A prevailing narrative in developmental cognitive neuroscience is that the increase in risk-taking behavior can be attributed to changes in frontostriatal circuitry that occur during adolescence, in particular in the mesolimbic striatum. It is certainly likely that neurobiological changes induce behavioral changes. However, the opposite may also be true: risk-taking behavior may help shape the brain in a similar fashion that experience more generally helps refine the brain across development.

### *Is Adolescent Risk-Taking Adaptive?*

Some adolescents engage in risky behaviors that are a threat to healthy development while others pass through this developmental window relatively unscathed. Scientists have long wondered what the adaptive aspects are of a brain that is hyperexcitable, responsive to the social environment, and primed for learning.

The brain is built this way to facilitate the important task of transitioning from a state of dependence on caregivers to one of relative independence. Imagine if such a period in life, when individuals actively sought out autonomy from their parents, did not exist. There would be minimal exploration of the environment, a lack of thirst for learning new things, and little curiosity to meet new people. Taken to an extreme, without this development stage, it is doubtful that our species would have survived. Growth of the human species is dependent on the motivation of individuals to innovate, create, and procreate utilizing a diverse gene pool. At no other time in life is there greater intrinsic motivation to explore the world than during adolescence. A model by Crone and Dahl (2012) emphasizes the positive and negative trajectories

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that can result from increased flexibility in the adolescent brain. Their model (Figure 14.3) has become a cornerstone of a nuanced depiction of adolescent brain development. It spans the period from puberty onset until the transition to adulthood, showing that goal-driven behavior is increasingly influenced by social input as well as cognitive flexibility because of the ongoing maturation of the social brain and cognitive control networks, respectively. Together, these changes have the possibility of yielding positive (e.g., adaptive exploration) as well as negative growth trajectories (e.g., mental health issues).

Youth are often at the forefront of new ideas; they are impassioned defenders of ideals, fervid leaders, and the ones having the most "fun" in their quest for autonomy. Despite possessing better cognitive, intellectual, and reasoning abilities than children, adolescents are not simply "mini-adults" nor are they overgrown children, despite immature emotion regulation, inexperience, and dependence on caregivers (Galván 2014). Instead, adolescents are in a distinct developmental stage that facilitates the creativity, rebellion, and progressive thinking that characterizes this period. Puberty jump-starts this process by giving individuals the biological means to procreate. This is followed by a few years of activities and behaviors that facilitate, and in some cases expedite, the move away from caregivers to establish independence—a period often marked by increased conflict with parents, more time spent with peers, frequently engaging in risk-taking behavior, and a greater desire for romantic partners. By late adolescence, independence is achieved. In the United States, for example, marriage often marked this move in years past, according to the U.S. Census

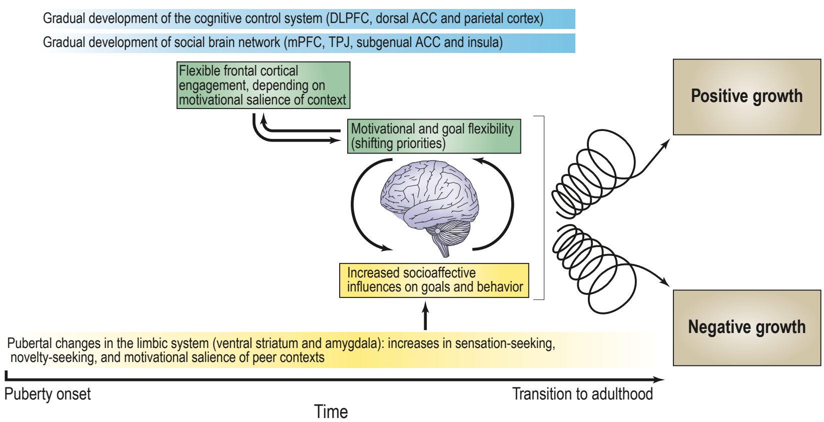


**Figure 14.3** Crone and Dahl's model of neurodevelopment illustrating the potential neurobiological mechanisms by which goal-driven behavior is increasingly influenced by social input and cognitive flexibility. Examples of trajectories that would lead to positive growth include adaptive exploration, mature long-term goals, and social competence. Examples of negative growth trajectories include diminished goals (e.g., depression, social withdrawal) and excessive motivation to achieve negative goals (e.g., substance use, excessive risk-taking). After Crone and Dahl (2012) with permission of Macmillan Publishers Ltd.

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Bureau. Nowadays, however, marriage plays a lesser role as many individuals simply leave their familial home to live with friends or romantic partners or to attend college.

Humans are not the only species to undergo this characteristic shift in seeking independence. In fact, risk-taking around the time of sexual maturation is also not unique to humans. Like their human counterparts, adolescent rats demonstrate a significant increase in the amount of time spent in social interactions with peers and at play (Varlinskaya and Spear 2008). American psychologist Jerome Bruner proposed that the function of being "immature" is so an organism can engage in experimental play, without serious consequences, and is able to spend considerable time observing the actions of skilled others in conjunction with oversight by and activity with its caregiver (Bruner 1972). Further, he suggested that this type of play helps the species practice and perfect imitative acts, such that "re-interpretive imitation" leads to innovation through extensive exploration of the limits on one's ability to interact with the world. Some have argued that this extended period of immaturity may serve the adaptive purpose of extending the period of neural plasticity (Steinberg 2014).

### *The Role of Peers in Risk-Taking*

Risk-taking is a very social behavior, particularly during adolescence. Teenagers spend an astonishing amount of time with their friends, not to mention the time spent planning or yearning to be with their friends. It is thus not surprising that most risky behavior occurs in the presence of friends. Could it be that being with friends amplifies the excitability of the mesolimbic system to an even greater degree than it already is in puberty? Although this is an interesting question, studying it faces major challenges, given the difficulties of capturing brain activity while teens are with their friends.

One approach, developed by Laurence Steinberg and Jason Chein, involves a clever fMRI experiment in which participants played a risk-taking video game in the presence of their peers while undergoing fMRI (Chein et al. 2011). Three groups of research participants—adolescents (14–18 years of age), college students (aged 19–22), and adults (aged 24–29)—were recruited to the study and each one played the "Stoplight Game." This game is a first-person task wherein participants must advance a car through a series of street intersections to reach a finish line as quickly as possible to receive a monetary reward. The risky component mimics real-life driving circumstances in which each intersection contains a stoplight that turns yellow as the car approaches: participants must decide whether to make a risky choice by running the yellow light or take a nonrisky choice of stepping on the brakes (and thus incurring extra time to get to the finish line). Each participant in the study played the game alone or in the presence of two same-aged, same-sex friends.

College students and adults exhibited the same behavior (i.e., they made the same number of risky and nonrisky choices) regardless of whether there

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was a peer watching them. Adolescents, however, made significantly more risky choices when a peer was present than when they were alone (Chein et al. 2011). This finding is especially interesting because risky behavior in adolescents did not differ from the other age groups in the alone condition. Interestingly, risky decisions in the presence of peers elicited greater activation in the mesolimbic circuitry (specifically in the ventral striatum) only in the adolescent group. This study provides compelling evidence that in the company of friends, reward sensitivity in adolescents is amplified when confronted with a risky choice. Similar studies using a "virtual" peer found similar results: the presence of a peer yielded worse cognitive control in the adolescent group, but not in young adults or adults (Breiner et al. 2018). This peer effect has also been observed in mice. A sample of mice raised in same-sex triads and tested for alcohol consumption, either as juveniles or as adults, showed that the presence of "peers" increased alcohol consumption among adolescent mice, but not adults (Logue et al. 2014).

### *The Role of Family in Risk-Taking*

Recent work has extended the study of how social relationships influence risk-taking and brain development by examining the role of the family unit on this behavior. The changing nature of family relationships during adolescence can have significant implications for risk-taking and associated health consequences, such as substance use and externalizing problems. Family obligation—the importance of spending time with the family, high family unity, family social support, and interdependence for daily activities (Fuligni et al. 1999)—is a key aspect of family relationships that may have significant consequences for adolescents' health.

Family obligation may reduce risk-taking because it is a meaningful activity that increases adolescents' motivation to control their own impulses and desires for the sake of their family, thus providing adolescents opportunities to practice engaging in self-control. For example, adolescents who value family obligation report greater negative consequences for engaging in risky behavior because risk-taking reflects poorly on their family (German et al. 2009). The negative consequences of risk-taking may be more consequential for these youth, and thus risk-taking becomes comparatively less rewarding. Likewise, adolescents who value family obligation may be more motivated to engage in self-control to avoid risky behaviors. To test this hypothesis, Telzer et al. (2013b) examined whether family obligation related to neural markers of risk-taking. Participants performed the Balloon Analogue Risk Task, a computerized assessment of risk-taking, while undergoing fMRI to derive measures of family obligation values and self-reported risk-taking behavior. Results suggest that adolescents with greater family obligation values show decreased activation in the ventral striatum when receiving monetary rewards and increased dorsolateral PFC activation during behavioral inhibition. Reduced activation

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in the ventral striatum correlated with less real-life risk-taking behavior and enhanced dorsolateral PFC activation correlated with better decision-making skills. Thus, family obligation may decrease reward sensitivity and enhance cognitive control, thereby reducing risk-taking behaviors (Telzer et al. 2013b).

## Conclusions and Unresolved Issues

In humans, the adolescent brain changes significantly until at least the mid-twenties. The next frontier for adolescent neuroscience research is to discover the factors that contribute to this significant period of neurobiological maturation. The influx of gonadal hormones at puberty certainly plays a significant role in refining and, in some cases, reforming the developing brain. However, we need to gain traction on other social, psychological, and physiological factors that contribute to adolescent brain development and dynamic brain coordination. To help anchor future directions in this area, I wish to highlight several promising areas of inquiry.

*What is adolescence?* As discussed, there are many issues involved in defining adolescence. An increasing number of scholars have argued that age-based boundaries of adolescence limit our understanding of the adolescent experience, the factors that mark the beginning and "end" of adolescence, as well as the policy, law, and education-relevant implications of this research. To progress, it may be useful instead to define adolescence based on neurobiological criteria, psychosocial responsibilities, and/or skill-based capabilities. Defining adolescence via these factors may help disambiguate who is considered an adolescent. To enable this, however, neurobiology needs to coalesce around the parameters of each of these operational definitions. For instance, which brain metric should be used to determine a "mature" versus an "immature" brain? Which skills are necessary for reaching maturation? These questions reveal an interesting set of issues that would benefit from discussions among scholars from interdisciplinary fields.

*Social influence*: The increasing importance of social relationships in adolescence is clear. What remains unknown, however, are the neurobiological and psychological mechanisms by which social relationships may serve to "sensitize" or trigger change in the adolescent brain. Research may profitably focus on the circumstances under which parental and peer influence may diverge, or the various factors that render adolescents more susceptible to influence from parental or peer sources. For example, parents may exert profound influence on adolescents' choices when values or moral concerns are made salient, whereas peers might be more influential in shaping adolescents' social activities and relationships at school.

*The positive attributes of adolescent brain maturation*: The majority of early studies on the adolescent brain focused on the negative or problematic attributes of neurobiological "immaturity" during adolescence. Fortunately,

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scientists have increasingly rectified this perception through empirical research which shows that the ontogenetic changes in the adolescent brain are adaptive for the individual and beneficial for society. Some have even argued that this extended period of immaturity may serve the adaptive purpose of extending the period of plasticity (Steinberg 2014). Like development itself, the science on the adolescent brain is a dynamic process. With every study, methodological advance, and collaboration with nonscientists, knowledge grows. By appreciating that the adolescent brain is sponge thirsty and receptive for new knowledge, rather than problematic, awareness of this significant period of life will continue to grow. New studies have begun to focus on the power of the adolescent brain to learn (e.g., Davidow et al. 2016), to engage in prosocial behavior, and to explore the environment in a healthy way. Greater research into the positive attributes of the brain and its dynamic coordination during this key developmental window is warranted.

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