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The Teenage Brain: Sensitivity to Rewards

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Abstract

Adolescence is characterized by heightened reward sensitivity. Accumulating evidence suggests that this behavior is associated with neurodevelopmental changes in reward-related neural circuitry. In this article, I review recent studies in animal models and humans that highlight the unique adolescent response to reward in the striatum, a reward-sensitive brain region. This work helps the field understand characteristic adolescent behavior and will be important in addressing policy questions related to this period of development.

Keywords

adolescence, reward, brain development

Adolescence is characterized by heightened reward sensitivity and risk-taking behaviors and often linked to high rates of drug use, reckless driving, and sexual promiscuity. However, adolescence is also an exciting developmental period during which individuals acquire the social, physical, and cognitive tools necessary to transition from dependence to independence. Heightened reward sensitivity may help individuals attain this developmental milestone, given that reward is known to facilitate approach behavior toward novel stimuli and experiences and learning from new surroundings and social interactions, both of which are critical for independence. In this review, reward sensitivity is operationalized as heightened behavioral motivation to obtain rewards and heightened arousal in response to rewards.

Early attempts to characterize adolescent reward sensitivity focused on the hormonal changes that emerge at the onset of adolescence. The advent of sophisticated neurobiological and neuroimaging tools has allowed the field to take a more mechanistic approach to this issue, and we have learned that adolescent behavior is more than just a product of “raging hormones.” Instead, pubertal hormones influence and interact with functional brain development, and together, hormones and brain play a significant role in adolescent reward-seeking behavior.

The goal of this review is to integrate evidence from the rich literature on adolescent reward sensitivity to illustrate the convergence on three critical points: (a) adolescent reward sensitivity is conserved across species; (b) heightened reward sensitivity in adolescents is linked to changes in dopamine-rich neurocircuitry; and (c) individual differences in neural

sensitivity to reward are critically important for predicting “real-world” reward seeking and risk-taking behavior. Collectively, these facets of adolescent reward sensitivity suggest that, despite the suboptimal outcomes that sometimes unfold from this behavior, it may serve a critical developmental role for normative maturation and growth.

Reward Sensitivity in Adolescence: Insight From Animal Studies

Reward sensitivity appears to be conserved across evolution, given that many mammalian species, including rodents and nonhuman primates, show patterns of reward-related behavior similar to those of humans (Spear, 2011). Several pieces of evidence suggest that adolescent rats exhibit inverted U-shaped developmental trajectories in the realms of reward and novelty seeking (Douglas, Varlinskaya, & Spear, 2003), risk taking, social interactions (Douglas, Varlinskaya, & Spear, 2004), and consummatory behavior (Friemel, Spanagel, & Schneider, 2010; Spear, 2011). They also demonstrate enhanced behavioral responses to novelty (Douglas et al., 2003) and to social peers (Varlinskaya & Spear, 2008), compared with adult rats. The increased proclivity toward drugs in human adolescents versus adults is also observed in rats (Brenhouse & Andersen, 2008; Torres, Tejada, Natividad,

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& O'Dell, 2008) and in nonhuman primates (Nelson et al., 2009). These remarkable behavioral parallels between animals and humans suggest that instead of heightened reward sensitivity in adolescence simply being a product of cultural norms and social opportunities, neural changes during this important developmental window may also contribute to this phenomenon.

The neurobiological mechanisms underlying reward sensitivity constitute an important area of research. Most studies focus on characterizing the developmental changes that occur in the dopamine system, which is essential for detecting, responding to, and learning from reward (Schultz, Dayan, & Montague, 1997). Burst firing of dopamine neurons occurs in dopamine target regions, including striatal regions, in response to rewards (Roitman, Wheeler, Wightman, & Carelli, 2008), social interactions (Robinson, Heien, & Wightman, 2002), and unexpected events and stimuli (Takahashi et al., 2009). Importantly, this neurobiological reactivity to reward leads to increased approach behavior (Robinson, Zitzman, Smith, & Spear, 2011), because an animal is more likely to exhibit behavioral modifications if there is an opportunity to receive a reward. Methodological limitations preclude researchers from investigating these dopaminergic changes at the neuronal level in human children. Therefore, the field relies on studies in animal models to understand how dopamine firing patterns change during adolescence (Robinson et al., 2011).

These investigations show that the mesolimbic dopamine system undergoes significant changes during adolescence. Dopamine D1 and D2 receptor expression in ventral striatum (VS) increases from preadolescence to adolescence (e.g., Andersen, Dumont, & Teicher, 1997), with some studies suggesting that binding in adolescence is higher than in adulthood (Doremus-Fitzwater, Varlinskaya, & Spear, 2010). Similar U-shaped trajectories are observed in the firing rates of dopamine neurons (McCutcheon & Marinelli, 2009) and the number of dopamine neurons that are activated in anticipation of reward (Sturman & Moghaddam, 2012), peaking in adolescence. Functional studies show that, compared with adults, the adolescent rat brain releases more dopamine if stimulated by environmental challenges (Laviola, Pasucci, & Pieretti, 2001) and exhibits longer sustained dopamine release following a social interaction (Robinson et al., 2011). These data indicate that heightened reward sensitivity in adolescents is linked to changes in dopamine-rich neurocircuitry in animals.

Neurobiological Correlates of Reward Sensitivity in Adolescence

There is evidence to suggest that human adolescents, like animals, display heightened sensitivity to different types of rewards, including gustatory, thrill-seeking, and monetary rewards. At the most basic gustatory level, adolescents are more sensitive to sweet substances than adults (Post & Kemper,

1993). In responses to self-report scales, there is a peak in reward-and sensation-seeking behaviors at approximately 12 to 15 years of age and 17 to 18 years of age, respectively (Steinberg et al., 2009). Studies that use monetary incentives also find that reward-seeking behavior follows an inverted U-shaped function, peaking at approximately 14 to 15 years of age and declining thereafter (Smith, Xiao, & Bechara, 2011).

The advent of functional MRI (fMRI) revolutionized the study of human brain development. fMRI is a tool that measures changes in blood oxygenation in the brain that are assumed to reflect neural activity. Thus, fMRI measures provide an index of neuronal activity but do not have the resolution to identify specific neurotransmitter (i.e., dopamine) activity. To investigate the neural phenotype of heightened reward sensitivity, researchers pair fMRI with monetary-reward-based tasks (see Fig. 1). From these studies, we have learned that, during adolescence, there is an exaggerated neural activation in the VS in response to reward (Ernst et al., 2005; Galván et al., 2006; Geier, Terwilliger, Teslovich, Velanova, & Luna, 2010; van Leijenhorst et al., 2010; see Fig. 1). However, it is important to note that some studies have reported diminished activation in response to reward (Bjork, Smith, Chen, & Hommer, 2010) and either hyperresponding or hyporesponding during different stages of reward processing (e.g., anticipation of reward versus reward receipt of reward; Geier & Luna, 2009). Plausible explanations for differences across studies, as well as implications for adolescent behavior, are reviewed elsewhere (Galván, 2010).

Our own work suggests nonlinear patterns of striatal development. In an fMRI study, children, adolescents, and adults performed a youth-friendly computerized reward task in which they were presented with three cues that were each associated with increasing monetary values (small, medium, and large; Galván et al., 2006). The task was similar to a reward-learning task previously used in monkeys to show that dopamine firing patterns temporally shift to track the most meaningful information in the task (Fiorillo, Tobler, & Schultz, 2003).

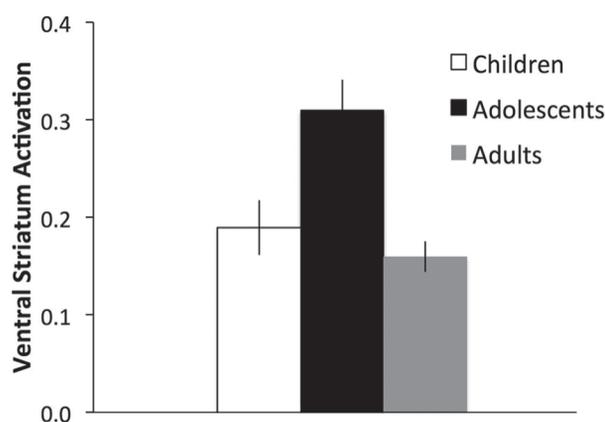


Fig. 1. Brain activity in the ventral striatum during reward processing in children, adolescents, and adults. (Galván et al., 2006).

In brief, the monkey work showed that at the beginning of the task, the dopamine response is greatest when reward is received; however, as the animal learns that a particular cue predicts the reward outcome, the dopamine neurons become increasingly more responsive to the reward-predicting cue. By the end of the experiment, the dopamine neurons are minimally responsive to the actual reward delivery and most responsive to the cue (Fiorillo et al., 2003). In our study, all age groups showed strong VS activation in response to the reward outcome. However, interesting developmental differences emerged when we examined how the temporal dynamics of the task influenced VS activation. By the end of the experiment, adolescents showed the most activation overall to the large monetary reward, whereas adults showed the least. However, within the adult group, the greatest activation was in response to the cue and not to the actual reward outcome, which paralleled the monkey data.

Particularly interesting is that these neural patterns of activation mapped onto the behavioral differences between groups. In the beginning of the experiment, none of the groups showed differences in reaction time (RT) to the three reward types. However, by the end of the experiment, adults had learned to discriminate between them, as evidenced by faster RTs in response to the large reward and slower RTs in response to the small reward. Adolescents became significantly slower in responding to the small reward and children continued to show no differences in reactions to the three reward types. From this study, we concluded that neural discrimination of reward value is paralleled by changes in behavior and that adolescents show heightened VS sensitivity to reward compared with children and adults (Galván et al., 2006).

Other work supports this hyperresponsive view as well. For example, a probabilistic monetary-reward task was used to show that adolescents demonstrated significantly more VS activation than adults when they earned money (Ernst et al., 2005). It has also been shown that adolescents exhibit heightened VS activity both in response to preparation for reward (Geier et al., 2010) and to expected (van Leijenhorst et al., 2010) and unexpected (Cohen et al., 2010) reward outcomes. Together, these findings demonstrate that across different labs, methodological techniques, participant samples, and reward tasks, the adolescent brain is hyperresponsive to one or more aspects of reward processing, as compared with other age groups. This unique sensitivity to reward is behaviorally meaningful and has been tied to task performance as well as to real-world reward sensitivity (e.g., drug use, thrill-seeking behavior).

Individual Differences in Reward Sensitivity

The central premise of this article is that adolescence is distinguished by a strong affinity for reward. However, it is important to note that not all adolescents exhibit heightened reward

sensitivity. In fact, the likelihood of reward-seeking behavior is largely influenced by individual differences, including the availability of reward, gender, and personality traits. For instance, reward-seeking and risk-taking behaviors are more frequent in individuals with elevated novelty and sensation seeking (Rao et al., 2011) and in those who report greater risk-taking among their peers. More recently, studies using fMRI have suggested that neural variability may also help explain individual differences in reward sensitivity.

Neuroimaging data in adults shows that individual differences in activation of the VS predict reward-related risks (Kuhnen & Knutson, 2005). For example, individuals who exhibit greater VS activation in response to appetitive cues are subsequently more likely to make risky choices to obtain monetary reward (Kuhnen & Knutson, 2005), to consume unhealthy snacks (Lawrence, Hinton, Parkinson, & Lawrence, 2012), to gain weight, and to report greater sexual desires (Demos, Heatherton, & Kelley, 2012). Recent work using positron emission tomography, a technique used to examine dopamine function in adult humans (Tatsch & Poepperi, 2012), found that individual differences in dopamine function in the VS and ventromedial prefrontal cortex were correlated with a willingness to expend greater effort for larger rewards (Treadway et al., 2012), further implicating dopamine in reward sensitivity.

These associations between VS activation and reward have also been observed in developmental populations. By examining individual neural responses to reward and correlating them with self-reported risk-taking behavior, we found a positive association between VS activation in response to monetary reward and the likelihood of engaging in risky behavior across development; that is, individuals more likely to report higher frequency of risky behavior in real life showed greater VS recruitment (Galván, Hare, Voss, Glover, & Casey, 2007). A more recent study found similar results in adolescents, with a positive association between individual differences in reactivity of the VS during anticipation of reward and externalizing behaviors such as drug use (Bjork, Smith, Chen, & Hommer, 2011).

Pubertal Hormones and Reward Sensitivity

This review has focused on how striatal changes during adolescence contribute to reward sensitivity in adolescents. However, it is important to touch upon the equally influential role that pubertal hormones play in reward sensitivity. Although there are many fewer published studies showcasing the bidirectional influence of striatal and pubertal changes during adolescence, recent calls in the field have underscored the importance of this work (Blakemore, Burnett, & Dahl, 2010; Sato, Schulz, Sisk, & Wood, 2008). Animal models provide evidence that gonadal hormones have significant activational and organization effects on brain development

and on the dopamine system in particular (an extensive review of this topic is beyond the scope of the current paper, but see Kuhn et al., 2010). In rodents, consumption and motivational incentive for palatable food reward increases during puberty (Friemel et al., 2010). In studies using fMRI reward tasks and hormonal assessments, several groups similarly report that higher levels of a pubertal hormone (testosterone) predicted increased reward-related activation in the VS (putamen) in adolescents (Forbes et al., 2010; Op de Macks et al., 2011). These findings suggest that although reward sensitivity may be developmentally normative across development, the onset of puberty may trigger an exaggerated sensitivity to reward. A deeper understanding of the neurobiological mechanisms underlying these interactions is warranted.

Future Directions

This paper focuses on the role of dopamine-rich striatal circuitry in adolescent reward sensitivity. However, there are other, equally important changes in the developing brain that directly and indirectly interact with an individual's own experience and personality traits to influence proclivity toward reward. For example, the relationship between striatal and prefrontal regions needs closer examination, given the protracted development of the prefrontal cortex (Sowell, Thompson, Holmes, Jernigan, & Toga, 1999) and its critical role in behavior regulation. Numerous investigations have begun to apply functional-connectivity techniques to study the cross-talk between this circuitry (Somerville, Hare, & Casey, 2011), but much more work in this area is needed.

In addition, it will be important for future research to delve more deeply into the contextual factors that can have significant sway on an individual's reward-related decision making. Preliminary studies show that factors such as stress (Galván & McGlennen, 2012; Porcelli & Delgado, 2009), peers (Chein, Albert, O'Brien, Uckert, & Steinberg, 2011), and psychopathology (Morgan, Olino, McMakin, Ryan, & Forbes, 2012) can have consequential effects on reward sensitivity and behavior.

Finally, the studies reviewed here provide clear evidence of how reward influences the approach behavior and novelty seeking necessary for independence. Less well-studied is whether heightened reward sensitivity also enhances learning during adolescence in humans, as it does in animals (Brenhouse, Dumais, & Andersen, 2010; Robinson et al., 2011). In future studies, it will be important to determine how activation of key learning nodes, such as the striatum and hippocampus, in response to feedback influence learning.

Conclusions

The developmental field has made significant progress in understanding teenage behavior by investigating normative

neural dynamics during adolescence. Probing more deeply into this question of reward sensitivity, investigators have asked why and how this happens and why it is important. Issues related to independence and maturation likely answer the *why* question, and the numerous investigations showing that reward sensitivity in adolescence is paralleled by changes in dopaminergic systems provide strong evidence for *how*. As for why this is important, it behooves us as a developmental field to translate these findings for laypeople, policy specialists, and lawmakers so that what we know about the adolescent brain and behavior from the lab may be used in meaningful ways in schools, at home, and in the courtroom.

Recommended Reading

- Galván, A. (2010). (See References). A more in-depth review of the fMRI studies that have examined the adolescent reward system.
- Somerville, L., & Casey, B. (2010). Developmental neurobiology of cognitive control and motivational systems. *Current Opinion in Neurobiology*, 20, 236–241. A comprehensive review that discusses the interaction between cognitive control and motivational systems during adolescence.
- Spear, L. (2011). (See References). An excellent review that presents the converging evidence on adolescent reward sensitivity from animal and human studies.
- Steinberg, L. (2009). Should the science of adolescent brain development inform public policy? *American Psychologist*, 64, 739–750. A review that discusses how developmental psychology and neuroscience can inform policy related to adolescents.

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