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Review article

What motivates adolescents? Neural responses to rewards and their influence on adolescents' risk taking, learning, and cognitive control

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ABSTRACT

Adolescence is characterized by pronounced changes in motivated behavior, during which emphasis on potential rewards may result in an increased tendency to approach things that are novel and bring potential for positive reinforcement. While this may result in risky and health-endangering behavior, it may also lead to positive consequences, such as behavioral flexibility and greater learning. In this review we will discuss both the maladaptive and adaptive properties of heightened reward-sensitivity in adolescents by reviewing recent cognitive neuroscience findings in relation to behavioral outcomes. First, we identify brain regions involved in processing rewards in adults and adolescents. Second, we discuss how functional changes in reward-related brain activity during adolescence are related to two behavioral domains: risk taking and cognitive control. Finally, we conclude that progress lies in new levels of explanation by further integration of neural results with behavioral theories and computational models. In addition, we highlight that longitudinal measures, and a better conceptualization of adolescence and environmental determinants, are of crucial importance for understanding positive and negative developmental trajectories.

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Thought by itself moves nothing

Adolescence is one of the periods in life well known for its changes in motivated, goal-directed, behavior. These changes are thought to result in a greater emphasis on potential rewards, such as a heightened behavioral motivation to obtain rewards and a heightened arousal in response to rewards (Galván, 2010). As a crucial aspect of almost all behavior and actions, motivated behavior has been investigated from a number of perspectives including economics, sociology, psychology, and neuroscience. Recent discoveries in neurocognitive research have led to new perspectives on the dynamic changes in motivated behavior during adolescence. In the current review we will discuss changes in adolescent's reward sensitivity by reviewing recent cognitive neuroscience findings in relation to behavioral outcomes.

1. Adolescence as a period of change in motivated behavior

Adolescence is defined as an important transitional period between childhood and adulthood in which individuals gain independence and develop mature social goals (Crone and Dahl, 2012). As such, adolescence represents a developmental time window characterized by strong needs for exploration, forming new relationships, increasing intimacy, and rapid adjustment to changing social environments. Although the age range of adolescence differs between countries and cultures, it is generally agreed upon that in Western societies adolescence approximately spans the period between ages 10 and 22 years. Puberty is an important phase of adolescence and characterized by a rapid rise in gonadal hormones (Blakemore et al., 2010). These hormones are released through the hypothalamus-pituitary-gonadal axis and have a large influence on bodily characteristics and brain development (Peper and Dahl, 2013; Goddings et al., 2014). Pubertal development reaches a plateau in mid-adolescence at approximately age 15–16 years (Braams et al., 2015). The end phase of adolescence, however, is culturally defined and is reached when individuals have achieved mature social and personal responsibilities (e.g., Cohen et al., 2016).

Adolescence has traditionally been interpreted as a period of changes in motivated behavior. Some of the earliest theories in developmental psychology have described adolescence as a period of storm and stress, including conflict with parents, mood disruptions and a variety of risk behaviors, which were thought to be universal and biological (Arnett, 1999; Hall, 1904). Epidemiological reports have indeed observed an increase in risk taking behavior in adolescence, such as a higher incidence of traffic accidents, delinquency, and substance abuse (see Eaton et al., 2011; Willoughby et al., 2013). To reconcile these findings with the general cognitive increase observed in adolescence (e.g., Crone 2009), research tuned to the role of affective-motivational processes in understanding changes in adolescent's behavior (e.g., Boyer, 2006). Developmental studies reported a surge in sensation seeking during adolescence (Zuckerman, 1994) that may lead to increases in peer influence and risky behavior (Steinberg et al., 2008; Romer, 2010). Recent approaches have linked these changes in motivated behavior to the long-lasting neurodevelopmental changes across adolescence.

Since the discovery that brain development continues throughout adolescence, research on adolescent brain development has expanded enormously. It was discovered that adolescence is a period of continuous changes in brain morphology. In grey matter there is an overall reduction in volume and cortical thickness (Giedd et al., 1999; Gogtay et al., 2004; Tamnes et al., 2010; Raznahan et al., 2011; Mills and Tamnes, 2014; Wierenga et al., 2014), which is thought to reflect synaptic pruning, occurring in a time- and region-specific manner (Huttenlocher 1990; Petanjek et al., 2011). At the same time white matter volume increases and undergoes changes in the organization of its connections (Lebel and Beaulieu, 2011; Simmonds et al., 2014). Together, these changes allow for greater specialization and strengthening of connectivity between brain regions. These changes in structural development are paralleled by changes in functional activity in the brain, such as activation in response to motivationally salient events (for an overview of studies, see Crone and Dahl, 2012; Crone et al., 2016), and changes in subcortical and cortical functional connectivity during rest (Gabard-Durnam et al., 2014; Fareri et al., 2015b; van Duijvenvoorde et al., 2016).

The structural and functional age-related changes in the brain have been summarized in neurocognitive models, which suggest that adolescent motivation is particularly tuned towards rewarding stimuli. According to these models, which are also referred to as dual processing or imbalance models, adolescent brain development can be described as an imbalance in neural maturational patterns between the cortical-control system (including brain regions such as the prefrontal cortex), important for the regulation of thoughts and emotion, and the limbic system (including brain regions such as striatum and amygdala), important for affective-motivational functioning (e.g., Ernst, 2014; Somerville et al., 2010; Steinberg, 2008). During adolescence the reactivity of the affective-motivational system may be particularly heightened and—depending on adolescents' motivations—may override controlled responses in emotionally-salient contexts (Somerville et al., 2010; Crone and Dahl, 2012). Consistent with these neurocognitive models, behavioral literature on adolescent risk-taking has indicated that in emotionally arousing situations, adolescents are more prone to taking risks. For instance, a recent meta-analysis showed that heightened risk taking in adolescents compared to adults, although particularly in contexts when rewards are encountered immediately (Defoe et al., 2015; see also Figner et al., 2009; van Duijvenvoorde et al., 2010). A similar finding is observed when adolescents are in the presence of peers (Gardner and Steinberg, 2005; Peake et al., 2013), or when approaching unknown situations (Blankenstein et al., 2016; Tymula et al., 2012).

New models in this tradition increasingly acknowledge the complexity of brain and behavioral changes across adolescence. In order to understand changes in adolescent motivated behavior these models stress a) the importance of studying brain-connectivity within and between limbic, affective-motivational, and cognitive control brain circuits (Casey, 2015; Casey et al., 2016), b) the influence of social context on observed neural sensitivities (Shulman et al., 2016; Nelson et al., 2016), and c) the importance of pubertal developmental changes and cortical-subcortical flexible interactions (Crone and Dahl, 2012). More specifically, the first model (Casey, 2015) highlights the hierarchical development of brain circuitry, in which development and sensitivity of subcortical circuits (e.g. subcortical–subcortical connections) precede others (e.g., top-down cortical control connections), in order to develop. The second model highlights that an imbalance between cortical and subcortical brain systems may not occur under all circumstances and depends on contextual factors, such as peer presence (Shulman et al., 2016). Finally, it has been proposed that increases in pubertal hormones at the onset of puberty trigger the limbic system to