



Review article

Reward-centricity and attenuated aversions: An adolescent phenotype emerging from studies in laboratory animals



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ABSTRACT

Adolescence is an evolutionarily conserved developmental period, with neural circuits and behaviors contributing to the detection, procurement, and receipt of rewards bearing similarity across species. Studies with laboratory animals suggest that adolescence is typified by a “reward-centric” phenotype—an increased sensitivity to rewards relative to adults. In contrast, adolescent rodents are reportedly less sensitive to the aversive properties of many drugs and naturally aversive stimuli. Alterations within the mesocorticolimbic dopamine and endocannabinoid systems likely contribute to an adolescent reward-sensitive, yet aversion-resistant, phenotype. Although early hypotheses postulated that developmental changes in dopaminergic circuitry would result in a “reward deficiency” syndrome, evidence now suggests the opposite: that adolescents are uniquely poised to seek out hedonic stimuli, experience greater “pleasure” from rewards, and consume rewarding stimuli in excess. Future studies that more clearly define the role of specific brain regions and neurotransmitter systems in the expression of behaviors toward reward- and aversive-related cues and stimuli are necessary to more fully understand an adolescent-proclivity for and vulnerability to rewards and drugs of potential abuse.

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1. Introduction

Reward-related behaviors guide organisms toward environmental stimuli that are necessary for individual, as well as species

survival. As individuals need to forage for food and fluids, engage in social interactions with conspecifics, locate safe habitats, and find a mate for sexual reproduction, natural rewards provided by procurement of these goals steer attention toward appropriate stimuli and reinforce behaviors leading to these goals. While some of these survival goals begin at birth, others gain importance over the course of development. During adolescence, many of these goals and behaviors take on new significance, with the gradual transition from dependence on adults and the family unit to relative indepen-

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dence and a focus on peer interactions (for review see Crone and Dahl, 2012; Spear, 2000). Thus, the adolescent transition between childhood and adulthood represents a unique ontogenetic niche during which adolescents often behave quite distinctly from their younger and older counterparts. This may be especially true with regards to reward-related neural systems and behaviors.

The goals of survival and reproduction are conserved across species, and thus it is not surprising that neural circuits and behaviors related to finding and consuming the necessary rewards to attain these goals likewise bear similarity across mammalian species. Indeed, research both with human subjects (e.g., Delgado, 2007; Haber and Knutson, 2010; O'Doherty, 2004; Sescousse et al., 2013) and in laboratory animals (e.g., McBride et al., 1999; Schultz, 2010; Sesack and Grace, 2010; Spanagel and Weiss, 1999) has demonstrated notable concordance across species regarding the neural substrates contributing to the detection, procurement, and receipt of rewards, as well as the behaviors promoted by these brain circuits. Moreover, the ontogenetic transition of adolescence itself has been shown to be an evolutionarily conserved developmental phase that is characterized by similar neural, hormonal, physiological, and behavioral alterations in a wide variety of mammals. In particular, the rodent appears to be a well-suited medium for investigating neural and behavioral transformations of adolescence, as adolescent rats and mice recapitulate elevations in peer-directed social interactions, risk-taking/novelty seeking, and drug and alcohol use that are observed in their human counterparts. Additionally, adolescent rodents have been reported to exhibit significant changes in motivational and reward-related behaviors (as reviewed below), as well as marked transformations in reward-relevant neural regions and related neurocircuitry, with similarity in these fundamental neural alterations again evident between human adolescents and laboratory animals (for reviews see Spear, 2000, 2011; Wahlstrom et al., 2010). The exact beginning and end of adolescence are equally imprecise events in both humans and rodents that are determined by a combination of neural, biological, behavioral, and social factors. Given these transitional “gray zones,” research studies have determined the approximate timing of adolescence to conservatively occur from postnatal days (P) 28–42 (see Spear, 2000 for review), but with broader boundaries identifying the six-week period from P28–55 as a more all-encompassing (early adolescence through late adolescence/emerging adulthood) definition of adolescence in rats (e.g., see Vetter-O'Hagen and Spear, 2012).

This review is guided by the hypothesis that adolescence is characterized by a reward-sensitive phenotype, where goal-directed behavior is dominant and receipt of rewards is particularly reinforcing. Such “reward-centricity” may not only favor a focus on primary rewards such as food, water, social, and, eventually, sexually attractive stimuli, but may direct behavior towards other rewarding stimuli as well. In many individuals, positive experiences and opportunities provide the scaffolding for adolescents to focus on rewards related to academic pursuits, sports, and other constructive activities that lead to immediate or future success (Telzer, 2016). Yet, the reward-sensitive phenotype of adolescence may also impart a liability at this age. Reward-centricity may promote sensation-seeking and risk taking behaviors directed toward the attainment of other, potentially detrimental rewards including drugs and alcohol. While some expression of these behaviors is normative during adolescence, in the presence of difficult and stressful environments or other vulnerabilities (e.g., risk-prone peers), the “reward-sensitive” phenotype of adolescence may prove maladaptive, leading for example to patterns of binge drinking and escalated drug use (e.g., D'Amico and McCarthy, 2006; Roberts et al., 2015; Simantov et al., 2000). Such propensities for alcohol/drug use during adolescence may not only be encouraged by an adolescent reward-sensitive phenotype, but also by (as we shall see)

an attenuated sensitivity to aversive stimuli, including the aversive properties of alcohol, nicotine, and illicit drugs. This pattern of increased rewarding but decreased aversive sensitivities may help to promote high levels of alcohol/drug use among susceptible adolescents—elevated use that has the potential to impact normative developmental changes in brain structure and function during this critical period, thus altering neural processes and behaviors occurring within adolescence, as well as into adulthood (see reviews by Silveri et al., 2016 and Spear, 2016).

2. Adolescent sensitivity to rewards

Adolescents differ notably from younger and older organisms in the ways in which they respond to meaningful stimuli in their environment. Sensitivity to rewarding stimuli often appears to peak in adolescence, an effect that is evident in both studies with humans (see van Duijvenvoorde et al., 2016) and in work with laboratory animals (e.g., Doremus-Fitzwater et al., 2010). Among human adolescents, for example, peer interactions and social rewards are of particular importance given that they interact more with peers than at other developmental periods (Hartup and Stevens, 1997), find peers to be a major source of positive experiences (e.g. Brown, 2004), and are more influenced by peers in their decision-making than adults (Gardner and Steinberg, 2005). When using self-reports to assess reward-related behavior across age, a peak in reward seeking was observed at 12–15 years of age, and at levels higher than seen at younger or older ages (Steinberg et al., 2009). When reward sensitivity was indexed via the Behavioral Approach System (BAS) scale, a developmental rise was observed in the BAS through early to late adolescence, followed by a decline in the early twenties (Urosevic et al., 2012). Likewise, reward seeking in a gambling task was reported to peak beginning at 14–15 years of age, while declining after 21 years – a notably different pattern of ontogenetic sensitivity than seen with avoidance behaviors that were low early in adolescence and only increased gradually over age (Coffman et al., 2010). Even the preference for a natural reward, sweet tastes, was found to be greater early in adolescence (11–15 years) than during late adolescence/emerging adulthood (19–25 years) (Desor and Beauchamp, 1987). A multitude of other studies have demonstrated enhanced sensitivity to rewarding stimuli in human adolescents for both decision-making/risk taking behaviors, as well as for cognitive control and learning behaviors, data that have been recently reviewed (see Andersen et al., 2002; and also in this issue: Luciana, 2016; Schulz and Sisk, 2016; Silveri et al., 2016; Spear, 2016; Vanderschuren et al., 2016; and van Duijvenvoorde et al., 2016).

Similar age-related enhancements in sensitivity to a variety of rewarding stimuli are evident in studies using rodents to examine the adolescent transition. Like their human counterparts, adolescent rodents are more sensitive to palatable foods and tastes than adults (Friemel et al., 2010; Willmouth and Spear, 2009). They additionally have been found to engage in higher overall levels of social behavior than adults, while displaying a different pattern of social interactions that emphasizes play, rather than more adult-typical social investigation (e.g., Vanderschuren et al., 1997; Varlinskaya and Spear, 2002, 2008). Adolescent rodents also exhibit enhanced novelty seeking (Adriani et al., 1998; Philpot and Wecker, 2008; Stansfield and Kirstein, 2006) relative to their more mature counterparts. The incidence of such behaviors may be especially high during adolescence because adolescents find these stimuli to be particularly reinforcing. Indeed, adolescents have been found to be more sensitive than adults to the rewarding effects of social peers (Douglas et al., 2004), as well as to novelty (Douglas et al., 2003), when indexed via conditioned place preferences (CPP) – i.e., the development of a preference for a place previously paired

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