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Pubertal status associations with reward and threat sensitivities and subcortical brain volumes during adolescence

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ABSTRACT

Adolescence is characterized by complex developmental processes that impact behavior, biology, and social functioning. Two such adolescence-specific processes are puberty and increases in reward sensitivity. Relations between these processes are poorly understood. The present study focused on examining unique effects of puberty, age, and sex on reward and threat sensitivities and volumes of subcortical brain structures relevant for reward/threat processing in a healthy sample of 9–18 year-olds. Unlike age, pubertal status had a significant unique positive relationship with reward sensitivity. In addition, there was a trend for adolescent females to exhibit higher threat sensitivity with more advanced pubertal development and higher reward and threat sensitivity with older age. Similarly, there were significant puberty by sex interaction effects on striatal volumes, i.e., left nucleus accumbens and right pallidum. The present pattern of results suggests that pubertal development, independent of chronological age, is uniquely associated with reward hypersensitivity and with structural differences in striatal regions implicated in reward processing.

1. Introduction

Adolescence is a period of transition into adulthood, involving biological, psychological, and social changes. An essential normative process during adolescence is the development of sexual maturity, or puberty. Increasingly, pubertal development has been empirically linked to the maturation of emotional processing functions that extend beyond sexual or reproductive contexts (e.g., Forbes et al., 2010; Quevedo, Benning, Gunnar, & Dahl, 2009; Silk et al., 2009; Stroud et al., 2009). Recently, another important normative process in adolescence related to emotional processing has gained empirical support—an increase in sensitivity to rewards (Casey, Jones, & Hare, 2008; Ernst, Pine, & Hardin, 2006; Nelson, Leibenluft, McClure, & Pine, 2005; Somerville, Jones, & Casey, 2010; Steinberg, 2008; Urošević, Collins, Muetzel, Lim, & Luciana, 2012). Theories posit that pubertal changes may drive the observed increases in reward sensitivity (Dahl, 2004; Forbes & Dahl, 2010; Steinberg, 2008), potentially through hormonal effects on the subcortical structures involved in emotional/reward processing (Blakemore, Burnett, & Dahl, 2010). However, empirical examinations of the associations between pubertal development and adolescent reward sensitivity and relevant subcortical brain structures are sparse. After a brief overview of relevant literature, the present study aims to address these empirical gaps by examining unique effects of sex, pubertal status, and chronological age on reward and threat sensitivities and subcortical brain volumes during adolescence.

1.1. Heightened reward sensitivity during adolescence

Over the last decade, empirical support for the hypothesis that reward sensitivity is excessive during adolescence has grown immensely. In epidemiological studies, adolescents exhibit greater rates of incentive-driven behavior with a high potential for negative consequences, such as substance use and unsafe sex (Eaton et al., 2006). In comparison to other ages, adolescents exhibit heightened reward sensitivity on self-report measures (e.g., Urošević et al., 2012), stronger effects of monetary incentives on task performance (Hardin, Schroth, Pine, & Ernst, 2007; Jazbec et al., 2006), and greater positive affect in response to the receipt of monetary rewards (Ernst et al., 2005). Similarly, in experimental paradigms assessing responses to variable rewards and risks, adolescents exhibit greater sensitivity to positive feedback compared to other ages (Cauffman et al., 2010). Finally, adolescents who prefer high-risk, high-reward choices in an experimental task also endorse more high-risk behaviors in the real world (Rao et al., 2011).

Abbreviations: BAS, behavioral activation/approach system; BIS, behavioral inhibition system; Nacc, nucleus accumbens; OFC, orbitofrontal cortex; PCA, principal component analysis; PFC, prefrontal cortex; VS, ventral striatum.

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Neuroimaging studies also provide support for greater reward sensitivity as indexed by greater ventral striatum (VS) activation in reward paradigms. Compared to adults, adolescents exhibit greater VS activation to receipt of monetary reward (e.g., Ernst et al., 2005) and in risk-taking paradigms with variable rewards (Galvan et al., 2006). Striatal activity in response to unexpected reward feedback also peaks during adolescence (Cohen et al., 2010), as well as VS activity in response to positively-valenced stimuli (Somerville, Hare, & Casey, 2011). Geier, Terwilliger, Teslovich, Velanova, and Luna (2010) observed decreased VS activity during reward cue evaluation, but increased VS activity during anticipation of behavioral responses to rewards. The VS, and the nucleus accumbens (Nacc) in particular, is a key node in the brain's reward system with a role in facilitating responses to reward stimuli by translating motivational tendencies to approach behavior (Depue & Collins, 1999). The VS also facilitates higher-order goal-directed behavior (Atallah, Lopez-Paniagua, Rudy, & O'Reilly, 2007; Voorn, Vanderschuren, Groenewegen, Robbins, & Pennartz, 2004).

Overall, increased VS activity during reward paradigms in adolescence, although present, may not be ubiquitous (Bjork, Smith, Chen, & Hommer, 2010; Bjork et al., 2004). However, bolstering the case for adolescence as a significant developmental period for VS functioning, structural imaging studies show striatal development continuing into early 1920s (e.g., Sowell, Thompson, Holmes, Jernigan, & Toga, 1999; Sowell, Trauner, Gamst, & Jernigan, 2002). Similarly, in a recent longitudinal study of healthy 9–23 year olds, Nacc volumes peaked in adolescence and then decreased into the early 1920s (Urošević et al., 2012).

This increased sensitivity to rewards during adolescence implicates an increased sensitivity of the behavioral approach system (BAS). The BAS is a behavioral-motivational system proposed to facilitate approach to rewards (e.g., Depue & Collins, 1999; Gray, 1991, 1994). The other behavioral-motivational system, the behavioral inhibition system (BIS), is involved in responses to threat and inhibits approach in situations of conflict between reward and risk (Gray & McNaughton, 2000). Both systems are implicated in theoretical models of adolescent behavior (Ernst et al., 2006; Luciana, Wahlstrom, Porter, & Collins, 2012). Adolescent BAS hypersensitivity is linked to substance use and other risky behaviors (e.g., Giles & Price, 2008; Knyazev, Slobodskaya, Kharchenko, & Wilson, 2004; O'Connor, Stewart, & Watt, 2009), whereas increased BIS sensitivity during adolescence is linked to increased anxiety-related behaviors, such as internalizing symptoms (Colder & O'Connor, 2004) and negative affective reactivity (Leen-Feldner, Zvolensky, & Feldner, 2004).

1.2. Theoretical and Empirical Associations between Pubertal Development and Adolescent Reward Sensitivity

Forbes and Dahl (2010) proposed that the hormonal changes in puberty provoke behavioral increases in appetitive motivation, particularly in the social domain. Furthermore, others have theorized that pubertal hormonal changes may lead to a reorganization of reward-related brain structures and/or dopaminergic pathways (e.g., Blakemore et al., 2010; Nelson et al., 2005). The potential influence of pubertal development on adolescents' dopaminergic pathways is intriguing given recent proposals for adolescents' reward hypersensitivity to be driven by developmental changes in reward-relevant striatal dopaminergic activity (Luciana et al., 2012; Spear, 2011; Wahlstrom, Collins, White, & Luciana, 2010). Despite the appeal of these theoretical models, empirical evidence of the hypothesized associations is still sparse, particularly in humans.

Recent cross-sectional studies are largely supportive of increased emotional sensitivity during adolescence as a function of pubertal stage. Neuroimaging studies using facial expression paradigms are inconsistent, with some supporting a link between pubertal development and overall emotional reactivity (Moore et al., 2012) and other studies showing less emotional reactivity in structures such as the amygdala with advanced pubertal development (Forbes, Phillips, Silk, Ryan, & Dahl, 2011). However, more advanced pubertal status has predicted increased negative affective reactivity, as measured by a range of psychophysiological indices (Stroud et al., 2009), enhanced startle reflex responses (Quevedo et al., 2009), and increased basal cortisol levels (Gunnar, Wewerka, Frenn, Long, & Griggs, 2009). Pubertal status also predicts overall emotional reactivity to both positively and negatively valenced stimuli as indexed by pupillary dilation and better recall of emotional words (Silk et al., 2009).

The very few studies examining pubertal development and reward processing in human adolescents are supportive of a positive association between these two processes. Forbes and colleagues (2010) linked more advanced pubertal development to greater medial PFC and less striatal activation (specifically in the caudate) in response to reward outcomes, but not reward anticipation, in a card-guessing task. In addition, the enhancement of the postauricular reflex, a psychophysiological measure proposed to tap into BAS and provoked by positively valenced stimuli, seems to emerge in mid-to-late puberty (Quevedo et al., 2009).

Studies examining the associations of sex hormones levels (e.g., testosterone and estradiol), as a proxy for pubertal development (Huang et al., 2012), and reward responsiveness are mixed. Plasma testosterone levels have been positively related to caudate activity during reward anticipation in boys, suggesting a positive association between reward sensitivity and pubertal status, but the same study supports a negative association between testosterone levels and caudate activity during reward receipt in both sexes (Forbes et al., 2010). In contrast, another study found a positive association between saliva testosterone levels and VS activity during reward versus loss receipt in both sexes (Op de Macks et al., 2011). To date, only one study has reported on the association between sex hormones and trait measures of reward (i.e., BAS) and threat (i.e., BIS) sensitivities, finding a positive association between estradiol levels and BAS sensitivity in both boys and girls (Vermeersch, T'Sjoen, Kaufman, & Vincke, 2009).

In sum, pubertal status appears to be positively related to overall increased emotional reactivity during adolescence (e.g., Moore et al., 2012; Silk et al., 2009). The few studies examining pubertal status in relation to reward processing are contradictory, with some reporting a negative relationship (e.g., Forbes et al., 2010) and others a positive relationship (Op de Macks et al., 2011; Vermeersch, T'Sjoen, Kaufman, & Vincke, 2009). Consequently, the direction and nature of puberty's association with reward sensitivity remains unclear. Inconsistencies across studies may be due to methodological issues, such as difficulties in using single measures of hormone levels to infer an individual's relative status (Shirtcliff, Dahl, & Pollak, 2009).

1.3. Pubertal Effects on Subcortical Brain Structures during Adolescence

Pubertal influences on the brain's development are most often hypothesized to occur through direct and/or indirect effects of fluctuating sex hormonal levels (e.g., Blakemore et al., 2010; Nelson et al., 2005), which are grouped into either activational or organizational effects. Activational effects of sex hormones influence existing neural structures to produce novel adult behaviors, whereas organizational effects influence the development of neural circuitry, including regional brain structure. Increased reward sensitivity may be driven by activational (and possibly organizational) effects of pubertal spikes in sex hormone levels on volumes