Psychoneuroendocrinology (2013) 38, 67—83

Available online at www.sciencedirect.com

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Social and emotional predictors of the tempo of puberty in female rhesus monkeys

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Received 25 January 2012; received in revised form 6 April 2012; accepted 30 April 2012

KEYWORDS
Menarche;
First ovulation;
Puberty;
Emotionality;
Social stress

Summary A cascade of neuroendocrine events regulates the initiation and progression of female puberty. However, the factors that determine the timing of these events across individuals are still uncertain. While the consequences of puberty on subsequent emotional development and adult behavior have received significant attention, what is less understood are the social and environmental factors that actually alter the initiation and progression of puberty. In order to more fully understand what factors influence pubertal timing in females, the present study quantified social and emotional behavior; stress physiology; and growth and activity measures in juvenile female rhesus monkeys to determine what best predicts eventual puberty. Based on previous reports, we hypothesized that increased agonistic behavior resulting from subordinate status in their natal group, in combination with slowed growth, reduced prosocial behavior, and increased emotional reactivity would predict delayed puberty. The analyses were restricted to behavioral and physiological measures obtained prior to the onset of puberty, defined as menarche. Together, our findings indicate that higher rates of aggression but lower rates of submission received from group mates; slower weight gain; and greater emotional reactivity, evidenced by higher anxiety, distress and appeasing behaviors, and lower cortisol responsivity in response to a potentially threatening situation, predicts delayed puberty. Together the combination of these variables accounted for 58% of the variance in the age of menarche, 71% in age at first ovulation, and 45% in the duration of adolescent sterility. While early puberty may be more advantageous for the individual from a fertility standpoint, it presents significant health risks, including increased risk for a number of estrogen dependent cancers and as well as the emergence of mood disorders during adulthood. On the other hand, it is possible that increased emotional reactivity associated with delayed puberty could persist, increasing the risk for emotional

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0306-4530/$ — see front matter
http://dx.doi.org/10.1016/j.psyneuen.2012.04.021

dysregulation to socially challenging situations. The data argue for prospective studies that will determine how emotional reactivity shown to be important for pubertal timing is affected by early social experience and temperament, and how these stress-related variables contribute to body weight accumulation, affecting the neuroendocrine regulation of puberty.

1. Introduction

The initiation and progression of female puberty is regulated by a cascade of neuroendocrine events leading to menarche and eventual first ovulation (Terasawa and Fernandez, 2001). However, the factors that determine the timing of these events across individuals are still uncertain. In addition to the importance of gene polymorphisms (Elks and Ong, 2011; Towne et al., 2005), a number of social and environmental signals likely alter the timing of puberty (Buck Louis et al., 2008). Apart from its importance for fertility, alterations in pubertal timing have lasting effects on both physical and emotional health (Golub et al., 2008; Walvoord, 2010). Because pubertal increases in gonadal steroids further stimulate brain maturation and behavioral development (Ahmed et al., 2008; Schulz et al., 2009; Sisk and Zehr, 2005; Vigil et al., 2011), it is possible that the hormonal consequences of puberty might prepare adolescents to adapt successfully to their social environment regardless of pubertal timing. However, this is not necessarily the case, as a number of studies show that early puberty is often associated with increased risk for mood and anxiety disorders as well as social impairments during late adolescence and adulthood, particularly in girls (Graber et al., 1997; Mendle et al., 2007; Nelson et al., 2005; Reardon et al., 2009; Zehr et al., 2007). The mechanisms responsible for the emergence of socioemotional problems in early developing individuals are poorly understood, but likely reflect the interaction of the social demands of adolescence and a developing brain (Angold and Costello, 2006; Blumenthal et al., 2009; Casey et al., 2010; Patton and Viner, 2007; Walker et al., 2004). While the consequences of puberty on subsequent emotional development and adult behavior have received significant attention, what is less understood are the social, physiological, and environmental factors that actually alter the initiation and progression of puberty.

Because exposure to psychosocial stressors has an inhibitory effect on the neuroendocrine regulation of fertility, particularly in women (Berga and Loucks, 2005; Warren and Fried, 2001) as well as nonhuman females (Baker et al., 2006; Bethea et al., 2008; Kaplan et al., 2010; Pope et al., 1986; Wagenmaker et al., 2009; Xiao et al., 2002), one critical factor affecting puberty timing could be exposure to psychosocial stress and activation of the limbic—hypothalamic—pituitary—adrenal (LHPA) axis prior to puberty, during childhood and adolescence. Indeed, social subordination in female macaques, known to be a potent psychosocial stressor in adults (Jarrell et al., 2008; Michopoulos et al., 2012, submitted for publication; Shively et al., 1997b), delays puberty and the occurrence of first ovulation (Wilson et al., 1986; Zehr et al., 2005). Furthermore, this delay in puberty is better predicted by social subordination during adolescence rather than at birth (Schwartz et al., 1985), suggesting that social stressor exposure imposed by subordination during development is a critical factor. Experimental studies in female rodents provide further evidence that an increase in stress hormones postnatally delays sexual maturation (Alves et al., 1993).

However, a different, more complex pattern emerges in studies of children (Mishra et al., 2009). Whereas positive family relations and the presence of an adult male engaged in child rearing predict a later pubertal age, exposure to a disruptive family environment is often associated with accelerated, not delayed, puberty (Ellis and Essex, 2007; Ellis and Garber, 2000; Ellis et al., 2011; Hulanicka et al., 2001; Kim and Smith, 1998). More recent studies show that the effects of an absent father on accelerating indices of puberty may be restricted to families of high socioeconomic status (Deardorff et al., 2011). In addition, the data suggest reactivity to an acute stressor interacts with the family environment to predict puberty timing (Ellis et al., 2011). The data are explained by a life-history theory that argues girls living in stressful environments have accelerated sexual maturation to initiate fertility and increase chances of producing more offspring (Ellis et al., 2011). However, the proximate neuroendocrine mechanisms produced by the stressful experiences during adolescence to account for the accelerated initiation of puberty are unknown. As noted previously (Cameron, 2004), it is difficult to reconcile how a stressful home environment could accelerate puberty, given that chronic stressor exposure consistently results in reproductive compromise in adults (Berga and Loucks, 2005; Warren and Fried, 2001). This is underscored by data showing girls with high urinary cortisol levels have a delayed growth spurt and a later age at menarche (Shi et al., 2011), and the data showing that adverse physical and psychological effects associated with wartime also delays age of menarche (Tahirovic, 1998).

Clearly, social, experiential, and innate temperamental factors can mitigate or accentuate the consequences of stress on puberty, as individuals can develop a differential neurobehavioral response that is shaped by a nurturing and supportive social environment in the face of stressor exposure during adolescence (Koolhaas et al., 1999). Importantly, this differential sensitivity—reactivity may be more predictive of pubertal timing than exposure to adverse experience during adolescence alone (Boyce and Ellis, 2005; Ellis et al., 2011). Thus, the degree of emotional and social reactivity (Barker et al., 2010; Freyberg, 2009; Heim and Nemeroff, 2001; McLaughlin et al., 2010; Richards et al., 1998; Slutske et al., 2010; Spear, 2000) could be predictive of pubertal timing. However, few studies have examined whether prepubertal emotional reactivity, as a proxy for the behavioral response to a socially stressful environment, affect the timing of puberty (Reardon et al., 2009). As noted above, measures of increased anxiety behaviors and reports of a more stressful family environment are often correlated with an eventual earlier age at menarche (Graber et al., 1995). In contrast, other studies report little or no predictive relation