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Surging Hormones: Brain-Behavior Interactions During Puberty

Jiska S. Peper[1] and **Ronald E. Dahl**[2,*]

[1]Department of Psychology, Leiden University, Wassenaarseweg 52, 2333AK, The Netherlands.
[2]Institute of Human Development, University of California, Berkeley, California 94707, USA.

Abstract

In this paper we discuss the surging hormones of puberty and their influences on adolescent behavior. We describe why these issues represent an interesting and important area of investigation, emphasizing their contributions to a specific set of developmental processes at the heart of the transition from childhood to adolescence. We briefly review the neuroendocrine underpinnings of human puberty. Our review focuses on evidence for behavioral (and neurobehavioral) effects of gonadal hormones, and emphasizes the social and affective dimensions of these hormonal effects. More broadly, we consider how these hormonal events contribute to brain-behavior interactions that can bias early adolescent trajectories in both positive and negative directions, and in ways that may begin as small influences, but can spiral into large-scale effects over time. These influences also appear to play an important role in functional and structural brain development during adolescence. Finally we offer some thoughts on directions for future research in these areas.

Keywords

behavior; puberty; social affective development; testosterone

THE INITIAL SURGE OF HORMONES OCCURS EARLY

Although the title of this special issue highlights The *Teenage* Brain, it is important to recognize that the foundational events at the onset of human adolescence—the surge of hormones that starts the cascade of physical changes known as puberty—typically begins *before* the teenage years. In girls, the average age of menarche (the onset of menstrual periods) in girls in the U.S. is 12.5 years of age. Moreover, menarche occurs near the final stages of puberty, and is usually preceded by 2–3 years of hormonal and physical changes (including breast development, the development of pubic and axillary hair, rapid physical growth, and sexually dimorphic changes in facial structure). This surge of hormones, which marks the end of childhood and the onset of adolescence, typically begins by 9–10 years of age in girls and by 10–12 years of age in boys. Thus, the effects these hormones have on developing bodies and brains (and behavior) are usually beginning well before the teens.

[*]**Corresponding author:** Ronald E. Dahl, Institute of Human Development, University of California, Berkeley, 1123 Tolman Hall, Berkeley, California 94707, USA, Phone: (510) 643-9063, rondahl@berkeley.edu.

It is important to acknowledge that some of the consequences of these rising hormonal levels can continue to grow in amplitude throughout the teen-age years and may influence brain-behavior interactions for several years (as will be described). However, in order to understand the proximal effects of this surge of pubertal hormones on neurobehavioral systems we should focus not on the teenage years, but rather, on this (usually) earlier window of development when there is a dramatic change in these hormonal levels from very low pre-pubertal levels to relatively high mid-pubertal levels.

Why Study the Effects of Surging Pubertal Hormones?

Until recently, relatively few studies of adolescent brain development have focused attention on puberty and pubertal hormones. In fact, there has been little consistency in the field as to how ‘adolescence’ is operationalized. This lack of consistency is reflected in the large variability in the age ranges selected as ‘adolescents’ (which can range from 10 to 25 years of age), and in the huge range and variability in developmental processes that occur across this interval. A strong case can be made for the scientific advantages of posing well-specified developmental questions about particular aspects of adolescent development.

Focusing on pubertal maturation—and more specifically on the hormonal components of puberty—represents one example of this approach. Moreover, there are at least four reasons to focus on this *particular* developmental process: 1) Puberty is *the* fundamental basis of the transition from childhood to adolescence. 2) The biological components of pubertal maturation provide targets to develop and test mechanistic hypotheses (e.g. the effects of particular hormones on specific neural systems at specific points in development). 3) Puberty creates unique opportunities for translational research with animal studies (i.e. it is very difficult to specify what ages in a mouse, rat, or monkey’s development correspond to ‘teen-age’ years in humans, while the sharp pubertal rise in testosterone and estradiol create direct parallels across species). 4) There is growing evidence for shifts in *social and affective processing during puberty* that may play a crucial role in biases developmental pathways in ways that can have enormous long-term effects on health, education, and well-being.

Why Focus on Social and Affective Influences of Pubertal Hormones?

As reviewed recently in (Crone & Dahl, 2012) amidst the myriad of social, emotional, cognitive and biological changes during adolescence, there is growing evidence in both humans and animals that pubertal hormones may influence (bias) some neural and neurobehavioral tendencies of social and affective processing. Examples of such neural and neurobehavioral correlates of social and affective processing include (but are not limited to) activity within the striatum during reward processing, activity within the amygdala and striatum during the processing of emotional stimuli and activity within the anterior medial prefrontal cortex and temporal-parietal junction during social-cognitive reasoning (for review see Crone and Dahl, 2012).

Changes in these brain areas and circuits appear to sensitize youth to their social world. A tendency to direct increased attention and motivation to social domains may have adaptive advantages in this developmental window. The fundamental task of adolescence—to achieve

adult levels of social competence—requires a great deal of learning about the complexities of human social interactions. Puberty appears to create a neurobehavioral nudge toward exploring and engaging these social complexities. These tendencies to explore and engage can promote adaptive social and affective learning across adolescence; however these same tendencies appear to create some vulnerabilities toward negative developmental trajectories.

The goal of this paper is to focus on the proximal roots of these changes—the specific neurobehavioral effects that occur during the initial surge of pubertal hormones, and consider how these contribute to a complex set of social and affective changes that can impact long-term developmental trajectories.

NEUROENDOCRINE AND HORMONAL ASPECTS OF PUBERTY

Puberty is an endocrinological event leading to sexual maturation. This surge in hormones plays a central role within a larger set of biological changes in the process of achieving reproductive maturity, which include rapid physical growth, sexually dimorphic alterations in facial structure, voice, and body characteristics, metabolic changes, the activation of new drives and motivations, changes in sleep and circadian regulation, and a wide array of social, behavioural and emotional changes.

The start of puberty is characterized by the reactivation of the hypothalamus-pituitary-gonadal (HPG)-axis. The first step is when the hypothalamus begins to release large amounts of gonadotrophin-releasing hormone (GnRH) in a pulsatile manner during sleep (Delemarre-van de Waal, 2002). The HPG-axis is active during prenatal and early postnatal life and then becomes quiescent throughout childhood. Puberty actually represents a re-activation. The exact mechanisms that trigger this reactivation of pulsatile GnRH release at puberty remain unclear, but there has been rapid progress in understanding several key aspects (Navarro & Tena-Sempere, 2012).

The first outward signs of puberty are breast development in girls and genital development in boys. The development of these first secondary sexual characteristics occurs on average at age 10 in girls and 11.5 in boys (for review see: (Euling et al., 2008). In addition to the gonadal hormones testosterone and estradiol, the adrenal androgen DHEA also plays a role in the development of secondary sexual characteristics, including pubic (girls/boys) and facial hair (boys) (Delemarre-van de Waal, 2002). Also Growth Hormone (GH) changes contributes to pubertal growth and metabolic changes. Other neuroendocrine systems (such as oxytocin and vasopressin) also appear to contribute to neurobehavioral changes at puberty, however, there is a dearth of data in humans to directly address these influences, and therefore most of this review will focus on gonadal hormones.

Developing reproductive capabilities does not only involve changes in the body, but also changes in neural systems. The brain is a major target for sex steroid hormones. Sex steroids act on the brain in two different ways: a) organizational effects of sex hormones that permanently change the structure of the brain (such as neuronal number, myelination, dendritic branching), and b) activational effects that temporarily change the activity of neural systems (such as the hormonal activation of neural systems that underpin mating behavior in animals after puberty) (McCarthy & Arnold, 2011). Until recently, it was

believed that organizational effects of sex hormones only took place during prenatal and early postnatal life, whereas puberty reflected only activational effects of sex hormones. However, recent animal work shows clear evidence of further organizational effects during puberty, such as the addition of new neurons to parts of the hypothalamus and amygdala (Ahmed et al., 2008). Evidence for brain organizational effects of pubertal hormones in humans also have been described, for instance global and focal gray matter decreases and white matter increases (Ladouceur, Peper, Crone, & Dahl, 2012; Peper, Hulshoff Pol, Crone, & van Honk, 2011). However, human studies have limited capacity to disentangle the direct effects of hormones from indirect effects that may be correlated with puberty. Accordingly, we will focus on activational effects of pubertal hormones, reviewing briefly the evidence for how specific hormones appear to influence behavior.

PUBERTAL HORMONES AND (NEURO-) BEHAVIORAL CHANGES DURING ADOLESCENCE

Testosterone

During adolescence, higher testosterone levels have been associated with increased approach-related behaviors, such as proactive aggression (van Bokhoven et al., 2006) and risk-taking (Vermeersch, T'Sjoen, Kaufman, & Vincke, 2008a) in boys, and sensation seeking and sensitivity to reward (Forbes et al., 2010) in both boys and girls.

With respect to brain activity, increased levels of testosterone in boys predict an enhanced activation in the ventral striatum after performing high-risk gambles (Op de Macks et al., 2011). The ventral striatum is a subcortical brain region that is active when a person receives or expects a reward (Haber and Knutson, 2010). Therefore, these findings might be interpreted as heightened gonadal hormones ‘sensitizing’ the brain’s reward system, making adolescents more reactive to rewards in general. However, there is also evidence that social rewards may be particularly important during this period of development, as pubertal testosterone is a strong predictor of status-relevant motivation and behavior. In boys, higher levels of testosterone predict increased social aggression controlled for age (Rowe, Maughan, Worthman, Costello, & Angold, 2004). The social environment plays an important role: The effect of testosterone on aggression was only found when the individual's status was threatened (Josephs, Mehta, & Carre, 2011; Josephs, Sellers, Newman, & Mehta, 2006). Moreover, bullied girls were found to produce less testosterone and bullied boys produced more testosterone than their non-bullied counterparts (Vaillancourt, deCatanzaro, Duku, & Muir, 2009). This study demonstrates that the social environment is not only able to mediate testosterone effects on behavior, but influences actual levels of testosterone itself.

Recent studies also suggest that it is not simply high levels of testosterone that predispose to these behaviors, but may involve interactions with other hormones or neurotransmitters (Montoya, Terburg, Bos, & van Honk, 2012). For example, relatively high levels of testosterone together with relatively low levels of cortisol have been implicated in delinquent behavior in adolescent boys (Popma et al., 2007; Yu & Shi, 2009).

Estradiol

Compared to testosterone, the role of estradiol in motivated behavior in humans is less well studied. In adolescent girls, a positive association was found between estradiol levels and (aggressive and non-aggressive) risk-taking, also when age-effects were taken into account (Vermeersch, T'Sjoen, Kaufman, & Vincke, 2008b). The effects varied across the menstrual cycle: the association between estradiol and risk-taking was strongest during the mid-luteal phase where estradiol levels are relatively high. Interestingly, female rats during the proestrus phase of the menstrual cycle (in which E2 levels are also high), exhibit attenuated inhibition when compared to rats with low levels of E2 (Quinlan, Duncan, Loiselle, Graffe, & Brake, 2010). Moreover, this effect was not seen until puberty indicating it is dependent on the surge of hormones at puberty (Quinlan et al., 2010). Taken together, these data suggest that increased pubertal estradiol in females relates to less behavioral inhibition and increased risk-taking. Moreover, with respect to brain activity in relation to risk-taking, it was found that higher estradiol levels in girls predict stronger activity within the ventral striatum after performing high-risk gambles, although this effect was somewhat weaker than testosterone in boys (Op de Macks et al., 2011).

This emphasis on social and affective influences is not intended to imply that these are the only neurobehavioral effects of pubertal hormones. Clearly some aspects of cognitive (and social cognitive) function are impacted by pubertal hormones. For example, there is evidence that estrogen shapes dopamine-dependent cognitive processes (Jacobs & D'Esposito, 2011) as well as a recent study reporting that pubertal hormones (testosterone, oestradiol and DHEA) directly influence brain activity within the anterior temporal lobe during social emotional processing (Goddings, in press). This is quite interesting given that, the anterior temporal lobe has been implicated in the processing of social emotions such as guilt and embarrassment (Zahn et al., 2007).

Pubertal Hormones and Models of Brain-Behavior Interactions

Recently, it has been proposed that pubertal maturation impacts social and affective processing in ways that contribute to an adolescent flexibility in cognitive engagement, depending on the social and motivational salience of the context (Crone and Dahl, 2012). The model suggests that interactions between social–affective processing systems in the brain and cognitive control systems can lead to healthy adaptation to the complex and rapidly changing social contexts of adolescence. However, these can also lead to negative trajectories such as substance abuse or depression. These negative trajectories may begin as small changes, but over time can lead to patterns of behavior that have cascading effects: brain-behavior interactions with spiraling impact across adolescence.

Pubertal Changes in Sleep as an Illustrative Example

To illustrate, in more depth, how a small pubertal change in one neuro-behavioral system can spiral into large-scale complex behavioral consequences, let us consider the powerful example of sleep and circadian changes during adolescent development. As has been observed now in several species (Hagenauer, Perryman, Lee, & Carskadon, 2009), pubertal maturation is associated with a small shift in the *tendency* to prefer sleeping later in the circadian cycle. In elegant work in mice, it recently has been shown that gonadal hormones

influence the way that the SCN (the biological master clock in the hypothalamus) responds to light (Karatsoreos, Butler, Lesauter, & Silver, 2011).

In human development, there is evidence for a similar circadian shift in sleep preferences at puberty. The direct effect of these pubertal changes appears to be relatively subtle—for example, a typical mid-pubertal 12 year old may experience a slight (biological) tendency to prefer staying up later and a tendency to sleep-in later into the morning on weekends. Moreover, for most of human history, this slight tendency to prefer staying up later at night was unlikely to result in large sustained effects on behavior (until the advent of electric lights) because the prevailing darkness at night presented adolescents with limited opportunities to activate their hypothalamus with the type of light signals that create large-scale biological shifts in the circadian clock. However, in contemporary society youth have access not only to bright lights at any hour of the night but it also appears that blue spectra light from TV, computer, and personal-device screens may have particularly strong effects on the human circadian system. Even more importantly, there are also several other social and motivational factors that increase the likelihood that many adolescents want to be using these arousing and light-signaling devices later into night (Carskadon, 2011).

Taken together, this combination of social and behavioral factors now contributes to a situation in the U.S. where the *average* school night bedtime among high-school seniors is after 11: 30 pm (despite the fact that the average wake-up time on school days for these students is 6:15 am). The resulting chronic sleep deprivation (and catch-up sleep on weekends on very late schedules) further amplifies the negative spiral of effects. It is currently estimated that up to 30% of high-school students in the U.S. are chronically sleep deprived as a result of these spiraling influences. Insufficient sleep has a cascade of negative effects on other aspects of emotion, behavior, cognition, and learning, which can in turn further interfere with sleep/arousal regulation (Carskadon, 2011).

The main point here is to illustrate how a relatively small pubertal change in specific neural systems—in this case an increased circadian sensitivity to the environment (light and social cues)—can become amplified by multiple social factors across adolescence. Thus, while the direct effects of the initial rise in pubertal hormones may appear relatively small, the longer-term effects on brain-behavior interactions can become large-scale effects over time. This framework helps us understand why the specific details of hormonal effects on neurobehavioral tendencies represent important scientific questions.

If we extend this example to consider the impact of a small pubertal increase in the motivational salience of acquiring social status, we can imagine a similarly complex cascade of changes (as with sleep patterns) interacting with complex contemporary social contexts. Most importantly, it highlights the power of social and cultural influences (for example the particular kinds of behaviors that bring increased attention and admiration early in the process) as well as the impact of early social failures. Clearly a great deal more research is needed to empirically test features of this model—and to advance understanding of the specific hormonal mechanisms (and specific neural systems) that underpin these changes.

CONCLUSIONS AND IMPORTANT AREAS FOR FUTURE RESEARCH

In brief, the most important conclusion is the need for more studies of adolescent brain development to focus on puberty-specific and hormone-specific developmental processes. Studying puberty-specific effects on developmental processes requires designing the studies to prioritize these questions—focusing on the early ages of onset, using longitudinal designs, and obtaining appropriate measures of pubertal development (Shirtcliff, Dahl, & Pollak, 2009). In addition it will require further development and refinement of heuristic models (and testing key features of these models) to advance understanding of how specific hormones impact specific neural systems to influence specific behavioral tendencies. This also requires recognition that the biological signals created by hormones can sometimes have little to with the *level* of the hormone in the blood or saliva, but rather the timing or pattern of hormone secretion reaching the target. For example, it has been well established that the fundamental trigger for the onset of puberty is the pulse frequency of gonadatropin releasing hormone (rather than the level of the hormone).

Other priorities for future research include the importance of considering (and investigating) a broad range of hormones that change at puberty. These include not only estradiol, testosterone, and the adrenal androgens dehydroepiandrosterone (DHEA) and dehydroepiandrosterone sulphate (DHEA-S) but also other neuroendocrine systems that appear to undergo developmental changes at puberty such as growth hormone regulation, and HPA axis regulation. One particularly interesting line of investigation focuses on oxytocin/vasopressin system that has been shown to be central to social bonding motivation and behaviors, and influences social cognitive processes like trust (and does this differently for ‘in’ groups and ‘out’ group contexts). Given the dynamic social changes in adolescence – establishing close friendships, intense motivations and emotions of early sexual and romantic relationships, as well as changes in family relationships – it would be surprising if pubertal changes in these oxytocin and vasopressin systems were not intertwined with some of these developmental changes. There are some animal data showing pubertal changes but very limited investigations translational or human research (see (Carter, 2003; Gordon, Martin, Feldman, & Leckman, 2011) for relevant reviews.

To conclude, our review demonstrates that pubertal hormones contribute to brain-behavior interactions. At least in some cases these effects appear to manifest as action-tendencies, or behavioral tendencies, which can in some ways appear to have relatively subtle effects. Yet, even small changes in behavioral tendencies (such as the biological shift in the tendency to go to sleep later) can in some contexts, over time lead to high-impact changes in patterns of behavior. There is growing evidence that these hormone-driven tendencies can impact long-term developmental trajectories, in both positive and negative ways. Achieving a better understanding of these important developmental processes represents an exciting and pioneering area for trans-disciplinary research.

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