



Review Article

Pubertal development and behavior: Hormonal activation of social and motivational tendencies

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ABSTRACT

Adolescence is a time of dramatic changes including rapid physical growth, the onset of sexual maturation, the activation of new drives and motivations, and a wide array of social and affective changes and challenges. This review focuses on behavioral changes in this interval and is organized by the claim that a key set of these adolescent changes are part of a more general *re-orientation of social behavior*. More specifically we hypothesize that pubertal maturation is associated with the *activation of social and motivational tendencies*, which in turn influence behavior and emotion in adolescence depending upon interactions with social context. We focus on evidence for two examples of these motivational changes: (1) increases in sensation-seeking (motivational tendency to want to experience high-intensity, exciting experiences) and (2) stronger natural interest in—and pursuit of—contact with peers and potential romantic partners. We consider how these motivational changes contribute to the broader social re-orientation of adolescence, including exploration of social experiences, development of skills and knowledge relevant to taking on adult social roles, individuation from family, and establishment of an individual identity, all of which represent core developmental tasks during this period in the life span (Blakemore, 2008; Dahl & Spear, 2004; Steinberg & Morris, 2000). The paper also emphasizes the importance of investigating and understanding the direct influences of puberty on behavior and disentangling these from the broader set of changes during adolescent development.

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1. Introduction

The onset of adolescence is a time of dramatic biological, behavioral, and social changes. These include rapid physical growth, sexual maturation, and emotional changes that range from igniting romantic interests to increased self-consciousness and social anxieties. Adolescence is also a time of new social challenges such as increasing academic pressures, competition with peers, and difficulties learning to balance desires for immediate gratification with an understanding of the importance of long-term goals and consequences (Dahl & Spear, 2004). Amidst this myriad of adolescent changes there are also sharply increasing rates of problems with the control of behavior and emotion, despite the fact that the regulatory capacities are improving across this interval of development. As discussed elsewhere in this issue, adolescence involves ongoing development of brain structure (Lenroot & Giedd (2010); Paus (2010)), sleep (Feinberg & Campbell (2010)), and brain function (Somerville, Jones, & Casey (2010)), including gradual in-

creases in capacities for cognitive control and executive function (Luna, Padmanabhan, & O'Hearn (2010)).

In the current paper, we examine pubertal maturation in relation to several aspects of adolescent behavior, with an emphasis on the increase in reproductive hormones that are instrumental to pubertal development. We review emerging evidence that pubertal maturation is closely associated with a set of affective (emotional and motivational) changes, which in turn influence some behavioral tendencies. We put forth the hypothesis that many (if not most) of the behavioral changes associated with pubertal maturation are linked to activation effects on specific motivational tendencies—including increased sensation-seeking, and stronger natural attraction to peer and romantic contexts—and that the subsequent influences on individual behavior are highly variable depending upon the social context as well as underlying individual differences.

Understanding these puberty-specific changes in behavior represents an important dimension of normal development in adolescence. It also has broad clinical and social policy relevance. Interactions between these motivational tendencies and the social contexts that amplify these tendencies are relevant to understanding the *health paradox* of adolescence. That is, adolescence represents one of the healthiest periods of the life span with respect

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to physical health, yet overall morbidity and mortality rates increase 200% (Centers for Disease Control, 2009; Ozer, Macdonald, & Irwin, 2002; Resnick et al., 1997). Rates of accidents, suicide, homicide, depression, alcohol and substance abuse, HIV, Hepatitis C, unwanted pregnancies, anorexia and bulimia rise sharply in this developmental period (Force, 1996; Ozer et al., 2002). On the one hand, these various types of adolescent health problems appear heterogeneous; on the other hand, the majority of these health consequences reflect difficulties with control of emotion and behavior.

An important framework for understanding some of these affective changes at puberty can be understood within the broader social re-orientation of adolescence. As noted by recent reviews on the social neuroscience of adolescence (e.g. Blakemore, 2008; Nelson, Leibenluft, McClure, & Pine, 2005) adolescence is marked by changes in social cognition and by functional and structural development of brain networks implicated in social processing. We hypothesize that the pubertal rise in reproductive hormones activates motivational tendencies—including appetitive motivations in the realm of social goals and rewards—that help to facilitate this social re-orientation. These are evident in adolescents' increasing motivations to attract friends and romantic partners, to attain social status, and more generally, in their natural tendencies to pay more attention to, care about, and react to peer, romantic, and sexual contexts.

The activation of these motivational tendencies can have positive effects on behavior—specifically, natural inclinations leading to learning and exploration of social environments in ways that contribute to acquiring relevant knowledge and skills. Yet, stronger attraction to peer and romantic pursuits—particularly in combination with increased sensation-seeking—can contribute to a wide range of risky adolescent behaviors associated with negative health consequences, especially in some social contexts.

We will review the evidence for puberty-specific changes in behavior. To begin, we will briefly describe the hormonal and physical changes of puberty and outline the limitations and challenges to research on puberty and behavior, and then describe emerging areas of progress in disentangling puberty-specific neurobehavioral changes. Next, we focus on two areas of investigation where there is strong evidence for puberty-specific behavioral changes—sensation-seeking and motivation for social status—and then consider these in relation to our model emphasizing motivational tendencies.

2. Pubertal development

Adolescence can be defined as that awkward period between the onset of sexual maturation and the attainment of adult roles and responsibilities (Dahl & Spear, 2004). The transition into adolescence is marked by pubertal development, which includes activation of the hypothalamic–pituitary–gonadal (HPG) axis and the hypothalamic–pituitary–adrenal (HPA) axis (see Buck Louis et al. (2008) for a detailed overview of pubertal development). Puberty is triggered by increases in the frequency and amplitude of nocturnal pulses of gonadotropin-releasing hormone (GnRH) in the hypothalamus. There is little research on the age at which GnRH pulses begin in humans, but studies of non-human primates suggest that there are individual differences in the function of the GnRH system and in the response to factors that influence GnRH function (Centeno, Sanchez, Cameron, & Bethea, 2007). Given this, and given sex differences in puberty onset in humans, it is difficult to estimate the age at which increased GnRH pulsing begins in humans.

A critical frequency of GnRH pulses activates pituitary release of luteinizing hormone (LH) and follicle-stimulating hormone (FSH) pulses, which in turn, activate the gonads. In girls, this leads to

ovarian secretion of estradiol, progesterone, and ovarian androgens, and eventually to the development of ovulatory menstrual cycles. In boys, LH pulses lead to testicular secretion of androgens. In addition to gonadal development, puberty also involves important changes such as increases in adrenal androgens, rapid growth in body size, changes in distribution of body fat, and development of secondary sex characteristics.

Importantly, puberty represents a re-activation of specific neuroendocrine systems. That is, the reproductive hormones that increase sharply at puberty represent a second activation of neuroendocrine axes that were also active in infancy (see Fig. 1 for an illustration of this pattern for males). This two-phase pattern of the effects of reproductive hormones in development has been described in relation to the *organizational–activational hypothesis* (Phoenix, Goy, & Young, 1967; see Romeo (2003) for a more recent review). This model focuses on the observation that the same hormones that initially organize sex differences in the body and the brain during fetal and early postnatal life are also the hormones that exert activational effects on behavior during puberty.

More recently, evidence from animal research on hormonal influences on behavior indicates that sex-steroid hormones can also have activational effects on brain development at puberty (Schulz, Molenda-Figueira, & Sisk, 2009). That is, puberty can be viewed as a period of re-activation of hormonal influences on behavior and the brain. Brain development is highly sensitive to hormone influence perinatally, but the activational effects of hormones do not simply occur during perinatal development, as once thought. Examples of puberty-related organization of behavior are evident in both males and females, as illustrated by the Syrian hamster model of pubertal hormone influence. In male hamsters, the organizing influence of pubertal hormones has been studied by castration after perinatal hormone influence but before puberty. As a result, testosterone at puberty appears to influence increases in male hamsters' sexual behavior and aggressive behavior (Schulz & Sisk, 2006), and their reduction in anxiety-related locomotor activity in a novel environment (Primus & Kellogg, 1989). In female hamsters, which have been less extensively studied, ovarian hormones at puberty influence food-guarding and feeding behaviors (Field, Whishaw, Forgie, & Pellis, 2004; Swithers, McCurley, Hamilton, & Doerflinger, 2008). At a neural level, organizational effects of pubertal hormones include cellular-level changes in brain circuits, such as testosterone influences on increases in white matter volume (Perrin et al., 2008). Importantly, pubertal hormones influence

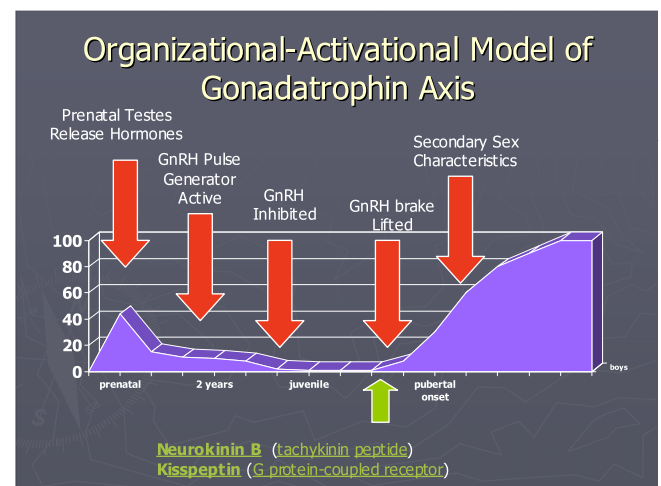


Fig. 1. Illustration of an organizational–activational model for boys, showing early activation of GnRH pulsing, a period of quiescence, then re-activation of the GnRH pulsing at the onset of puberty. GnRH: gonadotropin-releasing hormone.

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