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Hormone-dependent adolescent organization of socio-sexual behaviors in mammals

Cheryl L Sisk

The adolescent transition from childhood to adulthood requires both reproductive and behavioral maturation as individuals acquire the ability to procreate. Gonadal steroid hormones are key players in the maturation of behaviors required for reproductive success. Beyond activating behavior in adulthood, testicular and ovarian hormones organize the adolescent brain and program adult-typical and sex-typical expression of sociosexual behaviors. Testicular hormones organize sexual and agonistic behaviors, including social proficiency — the ability to adapt behavior as a function of social experience. Ovarian hormones organize behaviors related to energy balance and maternal care. These sex differences in the behaviors that are programmed by gonadal hormones during adolescence suggest that evolution has selected for hormone-dependent sex-specific organization of behaviors that optimize reproductive fitness.

Address
Neuroscience Program, Michigan State University, 293 Farm Lane, East Lansing, MI 48824, USA

Corresponding author: Sisk, Cheryl L (sisk@msu.edu)

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Introduction

The adolescent transition from childhood to adulthood requires a metamorphosis of brain and behavior as individuals acquire the ability to procreate and provide for themselves and their offspring. The beginning of adolescence is marked by the onset of puberty, when activation of the hypothalamic–pituitary–gonadal axis results in the maturation of gametes, elevated levels of sex steroid hormones, the appearance of secondary sex characteristics, and fertility. But merely being fertile is not sufficient for reproductive fitness in most mammals. Sexual reproduction usually requires complex social behaviors for bringing sperm and egg together, and additional behavioral capacities are needed to successfully rear young. Thus, full attainment of adulthood encompasses not only pubertal maturation of the reproductive system, but also adolescent maturation of the social and behavioral skills necessary for successful reproduction. The scope of this review is therefore not limited to adolescent maturation of male and female sexual behavior *per se*; it includes adolescent maturation of the range of behaviors that together lead to passing along one's genes. The central thesis of this review is that testicular and ovarian hormones, when elevated at the onset of puberty, program behavioral responses to hormones and social experiences in adulthood. The particular behaviors that are organized by gonadal hormones are different in males and females, but in each sex, hormones program adult behaviors that are important for reproductive success.

Organizational versus activational effects of gonadal steroid hormones

Steroid hormone action in the nervous system can be dichotomized as activational or organizational. Activational effects refer to the ability of steroids to modify the activity of target cells in ways that facilitate expression of particular behaviors in specific contexts. Activational effects are transient; they come and go with the presence and absence of hormone and are typically associated with steroid action in the adult brain. In contrast, organizational effects refer to the ability of steroids to sculpt nervous system structure and function during development. Organizational effects are long-lasting, persist beyond the period of developmental exposure to hormone, and program activational responses to hormones in adulthood.

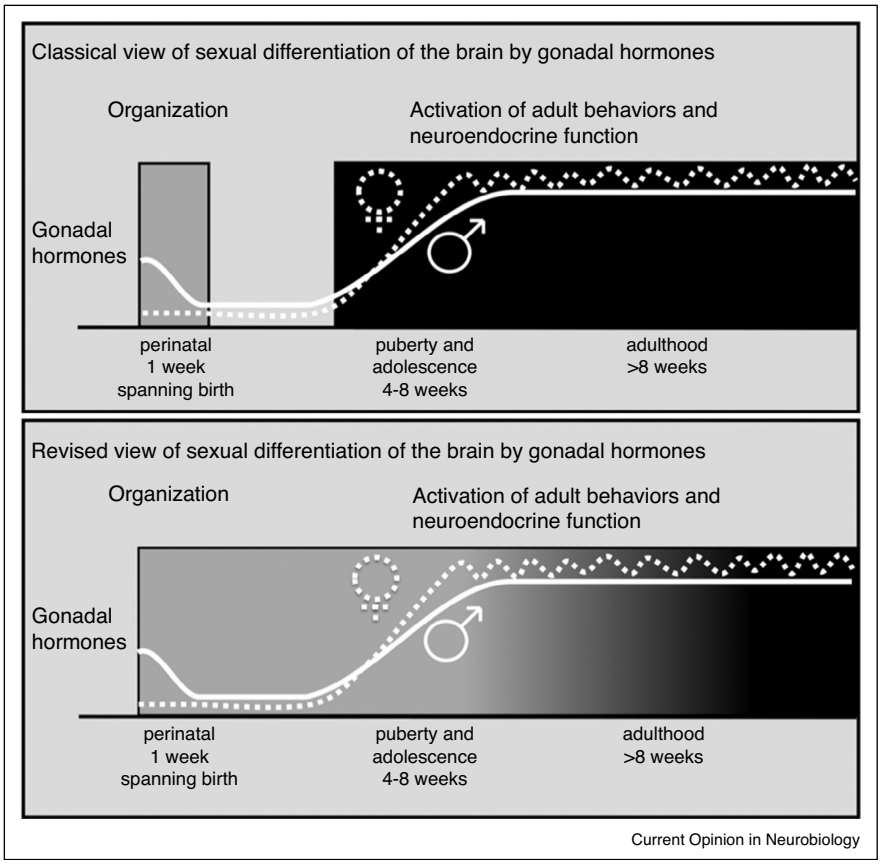
Conceptualization of the relationship between organizational and activational effects of steroid hormones has evolved over the past fifty years. In order to explain sex differences in behavioral responses to hormones in adulthood, Phoenix and colleagues [1] first proposed that sex-typical adult behavioral (activational) responses to steroid hormones are programmed (organized) by steroid hormones acting on the nervous system during early development. Subsequently, scores of experiments led to the identification of a sensitive period for hormone-dependent sexual differentiation (organization) of the brain during prenatal and early neonatal development in non-human primates and rodents (reviewed in [2–5]). Research over the past twenty years has revealed that in addition to the perinatal period of hormone-dependent organization of behavioral neural circuits, adolescence is another period of development during which gonadal hormones organize the nervous system [6,7,8••]. The current conceptual framework of organizational and activational effects of

gonadal steroid hormones is a two-stage model of development in which the perinatal period of hormone-dependent organization is followed by a second wave of organization during puberty and adolescence (Figure 1). During this second wave, pubertal hormones first organize neural circuits in the developing adolescent brain, and then facilitate the expression of adult sex-typical behaviors in specific social contexts by activating those circuits. Thus, adolescent organization reinforces and refines the sexual differentiation that occurred during perinatal neural development by inducing long-lasting structural changes in the nervous system that determine adult behavioral responses to hormones and socially-relevant sensory stimuli. One important distinction between the perinatal and pubertal periods of organization is the contribution of ovarian hormones. Perinatal organization is accomplished primarily through the masculinizing and defeminizing effects of testicular hormones; ovarian hormones, which are not elevated perinatally, do not play a major role, and the developing brain is not actively feminized. In contrast, both testicular and ovarian hormones are actively involved in the pubertal organization of behavior in males and females.

Adolescent organization of sociosexual behaviors in males

The general experimental strategy used to determine whether behavioral circuits are organized during adolescence is to manipulate gonadal hormones during that time and assess behavior in adulthood. Typically, animals are gonadectomized prior to the onset of puberty to allow adolescent development in the absence of testicular hormones, and then testosterone is replaced in adulthood prior to behavioral tests. The behavior of males treated in this way is compared with that of males that were similarly treated, except that gonadectomy, washout period, and testosterone replacement all occurred in adulthood. With this experimental design, the observed deficits in adult behavior of males that did not experience testicular hormones during adolescence can be attributed

Figure 1



Schematic representation of the classical and revised views of sexual differentiation of the rodent brain and behavior. In the classical view, brain architecture is permanently modified by exposure of the male brain to testicular hormones during a brief perinatal period. In the revised view, the period of organization/structural differentiation is extended, continuing well through puberty and adolescence, during which both testicular and ovarian hormones impact the structure of the male and female brain, respectively. Adolescence encompasses puberty, which refers specifically to reproductive maturation. Although fertility is attained within 2–3 weeks of the onset of puberty, additional maturation occurs during later adolescence before adult brain and behavioral phenotypes are achieved. From [43••].