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The organizational effects of pubertal testosterone on sexual proficiency in adult male Syrian hamsters

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HIGHLIGHTS

- Male hamsters deprived of pubertal testosterone fail to become sexually proficient.
- Pubertal testosterone programs behavioral adaptations to sexual experience.
- Pubertal testosterone may organize neural circuits underlying behavioral flexibility.

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ABSTRACT

Social proficiency requires making appropriate behavioral adaptations as a result of social experience. For example, male rodents become sexually proficient with experience as demonstrated by a reduction in ectopic (misdirected) mounts, mount-to-intromission ratio, and latency to ejaculation. We previously found that over a series of timed tests with a receptive female, male hamsters deprived of testosterone specifically during puberty (NoT@P) have overall lower levels of sexual behavior and continue to display high levels of ectopic mounts, compared with males that experienced endogenous testosterone during puberty (T@P). These results suggested that pubertal testosterone programs sexual proficiency in adulthood, but because NoT@P males engaged in less sexual behavior than T@P males in these tests, the amount of sexual experience may have been insufficient to improve sexual proficiency. To more rigorously test the hypothesis that pubertal testosterone is necessary for social proficiency in adulthood, the present study compared the behavior of NoT@P and T@P males in a series of 4 trials with a 48-h interval between each trial. Sexual experience was equated by limiting each trial to 5 intromissions. Sexually-naïve males were either gonadectomized prepubertally (NoT@P) or in adulthood (T@P) and received subcutaneous testosterone capsules four weeks later. Two weeks after testosterone replacement, these groups and a group of adult gonad-intact controls began sexual behavior testing. We found that NoT@P males had more ectopic mounts/min across all four tests compared to gonad-intact and T@P males. Moreover, both gonad-intact and T@P males, but not NoT@P males, showed an increase in the number of mounts and intromissions/min between trials 1 and 3. Unexpectedly, both gonad-intact and T@P, but not NoT@P, males showed a decrease in sexual behaviors during trial 4. Thus, T@P males display multiple behavioral adaptations to sexual experience that are not observed in NoT@P males: a reduction in ectopic mounts after repeated encounters with a receptive female and an inverted U-shape pattern in mounts and intromissions when these encounters do not lead to ejaculations. These results support the hypothesis that pubertal testosterone organizes neural circuits underlying behavioral flexibility and adaptability to promote sexual proficiency in adulthood.

1. Introduction

During puberty and adolescence, the focus of social interactions shifts from family to peers. As a result, individuals must acquire a new set of social behaviors and, through social experience, develop new social skills and proficiency. Social proficiency, also referred to as social competency, increases the likelihood of efficacious social interactions with conspecifics. One critical social behavior that emerges during adolescence is sexual behavior, which is induced by the pubertal rise in gonadal hormones. Competent sexual behavior is essential for reproductive fitness, and sexual experience generally increases sexual proficiency through learning and behavioral adaptations.

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Research in the male Syrian hamster has identified multiple roles for testosterone in the adolescent maturation of sexual behavior. First, the pubertal rise in testosterone increases the incentive salience and rewarding properties of female pheromones, the chemosensory stimuli necessary for expression of sexual behavior in this species [1,2,15]. This effect of testosterone is activational and can be induced in both prepubertal and adult male hamsters, and also in male hamsters gonadectomized prepubertally and treated with testosterone in adulthood [1,5]. Second, testosterone programs sexual performance via long-term, organizational influences. In this instance, sexual performance in adulthood is compromised if male hamsters are deprived of testosterone during adolescence, even after testosterone replacement in adulthood. For example, in timed trials with a receptive female, male hamsters that do not experience testosterone during puberty (i.e., gonadectomized prior to puberty and receiving testosterone replacement several weeks later, in adulthood; defined as NoT@P) display fewer mounts, intromissions, and ejaculations compared with males that do experience testosterone during puberty (i.e., gonadectomized in adulthood and receiving testosterone replacement several weeks later; defined as T@P) [10,11]. Third, testosterone appears to program sexual proficiency, that is, the ability to adapt behavior with sexual experience that increases behavioral competence. For example, both gonad-intact adult and T@P male hamsters show a significant decrease in ectopic (mis-directed) mounts with increasing sexual experience, whereas NoT@P males continue to show high numbers of ectopic mounts *even after sexual experience* [11].

The failure of NoT@P males to adapt their behavior with experience may be because they are more impulsive or lack the ability to inhibit maladaptive behavior due to the absence of organizational effects during puberty. Alternatively, because NoT@P males achieve fewer intromissions than T@P males in timed trials, they experience less sensory feedback to respond to appropriately. In the current study, we asked whether NoT@P and T@P males would both show a decrease in ectopic mounts if given equivalent sexual experience. If NoT@P males are less capable than T@P males in adapting their behavior, then they should show consistent rates of ectopic mounts after sexual experience, while the rate of ectopic mounts in T@P males should decrease with similar experience.

2. Materials and methods

2.1. Animals

Sexually naïve male Syrian hamsters were ordered from Harlan Laboratories (Madison, WI) and individually housed upon arrival in clear polycarbonate cages (30.5 × 10.2 × 20.3 cm) with ad libitum access to food and water in a 14:10 light/dark cycle (lights out at 1400 h). The male hamsters were used as experimental animals and 48 ovariectomized, sexually experienced female Syrian hamsters (2–3 months of age) from our colony (also from Harlan Laboratories) were used as stimulus animals in sexual behavior tests. All animals were treated in accordance with the NIH Guide for the Care and Use of Laboratory Animals and protocols were approved by the Michigan State University Institutional Animal Care and Use Committee.

2.2. Experimental design (Fig. 1)

In order to create NoT@P and T@P experimental groups, fifteen prepubertal and sixteen adult male hamsters arrived in the laboratory at 26 (P26) and 56–63 (P56–63) days of age, respectively. Two days after arrival, all hamsters were gonadectomized (P28 and P58–65, respectively). Thus, the males gonadectomized at P28 did not experience testosterone during the normal time of puberty and adolescence (~P28-P56; NoT@P), whereas the hamsters gonadectomized in adulthood at P58–65 had undergone normal pubertal development with exposure to endogenous testosterone (T@P). Four weeks after gonadectomy, all NoT@P (P56) and T@P (P86–93) males were implanted with two subcutaneous testosterone capsules (13 mm and 5 mm of testosterone with 4 mm of sealing glue on both ends; inner diameter 1.98 mm; outer diameter 3.18 mm) as previously used to produce adult-levels of circulating testosterone [3,6]. Two weeks following testosterone replacement, sexual behavior testing began (P70 for NoT@P males and P100–107 for T@P males). In order to compare the behavior of NoT@P and T@P males with that of gonad-intact males, ten adult male hamsters arrived in the laboratory on P56–70, and two weeks later, sexual behavior testing began when they were P70–84.

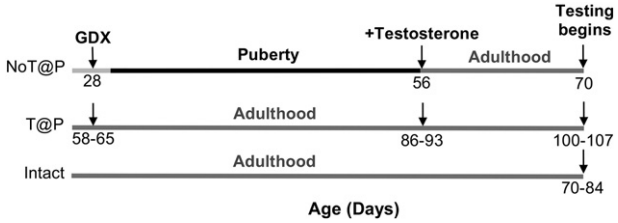

Fig. 1. Experimental model prepubertal (NoT@P) and adult (T@P) male hamsters are castrated such that animals go through adolescent development either without or with endogenous testosterone, respectively. Four weeks later in adulthood, all NoT@P and T@P males receive testosterone-filled capsules two weeks before behavior testing begins. Intact males are received as adults and do not experience any manipulations before behavior testing begins.

2.3. Stimulus females

Ovariectomized females were used to gain experimental control of the timing of receptivity. Behavioral receptivity was induced in the stimulus female hamsters by treatment with estradiol benzoate (10 μg in 0.05 mL sesame oil, sc injection) and progesterone (500 μg in 0.1 mL sesame oil, sc injection) 52 h and 4–5 h, respectively, prior to use in sexual behavior tests with males. Each receptive female was used only once per sexual behavior test and was never paired with the same male more than once.

2.4. Sexual behavior tests

Testing began 1 h into the dark-cycle under dim red light in clean large glass aquaria. Four tests were conducted at 48-hour intervals. Following a 2-minute acclimation period to the aquaria, each male was allowed to interact with a receptive female until the male achieved 5 intromissions or up to 30 min if 5 intromissions did not occur. Behavior was video recorded for later quantification.

2.5. Sexual behavior analysis

The three behaviors investigated were ectopic mounting (male grips female tightly and displays fast thrusting, but the mount is not vaginally oriented), mounting (male orients himself up on the female's hind flanks, grips her tightly with his forepaws, and displays fast thrusts), and intromissions (male is vaginally-oriented and makes a long-lasting thrust resulting in vaginal penetration). Ejaculations did not occur during any of the trials. Because males reached the 5-intromission criterion within varying times, the frequency of the behaviors displayed was divided by the total test time per male per trial. If a male displayed no mounts of any kind within 30 min, then his ectopic mounting data (i.e., zero) for that trial were not included in the statistical analysis. This was done because including the absence of ectopic mounts when there was never an attempt to engage in sexual behavior would skew the group mean to reflect more efficient behavior (i.e., less ectopic mounting during sexual behavior) than actually displayed.