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Partner preference in male hamsters: Steroids, sexual experience and chemosensory cues

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Abstract

This study investigated the effects of gonadal steroids on sexual motivation in male Syrian hamsters, using partner preference as a model. Male hamsters were assigned to 5 groups: control ($n=4$), Intact→Orchx ($n=8$), Orchx→Orchx+T ($n=7$), olfactory bulbectomy (BulbX, $n=5$), and vomeronasal organ lesion (VnoX, $n=8$). Each male was tested for partner preference before and after sexual experience. Unlike rats, sexually-inexperienced gonad-intact male hamsters preferred the receptive female to a stimulus male. However, sexual experience did not enhance preference for the stimulus female. Castration (Orchx) reduced sexual motivation: Orchx males showed no significant preference for the stimulus female. Subsequently, intact males were castrated (Intact→Orchx) and Orchx males received a testosterone implant (Orchx→Orchx+T) to determine the time course of gonadal hormones on partner preference and mating behavior. Partner preference changed significantly in both groups within 6 weeks. In Intact→Orchx males, preference for the stimulus female decreased while Orchx→Orchx+T males increased their preference for the stimulus female. However, significant changes in mating behavior preceded the alterations in partner preference. Chemosensory cues are also important for partner preference. After BulbX, preference for the stimulus female significantly decreased. However, VnoX failed to block partner preference. These results show that partner preference may be even more dependent on testosterone than is sexual behavior. Furthermore, while chemosensory cues are essential for sexual motivation, the vomeronasal organ is not required for partner preference.

Keywords: Testosterone; Sex behavior; Animal; Vomeronasal organ; Olfactory bulb

1. Introduction

The aim of the present study was to determine the importance of gonadal steroids, chemosensory cues, and sexual experience on sexual motivation in male hamsters, using partner preference as a model for appetitive sexual behavior. In the context of male sexual behavior, testicular steroid hormones have two important purposes: to promote sexual motivation and to induce copulation [1]. When endogenous steroid levels are low (i.e. before puberty and during seasonal reproductive suppression) or eliminated by castration (Orchx), mating is abolished [2,3]. However, gonadal steroids also promote sexual motivation. Previous studies have shown that castrated male hamsters spend less time in contact with an estrous female and show less chemoinvestigatory behavior towards females or their odors [4–7]. In rats, castration eliminates partner preference [8] and reduces operant responding for an estrous female [9]. These effects are reversed by testosterone replacement. In the present study, we used partner preference in male hamsters to compare hormonal responsiveness of sexual motivation and copulation.

Although hormones are essential for mating, sexual behavior is only expressed in response to sensory stimuli from a potential sexual partner. In most male rodents, attraction to females is mediated by chemosensory cues which are detected in the vomeronasal organ and olfactory mucosa [see 10]. The olfactory mucosa responds to volatile odors, while the vomeronasal organ is especially sensitive to non-volatile stimuli from conspecifics. Sexual attraction is initiated through odors transduced in the olfactory mucosa, leading to investigation at close range and subsequent activation of the vomeronasal system. Even at low concentrations (1/100), gonad-intact male hamsters are highly attracted to female hamster vaginal secretion (FHVS; [11]). Removal or deafferentation of the

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olfactory bulbs abolishes consummatory sexual behavior, and eliminates preference for vaginal secretions from conspecific females [12]. To determine the importance of chemosensory cues from the olfactory mucosa and vomeronasal organ on sexual motivation, the present study compared partner preference after bilateral olfactory bulbectomy (BulbX) or removal of the vomeronasal organ (VnoX).

In rats, sexual experience modulates attraction to females [13]. Sexually-naïve male rats do not express a consistent preference for female odors [14]. By contrast, hamsters are attracted to FHVS even when sexually-inexperienced [12]. The present study determined if prior sexual experience is required for partner preference in male hamsters.

2. Materials and methods

2.1. Animals

33 adult male Syrian hamsters (*Mesocricetus auratus*, 130–150 g, Charles River Laboratories) were housed under a long-day photoperiod (14:10 LD) and stable ambient temperature (24 °C). Food and water were available at all times, except during testing. All experimental procedures were in accordance with the "Guide for the Care and Use of Laboratory Animals" [15].

Initially, all males were sexually-inexperienced. Males were pair-housed with another male from the same experimental group. 8 female hamsters used as stimulus animals were ovariectomized via bilateral dorsal flank incision, and received a 4-mm Silastic estradiol implant sc (id: 1.98 mm, od: 3.18 mm; Dow Corning, MI) to maintain chronic physiologic levels of estrogen. To induce estrus, females received 250 ug progesterone in cottonseed oil sc approximately 4 h prior to testing (see [16]).

Based on the observation that a sexually-motivated male will prefer a receptive female to a stimulus male, partner preference was used to measure sexual motivation [10]. Mating tests were used to measure sexual behavior. To compare the time course of extinction and recovery of sexual motivation and mating behavior, males were tested at intervals before, during, and after castration and testosterone replacement.

2.2. Partner preference tests

Males were tested for partner preference in a clear plastic cage (see Fig. 1: 40×23.5×21 cm, Penn Plax, Garden City, NY). A gonad-intact male and estrous female used as stimulus animals were confined in small clear plastic compartments (13×13×12.5 cm) attached at either end of the test cage via a perforated concave bubble cap (5 cm diam, 4.5 cm deep; Penn Plax) to provide visual, auditory and volatile chemosensory cues. The location of the male and female stimulus animal was randomized between tests to eliminate side preferences.

Partner preference was recorded for 10 min on a PDA (Zire 21, Palm One Inc.) running Spectator Go! software (Biobserve GmbH, Bonn, Germany). Spectator Go! allows the user to enter time-stamped states or events on a PDA which are later analyzed with a standard spreadsheet application (Microsoft Excel). For partner preference testing, the parameters measured were time

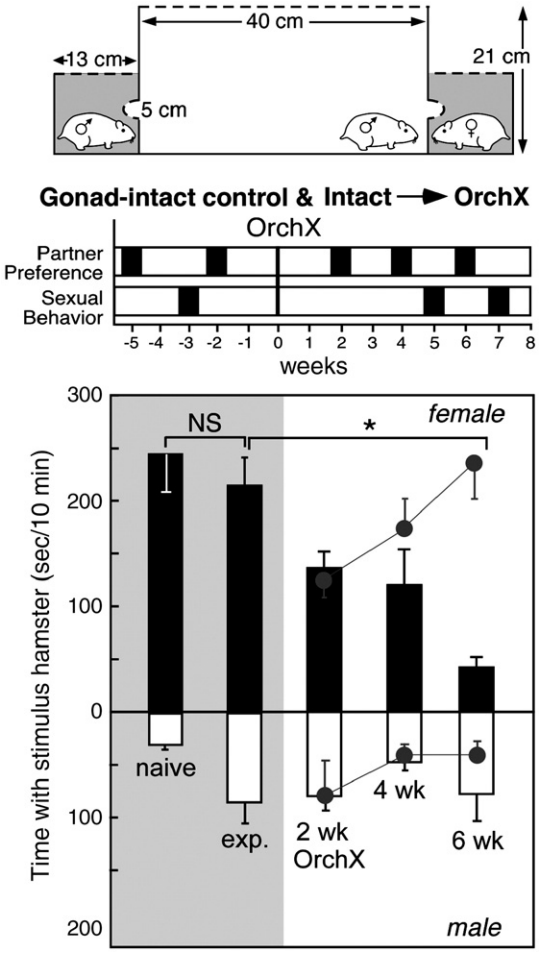

Fig. 1. Top: schematic of apparatus for testing partner preference in male hamsters. Middle: timeline for partner preference and copulation tests in male hamsters before and after sexual experience and castration (Orchx). Bottom: time (mean±SEM) with an estrous female (black bars) or male stimulus animal (white bars) in 10-min partner preference tests before (n=12, shaded area) and after castration (n=8) in male Syrian hamsters. Asterisk indicates significant effect of time post-castration. Gray symbols indicate behavior of gonad-intact control males tested at the same intervals.

spent with the male and time spent with the female. Investigation of the stimulus animal was defined as the time the test male spent with his head in the bubble cap past the level of his eyes. Preference was calculated as the time spent investigating the stimulus female minus the time with the stimulus male.

2.3. Mating tests

Mating behavior with an estrous female was tested for 10 min in the female's home cage. The behavior of the test male was recorded each second on a PDA as described previously [17]. Behaviors measured included self-grooming, investigation of the female, anogenital investigation, mounting, intromission, and ejaculation.

2.4. Experimental groups

There are 5 experimental groups: Control, Intact→Orchx, Orchx→Orchx+T, BulbX, and VnoX. The time-course of