

Sexual behavior in male rodents

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Abstract

The hormonal factors and neural circuitry that control copulation are similar across rodent species, although there are differences in specific behavior patterns. Both estradiol (E) and dihydrotestosterone (DHT) contribute to the activation of mating, although E is more important for copulation and DHT for genital reflexes. Hormonal activation of the medial preoptic area (MPOA) is most effective, although implants in the medial amygdala (MeA) can also stimulate mounting in castrates. Chemosensory inputs from the main and accessory olfactory systems are the most important stimuli for mating in rodents, especially in hamsters, although genitosensory input also contributes. Dopamine agonists facilitate sexual behavior, and serotonin (5-HT) is generally inhibitory, though certain 5-HT receptor subtypes facilitate erection or ejaculation. Norepinephrine agonists and opiates have dose-dependent effects, with low doses facilitating and high doses inhibiting behavior.

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Introduction

Reproductive behaviors and their neural and hormonal regulation vary widely across species. Yet much research has focused on relatively few animals. We describe the behaviors of male rodents and their neural, hormonal, and experiential regulation. We begin with rats, the most common subjects of laboratory research. We then describe the behaviors of male mice, hamsters, and guinea pigs, noting similarities and differences among species. Sexual behavior is highly interactive; here we concentrate on the male, keeping in mind that the contributions of the female are equally important. Because of the vast amount of research on rodents, and the page limits for this manuscript, we can cite only a small portion of it. For additional details, please consult Hull et al. (2006) or Hull et al. (2002).

Description of male rat copulatory behaviors and *ex copula* reflexes

Male rats usually begin a sexual encounter by investigating the female's face and anogenital region. Both partners may emit

mutually arousing 50 kHz ultrasonic vocalizations. The male approaches from the female's rear, mounts, and gives several rapid shallow thrusts (19–23 Hz) with his pelvis; if he detects the female's vagina, he gives a deeper thrust, inserting his penis into her vagina for 200–300 ms (Beyer et al., 1981). He then springs backward rapidly and grooms his genitals. After 7 to 10 intromissions, 1 to 2 min apart, he will ejaculate. Ejaculation is characterized by a longer, deeper thrust (750–2000 ms) and much slower dismount (Beyer et al., 1981). It is accompanied by rhythmic contractions of the bulbospongiosus and ischiocavernosus muscles at the base of the penis, and of anal sphincter and skeletal muscles (Holmes et al., 1991). After ejaculation, he grooms himself and then rests during the postejaculatory interval (PEI), which may last for 6 to 10 min before resuming mating. During the first 50–75% of the PEI, the male will not copulate again and emits 22 kHz ultrasonic vocalizations. During the latter 25%, he may resume copulation if presented with a novel female or a mildly painful stimulus. After 7–8 ejaculations males reach satiety and usually will not copulate again for 1 to 3 days. Previous sexual experience confers greater copulatory “efficiency” and increased resistance to the effects of various lesions, castration, and stress (reviewed in Hull et al., 2006).

Copulatory ability is acquired between 45 and 75 days of age (reviewed in Meisel and Sachs, 1994). Prepubertal castration

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prevented the onset of mating behavior, and exogenous testosterone (T) or estradiol (E₂) hastened its development. Aging male rats lose the ability to ejaculate, which is not restored by exogenous T (Chambers et al., 1991). A decline in estrogen receptors (ER) (Roselli et al., 1993), but not androgen receptors (AR) (Chambers et al., 1991), may underlie the deficit in old males. *Ex copula* reflexes can be observed in several contexts. Spontaneous or drug-induced erections occur in the home cage or neutral arena. Volatile odors from an estrous female elicit noncontact erections, which may be a model for psychogenic erections in humans. In rats “touch-based” erections can be elicited by restraining the male on his back and retracting the penile sheath. These erections result from engorgement of the corpus spongiosum, which produces tumescence of the glans penis (reviewed in Hull et al., 2006; Meisel and Sachs, 1994). Anteroflexions also occur; these result from contractions of the ischiocavernosus muscle and erection of the corpus cavernosum, causing the penis to rise from its normal postero-flexed position. Occasionally, seminal emission occurs in this context. The continuing pressure of the retracted sheath around the base of the penis provides the stimulus for these touch-based reflexes. Finally, the urethrogenital reflex has been studied in anesthetized male and female rats as a model of orgasm in humans (McKenna et al., 1991). It is elicited by urethral distension, followed by release; it consists of clonic contractions of the perineal muscles.

Hormonal factors in the activation of male rat mating behavior

Male sexual behavior in virtually all vertebrate species is dependent on T, secreted by the Leydig cells of the testes and metabolized in target cells to either E₂ (by aromatization) or dihydrotestosterone (DHT, by 5 α -reduction). Plasma T is undetectable within 24 h of castration (Krey and McGinnis, 1990); however, copulatory ability decreases gradually over days or weeks. Five to ten days of T is usually required to reinstate mating (McGinnis et al., 1989). However, E₂ increased chemo-investigation and mounting by castrates within 35 min (Cross and Roselli, 1999). Therefore, rapid, probably membrane-based, hormonal effects may contribute to sexual motivation, but longer-term genomic effects are required for full restoration of mating.

The major hormone to activate sexual behavior in male rats is E₂, as proposed by the “aromatization hypothesis” (reviewed in Hull et al., 2006). DHT, which is nonaromatizable and has greater affinity for ARs than does T, is ineffective when administered alone. However, E₂ does not fully maintain male rat sexual behavior (McGinnis and Dreifuss, 1989; Putnam et al., 2003) or partner preference (Vagell and McGinnis, 1997). Thus, androgens contribute to motivation and performance and are also necessary and sufficient to maintain *ex copula* genital reflexes (Cooke et al., 2003; Manzo et al., 1999; Meisel et al., 1984). Although E₂ was ineffective in maintaining *ex copula* reflexes, it did maintain vaginal intromissions *in copula* (O’Hanlon et al., 1981). Sachs (1983) suggested that E activates a “behavioral cascade” that can elicit genital reflexes *in copula*, but cannot disinhibit them *ex copula*.

Effects of systemically administered drugs on male rat sexual behavior

Transmitters often act synergistically in multiple sites, and the site of action often is not known *a priori*. Therefore, systemic drug administration can be useful. Table 1 summarizes the effects on male rat sexual behavior of drugs and treatments that affect neurotransmitter function in more than one brain area.

Brain areas that regulate male rat sexual behavior

Chemosensory input from the main and vomeronasal systems is probably the most important stimulus for male rodent sexual behavior. Bilateral olfactory bulbectomy, which removes both the main and vomeronasal pathways, produced variable impairment of copulation and noncontact erections, with sexually naive males being more susceptible to impairment (reviewed in Hull et al., 2006). Information from the main and accessory olfactory systems is processed in the medial amygdala (MeA), along with somatosensory input from the genitals, relayed through the parvocellular portion of the subparafascicular nucleus (SPFp), which is also part of an ejaculation circuit in several species (reviewed in Hull et al., 2006). Input from the MeA, both directly and via the bed nucleus of the stria terminalis (BNST), to the medial preoptic area (MPOA) is critical for copulation in male rats (Kondo and Arai, 1995).

The MPOA is arguably the most critical site for orchestrating male sexual behavior. It receives sensory input indirectly from all sensory systems and sends reciprocal connections back to those sources, thereby enabling the MPOA to influence the input that it receives (Simerly and Swanson, 1986). It also sends output to hypothalamic, midbrain, and brain stem nuclei that regulate autonomic and somatomotor patterns and motivational states (Simerly and Swanson, 1988). Many studies have reported severe and long-lasting impairment of copulation following lesions of the MPOA (reviewed in Hull et al., 2006). However, male rats with MPOA lesions continued to show noncontact erections (Liu et al., 1997a,b) and bar-press for a light that had been paired with access to a female (Everitt, 1990). Everitt (1990) suggested that the MPOA is important only for copulation, and not sexual motivation. However, MPOA lesions impaired sexual motivation in other contexts, including preference for a female partner (Edwards and Einhorn, 1986; Paredes et al., 1998) and pursuit of a female (Paredes et al., 1993).

Conversely, stimulation of the MPOA facilitated copulation, but did not elicit mating in sated males (Rodríguez-Manzo et al., 2000). Stimulation also increased intracavernosal pressure in anesthetized males (Giuliano et al., 1996) and elicited the urethrogenital reflex without urethral stimulation (Marson and McKenna, 1994a,b). The MPOA does not project directly to the lower spinal cord, where erection and seminal emission are controlled; thus, it must activate other areas that, in turn, elicit those reflexes.

The MPOA is the most effective site for hormonal stimulation of mating in castrated rats; however, T or E₂

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