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ANABOLIC-ANDROGENIC STEROIDS AND APPETITIVE SEXUAL BEHAVIOR IN MALE RATS

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Abstract

Anabolic-androgenic steroids (AAS) increase libido and sexual behavior, but the underlying behavioral mechanisms are unclear. One way AAS may enhance expression of sexual behavior is by increasing the willingness to work for sex. In the present study, sexually-experienced male rats received daily injections of testosterone at supraphysiologic doses (7.5 mg/kg in water with 13% cyclodextrin) or vehicle and were tested for appetitive sexual behavior measured by operant responding for access to an estrous female. Initially, rats were trained in their home cage to respond on a nose-poke under a 10-min fixed-interval schedule for food reward. Once rats achieved stable response rates, the food was replaced by a female, followed by mating for 10 min. There was no effect of testosterone on operant responding for food (28.1 ± 4.4 responses/10 min for testosterone, 30.6 ± 4.3 for vehicle) or sex (35.0 ± 4.0 responses/10 min for testosterone, 37.3 ± 5.2 for vehicle). However, rats made significantly more responses for sex than for food ($p < 0.05$), and responses for food and sex were positively correlated among individuals ($R^2 = 0.6$). Additional groups of rats were trained to respond on a lever for the female under a 2nd-order schedule of reinforcement, where 5 responses opened a door to show the female for 5 seconds. After 15 door openings, the male gained access to the female. There was no effect of testosterone on time to complete 75 responses: 38.4 ± 7.8 minutes for vehicle controls vs 43.3 ± 6.6 minutes for testosterone-treated rats ($p > 0.05$). These findings suggest that chronic high-dose testosterone does not enhance appetitive drive for sexual behavior.

Keywords

anabolic agents; androgen; food reward; operant behavior; sex behavior; animal

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INTRODUCTION

Anabolic-androgenic steroids (AAS) are performance-enhancing substances. Misuse of AAS by athletes is widely acknowledged, but potential health risks are not well-understood. These include not only cardiovascular, hepatic and reproductive dysfunction, but also alterations in brain and behavior (Pope et al, 2014a). Many AAS users meet Diagnostic and Statistical Manual of Mental Disorders (DSM) criteria for psychoactive substance dependence, including continued use despite negative side effects, and withdrawal symptoms when steroids are discontinued (Brower et al, 1991). However, unlike other illicit drugs, AAS have only a limited capacity to cause acute intoxication or other immediate physiologic responses (Kanayama et al, 2009). However, there is concern that AAS may have a negative impact not only on steroid users, but also on those around them. Steroid use has been implicated in enhanced aggression (Conacher and Workman, 1989; Pope and Katz, 1990; Pope et al, 1996; Schulte et al, 1993), known popularly as "roid rage". AAS also promote excessive and inappropriate sexual behavior (Moss et al, 1993; Choi and Pope, 1994). Clinical investigations of sexual response in human volunteers receiving injections of AAS have observed positive mood including sexual arousal and desire (Anderson et al, 1992; Choi and Pope, 1994; Daly et al, 2001; Hannan et al, 1991; Moss et al, 1993; Pope et al, 2000; Su et al, 1993). From a clinical perspective, the potential for AAS to enhance sexual performance is not problematic. However, the potential for AAS to facilitate sexual violence and non-consensual intercourse is a concern (Schulte et al, 1993).

Investigating AAS use in humans is complicated by the user's motivation for increased strength and muscle mass (Brower et al, 1991; Kanayama et al, 2009). Animal studies can explore consequences of AAS in an experimental context where appearance and athletic performance are irrelevant. Such studies show that AAS are rewarding (reviewed in Wood (2008)), as demonstrated by self-administration and conditioned place preference (CPP). Furthermore, AAS stimulate social behavior, particularly mating and aggression (Clark and Fast, 1996; Cunningham and McGinnis, 2006, 2007; Farrell and McGinnis, 2003, 2004; McGinnis, 2004; Melloni et al, 1997). In our study of oral testosterone self-administration in hamsters, testosterone stimulated sexual behavior in a dose-dependent manner (Wood, 2002). Other investigators have shown that anabolic steroids reduce the latency to initiate mating, and increase the efficiency of sexual performance in male rats (Farrell and McGinnis, 2003, 2004; McGinnis, 2004).

Up to this point, studies of AAS and mating have mostly focused on consummatory aspects of sexual behavior (mounts, intromissions, ejaculation). The present study addressed the ability of chronic high-dose testosterone to facilitate appetitive sexual behavior. In this regard, the reinforcing effects of mating in males are well-documented (reviewed in Hull et al, 2006). Male rats develop CPP for environments where they have previously mated. They will run rapidly towards a goal box or press a lever on a 2nd-order schedule of reinforcement for access to a female. These responses require gonadal steroids: castrated males do not mate, and show little interest in females. Testosterone restores both appetitive and consummatory aspects of sexual behavior. Since androgens promote mating, and both mating and androgens are rewarding, we hypothesized that high-dose androgens would enhance operant responding for sexual behavior.

MATERIALS AND METHODS

Animals

Adolescent male Long-Evans rats (4 weeks of age, ca. 200 g BW at the start of the study, Charles River Laboratories, MA) were individually housed under a reversed 14L:10D photoperiod. They remained gonad-intact to approximate AAS use in humans. Female rats 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 (Bridges, 1984). To induce estrus, females received 250 ug progesterone in cottonseed oil sc approximately 4h prior to testing. Females were rotated among the different test males. Behavior was tested under dim red light during the first 4h of the dark phase when activity peaks. Experimental procedures were approved by USC's Institutional Animal Care and Use Committee and were conducted in accordance with the Guide for the Care and Use of Laboratory Animals, 8th Ed (National Research Council, National Academies Press, Washington DC; 2011).

AAS treatment

Beginning at 5 weeks of age, rats received testosterone (7.5 mg/kg; Steraloids, RI) or vehicle (3% ethanol and 13% cyclodextrin (RBI, MA) in water) by daily sc injection 5 days/week. The 7.5 mg/kg dose approximates a heavy steroid dose in humans, and has been used previously to demonstrate AAS effects on mating and aggression in rats (Clark and Fast, 1996; Clark et al, 1998; Cooper et al, 2014; Wood et al, 2013). Testosterone treatment was initiated in adolescent rats to model human users. A typical AAS user is a young man in his late teens or early 20's (Pope et al, 2014a). Among U.S. high school students, 4–6% of boys have used AAS, comparable to the rates of crack cocaine or heroin use (Johnston et al, 2013). It is estimated that AAS use among men in their 20's is even higher (Pope et al, 2014b).

Experimental Design

To determine the effects of chronic high-dose testosterone on appetitive sexual behavior, male rats were trained in their home cage to make operant responses for access to a receptive female. Before training, all males received sexual experience with an estrous female on two occasions for 30 min each. Operant training began after at least 4 weeks of exposure to testosterone or vehicle. Injections of testosterone or vehicle continued throughout training and testing for food reward and for access to a female. Testosterone- and vehicle-treated rats were trained and tested on the same schedule, and there was no effect of testosterone on task acquisition.

The first experiment used a 10-minute fixed-interval (FI) schedule of reinforcement (FI-10), according to methods of Wood et al (2013) as modified from Scott et al (1994) and Fish et al (2008). A second experiment provided access to the female on a 2nd-order schedule of reinforcement (2nd-order FR), using modifications of Everitt et al (1987). In Everitt et al (1987), access to the reinforcer (estrous female) was paired with a neutral conditioned stimulus (CS, a stimulus light) activated by operant responses on a lever. In the present study, access to the reinforcer (estrous female) was paired with a sexually- salient CS (brief

visual presentation of the female) activated by operant responses on a lever. The assumption was that a sexually-salient CS would enhance rates of operant responding under 2nd-order FR. To facilitate training because copulatory behavior is impaired when males are mated daily (Everitt et al, 1987), rats were initially trained in daily sessions to respond for a small food reward (Froot Loops, Kellogg's, Battle Creek, MI). To compare appetitive and consummatory sexual behavior in both experiments, mating was recorded on videotape during presentation of the female, and was scored by an observer blinded to the treatment groups. Measures of sexual behavior included the number of mounts+intromissions, and latency to the first intromission and ejaculation.

FI-10

An operant conditioning panel containing a nose-poke with stimulus light (Med Associates, VT) was introduced into the home cage 10 minutes after injection of testosterone or vehicle (n=7 each). The reward (initially a Froot Loop, later an estrous female rat) was present behind a perforated Plexiglas screen adjacent to the nose-poke, permitting transmission of visual, auditory and olfactory stimuli. Responses on the nose-poke were recorded and reinforced on a FI schedule, as in previous studies of aggressive motivation in mice (Fish et al, 2008) and rats (Wood et al, 2013). The initial FI was 30 sec, subsequently increased to 1 min, and by 1-min increments thereafter until a 10 min FI was reached. Testing for food reward on the FI-10 schedule continued until response rates stabilized (8 days of testing at FI-10 for both testosterone- and vehicle-treated rats). At this point, an estrous female was substituted for the Froot Loop behind the Plexiglas screen, with access to the female for 10 minutes as the reinforcer. Testing continued twice weekly until behavior stabilized. In addition, sexual behavior of each male was videotaped on one occasion upon presentation of the female at the end of the 10-min FI. In 3 subsequent trials, males were tested with an anestrous female.

Data were analyzed using JMP 9.0 statistical software (SAS Institute, NC), and $p < 0.05$ was considered significant for all analyses. Effect sizes for significant relationships from unpaired comparisons, pairwise comparisons, and ANOVA's were estimated using Cohen's d and η^2_p using online tools (<http://www.cognitiveflexibility.org/effectsize/> and <http://www.campbellcollaboration.org/escalc/html/EffectSizeCalculator-SMD-main.php>). Operant responses for food during initial training in vehicle- and testosterone-treated rats were compared by RM-ANOVA with increasing FI as the repeated measure. Operant responses for access to food or females in each male were averaged over the last 3 days of testing. Individual responses were then averaged across the two experimental groups (vehicle and testosterone), and compared by Student's t -test. Measures of sexual behavior (numbers of mounts+intromissions, latency to first ejaculation) in vehicle- and testosterone-treated rats were likewise compared by Student's t -test.

2nd-order FR

As with FI-10, an operant conditioning panel containing a lever with stimulus light (Med Associates, VT) was introduced into the home cage 10 minutes after injection of testosterone or vehicle (n=9 each). Unlike FI-10, the panel separating the male from the Froot Loop or estrous female was opaque, with an automated guillotine door that opened to

a perforated Plexiglas screen. Responding on the lever opened the guillotine door for 5 seconds, thereby providing access to visual, olfactory and auditory stimuli from the female. As with FI-10, rats were trained first to respond for food in 5 trials/day. For each trial, the door opened after 1 response on the lever (FR1), and the rat was rewarded for each door opening (FR1:1). The number of door openings to obtain a food reward was gradually increased to 15, with 2 lever presses per opening (FR2:15).

Once training for food reward on the FR2:15 schedule stabilized, an estrous female was substituted behind the Plexiglas screen. Males were tested in a single trial twice weekly, and response requirements open the guillotine door were increased from FR2:15 to FR5:15. Latency to each door opening and the time to complete all responses (45, 60 and 75 responses at FR3:15, FR4:15, and FR5:15, respectively) was recorded, with a maximum test duration of 70 minutes. Rats that failed to complete all responses in 70 minutes were excluded from the experiment. Rats were then tested on FR5:15 for 5 consecutive days without the female behind the screen. Subsequently, operant responses were recorded for 3 additional days with the guillotine door disabled and no female present.

For each response requirement (FR3:15 - FR5:15), time to complete all responses from the last 3 trials were averaged for each male. Individual values from the two experimental groups (vehicle and testosterone) were compared by RM-ANOVA with response requirement as the repeated measure. At FR5:15, total elapsed time at each door opening was compared in vehicle- and testosterone-treated rats by RM-ANOVA with door openings as the repeated measure. Also at FR5:15, time to completion in the last 3 trials with a female present, no female, or no door opening was averaged for each male. Individual values from vehicle- and testosterone-treated males were compared by RM-ANOVA with stimulus ($\pm$ female/door) as the repeated measure. Subsequently, stimulus effects were compared by ANOVA. As with FI-10, measures of sexual behavior in vehicle- and testosterone-treated rats were compared by Student's t-test.

RESULTS

FI-10

Figure 1 shows operant responding for Froot Loops. As the FI increased during initial training (Fig. 1A), vehicle- and testosterone-treated rats increased the number of responses to obtain a food reward. Once operant responding stabilized at FI10, there was no difference in response rates between vehicle- (30.6 ± 4.3 responses/10 min) and testosterone-treated rats (28.1 ± 4.4 , $p > 0.05$). Overall operant responding for food reward on an FI10 schedule was similar to that reported previously (Scott et al, 1994). Although initial body weights were not different, body weight in testosterone-treated rats was significantly lower at the end of the study (553.3 ± 10.0 g vs 612.5 ± 23.0 g in vehicle controls, $p < 0.05$, $d = 1.6$), as reported previously (Wood et al, 2013).

As with operant responding for food reward, there was no difference between testosterone- and vehicle-treated rats in the number of responses for access to an estrous female on an FI10 schedule (35.0 ± 4.0 vs 37.3 ± 5.2 , respectively, Fig 2A). Male rats in both treatment groups displayed vigorous sexual behavior upon access to the estrous female at the end of

the 10-minute interval. Latency to the first intromission was less than 5 seconds (data not shown). Rats made relatively few mounts (testosterone: $4.0 \pm 1.2/10$ min and vehicle: $6.7 \pm 1.6/10$ min, $p > 0.05$). The numbers of mounts+intromissions (vehicle: $25.9 \pm 7.5/10$ min, testosterone: $22.2 \pm 7.3/10$ min; Fig 2C) and latency to the first ejaculation (vehicle: 4.4 ± 0.9 min, testosterone: 6.2 ± 0.7 ; Fig 2D) were not different between groups. Operant responding persisted when males were tested on 3 occasions with an anestrus female (Fig 2B).

Figure 3 compares response rates for food and sex in individual rats across the two groups. As shown in Fig 3A, there was a significant positive correlation between responses for food and for sex ($R^2 = 0.6$, $p < 0.05$). Rats that showed vigorous responding for food reward also made the highest number of nose-pokes for access to an estrus female. By paired t-test, males made significantly more responses for sex than for food ($p < 0.05$, $d = 0.5$; Fig 3B).

2nd-order FR

As with FI-10 reinforcement, there was no effect of testosterone on responding for an estrus female under a 2nd-order FR schedule of reinforcement. Fig 4A illustrates time to gain access to a female under FR3:15, 4:15, and 5:15. By RM-ANOVA, rats took longer to complete the task at higher response ratios ($F_{2,13} = 5.9197$, $p < 0.05$, $\eta_p^2 = 0.48$), but there was no effect of testosterone and no interaction. At FR5:15, vehicle-treated rats averaged 38.4 ± 7.8 minutes to complete 75 responses; testosterone-treated rats took 43.3 ± 6.6 minutes. As illustrated in Figure 5, time between successive window openings averaged 3.0 ± 0.5 minutes for testosterone-treated rats vs 2.6 ± 0.4 minutes for vehicle controls ($p > 0.05$), and did not vary across the task or with testosterone treatment. The latency to first ejaculation was significantly shorter in testosterone-treated rats (4.5 ± 0.4 min) compared with vehicle-treated males (6.9 ± 1.0 min, $p < 0.05$, $d = 1.9$), and testosterone-treated males made fewer mounts+intromissions during the 10-min test ($p < 0.05$, $d = 1.6$; Fig 5B and C). However, there were no differences in the number of ejaculations during the 10-minute test (not shown).

At FR5:15, there was a significant effect by RM-ANOVA of blocking the CS ($F_{2,13} = 4.242$, $p < 0.05$, $\eta_p^2 = 0.39$), either omitting the female behind the screen or disabling the door (Fig 4B). Nonetheless, responses of testosterone- and vehicle-treated rats were equivalent. When the female was not present, the time to complete the response requirements at FR5:15 was unchanged. However, only 5/7 testosterone- and 7/8 vehicle-treated rats completed 75 responses within 70 minutes (those that failed were assigned a time of 70 minutes). When the door was disabled, few rats completed the response requirements within 70 minutes (testosterone: 3/7; vehicle: 4/8), and time to completion was significantly longer (testosterone: 59.6 ± 4.7 minutes; vehicle: 48.2 ± 8.9 minutes) vs FR5:15 with the female present.

DISCUSSION

The present study investigated the relationship between AAS and appetitive sexual behavior in male rats. Sexually-experienced males treated chronically with high-dose testosterone or vehicle were trained make operant responses for access to a sexually-receptive female under a FI or 2nd-order FR schedule of reinforcement. As with our previous study of aggressive motivation (Wood et al, 2013), AAS failed to increase operant responses for the opportunity

to mate. While previous studies have demonstrated that castration in rats reduces both sexual motivation and sexual performance (reviewed in Hull et al, 2006) and that testosterone replacement in hypogonadal men increases libido (Morales et al, 1997), exposure to exogenous androgens at pharmacologic levels does not further increase the willingness to work for access to females. These results have implications for understanding sexual behavior in human AAS users.

Since AAS are derivatives of testosterone and testosterone is essential for male sexual behavior, it is not surprising that exogenous AAS influence sexual activity in rats (Clark and Fast, 1996; Farrell and McGinnis, 2003, 2004; McGinnis, 2004; Wood, 2002). The effects may be stimulatory or inhibitory, depending on the specific AAS administered, the dose, and the hormonal status of the recipient (normal gonad-intact vs castrate). In our study of oral testosterone self-administration in hamsters, testosterone stimulated sexual behavior in a dose-dependent manner (Wood, 2002). Other investigators have shown that chronic high-dose testosterone increases mating in rats, including reduced latency to initiate mating, and increased efficiency of sexual performance (Clark and Fast, 1996; Farrell and McGinnis, 2003, 2004). Testosterone also reduces the refractory period after mating, allowing a more rapid restoration of sexual activity after sexual satiety (Philips-Farfan et al, 2008). In the present study, all rats were highly trained to anticipate sexual activity once the response requirements were fulfilled, and their latency to the first intromission was extremely short. Although the study was not optimized to observe increases in sexual behavior, testosterone-treated rats tested under 2nd-order FR did show reduced latency to ejaculation compared with vehicle-controls.

Instead, our focus was on the effects of chronic high-dose testosterone to enhance operant responding for access to a receptive female, in part because the effects of AAS on appetitive sexual behavior have not previously been studied in detail. Considering the stimulatory effect of exogenous testosterone on mating (Hull et al, 2006), and the reinforcing effects of testosterone itself (Wood, 2008), we were surprised that testosterone failed to increase operant responding for access to an estrous female under FI or FR schedules of reinforcement. The effects of androgens on sexual motivation in rodents have been demonstrated previously using partner preference for a receptive female (Feinberg et al, 1997; Agmo, 2003; Wesson and McGinnis, 2006), searching in a multi-level chamber (Roselli et al, 2003), or operant responding for the opportunity to mate (Everitt and Stacey, 1987). The design of the present study was based on modifications of previous studies using FI- (Fish et al, 2008) and 2nd-order FR-schedules to evaluate operant responding for social behavior. Fish et al (2008) measured alcohol-induced aggressive motivation by responses on an FI-10 schedule in the home cage. We recently applied this model to study AAS-induced aggressive motivation (Wood et al, 2013). Because response rates for an estrous female under FI-10 were relatively modest, we subsequently developed a 2nd-order FR task based on Everitt et al (1987). Pressing a lever to obtain food or drugs has been a powerful tool to evaluate reward processes. However, unlike the rapid delivery of a small food pellet or drug infusion as reinforcement, it is difficult to offer social rewards in incremental doses. In Everitt et al (1987), the CS was a stimulus light. In the present study, the estrous female served as both CS and reinforcer. The assumption was that brief presentation of the female as a CS (not unlike a pornographic peep show) would enhance rates of operant responding.

However, testosterone-treated rats failed to demonstrate increased responding compared with gonadally-intact controls. Therefore, our results argue that chronic high-dose testosterone does not enhance appetitive sexual behavior. This conclusion is consistent with previous studies of sexually-relevant behaviors (partner preference for an estrous female, scent marking or ultrasonic vocalizations) where 5 mg/kg testosterone had no effect (Wesson and McGinnis, 2006). Similarly, sexual arousal, sexual satisfaction, kissing and fondling were not significantly increased in men by treatment with testosterone at 200 mg/week (Bagatell et al, 1994). The implication is that chronic high-dose androgens may improve sexual functioning without altering the willingness to work for sexual behavior.

Operant responses for mating on an FI-10 schedule in the present study were similar to our recent study of aggressive motivation (Wood et al, 2013). In that study, testosterone increased aggressive behavior, as demonstrated previously (McGinnis, 2004). Impulsive aggression (so-called 'roid rage') is probably the most widely-recognized behavioral consequence of AAS use. However, as in the present study, operant responses for access to an intruder male were not different in testosterone- and vehicle-treated males. The similar results in these two studies underscore the parallels between mating and aggression. Both are rewarding social behaviors stimulated by testosterone in response to olfactory stimuli from conspecifics (Fish et al, 2005; Hull et al, 2006; Melloni et al, 2010). Since testosterone increases consummatory aspects of mating and aggression without similar increases in appetitive motivation, other behavioral effects of AAS may play a role.

One possibility is that AAS-induced impulsivity may contribute to the increased expression of sexual and agonistic behavior. We have tested the effects of testosterone on aspects of impulsive and risk-taking behavior in rats. Testosterone selectively reduces sensitivity to punishment (footshock) and delay (Cooper et al, 2014; Wood et al, 2013), even as it increases sensitivity to reward uncertainty (Wallin and Wood, 2013). As applied to human sexual behavior, AAS users would be expected to be less susceptible to punishment (future negative consequences), and would be more likely to engage in risky sexual activity. This prediction is supported in surveys of current AAS users. Compared with non-users, human AAS users report increased sex drive (Moss et al, 1993) and increases in risky sexual behaviors [increased numbers of partners, infrequent condom usage (Midgley et al, 2000), as well as unprotected anal intercourse among HIV-positive gay men (Bolding et al, 2002)]. There is some debate whether AAS use is associated with a constellation of risky behaviors (Middleman et al, 1995) or whether sexual risk-taking predominates (Bolding et al, 2002; Midgley et al, 2000). Among American high school students, AAS use correlated with both sexual (not using a condom, history of sexually-transmitted disease) and non-sexual risks (alcohol consumption, not wearing a helmet or seatbelt, suicide attempt) (Middleman et al, 1995). Conversely, while AAS use was associated with risky sexual behavior among men recruited from British gyms (Bolding et al, 2002; Midgley et al, 2000), needle-sharing was uncommon.

And, finally, there is overlap of sexual and aggressive behavior, which may be sensitive to AAS. Normal male rats will attack a male intruder, but do not attack females even when provoked with tail-pinch. By contrast, AAS-treated males attack anestrus females in response to tail-pinch (Cunningham and McGinnis, 2006). This suggests that AAS-treated

rats are especially sensitive to reward omission (no mating when paired with an anestrus female), similar to our recent study showing increased response to uncertainty (Wallin and Wood, 2013). Reward omission combined with stress (tail-pinch) may elicit an impulsive aggressive response. There are parallels with human behavior: AAS users are more violent towards women compared to non-AAS users (Choi and Pope, 1994; Pope et al., 1996). And, there is a case report of child sexual abuse in a man using AAS (Driessen et al, 1996).

Thus, the effects of AAS abuse on social behavior are unpredictable. Sexual and aggressive behavior are increased, but the willingness to work for these behaviors is not. Instead, the decision to fight or to engage in sexual activity may reflect a spur-of-the-moment decision made without regard for potential risks.

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Highlights

- Male rats were tested for sexual motivation under fixed-interval and 2nd-order schedules of reinforcement.
- Chronic high-dose testosterone did not increase operant responding for access to a receptive female.
- Our data suggest that testosterone at supraphysiologic levels does not increase sexual motivation.

Figure 1.

Top: Operant responses (mean $\pm$ SEM) under a fixed-interval (FI) schedule for access to food reward in male rats treated chronically with high-dose testosterone (*closed symbols*) or vehicle (*open symbols*). Operant behavior during acquisition (A), and during a 10-min FI (B). C: *Initial* body weights (BW) were similar in testosterone- (*closed bars*) and vehicle-treated rats (*open bars*). At the end of the study, BW among testosterone-treated males was significantly lower. Asterisk indicates significant difference between treatment groups.

Figure 2.

A: Operant responses (mean $\pm$ SEM) under a fixed-interval (FI) schedule for access to an estrous (A) or anestrous female (B) in male rats treated chronically with high-dose testosterone (closed bars) or vehicle (open bars). Measures of sexual behavior with 10-min access to an estrous female, including mounts+intromissions (C) and ejaculation latency (D). Compared with vehicle-treated rats, there was no effect of testosterone on appetitive or consummatory sexual behavior.

Figure 3.

A: Correlation among individual rats treated with high-dose testosterone (*closed symbols*) or vehicle (*open symbols*) in operant responding for food reward and for sex. B: Operant responses (mean $\pm$ SEM) for food and sex among all rats (*gray bars*). Asterisk indicates significant difference.

Figure 4.

A: Time to complete response requirements (FR3:15-5:15) for access to an estrous female rat in male rats treated chronically with high-dose testosterone (*closed bars*) or vehicle (*open bars*). B: Time to completion at FR5:15 with and without female present, or with guillotine door closed. See text for details. *Numbers* indicate proportion of rats completing the task within 70 minutes. *Asterisk* indicates significant difference in response time with door closed vs with female.

Figure 5.

A: Elapsed time at each door opening at FR5:15 for access to an estrous female rat in male rats treated chronically with high-dose testosterone (*closed bars*) or vehicle (*open bars*). Measures of sexual behavior with 10-min access to the female, including mounts +intromissions (C) and ejaculation latency (D). Asterisks indicate significant differences.