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# Sexual experience and conditioned place preference in male rats

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**Abstract**

We have previously shown that sexual behavior induces a reward state, as evaluated by conditioned place preference (CPP), only when males or females are able to control the rate of sexual interaction. In the present experiment, we evaluated if male rats that are repeatedly tested in a situation in which they are not able to control the sexual interaction eventually develop CPP. Three groups of sexually naïve male rats were used. One group never mated. A second group was tested once a week for 10 consecutive weeks in a chamber in which they controlled the rate of the sexual interaction. The third group was mated for the same number of weeks in a chamber in which the female, but not the male, controlled mating. The three groups were then tested for CPP. Only the group able to control the sexual interaction developed CPP. The group that had no control over the rate of the sexual interaction did not develop CPP even after 10 tests in which they consistently displayed sexual behavior. These results suggest that an estrous female and/or sexual behavior are powerful incentives that maintain mating even if the rewarding properties of the incentive are reduced.


*Keywords:* Conditioned place preference; Mating; Control; Sexual experience; Sexual incentive

## 1. Introduction

The conditioned place preference (CPP) paradigm is extensively used in studies of reinforcing qualities of drugs, and it can also reveal incentive motivational responses to reward-related stimuli by measuring approach responses to an environment where a reinforcing (positive or negative) event has occurred (for a review, see Carboni and Vacca, 2003; Schechter and Calcagnetti, 1993; Tirelli et al., 2003). In this paradigm, an initially nonpreferred compartment is associated with the rewarding properties of a stimulus in two or three conditioning sessions. On alternate days, the initially preferred compartment is associated with a neutral stimulus. At the end of conditioning, the experimental subjects spent more time in the initially nonpreferred (reinforced) compartment, indicating that the stimuli produced a reward state of sufficient intensity and duration to induced conditioning. This was clearly demonstrated in early studies showing that systemic or intracerebral morphine induced CPP (Mucha and Iversen, 1984; Mucha et al., 1982; van der Kooy et al., 1982).

Sexual activity functions as a reinforcer in a way similar to that of classical primary reinforcers, such as water or food (Bermant and Westbrook, 1966; Gilman and Westbrook, 1978). The rewarding effects of sexual behavior in male and female rats have been clearly identified in the laboratory using CPP (Agmo and Berenfeld, 1990; Hughes et al., 1990; Martinez and Paredes, 2001; Mehrara and Baum, 1990; Miller and Baum, 1987; Paredes and Alonso, 1997; Paredes and Vazquez, 1999). The ability to control or "pace" the sexual interaction is a crucial factor for sex to induce CPP. In a series of studies, we have demonstrated that sexual behavior is rewarding for female rats only if they are able to pace their sexual interactions. There are different methodologies available to evaluate pacing behavior (reviewed in Paredes and Vazquez, 1999). We use a chamber divided by a wood partition with a small hole. Due to the small size of the hole, only the female can enter or exit the half of the cage in which the male is confined. Using this methodology, the animals copulate in a mating cage and are put into an adjacent conditioning chamber immediately after sexual interaction (Paredes and Alonso, 1997; Paredes and Vazquez, 1999). Therefore, the affective state evaluated by CPP is not limited to the execution of sexual behavior but allows environmental cues to be associated with the physiological

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state induced by mating. Females not allowed to pace do not develop CPP (Martinez and Paredes, 2001; Paredes and Alonso, 1997).

Early studies in male rats, clearly demonstrated that sexual behavior (Hughes et al., 1990; Mehrara and Baum, 1990; Miller and Baum, 1987) and ejaculation (Agmo and Berenfeld, 1990) induce a reward state. These studies were done in a traditional copulatory testing model (one male, one female) in which the male controls the coital stimulation. However, when males were tested for CPP in a mating situation with a wood partition, in which they do not control the rate of sexual interaction, no change of preference was observed (Martinez and Paredes, 2001). These results clearly indicate that sexual interaction is rewarding only if the animals can control the rate of sexual stimulation.

In the present experiment, male rats were allowed to mate in a situation in which they control their sexual contacts. Another group mated in a pacing chamber in which the female, but not the male, controlled the rate of sexual interaction. Both groups were tested once a week for 10 consecutive weeks. On Week 11, CPP was evaluated for each group and for a control group that never mated. This would allow us to determine if sexual behavior is modified after several weeks of testing in a situation in which, in theory, sex is not rewarding for the male. On the other hand, we could also determine if repeated testing in a situation in which the female controls the sexual interaction eventually becomes rewarding for the male.

## 2. Methods

### 2.1. Subjects

Sexually naive male Wistar rats from a local colony weighing 300–350 g were maintained in a room with a reversed light–dark cycle (12 h light, 12 h dark; lights off at 0900 h). Commercial rat pellets (LabDiet, Nutrition International, Brentwood, MO) and water were always available. Subjects were housed four per cage, with animals of the same group living together. Stimulus females of the same strain (250–300 g) were bilaterally ovariectomized following anesthetization with a mixture of ketamine (95 mg/kg) and xylazine (12 mg/kg). They received subcutaneous injections of 25 μg/rat of estradiol benzoate (EB) 48–52 h before mating tests plus 1 mg/rat of progesterone 4 h before testing. The steroids were dissolved in corn oil and injected in a volume of 0.2 ml/rat. We use this treatment routinely to induce high levels of receptive and proceptive behavior in females.

### 2.2. Apparatus

The mating cages (40 × 60 × 40 cm) had wood shavings on the floor and a front wall made of glass for observation. When females were allowed to pace, a removable wood partition was placed in the middle of the mating cage. The partition had a small hole (4 cm diameter) through which only the female could move freely from one side to the other; the hole was too small for the male to go through. When males were allowed to control the sexual interaction, they mated without the removable wood partition having free and continual access to the female. In each test, a stimulus female was placed in the mating cage 2 min before the male was introduced.

The place preference apparatus consisted of a three-compartment box made of wood. The middle compartment (22 × 24 × 32 cm) painted gray, communicated with the lateral compartments through a sliding door (10 × 10 cm). One of the lateral compartments (23 × 37 × 32 cm) was painted white and the floor was covered with clean wood shavings. The opposite lateral compartment was painted black, had no bedding, and was moistened with a 2% solution of glacial acetic acid immediately before an animal was placed in it. In this way, the lateral compartments offered distinct stimuli in odor, color and texture. The animals were observed through the front wall of the middle compartment made of fine wire mesh. The place preference cages were located in a room illuminated with dim white light.

### 2.3. Procedure

Subjects were randomly assigned to one of the following groups: Group 1 never mated; Group 2 mated once a week for 10 weeks in a situation in which the female, and not the males, controlled the sexual stimulation (“no control”); that is, the mating cage was divided by the wood partition; Group 3 mated once a week for 10 weeks without the partition; that is, males controlled the sexual interaction (“control”). Each group had 11 animals.

#### 2.3.1. Conditioning

We followed a procedure described in detail elsewhere (Martinez and Paredes, 2001; Paredes and Alonso, 1997). Briefly, the procedure consisted of a pretest, six conditioning sessions and a test. In the pretest session, each animal was placed in the middle compartment, and the time spent in each of the lateral compartments was recorded for 10 min to determine the initial preference. On the first, third and fifth sessions, subjects were placed in the preferred compartment for 30 min directly from their home cage without copulation. On alternate test days, second, fourth and sixth sessions, animals from Group 1 were placed in the nonpreferred compartment directly from their home cage. Animals from Groups 2 and 3 were mated until ejaculation and placed in the nonpreferred compartment for 30 min. Males from Group 2 were not able to control copulation because they mated with the wood partition and hence the females paced the sexual contacts. Males from Group 3 mated without the wood partition controlling the sexual interaction. After

these conditioning sessions, the preference for each compartment was tested again in exactly the same way as before conditioning (test session). The following sexual behaviors were scored: latency to the first mount and intromission (calculated from the time the male was introduced in the mating cage until the occurrence of the behavior), the number of mounts, intromissions and ejaculations as well as the ejaculation latency. The inter-intromission interval was also calculated. Because at the beginning of the experiment, all subjects were sexually naïve, all tests lasted 45 min or until ejaculation occurred.

### 2.4. Statistical analysis

The sexual behavior data for the 10 weeks before conditioning were evaluated by a 2 (groups) × 10 (weeks) ANOVA followed by Fisher's LSD. The analysis was done for those subjects actually displaying the behavior. The sexual behavior data during conditioning was evaluated by a 2 (groups) × 3 (sessions) ANOVA followed by Fisher's LSD.

To evaluate place preference conditioning, two criteria were used: The difference between time spent in the non-reinforced compartment and time spent in the reinforced compartment had to be significantly reduced after conditioning. The preference score [(time in reinforced compartment/(time in reinforced compartment + time in nonreinforced compartment)] should increase after conditioning. The use of both criteria reduces the possibility of spurious effects. The data were analyzed by a 2 (test) × 3 (group) ANOVA with repeated measures on the test factor (pretest–test). All probabilities were two-tailed.

## 3. Results

### 3.1. Sexual behavior

Table 1 shows different sexual behavior parameters in the 10 weeks of testing for the group not controlling the rate of sexual stimulation (no control) and for the group controlling the sexual interaction (control). No significant differences were observed during the first 5 weeks of testing in mount and intromission latency between the groups (Table 1A). However, during last 5 weeks, the group that had no control over the sexual interaction consistently showed (except for Week 8) a significant reduction in mount ([$F(1,25) = 15.65$, $P < .001$] group [$F(9,25) = 3.90$, $P < .001$]; Group × Weeks [$F(9,25) = 1.85$, $P = .060$]) and intromission ([$F(1,25) = 15.27$, $P < .001$] group [$F(9,25) = 5.58$, $P < .001$]; Group × Weeks [$F(9,25) = 0.96$, $P = .47$]) latencies. The number of mounts was consistently reduced along the 10 weeks of testing for the group not controlling the sexual interaction ([$F(1,25) = 44.91$, $P < .001$] group [$F(9,25) = 3.17$, $P < .001$]; Group × Weeks [$F(9,25) = 1.84$, $P = .061$]). The number of intromissions was lower for the group not controlling the sexual interaction in Weeks 2 through 6 ([$F(1,25) = 24.09$, $P < .001$] group [$F(9,25) = 3.085$, $P = .001$]; Group × Weeks [$F(9,25) = 0.79$, $P = .62$]). However, no significant differences were observed in the number of intromissions in the last weeks of testing (Table 1B). Similar results were observed for the inter-intromission interval. During conditioning, the no-control group had a reduced number of mounts and reduced ejaculation latency in Session 2 and reduced mount latency in Session 3 compared to the group that controls the sexual interaction (Table 2).

### 3.2. Conditioned place preference

The ANOVA of the difference between compartments revealed an effect of session [$F(1,30) = 10.91$, $P = .002$]; group [$F(2,30) = 0.31$, $P = .734$]; and Group × Session [$F(2,30) = 0.44$, $P = .645$]. The test of simple main effects showed a significant reduction in the differences between compartments in the group of males controlling their sexual interaction. (see Fig. 1).

The preference score in the group that controlled their sexual interactions showed a significant increase. The ANOVA revealed a significant effect of session [$F(1,30) = 9.02$, $P < .005$]; group [$F(2,30) = 2.53$, $P = .097$]; and Group × Session [$F(2,30) = 1.20$, $P = .315$]. The test of simple main effects revealed a significant increase in the preference score in the group that controlled their sexual contacts (see Fig. 1). No changes in preference were seen in the other groups.

## 4. Discussion

The results of the present experiment clearly show that only males able to control the sexual interaction develop CPP. No change of preference was observed in males that were not allowed to control the rate of sexual stimulation. The results of the present experiment further demonstrate that only paced coital contacts in females (Paredes and Alonso, 1997; Paredes and Vazquez, 1999) and being able to control the sexual interaction in male rats (Martinez and Paredes, 2001) produce a positive affect of sufficient intensity and duration to induce conditioning.

A reduction in mount and intromission latency as well as in the number of mounts was observed in the no-control group before and during conditioning sessions. Although the effects were not significant every week before conditioning or in every session during conditioning, the same parameters were consistently affected. Only the males that paced their sexual interaction developed CPP. If sexual behavior is not rewarding when males do not control the rate of sexual interaction, why then do they continue to mate? At least two possible explanations can be considered. First, sexual behavior is indeed rewarding even if males cannot control the sexual stimulation, but the CPP paradigm is not sensitive enough to reveal a reward state. Second,

Table 1
Sexual behavior parameters in males controlling (control) the sexual stimulation and in males not controlling the sexual interaction (no control)

(A)

| Behavior parameter | Weeks | | | | |
|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 |
| *Mount latency* | | | | | |
| Control | 370 ± 114 | 387 ± 132 | 227 ± 64 | 305 ± 87 | 169 ± 45 |
| No control | 431 ± 144 | 199 ± 46 | 108 ± 19 | 268 ± 128 | 68 ± 16 |
| *Intromission latency* | | | | | |
| Control | 922 ± 213 | 691 ± 273 | 417 ± 122 | 512 ± 146 | 366 ± 126 |
| No control | 567 ± 157 * | 64 ± 122 | 270 ± 56 | 435 ± 123 | 143 ± 54 |
| *Ejaculation latency* | | | | | |
| Control | 1705 ± 44 | 815 ± 204 | 879 ± 81 | 808 ± 131 | 924 ± 95 |
| No control | 967 ± 123 * * | 1192 ± 141 | 1028 ± 153 | 628 ± 113 | 577 ± 95 * * |
| *Number of mounts* | | | | | |
| Control | 22 ± 6.7 | 25 ± 6.7 | 17 ± 2.7 | 27 ± 3.5 | 19 ± 2.3 |
| No control | 12 ± 1.8 * * | 12 ± 2.6 * * | 12 ± 2.6 | 6 ± 1.0 * * | 7 ± 1.6 * * |
| *Number of intromissions* | | | | | |
| Control | 15 ± 4.7 | 21 ± 7.6 | 17.5 ± 2.2 | 15 ± 2.4 | 14 ± 1.0 |
| No control | 12 ± 2.9 | 14 ± 1.6 * | 10 ± 0.8 * * | 9 ± 0.6 * * | 8 ± 1.0 * * |
| *Inter-intromission interval* | | | | | |
| Control | 74 ± 1.9 | 49 ± 7.2 | 58 ± 6.6 | 44 ± 4.3 | 65 ± 5.3 |
| No control | 126 ± 43.5 | 108 ± 21.5 * | 103 ± 18.9 * * | 80 ± 21.8 | 77 ± 16.5 |

(B)

| Behavior parameter | Weeks | | | | |
|---|---|---|---|---|---|
| | 6 | 7 | 8 | 9 | 10 |
| *Mount latency* | | | | | |
| Control | 410 ± 100 | 301 ± 90 | 153 ± 76 | 358 ± 107 | 409 ± 128 |
| No control | 88 ± 20 * * | 34 ± 5 * * | 112 ± 15 | 114 ± 61 * * | 176 ± 50 * |
| *Intromission latency* | | | | | |
| Control | 599 ± 123 | 379 ± 89 | 328 ± 119 | 563 ± 148 | 494 ± 127 |
| No control | 181 ± 34 * * | 62 ± 22 * | 279 ± 123 | 205 ± 95 * * | 238 ± 58 |
| *Ejaculation latency* | | | | | |
| Control | 822 ± 131 | 761 ± 70 | 518 ± 84 | 693 ± 95 | 663 ± 85 |
| No control | 586 ± 99 * | 349 ± 57 * * | 452 ± 111 | 515 ± 100 | 477 ± 66 |
| *Number of mounts* | | | | | |
| Control | 20 ± 3.4 | 16 ± 2.7 | 15 ± 2.6 | 15 ± 2.9 | 20 ± 4.3 |
| No control | 11 ± 2.6 * | 7 ± 1.0 * | 7 ± 1.8 * | 5 ± 0.8 * * | 10 ± 2.3 * * |
| *Number of intromissions* | | | | | |
| Control | 15 ± 1.4 | 14 ± 1.7 | 14 ± 1.6 | 14 ± 1.2 | 12 ± 1.3 |
| No control | 11 ± 1.8 * | 11 ± 1.5 | 11 ± 1.6 | 11 ± 1.4 | 10 ± 0.9 |
| *Inter-intromission interval* | | | | | |
| Control | 55 ± 7.3 | 55 ± 5.8 | 38 ± 4.2 | 50 ± 4.7 | 67 ± 13 |
| No control | 74 ± 9.4 | 34 ± 4.3 | 41 ± 4.5 | 59 ± 13.6 | 69 ± 22 |

Subjects were observed once a week for 10 weeks. $n = 11$ for each group.
* Different from control group, $P < .05$.
** Different from control group, $P < .01$.

sexual behavior and females are powerful incentives for the male even without reward or when the value of the reward associated with sex is reduced.

Different lines of evidence indicate that CPP is a powerful methodology to evaluate whether a stimulus induces a positive affect. As already described in the introduction,

Table 2
Sexual behavior parameters in males controlling (control) the sexual stimulation and in males not controlling the sexual interaction (no control) during conditioning sessions

| Behavior parameter | Session | Control | No control |
|---|---|---|---|
| Number of mounts | 1 | 21.4 ± 3.7 | 21.5 ± 7.6 |
| | 2 | 27.6 ± 5.5 | 14.1 ± 5.9 * |
| | 3 | 14.4 ± 3.1† | 8.3 ± 2.6† |
| Number of intromissions | 1 | 12 ± 1.4 | 10.3 ± 1.0 |
| | 2 | 12.6 ± 1.9 | 9.8 ± 1.0 |
| | 3 | 10.5 ± 1.0 | 8.5 ± 0.9 |
| Mount latency | 1 | 178.5 ± 81.4 | 109.8 ± 40.8 |
| | 2 | 344.8 ± 160.6 | 131.3 ± 63.6 |
| | 3 | 423.5 ± 166.7† | 86 ± 34.3 * * |
| Intromission latency | 1 | 365.1 ± 160.1 | 363.1 ± 112.8 |
| | 2 | 547.6 ± 225.6 | 186.5 ± 69.3 |
| | 3 | 533.4 ± 171.4 | 185.4 ± 79.8 |
| Ejaculation latency | 1 | 544 ± 74.7 | 721.4 ± 169.1 |
| | 2 | 833.9 ± 185.2 | 489.3 ± 128.4 * |
| | 3 | 616.1 ± 127.1 | 532.6 ± 92.9 |
| Inter-intromission interval | 1 | 58 ± 8.7 | 72 ± 17.0 |
| | 2 | 64.6 ± 10.7 | 48.3 ± 11.1 |
| | 3 | 57.5 ± 9.9 | 70.6 ± 20.9 |

$n = 11$ for each group.
* Different from control group, $P < .05$.
** Different from control group, $P < .01$.
† Different from Session 1 in the same group, $P < .05$.

not only sexual behavior for males (Agmo and Berenfeld, 1990; Hughes et al., 1990; Mehrara and Baum, 1990; Miller and Baum, 1987) and females (Gans and Erskine, 2003; García-Horsman and Paredes, 2004; Martinez and Paredes, 2001; Paredes and Alonso, 1997; Paredes and Vazquez, 1999) but also different pharmacological treatments (see Tirelli et al., 2003 for a review) can induce a reward state as evaluated by CPP. Other stimuli, like drinking in water-deprived rats (Agmo et al., 1993), food (Bechara and van der Kooy, 1992), hormone administration (King et al., 1999; Schroeder and Packard, 2000), kindling-like stimulation (Corcoran et al., 1992; Barnes et al., 2001; Paredes et al., 2000), and vaginal lavage (Walker et al., 2002), and behaviors, like intermale aggression (Martinez et al., 1995) and wheel running (Lett et al., 2000, 2001), can reliably induce CPP. Although no direct comparisons have been made as to the incentive value of sex and the behaviors described above, parsimony will suggest that the incentive value of sex is probably at least similar to the other behaviors, if not greater. It is therefore unlikely that sexual behavior when the males do not control the sexual interaction induces a reward state not detected by CPP. Moreover, it has been shown that delayed backward conditioning of wheel running can be detected by CPP (Lett et al., 2002). Different groups of rats had access to a period of wheel running. Subjects were then exposed to the conditioning chamber 0, 10 or 30 min after wheel running. Only the groups with a delay of 0 or 10 min developed a reliable CPP with the strength of conditioning decreasing as the delay increased. The authors suggest that the reward state initiated by wheel running is maintained sometime after running stops (Lett et al., 2002). In the present experiment, the animals were placed in the originally nonpreferred compartment immediately after ejaculation (for the two groups that copulated), minimizing any possible effect of delay in the reward associated with conditioning.

More evidence supports the second possibility; that is, sexual behavior and females are powerful incentives for the male even when the value of the reward associated with sex is reduced. For example, it has been demonstrated that the intensity of sexual behavior appears to be directly related to the efficacy of sex as a reinforcer. Kagan (1955) tested independent groups of male rats in a T maze with a receptive female as the reinforcer in one goal box and a stimulus male in the opposite goal box. One group of subjects was only allowed to mount after each choice to the female side. Another group was allowed to mount and intromit but not ejaculate, and a third group was allowed to copulate until ejaculation. The ejaculation group showed the most consistent choice to the female side of the maze. In a similar study, also using a T maze (Whalen, 1961), male rats that were allowed to make four intromissions ran faster to the female than those males allowed a single intromission. Males allowed only mounts ran much slower but still

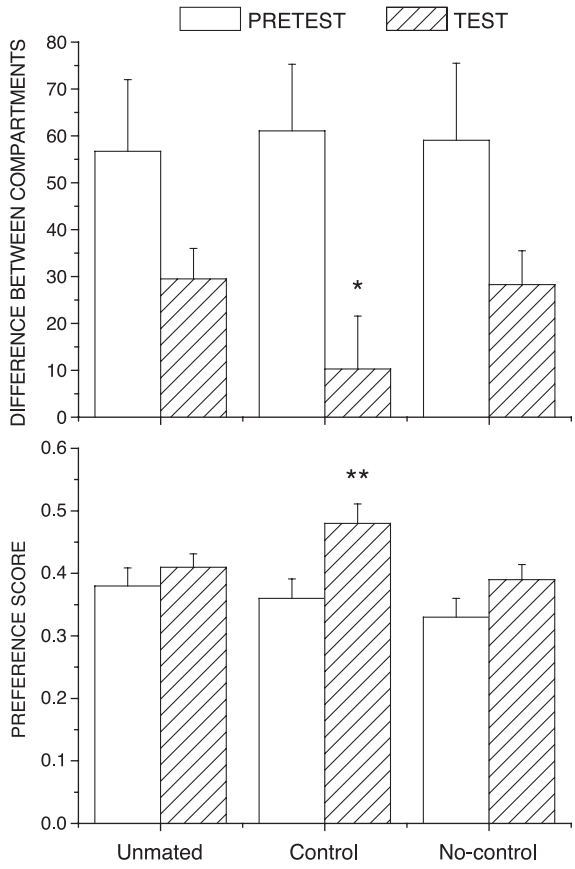


Fig. 1. Difference between compartments (top panel) and preference score (bottom panel) at pretest and test in males controlling the sexual stimulation and in males not controlling the sexual interaction (no control). $n = 11$ for each group. Data are expressed as mean ± S.E.M. * Different from pretest, $P < .05$; * * $P < .01$.

showed a preference for the female (Whalen, 1961). That is, when the reward is reduced, as presumably occurs when the males are allowed to mount or intromit but not ejaculate, sexual behavior is still displayed. Unpublished observations from our laboratory further support this hypothesis, male rats that control the rate of sexual interaction but that are allowed only 10 intromissions without ejaculation, do not develop CPP. In the present experiment, male rats that did not control the rate of sexual stimulation did not develop CPP but continued mating, suggesting that sex and the female still had a high incentive value.

An incentive is defined as any stimulus that activates an approach behavior. In this case, the approach behavior is induced by a sexual stimulus, a female. A procedure for studying unconditioned sexual motivation has recently been described (Agmo, 2003). In these tests, the subject is placed in a large arena where it can choose between a sexual and a social incentive located in cages adjacent to the arena. The subjects can see, hear and smell the incentive animals but do not have physical contact with them because the stimuli are confined behind wire mesh openings (Agmo, 2003). The proportion of time spent in an area outside the female incentive is the measure of motivation. In this test, no sexual experience is necessary, and the test constitutes a convenient procedure for evaluating unconditioned sexual motivation. It would be interesting to determine in future studies if males not allowed to control their sexual interaction show a reduced incentive motivation for a receptive female.

The reduction in the value of the reward does not necessarily make the animal stop mating. Indeed, different lines of evidence demonstrate that is not easy to inhibit sexual behavior specifically and consistently. For example, many pharmacological treatments that inhibit sexual behavior usually modified one or two parameters of a very complex behavior. Moreover, the inhibitory effects produced by dopaminergic (Agmo and Fernandez, 1989; Paredes and Agmo, submitted for publication) or GABAergic (Agmo et al., 1987; Paredes and Agmo, 1992) compounds upon sexual behavior are clearly associated with strong motor effects. That is, sexual behavior is inhibited only in doses where motor function is greatly impaired (see Paredes and Agmo, in press for a review). Interestingly, dopaminergic drugs modify sexual incentive motivation only in doses that significantly affect ambulatory activity, suggesting that modifications of dopaminergic activity do not affect sexual motivation to any significant extent in male rats (Agmo, 2003).

Several studies have demonstrated that when females control the rate of sexual interaction in a pacing (Blaustein and Erskine, 2002; Erskine, 1989; Gans and Erskine, 2003) or a bilevel chamber (Mendelson and Pfaus, 1989), they lengthen the time between successive mounts, intromissions and ejaculations compared to the times between sexual contacts when females cannot avoid males. As well, it has been reported that in paced mating tests, males usually ejaculate with fewer intromissions than in nonpaced tests (Erskine, 1989). In the present experiment, males that mated in a situation where the female but not the male (no control) controls the rate of sexual stimulation displayed fewer intromissions before ejaculation in the first weeks of testing. No differences in the number of intromissions were observed in the last 4 weeks of testing. These results further support the observations that males modified the mating sequence depending on the testing conditions (Pfaus et al., 1990; Kippin and Pfaus, 2001). It should also be noted that in the previous studies of paced mating, the stimulus animals used to evaluate female sexual behavior are usually sexually experienced males. In the present experiment, all males were sexually naïve and the stimulus females were sexually experienced. Further studies are needed to determine if behavior changes similarly in sexually naïve males and females tested in different environmental conditions, i.e., controlling or not controlling the sexual interaction.

To summarize, males not allowed to control the rate of sexual stimulation do not develop CPP and they continue to display sexual behavior. It is suggested that an estrous female and/or sexual behavior are powerful incentives that are able to maintain the expression of copulation even if the rewarding properties of the incentive are reduced.

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