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Effects of Copulation on Apomorphine-Induced Erection in Rats

BENJAMIN D. SACHS,[1] KEIKO AKASOFU AND SARA S. McELDOWNEY

Department of Psychology, University of Connecticut, Storrs, CT 06269-1020

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SACHS, B. D., K. AKASOFU AND S. S. McELDOWNEY. *Effects of copulation on apomorphine-induced erection in rats.* PHARMACOL BIOCHEM BEHAV **48**(2) 423–428, 1994.—By testing the effects of antecedent copulation on subsequent apomorphine-induced penile erection we sought to test an implicit assumption in the research on drug-induced "spontaneous" erection—namely, that this research provides information relevant to the regulation of erection in copula. In experiment 1, male rats were observed after being injected SC with 0, 15, 30, 60, or 120 μg/kg apomorphine (APO); 60 μg/kg yielded the maximum probability of erection and yawning. In experiment 2, males were injected with 60 μg/kg APO after no exposure to females, after three intromissions, or after copulation to sexual satiety. There was no significant effect of three intromissions, but sexually sated males displayed no erections, the first evidence that copulation affects drug-induced erections. In experiment 3, males had one ejaculation, three intromissions, or no exposure to females immediately before injection with APO (60 μg/kg, SC) or ascorbic acid vehicle. APO induced both erection and yawning, but neither behavior was reliably affected by copulation in APO-treated males. Among vehicle-treated males, those having three intromissions or one ejaculation before the test had shorter erection latencies and more erections than males not exposed to females. Thus, a relatively small amount of copulation resulted in a level of erectile response similar to that of APO-treated males. Optimal doses of APO may be no more effective in promoting erection in male rats than are the natural neurochemical sequelae to copulation.

Penile erection Copulation Yawning Apomorphine Dopamine

FOR over 20 years, a major tool in the study of the neurochemical basis of erection has been the use of pharmacological agents that promote "spontaneous" penile erection in isolated male rats (2,5,6,11,13–16,25,26,29). In much of the research on drug-induced erection there appears to be an implicit assumption that this approach provides information relevant to the regulation of erection *in copula*. Apomorphine (APO), a D_1/D_2 dopamine agonist, is among the most frequently used of these drugs because of its efficacy with systemic injection (14,16,27,29), and its use has been proposed as a reference model for the study of the physiological regulation of erection (16). However, the relation of drug-induced erections to erections occurring in other contexts remains untested, and therefore uncertain, because the physiological regulation of erection is known to vary with the context. For example, hypogonadal men have an expected decrement in spontaneous erections, including nocturnal penile tumescence, and in encounters with sexual partners, but these men have normal erections while viewing erotic videos (7,19). Castrated male rats treated with estrogen have erections adequate for copulation but fail to display reflexive erections, whereas dihydrotestosterone maintains reflexive erections but not copulation (10,17,24).

Evidence that antecedent copulation affected subsequent reflexive erection (28,34) helped to demonstrate the sexual relevance of reflexive erection tests. In contrast, the failure of ejaculation induced by brain stimulation to influence subsequent copulation was taken to mean that this mode of ejaculation involved mechanisms that were not relevant to copulatory behavior (3). If drug-induced erections have relevance to sexual activity, then antecedent copulation should affect them. Therefore, we inquired whether copulation would influence subsequent APO-induced erections.

EXPERIMENT 1

This experiment served to determine which dose of systemically administered APO best promoted penile erection under our testing conditions. APO and many other drugs that induce erections in rats also induce yawning and, sometimes, stretch-

[1] Requests for reprints should be addressed to Benjamin D. Sachs, Department of Psychology, U-20, University of Connecticut, Storrs, CT 06269-1020.

ing. The concurrence of these responses has been referred to as the penile erection/stretching/ yawning syndrome (4,14), although the responses are readily dissociable, depending on the drugs used (15). To determine how this "syndrome" responded to antecedent copulation we observed rats for episodes of yawning and stretching as well as penile erection.

Method

Subjects and housing. The subjects, 40 sexually inexperienced Long-Evans rats (Blue Spruce, obtained from Harlan Sprague-Dawley, Indianapolis), were 12 weeks old at the start of testing and weighed 310–390 g. They were housed as pairs in hanging wire-mesh cages (43 × 34 × 20 cm) under a 12-h light-dark cycle, with lights off at 1100. All tests were conducted between 1100 and 1600. Ambient temperature was maintained at a mean of 23°C; pelleted commercial rodent chow and tap water were always available in the home cage.

Procedure. Sexually inexperienced rats were weighed and transported to a testing room where they were injected SC with APO (Sigma Chemical Co., St. Louis) dissolved in 0.1% ascorbic acid at doses of 0, 15, 30, 60, or 120 μg/kg. Each male was tested at only one dose. Immediately after injection rats were placed in the test chamber, a glass-bottomed aquarium (51 × 30 × 29 cm) divided in half by a plywood partition. A mirror placed at an angle below the aquarium permitted simultaneous lateral and ventral viewing. One rat was placed on each side of the barrier and they were observed for 30 min. Penile erection was scored when the glans emerged from the preputial sheath, an action that was usually accompanied by intense penile grooming and slight hip movements. Erections normally lasted 10–15 s and often included full glans engorgement ("cup") and anteroflexion ("flip") [illustrated in (20,31)]. Yawning was scored when the rat sustained an open mouth for more than a second. Stretching occurred so rarely that it was ignored.

Results and Discussion

As evident from Table 1, only the 60- and 120-μg/kg doses of APO increased significantly the proportion of males responding with erection ($\chi^2 = 15.00$, $p < 0.005$). When only responding males were considered, analysis of variance (ANOVA) revealed that the dose did not reliably affect the erection latency or the number of erections displayed, $F(3, 16) = 0.72$ and 0.55, respectively. Yawns showed a similar dose/response function with respect to proportion of males responding ($\chi^2 = 17.78$, $p < .001$) as well as latency and number of yawns, $F(3, 14) = 0.90$ and 0.18, respectively. The 60-μg/kg dose that was maximally effective for both erections and yawns is within the range reported by other investigators to be the optimum dose (16,26,29) and was therefore used in the following experiments.

Close observation and occasional inspection of the penis yielded no evidence of ejaculation accompanying APO-induced erections. Although reports of APO- and other drug-induced erections occasionally indicate that seminal emission accompanies the behavior, we know of no supporting evidence, such as plug weight or sperm count. It may be that emission has been inferred from the purported similarity between drug-induced erections and *in copula* ejaculatory patterns. However, except for the occurrence of genital grooming and the occasional more vigorous hip thrusts, those familiar with the copulatory behavior of male rats would be unlikely to characterize typical APO-induced erections as similar to intromissive or ejaculatory patterns.

EXPERIMENT 2

Previous studies have demonstrated that the probability of reflexive erections evoked from supine rats increases after a few intromissions, or even after one ejaculation (18,22,28, 33,35). In contrast, reflexive erections are eliminated by antecedent sexual satiety (exhaustion)—that is, no copulatory attempts within 30 min after the last of a succession of ejaculations (28,33,34). A minimum condition for the demonstration of an interaction between copulation and APO-induced erections would be an inhibition of these erections in sexually sated rats.

Method

At the start of testing the 27 males were 16 weeks old. Ten of the rats had received a single 60–100-μg dose of APO at least a week before this experiment. In the week before testing, all males copulated to a single ejaculation three times, and they were randomly assigned to one of three treatment groups, identified by the copulation condition that preceded APO injection: 1) no copulation and no exposure to an estrous female; 2) three intromissions; and 3) sexual satiety, defined as no intromission within 30 min of the last ejaculation, despite a change in the stimulus female 10–20 min after ejaculation.

TABLE 1

ERECTIONS AND YAWNS IN RATS AFTER INJECTION WITH APOMORPHINE

	Apomorphine Dose (μg/kg, sc)				
	0	15	30	60	120
Erections					
Males responding	0/8	3/8	4/8	7/8*	6/8*
Latency (min)	–	15.9 ± 6.5	11.7 ± 0.7	14.8 ± 2.2	10.6 ± 2.6
Number of responses	–	1.3 ± 0.3	1.5 ± 0.3	2.0 ± 0.4	2.3 ± 0.8
Yawns					
Males responding	0/8	2/8	4/8	8/8*	4/8
Latency (min)	–	23.9 ± 1.6	16.6 ± 3.8	16.1 ± 2.2	16.7 ± 2.6
Number of responses	–	3.0 ± 1.0	5.0 ± 2.4	6.3 ± 2.4	5.0 ± 2.7

Data for latency and number of responses are presented as means ± SEMs. *$p < 0.05$, relative to 0 μg/kg, by Fisher exact probability test.

After the antecedent condition was satisfied, males were transported to the test room, placed in the observation chamber, and allowed to acclimate for 10 min. They were then injected with APO (60 μg/kg in 0.1% ascorbic acid) and observed for 30 min. Erections and yawns were recorded.

Results and Discussion

As indicated in Table 2, none of the sexually satiated males exhibited erections, compared with 6/9 males after no copulation and 8/9 males after three intromissions, $\chi^2(2) = 15.43$, $p = 0.0004$. The last two groups differed reliably from the sexually satiated males ($p < 0.01$, Fisher exact probability test) but not from each other. Neither the latency to the first erection, $F(1, 12) = 0.08$, nor the number of erections ($F = 1.25$) reliably distinguished the no-copulation and three-intromission groups.

With respect to yawning, antecedent copulation did not significantly affect the proportion responding, and ANOVA revealed no significant effect of treatment on the latency or number of yawns, $F(2, 20) = 1.58$ and 1.97, respectively; $p > 0.15$.

The absence of APO-induced erections in sexually satiated male rats demonstrates at least some effect of copulation on these responses. Although satiety represents an extreme sexual condition, this may be the first evidence that drug-induced erections interact with copulatory behavior. The dissociation between erections and yawns in sexually sated males indicates that the effect of copulation may be specific to erection, and perhaps other sex-relevant acts, but does not generalize to all dopamine-sensitive behavior patterns.

EXPERIMENT 3

In experiment 2, sexual satiety blocked APO-induced erection, but there were no vehicle-injected males in that study. Furthermore, the three copulatory experiences of the males during the week preceding the test may have reduced the probability of males showing an effect of three intromissions. Therefore, in this experiment we repeated the three-intromission condition and inquired whether a single ejaculation would alter the effect of APO on erections.

Method

Subjects and housing. The 48 males, derived from the same source and maintained in the same conditions as in experiment 1, were 12 weeks old at the start of testing and weighed 340–420 g.

Procedure. All tests were conducted between 1100 and 1700. Prior to testing, males were given two copulatory experiences (to ejaculation with hormonally induced estrous females) and two 10-min acclimation sessions in the ventral viewing apparatus used in experiment 2, but without a partition. Males were then divided randomly into six groups for the 3 × 2 factorial design. Three antecedent behavioral conditions were used: 1) no exposure to a female, 2) copulation to three intromissions, or 3) copulation to one ejaculation. Males in the no-exposure condition were placed alone in a copulation test chamber for 6.25 or 11.25 min ($n = 3$ for each duration), which were, respectively, the mean times to reach three intromissions or one ejaculation in the sexual experience tests. Immediately after reaching the temporal or behavioral criterion males were injected with APO (60 μg/kg, SC) or vehicle (VEH; 0.1 ml/kg 0.1% ascorbic acid), placed in the ventral viewing apparatus, and observed for 30 min. Penile erection and yawning were scored as in experiment 1.

Results

Erection latency was reliably affected by the treatments, $F(5, 35) = 5.26, p < 0.001$ (Fig. 1). There was no main effect of drug treatment, $F(1, 35) = 1.15, p = 0.29$, but copulation reduced the erection latency, $F(2, 35) = 8.96, p < 0.001$, and there was a reliable Drug × Copulation interaction, $F(2, 35) = 3.60$, $p < 0.05$. Post hoc Tukey tests revealed that for VEH males the erection latency after no exposure (to females) was longer than after three intromissions or one ejaculation. No other erection latency differences were significant, despite the apparent decline in latency across copulation conditions for APO males.

Although the omnibus ANOVA for number of erections was not significant, $F(5, 35) = 1.94$, $p > 0.10$), a reliable main effect of copulation was indicated, $F(2, 35) = 4.22$, $p < 0.025$. We consider that effect anomalous, since Tukey

TABLE 2

ERECTIONS AND YAWNS IN RATS INJECTED WITH APOMORPHINE (60 μg/kg, sc) AFTER THREE INTROMISSIONS OR ACHIEVEMENT OF SEXUAL SATIETY

	Antecedent Copulation		
	None	Three Intromissions	Sexual Satiety
Erections			
Males responding	6/9	8/9	0/9*
Latency (min)	14.8 ± 4.4	16.3 ± 2.7	–
Number of responses	2.2 ± 0.6	3.0 ± 0.5	–
Yawns			
Males responding	6/9	8/9	9/9
Latency (min)	12.0 ± 2.3	16.4 ± 2.4	12.4 ± 1.2
Number of responses	7.8 ± 2.9	3.8 ± 0.9	8.4 ± 1.2

Data for latency and number of responses are presented as means ± SEMs. *$p < 0.01$, relative to other conditions, by Fisher exact probability tests.

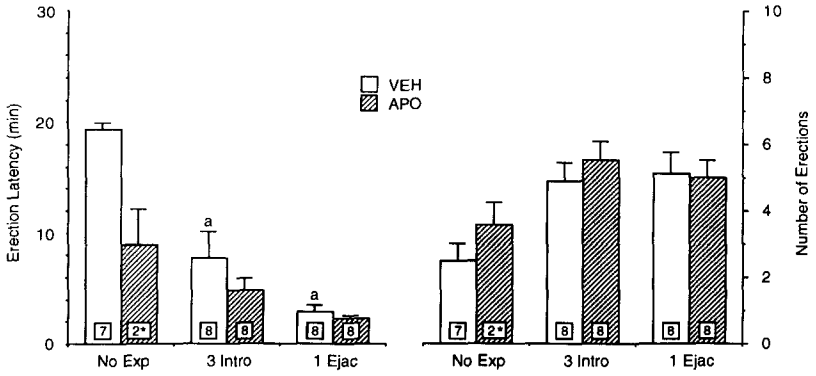

FIG. 1. Erection latency and number of erections of males treated with apomorphine (APO; 60 μg/kg, SC) or vehicle (VEH) after no exposure to estrous females (No Exp), three intromissions (3 Intro), or one ejaculation (1 Ejac). Values are means + SEMs and are based on males displaying the response, as shown in each column (repeated on each side of figure). $^{*}p < 0.05$ vs. VEH males, Fisher exact probability test. $^{a}p < 0.05$ vs. NoExp/VEH males, Tukey HSD test. See text for additional information on statistical comparisons.

tests confirmed the ANOVA in revealing no significant differences among groups.

The treatments reliably affected yawn latency, $F(5, 22) = 4.02$, $p < 0.01$, and number of yawns ($F = 3.39$, $p < 0.025$) (Fig. 2). Both effects were due entirely to APO injection: latency, $F(1, 22) = 17.55$, $p < 0.001$; number, $F = 6.12$, $p < 0.025$. There was no reliable effect of copulation for either variable, nor was there a Drug × Copulation interaction. Comparison of latencies in Figs. 1 and 2 indicates that erection generally preceded yawning after APO injection.

DISCUSSION

With regard to yawning, injection of APO increased its incidence, as expected from previous studies (2,14,15,26,27), but neither APO- nor vehicle-injected males showed an effect of copulation on yawning. We infer that yawning and erection are readily dissociable and that any changes in brain dopamine resulting from copulating to ejaculation (1,9,23,30) are not sufficient to promote reliable changes in yawning latency or frequency.

Experiment 2 had demonstrated no influence of three intromissions on APO-induced erection, but there was a strong inhibitory effect of sexual satiety. In experiment 3, three intromissions were again without reliable effect on APO-induced erection, as was one ejaculation. Since a few intromissions or one ejaculation have repeatedly been shown to enhance reflexive erections, it appears that APO-induced erections are less susceptible than reflexive erections to the influence of antecedent copulation. Nonetheless, in experiment 3 there was a nonsignificant progressive reduction in the erection latencies of APO-injected males after three intromissions or one ejaculation. This reduction may hint at the possibility of an effect that might be revealed under other experimental conditions

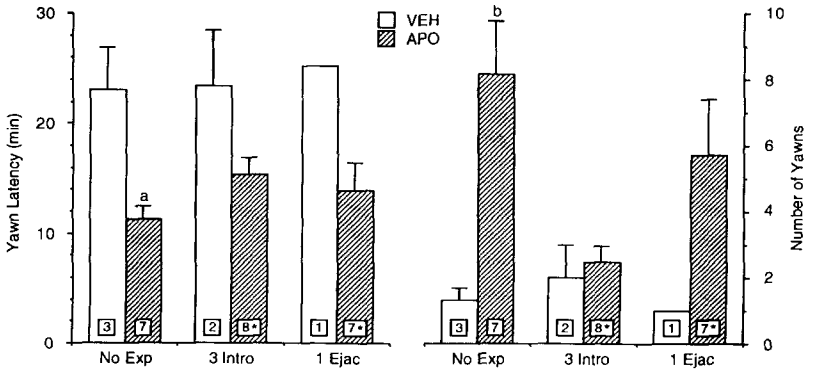

FIG. 2. Yawn latency and number of yawns of males treated with apomorphine (APO; 60 μg/kg, SC) or vehicle (VEH) after no exposure to estrous females (No Exp), three intromissions (3 Intro), or one ejaculation (1 Ejac). Values are means + SEMs and are based on males displaying the response, as shown in each column (repeated on each side of figure). $^{*}p < 0.05$ vs. VEH males, Fisher exact probability test. $^{a}p < 0.05$ vs. NoExp/VEH males, Tukey HSD test. $^{b}p < 0.025$ vs. NoExp/VEH, Tukey HSD test. See text for additional information on statistical comparisons.

(e.g., in males given a suboptimal dose of APO). Pending such evidence, however, an interaction between subsatiety amounts of copulation and APO-induced erections remains to be demonstrated.

Unexpectedly, three intromissions or one ejaculation reliably increased the probability of spontaneous erections in vehicle-injected rats in the absence of a female. In fact, these treatments were no less effective than 60 μg APO in promoting erection, and the erectile response pattern appeared to be identical to APO-induced erection. Brain levels of dopamine and other neurotransmitters change dramatically during and after copulation (1,23,30), or even with noncontact exposure to estrous females (9,21). Such changes may have contributed to the display of postcopulatory erections. In any case, it appears that optimal doses of APO may be no more effective than the natural neurochemical sequelae to copulation in promoting erection in male rats.

Psychogenic erection is commonly regarded as erection that results from fantasy, spontaneous brain activity, or noncontact exposure to sexual stimuli, and reflexive erections are those resulting from somesthetic stimulation, especially of the perigenital area (8,11,12,25,32). Erections *in copula* probably include elements of both sources of stimulation. The postcopulatory occurrence of erection in male rats for several minutes after removal of the female has elements of reflexive erection, in that genital stimulation precedes the erections, and of psychogenic stimulation, in that erections appear to occur spontaneously for several minutes after genital stimulation. Appropriate categorization of the response is less important than—and is likely to follow from—analysis of the bases for the response. Research in progress addresses the stimulus basis (32) and physiological mediation (35) of psychogenic erection in rats.

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