Pergamon

Pharmacology Biochemistry and Behavior, Vol. 48, No. 4, pp. 929–934, 1994

0091-3057/94 $6.00 + .00

0091-3057(94)E0054-L

Effects of Alcohol on the Sexual Motivation of the Male Rat

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Received 30 April 1993

SCOTT, M. P., A. ETTENBERG AND D. H. OLSTER. *Effects of alcohol on the sexual motivation of the male rat.* PHARMACOL BIOCHEM BEHAV 48(4) 929–934, 1994.—Previous research measuring the effects of alcohol on sexual behavior has primarily focused on its effects on copulation. The present experiment was designed to investigate the effects of alcohol on the sexual motivation of the male rat by requiring operant responding to gain access to a sexually receptive female. A novel apparatus was used that allowed both visual and olfactory cues from an estrous female to reach the male. Lever presses resulted in the opening of a door that permitted the male rat to enter an adjacent chamber where a receptive female was located. Treatment with low to moderate doses of alcohol (0.5 g/kg and 1.0 g/kg) resulted in increased latencies to emit the first response of the males working for access to females, but did not affect response rate or subsequent mount or ejaculation latencies, when these males were allowed access to the receptive female. Furthermore, alcohol failed to show any response-reinstating or disinhibitory effects when tested following a period of nonreinforced extinction trials. An additional experiment, in which rats received equivalent doses of alcohol, revealed no decrease in spontaneous locomotion. Taken together, these data suggest that the response-reducing effects of alcohol are probably not a result of general drug-induced reductions in activity, but rather an attenuating action of the drug on sexual motivation.

Sexual motivation Ethanol Sexual reinforcement

A GREAT deal of research has been done to elucidate the effects of alcohol on the sexual behavior of male rats. The general finding is that under most conditions, alcohol has dose-dependent, disruptive effects on many measures of copulatory behavior (3,12,17). Even comparatively low doses of alcohol, in the range of 0.25 g/kg to 1.0 g/kg, have been shown to have deleterious effects on several measures of copulatory behavior, including mount latency, intromission latency, ejaculatory latency, and number of intromissions and ejaculations (17). Unfortunately, these types of experiments do not clearly discriminate between effects of alcohol on the copulatory competence of the animal vs. those on sexual motivation. For example, Pfaus and Pinel (17) trained male rats to inhibit their sexual responding by giving them repeated training sessions with unreceptive females. When given low doses of alcohol, the males reinstated their copulatory behavior, an effect that the authors attributed to an alcohol-induced disinhibitory effect on restrained sexual behavior.

The distinction between sexual motivation and copulation is an important one, because sexual motivation may be present without subsequent consummatory behavior. For example, lesions of the preoptic-anterior hypothalamic area create marked decreases in sexual behavior (i.e., performance) in rats, but do not affect partner preference for an estrous female over an anestrous one, nor do they decrease instrumental responding by males to gain access to sexually receptive females (9,15). Conversely, lesions of the basolateral amygdala have been shown to disrupt instrumental responding for a female, without significantly influencing measures of unconditioned sexual behavior such as mount latency and intromission latency (7). These data suggest that sexual motivation and copulation are controlled by separate mechanisms, and any attempt to study sexual motivation must look beyond copulation as a measure of motivation.

One method for assessing sexual motivation has been to require some type of instrumental responding to gain access to a sexually receptive female, but it has proved difficult to train males to respond for a sexual reinforcer, or at least, respond at adequate rates [see review, (8)]. The most recent and successful method used to assess sexual motivation was described by Everitt et al. (8). In that experiment, classical conditioning was employed in training male rats to associate a conditioned stimulus (a light or tone) with copulation. Males were then required to lever press to gain access to a receptive fe-

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male, and their responding was maintained at high levels by the presentation of the tone or light under a second-order schedule.

Due to the profound importance of olfaction to both sexual motivation and copulation in the male rat (5,13,16), the present study employed an apparatus that allowed both olfactory and visual cues from an estrous female to reach a male trained to lever press to gain access to the female. The effects of alcohol on lever-press behavior were then determined during reinforced behavior and again after a period of nonreinforced extinction responding [the latter was employed to test the disinhibition hypothesis of Pfaus and Pinel, (17)]. Assuming that the documented disruptive effects of alcohol on sexual behavior (3,12,17) result, in part, from a change in motivational state, it was hypothesized in the present study that alcohol treatment would induce a parallel increase in the latency to emit the first lever-press response. After operant responding had undergone extinction (i.e., a behavioral form of inhibition), it was hypothesized that alcohol administration would result in disinhibition, as reflected by a decrease in the subjects' latency to emit the first response. Finally, to assure that any effects of alcohol on instrumental responding were due to motivational factors rather than nonspecific motoric effects of the drug, alcohol-induced changes in locomotor activity were also examined.

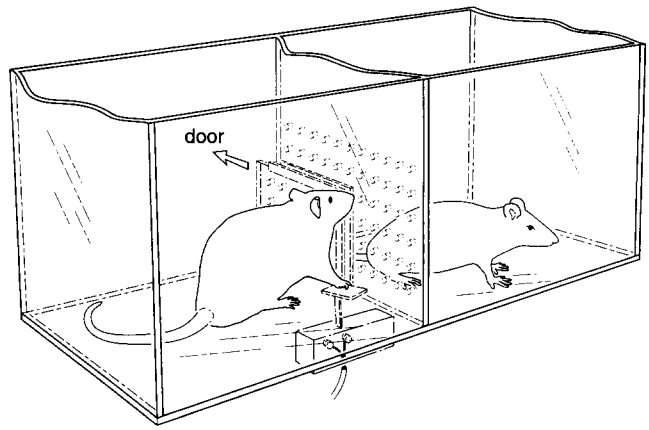

FIG. 1. Experimental apparatus used to measure appetitive behavior (lever pressing) of a male rat responding for a receptive female. Upon completion of appropriate responses, the door in the partition is opened, allowing access to the female. The partition is studded with small holes to allow for olfactory cues from the female to reach the male.

METHOD

Subjects and Surgery

Ten male Long-Evans and seven female Sprague-Dawley rats were purchased from Charles River Laboratories (Wilmington, MA). Upon delivery the males weighed 350–400 g, and the females 225–275 g. Animals were handled for a few minutes per day over 10 days to gentle them prior to training. Each subject was individually housed in a hanging metal cage residing within a temperature-controlled room (22°C) that was maintained on a reversed 14 L : 10 D schedule (lights out at 1400 h). Fifteen additional males (250–300 g) were purchased for the locomotor activity experiment, and were maintained under identical conditions. Animals were given food and water ad lib, except where indicated below.

The seven rats to be used as stimulus females were ovariectomized under anesthesia produced by a combination of chloral hydrate (106 mg/kg IP) and sodium pentobarbital (22 mg/kg IP), supplemented when necessary by methoxyflurane (Metofane, Pittman-Moore, NJ). After ovariectomy and while still under anesthesia, the rats were implanted with two 5 mm Silastic (i.d 1.47 mm, o.d. 1.96 mm, Dow-Corning, Midland, MI) capsules containing crystalline 17β-estradiol. The methods used to prepare and insert the capsules have been described elsewhere (2). These rats were made sexually receptive by SC injections of 0.5 mg progesterone (in propylene glycol), 4 h prior to use in the training/testing sessions.

Apparatus

Testing was carried out in a custom-built rectangular Plexiglas box measuring 60 cm in length × 30 cm in width × 60 cm in height with an open top (Fig. 1). The interior of the box was divided by a Plexiglas wall into two equal halves measuring 30 × 30 × 60 cm. To allow for transmission and reception of olfactory cues, the bottom half of this dividing Plexiglas wall was perforated with holes. The holes were arranged in eight rows of 10 each, with the holes measuring 0.5 cm in diameter and spaced about 3.0 cm apart. A sliding door 15 cm long and 10 cm high was located in the dividing wall. This door could be opened from the outside by sliding it through an opening in the opaque side of the box. Once open, a rat had access to both sides of the box. A single response lever was located 3 cm from the dividing wall, centered in front of the immovable section of the partition. The lever measured 2.5 × 5 cm and was positioned approximately 3 cm from the floor of the chamber. The box was equipped with counting and timing devices that measured the subjects' latency to emit the first response (time elapsed between introduction of the animal into the box and the first lever press), response time (time elapsed from the first response to door opening), total elapsed trial time (time from introduction of the animal to its removal), as well as total number of lever-press responses.

The locomotor activity apparatus (11) was housed in a sound-attenuated isolation room and consisted of 16 hanging wire activity chambers (each 25 × 36 × 20 cm). Each chamber was equipped with two infrared photocell detectors, positioned at the front and back of the cage on the long axis. Interruptions of an infrared beam registered counts which were summed across 5-min intervals for data analysis.

Drug Administration

Ethanol (95%) was diluted with 0.9% saline in a 25% v/v solution and 12.5% v/v solution and injected intraperitoneally in doses of 0.5 g/kg (12.5% solution), or 1.0 g/kg (25% solution), 1 h prior to testing. A saline (0.9%) vehicle was used in the control condition and was administered in equal volumes. After injection, animals were replaced in their home cages and then removed 1 h later for testing. All training and testing was done between 1400 and 1700 h, during the dark phase of the photocycle.

Training

Males were first trained to press the lever to gain access to a reinforcement consisting of a single Hershey brand chocolate chip, placed in a small bowl on the adjoining side of the box. When the lever was depressed, the sliding door was opened, thereby allowing access to the reinforcement side of

the box. Each male was given five consecutive trials each day during which they were gradually shaped to respond on a fixed ratio (FR)-10 schedule of reinforcement with the average latency to their first response of about 10 s, and the average response time to complete an FR-10 segment of about 30 s. To expedite the learning process, the rats were food restricted for 3 days by limiting their consumption to approximately 15 g of food per day. During these 3 days, none of the animals fell below 90% of original body weight, and all rats were provided ad lib access to food and water thereafter. In addition to operant training, the males were given copulatory experience with sexually receptive females in a different chamber.

After achieving adequate responding for the chocolate, the animals were then trained to lever press for access to a sexually receptive female. Training began on an FR-10 schedule of reinforcement, with the tenth response resulting in the opening of the sliding door, which allowed access to both sides of the box for both the male and female. When both animals were on the female's side, the door was closed and copulation was allowed to proceed until ejaculation by the male or 20 min had passed. If the male was engaged in an active copulatory sequence, he was allowed to continue until ejaculation without regard for time. Each rat was given one trial daily, and the animals were considered trained when 9 of the 10 rats had copulated to ejaculation at least once with a female in the testing chamber, and the measures of instrumental responding were consistent and adequate. The entire training period, including the training with chocolate, lasted 19 days.

Preextinction Testing

A within-group design was employed in which each of 10 trained rats experienced all three test conditions in a spaced and counterbalanced manner. Initially, each rat was assigned to one of three conditions: vehicle (saline 0.9%), low alcohol (0.5 g/kg EtOH), or high alcohol (1.0 g/kg EtOH). Animals were injected at the beginning of the dark cycle, placed back in their home cages, and removed 1 h later for testing. The testing procedure was identical to the training trials. The subjects' latency to emit their first response and the rate at which the FR10 was completed were measured. Response rates were calculated as 10 (the number of emitted responses)/(the time required to complete the FR10 minus the latency to first response). Once on the female's side of the box, the males' latencies to first mount and ejaculation, indices of copulatory performance, were recorded. Animals that did not mount or ejaculate were assigned for these measures a value of 20 min (1200 s), the length of time they remained on the female's side of the box. Following testing the animals were returned to their home cages where they remained undisturbed for 48 h to allow for any lingering effects of the drug to dissipate. This period was followed by 2 days of baseline testing to verify that responding had returned to normal predrug levels. This baseline testing was identical to training. After the 2 baseline days, the animals were reassigned to different drug groups and tested again. This entire process was repeated once more, so that by the third testing day, all the animals had been tested under all drug conditions, at 5-day intervals.

Extinction

Nonreinforced extinction trials began the day after the last test day and continued for 11 days. Each animal was given three trials a day at 1-h intervals, with each trial lasting 4 min in the experimental box. During extinction, the latency to first response and the total number of emitted responses were recorded for each subject on each trial. Although a receptive female was present in the operant box, on no trial was the adjoining door opened. Operant lever pressing was considered extinguished when the average latency to first response had doubled in comparison to the first day of extinction, and the average response rate had dropped to 25% of the original response rate.

Postextinction Testing

Following extinction, an additional alcohol dose–response curve was obtained for reinforced behavior in a manner identical to that described under the Preextinction Testing section. In this phase, the response rate was calculated as the total number of lever-press responses/(4 min minus the latency to first response). The intent here was to determine whether ethanol would serve to reinstate (i.e., disinhibit) the previously sexually reinforced operant behavior. Copulatory performance was not measured in this condition, as the males were not permitted access to the receptive female.

Locomotor Activity

Fifteen new males were placed in the locomotor activity chambers where activity counts were taken every 5 min for 2 h. Twenty-four hours later, this procedure was repeated following treatment 1 h earlier with either saline (0.9%; $n = 5$), a low dose of alcohol (0.5 g/kg EtOH; $n = 5$), or a higher dose of alcohol (1.0 g/kg EtOH; $n = 5$). Time and dose parameters used here were chosen to correspond to those employed in the sexual motivation experiment.

Data Analysis

The data from two animals were discarded. One of these died after completing the preextinction phase of the experiment; during those tests, this rat never attempted to mount the receptive female. The other was an animal whose performance on both saline trials was more than 2 standard deviations from the group mean; this rat also never attempted to mount a receptive female on the saline or alcohol tests, something that was not observed in any of the remaining eight rats.

Separate two-factor (test condition/drug) analyses of variance (ANOVAs, with repeated measures on both factors) were performed on the latency and response rate data. The test conditions were preextinction and postextinction, and the drug factor represented alcohol dose/treatment. The mount and ejaculation latencies following alcohol treatment during the preextinction trials were analyzed by ANOVA for repeated measures (drug dose). The percentages of animals copulating to ejaculation under these conditions were analyzed by the Cochran Q test (18). The data from the locomotor activity test were analyzed using a two-factor (time/drug) ANOVA with time representing the repeated measures variable and drug the between-groups treatment variable.

RESULTS

Figure 2 represents the effects of alcohol on the latency to emit the first operant response upon introduction into the box. There was a marginal effect of test condition, $F(1, 7) = 4.24$, $p = 0.078$, with the response latencies being somewhat slower in the postextinction condition compared to those obtained prior to extinction. There was a significant main effect of alcohol, $F(2, 14) = 3.83$, $p < 0.05$, but no drug × test interaction, $F(2, 14) = 1.48$, $p = 0.262$, thereby demonstrating a reliable effect of alcohol dose across both pre- and post-

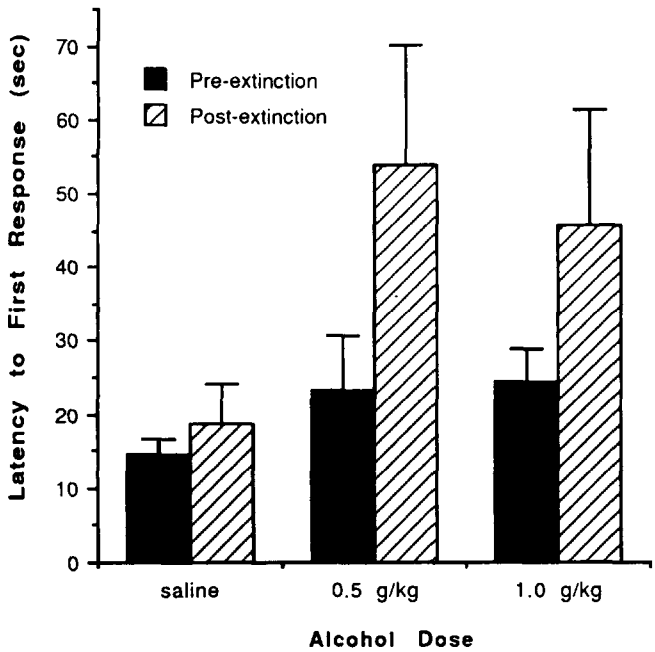

FIG. 2. Mean latencies to emit the first operant response (±SEM) for each drug group (n = 8). Data represent performance of subjects during two identical test sessions run prior to and after an 11-day period of nonreinforced extinction trials.

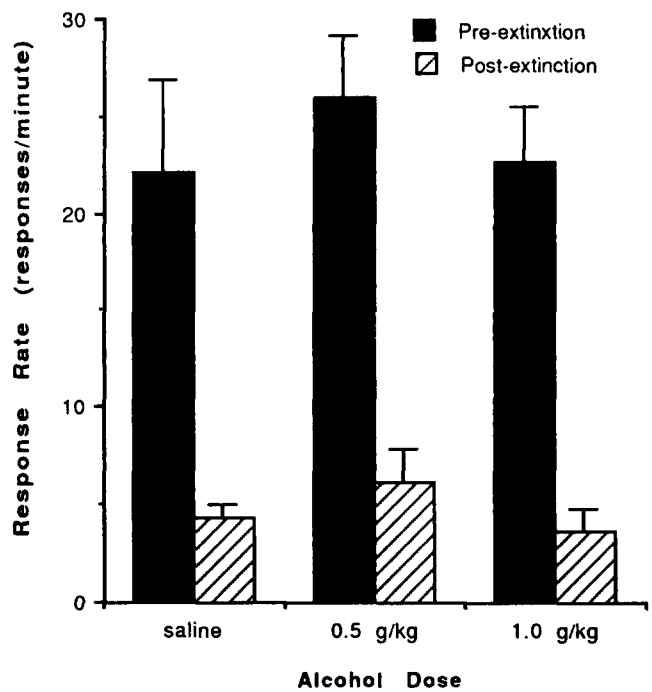

FIG. 3. Mean response rates (±SEM) for each drug group (n = 8). Data represent performance of subjects during two identical test sessions run prior to and after an 11-day period of nonreinforced extinction trials.

extinction test sessions. The lack of an interaction indicates that the effects of alcohol were relatively comparable in the two test conditions.

The response rates for the different alcohol treatments during the pre- and postextinction drug trials are depicted in Fig. 3. There was a highly significant reduction in operant response rate after extinction compared to the preextinction condition, $F(1, 7) = 78.08, p < 0.0005$. However, alcohol itself had no reliable effect on response rate, $F(2, 14) = 1.04, p = 0.379$, and there was no significant interaction between test condition and drug dose, $F(2, 14) = 0.06, p = 0.946$.

The copulatory performance data from rats during the preextinction phase of the experiment are shown in Table 1. Although the mount latencies tended to be higher in alcohol-treated rats, there was no significant effect of the alcohol treatment on the animals' latencies to first mount or ejaculation. Nor was there a significant effect of alcohol on the percentage of animals copulating to ejaculation.

The results of the locomotor activity test are shown in Fig. 4. While there was no effect of alcohol dose on activity level, $F(2, 12) = 0.972, p = 0.406$, there was a highly reliable effect of time on activity level, $F(2, 15) = 0.95, p < 0.0001$, with all animals becoming less active as the trial progressed. Once again, there was no time × drug interaction, $F(2, 30) = 0.95$, $p = 0.545$.

DISCUSSION

The apparatus used for assessing the sexual motivation of the male rats was successful in producing both high levels of responding and fairly easy acquisition of the required operant response. For example, during a single extinction trial, one rat pressed the lever over 200 times in 4 min to gain access to the female. The olfactory cues permitted by the holes in the partition between the male and female rats clearly provided for an important source of motivational stimulation, because a vast majority of the animals spent a great deal of time engaged in sniffing at this location. In addition, females would occasionally exhibit hop-darting, a form of proceptive behavior, while the male was still on the other side of the box. This apparatus, therefore, provides a reliable, simple method for the separate assessment of both appetitive and consummatory aspects of sexual behavior. We cannot, of course, rule out the possibility that the male operant behavior was socially motivated and, hence, reflected responding for the opportunity to interact with another rat, regardless of its sexual status. However, this does not seem likely in view of the fact that other investigators have shown that upon repeated trials with anestrous, rather than estrous, females as the reinforcer, male rats show a 60–70% decrease in instrumental responding (8).

As predicted, alcohol in levels of 0.5 g/kg and 1.0 g/kg produced significant increases in the time it took males to make their first response (on an FR10 schedule) for gaining access to an estrous female. The latencies to the first lever press following ethanol administration increased 61–70% and 143–187% during the training and extinction phases, respectively. The observed increase in the subjects' latency to emit the first response is probably not due to some nonspecific action of alcohol, because neither response rate nor locomotor behavior were affected at the alcohol doses under investigation. These results, therefore, suggest that the disruption of copulation observed in male rats under low to moderate doses of alcohol may be due to a decrease in motivation.

Given that separate mechanisms have been proposed to govern sexual motivation vs. copulatory performance (7,9, 15), it is noteworthy that these doses of alcohol (0.5–1.0 g/kg)

TABLE 1

EFFECTS OF ETHANOL (EtOH) TREATMENT ON COPULATORY PERFORMANCE IN MALE RATS

	Saline	0.5 g/kg EtOH	1.0 g/kg EtOH	*p* value
Mount Latency (s)*	350 ± 186	812 ± 196	808 ± 196	0.27, NS
Ejaculation Latency (s)*	951 ± 137	1124 ± 110	1001 ± 115	0.55, NS
Copulating to ejaculation	62.5% (5/8)	37.5% (3/8)	37.5% (3/8)	0.5–0.7, NS

*All data are mean ± SEM (n = 8 rats, each tested under all treatments, preextinction trials only).

did not disrupt male copulatory performance. Previous work from one laboratory has shown that administration of 0.5 g/kg ethanol produces moderate decrements in some measures of male sexual behavior, but it is not until higher doses (1.0–2.0 g/kg) are administered that all features of copulatory performance are severely compromised (17). In another study, an ethanol dose of 2.0 g/kg was needed to observe deficits in tests of male sexual behavior with females and in ex copula penile reflex tests (12). It is difficult to compare these studies with the present one; in these earlier experiments, tests of male sexual behavior with females did not include a separate measure of sexual motivation, independent of copulatory performance. In the present study the lever-press effects of ethanol occurred before the animals gained access to the female and, again, suggests a more motivational interpretation of the results.

Although alcohol slowed the latency to first response, it had no effect on response rates. Thus, once the initial response was made, the rate of additional responses remained unaffected by the different doses of alcohol. The fact that alcohol did not disrupt response rates but did disrupt latency to first response, further supports the hypothesis that these latency effects were due to a change in motivational state as opposed to a disruption in motor performance. This observation is also consistent with the notion that the latency to emit the first response may be a more sensitive index of motivation than response rate to the effects of ethanol. Presumably, the visual, olfactory, and conditioned cues that together serve as motivating stimuli, are less effective in generating the initiation of sexually motivated behavior (in this case, the lever pressing). However, once the behavior is activated, it proceeds normally (at least under the influence of the low doses of alcohol examined here).

There are, however, several other possibilities that may account for the results. For example, it may be that, as a central nervous system depressant, alcohol interfered with the rats' sensitivity to the available cues, such as odor and proceptive behavior, which indicate a receptive female. Once these cues are belatedly recognized, the responding begins and continues unaffected. Alternatively, it is possible that the increase

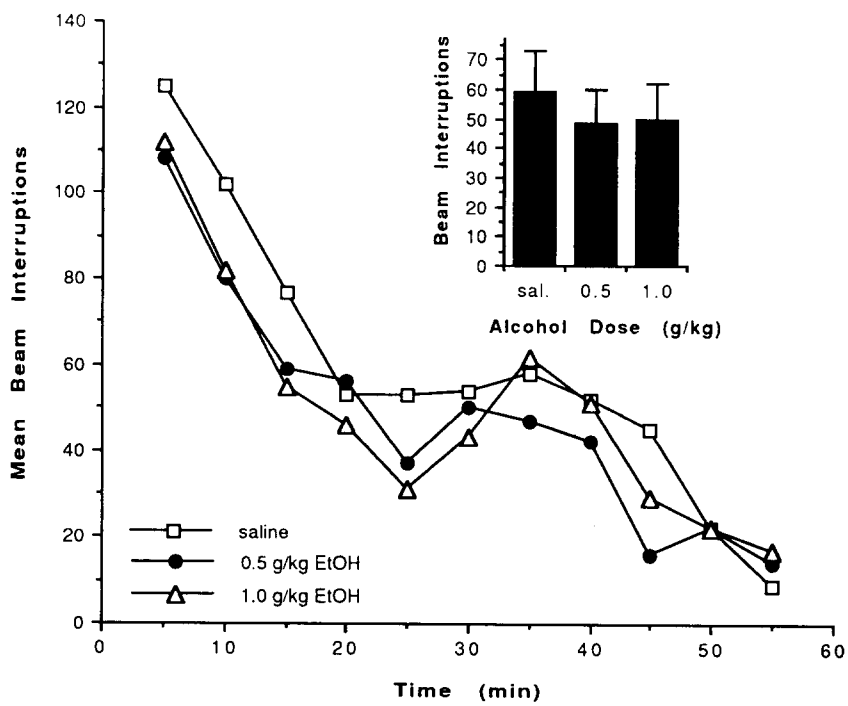

FIG. 4. Effects of alcohol on locomotor activity (beam interruptions) during a 60-min session conducted approximately 1 h postinjection (n = 5/group). Inset: mean total activity over the course of 60-min test session (±SEM).

in latency to first response may be the result of the general rate-reducing properties that alcohol has been shown to have on rats responding for other rewards (1,4,6,10,14), rather than a specific effect on sexual motivation. It is difficult to compare our study with this previous work. Most reports of this nature have focused on effects of ethanol on operant response rates, rather than effects of the drug on the latency to emit the first response. The higher dose used in this study (1.0 g/kg) appears to be just at or below a threshold for decreasing response rates for food or water reinforcers (4,10,14), although inhibitory effects of lower doses of alcohol on instrumental responding have been observed (6). We found no significant effect of ethanol on lever press response rates for access to a sexually receptive female.

Contrary to the results of Pfaus and Pinel (17), alcohol showed no disinhibitory effect on sexually motivated operant responding. In fact, treatment with ethanol continued to increase the latency to first response postextinction, as it had done in the preextinction trial. These results are not consistent with those of Pfaus and Pinel (17); however, in their study, the emphasis was placed on consummatory aspects of sexual behavior and the authors used unreceptive females to extinguish male advances. Conversely, in the present study, noncopulatory appetitive aspects of sexual behavior were emphasized and response inhibition was developed by preventing access to sexually receptive females. Therefore, the differences in results between the current paper and those reported by Pfaus and Pinel (17) may be due to differences in the means used to create response inhibition in the rats, and/or the nature of the behavior (consummatory vs. appetitive) under investigation.

ACKNOWLEDGEMENTS

This work was supported by NIH Grants HD 23483 (awarded to D.H.O.) and DA 05041 (awarded to A.E.). The assistance of Mr. Alexander Eremia in surgery and testing the animals is gratefully acknowledged.

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