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STIMULUS VARIABLES INFLUENCING CONDITIONED SUPPRESSION OF COPULATORY BEHAVIOR IN MALE RATS

Iowa State University PH.D. 1985

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Stimulus variables influencing conditioned suppression of copulatory behavior in male rats

by

Bonnie Lee Blythe

A Dissertation Submitted to the
Graduate Faculty in Partial Fulfillment of the
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DOCTOR OF PHILOSOPHY

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Iowa State University
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INTRODUCTION

The sequence of copulatory behaviors displayed by male rats consists of a series of mounts and intromissions (mounts with vaginal penetration) that culminate in an ejaculation (Beach, 1942). Attempts have been made to modify these copulatory behaviors using shock as an aversive stimulus (Beach, Conovitz, Steinberg, & Goldstein, 1956; Hayward, 1957; Zimbardo, 1958). Although decrements in sexual performance were observed, these decrements could be attributed to conditioned emotional responses (CERs) evoked by the testing environment. Such decrements were not observed when the rats were tested in a novel environment.

Other researchers have attempted to modify the copulatory behaviors of rodents by pairing relevant copulatory cues with toxicosis in experiments analogous to those of learned taste aversion research. In the traditional taste aversion learning paradigm, ingestion of a novel food substance is followed by an experimentally-induced illness caused by exposure to radiation or administration of certain toxic agents [e.g., lithium chloride (LiCl)]. After such a pairing, the animal will subsequently avoid ingestion of that substance (Garcia, Kimeldorf & Koelling, 1955; Revusky & Garcia, 1970).

Although taste aversions are routinely acquired in one

trial (Milgram, Krames & Alloway, 1977), decrements in copulatory behaviors have not been consistently observed after a single pairing of sexual experience with toxicosis. Emmerick and Snowdon (1976) reported that male hamsters injected with methylatropine nitrate following a single 5-min encounter with a receptive female did not subsequently modify their copulatory behaviors. Other males injected with LiCl after a single mount subsequently displayed normal copulatory behaviors. When LiCl was paired with a novel taste/odor cue (phenylacetic acid), increased anogenital sniff-licking latencies were the only changes in the male hamsters' behavior toward receptive females bearing this cue. Johnston, Zahorik, Immler, and Zakon (1978) allowed sexually naive male hamsters to consume vaginal secretions and then immediately injected the animals with LiCl. When paired with receptive females two days later, the males mounted less frequently and had longer latencies to mount than animals that had received saline injections. These longer latencies were interpreted as hesitancy to initiate copulatory behavior, but all males ejaculated.

Recent research (Peters, 1983; Peters, Blythe, & Kueker, 1985) has demonstrated that decrements in copulatory behaviors in male rats can be established with a multiple-trial

conditioning procedure. Peters (1983) reported that male rats injected with .15 M LiCl (20 ml/kg) immediately following each pairing with an estrous female continued to ejaculate during the first few trials, but showed a gradual increase in latency to initiate the copulatory sequence. During the later test sessions, the male rats began to exhibit paw treading (repetitive treading movements with the front paws, e.g., Garcia, Clarke, & Hankins, 1973). After five to ten pairings, the males ceased to copulate entirely.

Peters et al. (1985) found that acquisition of copulation-illness associations (CIAs) was more rapid with a higher concentration of LiCl. Male rats that received an injection of .3 M LiCl after each pairing with an estrous female stopped copulating after fewer trials than did rats that had received .15 M LiCl. Once established, CIAs were retained over a 60-day interval. Delaying administration of LiCl for 5 or 15 min after each pairing with an estrous female did not influence CIA acquisition. Although copulatory decrements were not observed when the delay interval was increased to 1 hr, these animals engaged in paw treading and/or chin rubbing behaviors similar to those displayed by rats that received contingent LiCl injections at shorter delay intervals. Chin rubbing has been described as a response sequence during

which a rat brings its mouth in direct contact with a substrate (e.g., floor) by lowering its head and projecting its upper body forward as a single extension, or as a series of extensions and relaxations (Grill & Norgren, 1978). Rats that received periodic electric shock for 10 min after each pairing with an estrous female did not display paw treading or chin rubbing, and they continued to ejaculate during all copulatory opportunities.

Therefore, in contrast with earlier reports, copulatory behaviors in male rats can be substantially modified when an injection of LiCl is paired with each encounter with a receptive female. It is not clear whether the failure to copulate in the CIA paradigm represents response-contingent punishment of instrumental responses involved in the copulatory sequence (e.g., mounts, intromissions, and ejaculations) or classical conditioning of aversive states to environmental cues (e.g., an estrous female). If a crucial component of the phenomenon is classical conditioning, then multiple pairings of LiCl with exposure to an estrous female when copulation is not possible should lead to a suppression of subsequent copulatory behavior in male rats.

A large body of literature (e.g., Campbell & Church, 1969) has focused on the effects of pairing an aversive stimulus (e.g., shock) with an initially neutral stimulus (CS). Ongoing behavior

is frequently disrupted with subsequent presentation of the CS. This selective suppression of behavior during CS presentation is called a CER. The amount of suppression typically serves as an index of the strength of the association between the CS and the aversive stimulus.

Copulatory decrements have been displayed by male rats that were allowed to copulate during conditioning trials (Peters, 1983; Peters et al., 1985). The general purpose of the present series of experiments was to determine whether similar decrements would be observed in male rats when LiCl was administered following trials in which various stimulus elements were present, but copulation was not permitted. The phrase conditioned suppression of copulatory behaviors was used to describe the decrements that were observed in these experiments, because this term is conventionally used in the CER paradigm.

EXPERIMENT 1

The primary purpose of Experiment 1 was to determine if conditioned suppression of copulatory behaviors in male rats could be established with the following procedure. Male rats received an injection of either LiCl or saline following each exposure to an estrous female that had been placed in a retaining cage.

Method

Subjects

The subjects were adult male and female Long-Evans hooded rats (Blue Spruce Farms, Inc., Altamont, New York). The animals were approximately 60 days old when they were received from the supplier. Except where noted below, the animals were individually housed in suspended wire-mesh cages and had free access to food (Teklad Mouse/Rat Diet, 4% fat) and tap water. Males and females were maintained in separate temperature-controlled (24 °C) rooms under a reversed 12:12 hr light/dark cycle with lights off at 0800.

Apparatus

Six identical black wooden compartments (96 x 30 x 50 cm) with front and rear glass walls were used for behavioral testing. Each of two observers was trained to record data simultaneously from three chambers. Each chamber was illuminated

with a 7.5-W red bulb, and the floor was covered with wood shavings. The test room was also illuminated with dim red light.

Stimulus animals

Female rats were ovariectomized under potential anesthesia (Chloropent 3 ml/kg ip) at 60 days of age. Approximately 48 and 24 hours before a test session, each female received a sc injection of .1 ml sesame oil containing 5 µg of estradiol benzoate. Five hours before a test session, each female received a sc injection of .1 ml sesame oil containing .5 mg progesterone. The females were screened for receptivity with stud males before each test session.

Procedure

Male rats were housed in groups of six or seven in suspended triple cages until their first pairing with a sexually experienced, estrous female at 90 days of age. The male was placed in the chamber 2-3 min before the introduction of a receptive female. Latencies to first mount (ML), first intromission (IL), and ejaculation (EL) were recorded from an electronic clock. Frequency counts were made of the number of mounts and intromissions preceding ejaculation. Male rats that intromitted within 900 sec and ejaculated within an additional 900 sec were considered sexually active. These sexually active males were randomly

assigned to treatment conditions and housed individually in suspended wire-mesh cages thereafter.

Following this initial screening for sexual activity, two conditioning sessions were conducted each week at 3-4 day intervals during the middle third of the dark cycle. During conditioning sessions, an estrous female was placed in a retaining cage made of hardware cloth (39 x 17 x 20 cm) that was positioned in the center of the chamber. Each male rat was paired with the inaccessible estrous female for 300 sec and then received a 20 ml/kg ip injection of either .3 M LiCl (n=8) or .3 M saline (n=7). Male rats were never paired with the same stimulus female on more than two occasions.

Two days after the eighth conditioning trial, male rats were tested for copulatory activity with receptive females. Retaining cages were removed from all chambers during copulation tests. As during their only other copulatory opportunity, a male had 900 sec to intromit and an additional 900 sec to ejaculate. Latency measures (ML, IL, EL) were recorded from an electronic clock, and frequency counts were made of the number of mounts and intromissions preceding ejaculation. The presence or absence of any paw treading and/or chin rubbing (Peters, 1983; Peters et al., 1985) was recorded.

Results and Discussion

Male rats that received LiCl immediately after each conditioning session failed to intromit when provided with the opportunity to copulate with an estrous female. Only one of eight animals initiated copulatory behavior during the 900 sec trial, and that was limited to one mount. All seven of the rats that had received saline ejaculated in less than 800 sec when provided with the opportunity to copulate with an estrous female.

During the fourth conditioning session, some of the rats receiving LiCl injections displayed paw treading and/or chin rubbing for a portion of the 5 min session. The number of animals that engaged in these agitated behaviors increased with each session. By the last conditioning session, all eight rats that received LiCl injections were paw treading and/or chin rubbing. These animals also seemed to spend the majority of the time in a corner away from the retaining cage. In contrast, rats that received saline injections spent most of their time investigating the female, and frequently crawled on top of the cage.

The series of conditioning sessions clearly influenced subsequent copulatory behavior. Multiple pairings of LiCl with an estrous female when copulation was not possible

induced subsequent suppression of copulatory behaviors in male rats. During the time the male rat occupies the chamber with the inaccessible estrous female, the male encounters a variety of cues prior to the aversive consequences induced by the LiCl. An estrous female provides particularly salient cues for the male rat. Proceptive female rats solicit sexual behavior with the visual cues of darting, hopping, and ear-wiggling (Beach, 1976). Chemical signals in preputial gland extracts, vaginal secretions, and urine provide powerful stimuli to encourage sexual behavior (Gawienowski, Orsulak, Stacewicz-Sapuntzakis, & Pratt, 1976; Lucas, Donohoe, & Thody, 1982; Orsulak & Gawienowski, 1972; Nyby, 1983). Most studies indicate that a sexually active male rat prefers the odors of estrous females over the odors of nonestrous (or ovariectomized) females (Carr, Loeb, & Dissinger, 1965; Landauer, Wiese, & Carr, 1977; Lydell & Doty, 1972; Schultz & Tapp, 1973; Stern, 1970).

EXPERIMENT 2

The suppression of copulatory behaviors observed in Experiment 1 may be attributed to associations formed between the unique cues of the estrous female rat and LiCl-induced illness. If the suppression of copulatory behaviors observed in the first experiment is mediated by associations formed with the unique cues of an estrous female, then less suppression would be expected for males that had been similarly paired with inaccessible nonestrous females. The specific cues of estrus would not be present during the conditioning trials, and generalization decrements would be expected on test trials with accessible females. If, however, similar suppression were observed in both groups, the intrinsic cues associated with female rats (estrous or nonestrous) may mediate the associations that suppress copulatory behaviors.

Further, any rat present in the retaining cage during conditioning sessions might provide sufficient cues for associations that subsequently suppress copulatory behavior. Pettijohn (1981) reported that adult male Mongolian gerbils formed conditioned social aversions to young male conspecifics if administered LiCl after a 5-min encounter. Administration of LiCl could be delayed for up to 30 min, but a much stronger aversion was formed if LiCl was injected within 15 min of the preliminary social pairing. This temporal gradient roughly parallels that reported by Hankins, Garcia, and

Rusiniak (1973) for suppression of water intake following odor-illness conditioning. Pettijohn, therefore, suggested that social aversion in the male gerbil may be primarily mediated by olfactory cues. The temporal gradient also parallels that reported by Peters et al. (1985) for CIAs. Thus, odor aversions formed with cues from stimulus animals may mediate a suppression of approach behavior (conditioned social aversion) which, in turn, results in copulatory decrements.

Traditionally, associations between exteroceptive cues and illness have been considered difficult to establish in the taste aversion learning paradigm (Domjan & Wilson, 1972; Garcia, Kimeldorf, & Hunt, 1961; Garcia & Koelling, 1966). Some investigators, however, have been successful in producing aversions to exteroceptive cues (Best, Best, & Mickley, 1973; Mitchell, Kirschbaum, & Perry, 1975; Rozin, 1969). Consequently, CERs associated with the test environment might also account for part, or all, of the suppression of copulatory behavior.

The primary purpose of Experiment 2 was to determine which of the stimulus variables present during conditioning trials are critical in the conditioned suppression of copulatory behavior in male rats. Four groups were added

to the original design to address the issues discussed above. As in the first experiment, an estrous female was present in the retaining cage during conditioning trials for two of the groups, one of which (Group E-LiCl) received injections of LiCl following each trial and the other (Group E-Sal) received saline. For a third group (NE-LiCl), a nonestrous female was present in the retaining cage. The cage contained an adult male conspecific for a fourth group (M-LiCl), and it remained empty for a fifth group (no rat, NR-LiCl). A sixth group (E-Noncon) received noncontingent injections of LiCl on the days following exposure to an inaccessible estrous female to control for possible nonassociative effects of repeated LiCl injections on copulatory behavior. An attempt was also made to quantify paw treading and/or chin rubbing, and measures of differences in proximity to the retaining cage noted in the first experiment were obtained.

Method

Subjects

The subjects were adult male and female albino rats (Holtzman Company, Madison, Wisconsin). Budget limitations favored the purchase of albino rats rather than the hooded rats used in Experiment 1. The animals were approximately 40 days old when they were received from the supplier.

Except where noted below, the animals were individually housed in suspended wire-mesh cages and had free access to food (Simonsen Rat/Mouse Diet) and tap water. Males and females were maintained in separate temperature-controlled (24° C) rooms under a reversed 12:12 hr light/dark cycle with lights off at 0800.

Apparatus

Nine identical black wooden chambers (75 x 55 x 38 cm) with glass fronts and hinged rear doors were constructed for behavioral testing in Experiment 2. Each chamber was contained within a larger wooden compartment which was lined with styrofoam on all sides except for the glass front necessary for observation. Each chamber was dimly illuminated with a 7.5-W red bulb, and the floor was covered with wood shavings. A blower fan provided ventilation for each sealed compartment, and created a noise level ranging between 69-74 dB (C scale weighting). The test room was also illuminated with dim red light.

Stimulus animals

The females were housed in pairs until they were ovariectomized under pentobarbital anesthesia (Chloropent 3 ml/kg ip) at 60 days of age. After surgery, these rats were housed individually for the remainder of the experiment. Estrus was induced as in Experiment 1. Females were screened

for receptivity with stud males prior to each test session. Ovariectomized females used as stimulus animals for Group NE-LiCl were never brought into heat. Sexually inactive male conspecifics served as stimulus animals for Group M-LiCl.

Procedure

Housing of male rats and initial screening for sexual activity were the same as those of Experiment 1. In addition, the males were briefly handled on two different occasions for five consecutive days when the animals were approximately 70 days of age.

Four days after the initial screening for sexual activity, animals were again paired with a receptive female and allowed to ejaculate. Therefore, the male rats in this experiment had two successful copulatory experiences prior to any conditioning sessions. The conditioning sessions were conducted at 3-4 day intervals during the middle third of the dark cycle. During conditioning sessions, each chamber contained a retaining cage made of hardware cloth (39 x 17 x 20 cm) placed lengthwise against the side wall. A black wooden lath extended from the glass wall across the floor of the chamber to the back door to equally divide the open area.

Six treatment conditions (n=9 per condition) were included in the experiment. In four groups, the male rats

received an injection of LiCl immediately after each exposure to one of four stimulus conditions present in the retaining cage during conditioning trials (estrous female rat, nonestrous female rat, male rat, or no rat). A red brick was used to stabilize the retaining cage in the "no rat" condition. One control group received saline rather than LiCl after each exposure to an estrous female during conditioning trials. An additional control group received noncontingent injections of LiCl on the days following exposure to an estrous female during the conditioning trial.

Each conditioning session lasted 300 sec. The male rat was always introduced to the middle portion of the chamber with its head facing the glass front and its limbs straddling the black wooden lath. An electronic clock was started when the hind paws touched the wooden shavings. Time spent in the portion of the chamber containing the wire-mesh cage and the duration of paw treading and chin rubbing were recorded on separate clocks. Immediately following each of the eight 5-min conditioning trials, all male rats received their appropriate injection (20 ml/kg ip of either .3 M LiCl or .3 M saline).

Precautions were taken to minimize the presence of estrous cues on trials not involving estrous females. First,

on each testing day, three of the nine compartments were used exclusively for activity that involved estrous female (e.g., screening for sexual receptivity and for conditioning sessions in which an estrous female was present in the retaining cage). Used chambers were cleaned with a dilute Lysol solution at the conclusion of each day, and new wood shavings were spread on the chamber floors before beginning the next conditioning trial. Second, the conditioning trials with estrous females were conducted on Mondays and Thursdays, while the other groups were run on Tuesdays and Fridays. Although this procedure confounds groups with days, it was judged to be more important to minimize possible estrous odor cues. Third, the ovariectomized females used for the trials in which a nonestrous female was present in the retaining cage were never brought into heat. Finally, males and females were housed in separate rooms as mentioned above.

Four days after the eight conditioning trials, each male was tested for copulatory activity with a receptive female. Retaining cages were removed from all chambers during copulation tests. As during their only other two copulatory opportunities, a copulation test was terminated after an ejaculation, a failure to intromit within 900 sec, or a failure to ejaculate within an additional 900 sec. Latency measures

(ML, IL, EL) were recorded from an electronic clock, and frequency counts were made of the number of mounts and intromissions preceding ejaculation. The presence or absence of paw treading and chin rubbing was also recorded.

Analyses of variance were performed on all dependent variables. Two-tailed *t* tests were used to evaluate the differences for planned comparisons. Fisher exact probability tests were used to analyze ejaculation frequency data.

Results and Discussion

There were no significant differences between groups for all dependent variables before conditioning. One rat (Group M-LiCl) developed an inner ear infection after the fourth conditioning trial and was sacrificed (its data were discarded).

The robust conditioning of Experiment 1 was not replicated in this experiment. As shown in Table 1, approximately half of the male rats in three experimental groups (E-LiCl, NE-LiCl, and M-LiCl) ejaculated when paired with an estrous female after the series of conditioning trials. Using the Fisher exact probability test, the proportions were significantly ($p<.05$) less than the 100% of Group E-Sal. Six of the nine rats in Group NR-LiCl ejaculated during the post-conditioning copulatory test. Although this proportion was not significantly

Table 1

Mean Performance Scores of Male Rats in Experiment 2 Pre- and Post-Conditioning Trials

Group	n	Pre			Post		
		ML	IL	% Ejaculated	ML	IL	% Ejaculated
Experimental							
E-LiCl	9	74	148	100	416*	421*	55.6†
NE-LiCl	9	118	267	100	517**	567**	44.4†
M-LiCl	8	54	77	100	506**	570**	50.0†
NR-LiCl	9	83	212	100	321	363*	66.7
Control							
E-Saline	9	118	158	100	65	79	100
E-Noncon	9	110	155	100	34	65	88.9

Note. ML and IL data are in sec.

*$p<.05$, two-tailed t tests.

**$p<.01$, two-tailed t tests.

†$p<.05$, one-tailed Fisher exact test.

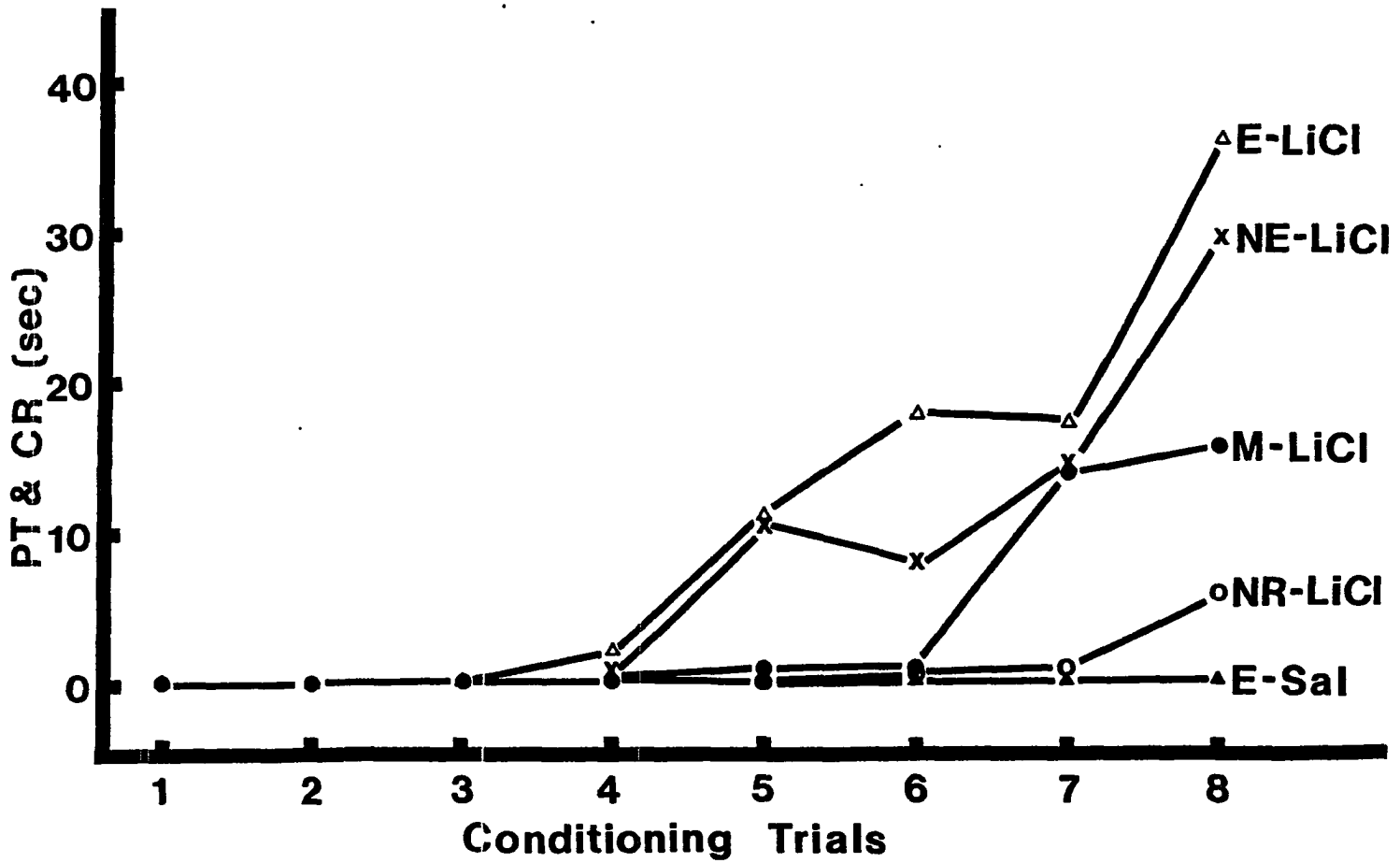
different from other experimental groups, it was also significantly different from Group E-Sal.

All four experimental groups had significantly longer mean latencies to first intromission compared to the control groups (Table 1). Comparisons of ML data yielded the same pattern of results. There were no significant differences between animals that received saline or noncontingent LiCl in any of the dependent measures. Only one control animal (Group E-Noncon) failed to ejaculate, and that animal intromitted five times before test trial termination.

Rats do not usually engage in paw treading or chin rubbing. Only one animal in each of the control groups (E-Noncon and E-Sal) ever displayed paw treading or chin rubbing, and on those two occasions, the durations were less than one sec (Figure 1). For more clarity, the data for Group E-Noncon were not displayed in Figure 1.

By the sixth conditioning trial, some animals from all experimental groups had begun to paw tread and/or chin rub (Figure 1). Animals would paw tread and chin rub against the floor, walls, and sometimes on the retaining cage. The amount of paw treading and chin rubbing displayed by these animals increased over trials ($p<.001$). By the eighth trial, 31 of 35 experimental animals had displayed paw treading

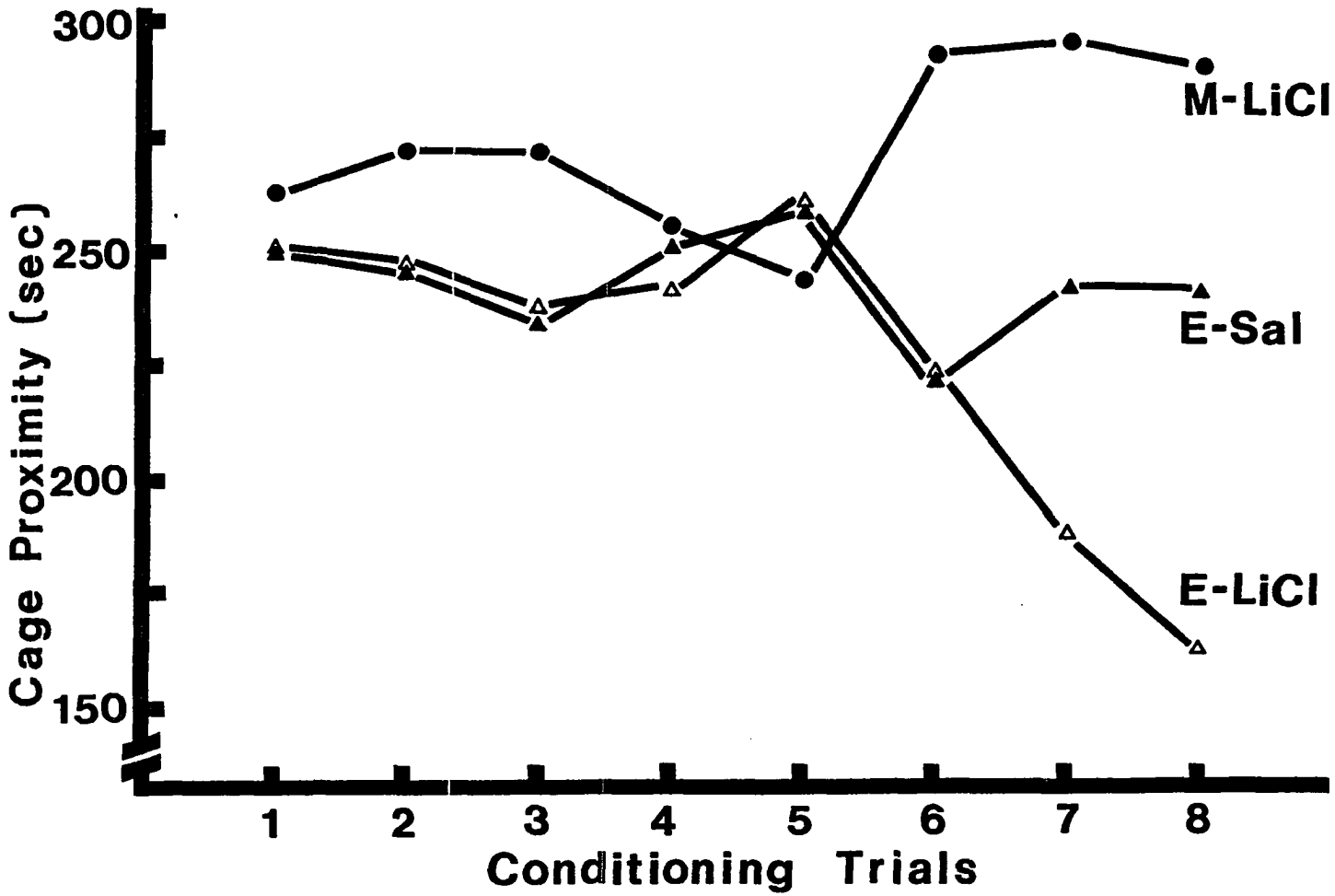
Figure 1. Mean paw treading (PT) and chin rubbing (CR) by experimental groups during conditioning trials in Experiment 2


40
30
20
10
0
PT & CR (sec)
E-LiCl
NE-LiCl
M-LiCl
NR-LiCl
E-Sal
1
2
3
4
5
6
7
8
Conditioning Trials

and/or chin rubbing on at least one occasion. The four exceptions were all in Group NR-LiCl. The Group x Trials interaction was significant [$F(30,282)=1.95$, $p<.01$] and on the last conditioning trial, males in Group E-LiCl were paw treading and chin rubbing significantly more than animals in Groups NR-LiCl and E-Sal ($t=2.49$, $df=16$, $p<.05$ and $t=3.06$, $df=16$, $p<.01$, respectively). The mean amount of paw treading and/or chin rubbing displayed by Group M-LiCl was also significantly greater than that displayed by Group E-Sal ($t=2.28$, $df=15$, $p<.05$). As illustrated in Figure 1, rats in NE-LiCl also displayed a great deal of paw treading and chin rubbing on the last conditioning trial. Due to the large amount of group variance, however, this mean was not significantly different from any other group mean on that trial.

Before conditioning, there were no significant differences between groups in the amount of time spent on the side of the chamber containing the retaining cage (cage proximity, see Figure 2). Based on casual observations in Experiment 1, it was predicted that animals in three experimental groups (E-LiCl, NE-LiCl, and M-LiCl) would spend increasingly less time than control animals near the retaining cage. While significant differences did develop among groups, means

Figure 2. Mean time spent on the side of the chamber containing the retaining cage (cage proximity) for groups during conditioning trials in Experiment 2


300
250
200
150
Cage Proximity (sec)
M-LiCl
E-Sal
E-LiCl
1
2
3
4
5
6
7
8
Conditioning Trials

for Group NE-LiCl were not significantly different from those of control animals (Groups E-Sal and E-Noncon) and of Group NR-LiCl. For more clarity, the means of Groups E-Noncon, NE-LiCl, and NR-LiCl were omitted from Figure 2.

By the sixth conditioning trial, animals in Group M-LiCl were spending virtually all 300 sec of each session on the side of the chamber with the retaining cage containing the stimulus male rat. Initially, rats from all groups would climb over the retaining cage, but by later trials, several rats in Group M-LiCl would remain on top of the cage for the entire session. This posture may have been a dominance gesture, since male rats will often try to urine-mark the top of a hardware cloth block covered with paper toweling that carries odors from a male conspecific (Brown, 1975). By the last conditioning trial, the mean cage proximity score for Group M-LiCl was significantly greater than the corresponding means for Groups E-Sal and E-LiCl (t=3.70, df=15, p<.01 and t=3.26, df=15, p<.01, respectively).

During the last two conditioning trials, rats in Group E-LiCl sharply decreased the amount of time spent near the estrous female. The group mean for the eighth trial approaches significance compared to Group E-Sal (t=2.02, df=16, p<.057).

Based on changes in latency scores and ejaculation rate following the series of conditioning trials, there appears to be uniform conditioning among the three experimental groups in which animals were present in the retaining cage and slightly less suppression of copulatory behavior demonstrated by male rats in Group NR-LiCl. At first glance, the amount of paw treading and chin rubbing displayed by experimental animals appears to correspond well to the subsequent decreases in copulatory behavior. The three experimental groups with the lowest ejaculation rates displayed the most paw treading and chin rubbing, while Group NR-LiCl displayed only a modest amount of these behaviors. Since all rats in Groups E-LiCl, NE-LiCl, and M-LiCl displayed paw treading and/or chin rubbing during conditioning trials, but only half of these rats ejaculated when later paired with an estrous female, paw treading and chin rubbing failed to predict whether a rat would subsequently ejaculate. The presence or absence of these behaviors during the post-conditioning copulation test also failed to predict ejaculation by animals in Group NR-LiCl (Fisher exact test, $p=.50$).

Several methodological differences may explain the failure to replicate the strong conditioning found in Experiment 1. The most obvious possibility is that albino rats may respond differently in this conditioning paradigm than hooded rats.

Since Peters (1983) reported successful modification of sexual behavior with both strains of rats, a strain difference was not expected, and the economic savings represented by the use of albino rats made the change necessary at the time.

The other major methodological change was in the apparatus. New test chambers were constructed. These chambers were more sound-isolated than those used in Experiment 1 because they were completely enclosed and lined with styrofoam. While noise from other animals in adjacent chambers would be diminished with the new apparatus, a different type of disturbance results from the opening and closing of the hinged doors. This additional noise and vibration may disinhibit copulatory behavior.

EXPERIMENT 3

The conditioned suppression of copulatory behavior in albino male rats in Experiment 2 was not as robust as that observed in Experiment 1 with hooded male rats. Therefore, the primary purpose of Experiment 3 was to replicate the robust conditioning of Experiment 1 with Long-Evans hooded rats. Two major changes were incorporated into this third experiment. First, Group NE-LiCl was not included in the design. Even with the precautions taken in Experiment 2, adequate control of estrous odors within the limitations of our research facilities was probably unrealistic.

Second, retaining cages were no longer used to contain the appropriate stimulus (estrous female rat, male rat, or no rat). At the beginning of the experiment, hardware cloth partitions were permanently installed to section off one end of each chamber. With this modification, structural environmental cues remained the same during both conditioning trials and copulation test sessions. It was also of interest to determine if rats in Group M-LiCl would still prefer to be near the stimulus male during later conditioning trials when a superior positioning in space was no longer possible.

Method

Subjects

The subjects were Long-Evans hooded rats (Blue Spruce Farms, Inc., Altamont, New York) housed as in Experiment 2. The animals were approximately 60 days old when they were received from the supplier.

Apparatus

The nine compartments used in Experiment 2 were modified before initial screening for copulatory behaviors. A vertical wall of hardware cloth was installed approximately 13 cm from one end of the chamber to isolate a portion of the chamber. The hardware cloth partitions were securely anchored with pieces of wooden lath extending across their base and nailed to the floor of each compartment. Preliminary study indicated that some rats climbed up the hardware cloth partition. Chicken wire was placed across the top of each chamber to restrict movement from one section into the other.

Stimulus animals

Females were ovariectomized, and estrus was induced as in Experiment 1. Females were screened for receptivity with stud males before each test session. Sexually inactive albino male rats from Experiment 2 served as stimulus animals for Group M-LiCl.

Procedure

When the animals were approximately 90 days old, males were paired with sexually-experienced receptive females. All copulation tests were conducted as in Experiment 2. After one successful copulatory sequence, each male was randomly assigned to a group.

Conditioning sessions were conducted as in Experiment 2 with two exceptions. First, all groups were run on the same test days, and all subjects within a group were run in the same chamber on each test day (i.e., 5 chambers were used per test trial). As in the previous experiments, animals were never paired with the same stimulus animal or run in the same chamber more than twice. Second, stimulus animals were placed in the small section of each chamber partitioned off by hardware cloth rather than in a retaining cage.

Results and Discussion

There were no significant differences among groups for any measures before conditioning.

Decrements in copulatory behaviors were observed in rats that had received LiCl injections immediately following each conditioning session. The percentages of rats that ejaculated in the experimental groups were all significantly ($p<.05$) different from 100% observed for both control groups. As

Table 2

Mean Performance Scores of Male Rats in Experiment 3 Pre- and Post-Conditioning Trials

Group	n	Pre			Post		
		ML	IL	% Ejaculated	ML	IL	% Ejaculated
Experimental							
E-LiCl	10	73	131	100	522**	608**	50†
M-LiCl	10	81	149	100	547**	547**	50†
NR-LiCl	10	98	182	100	538**	543*	60†
Control							
E-Saline	10	72	148	100	28	65	100
E-Noncon	10	48	95	100	13	37	100

Note. ML and IL data are in sec.

*$p<.01$, two-tailed t tests.

**$p<.001$, two-tailed t tests.

†$p<.05$, one-tailed Fisher exact test.

shown in Table 2, approximately half of the rats in each experimental group ejaculated. Further, all three experimental groups had significantly longer latencies to first mount and to first intromission than control animals. Finally, there were no significant differences among experimental groups for these measures.

The conditioned suppression of copulatory behaviors roughly paralleled that observed in Experiment 2. Since copulatory behaviors were comparably suppressed in albino and hooded male rats in Experiments 2 and 3, strain differences cannot account for the differential suppression observed in the first two experiments. The decreased suppression may have been due to the use of new test chambers. A more likely explanation, however, is that the complete suppression of copulatory behaviors in Experiment 1 was exceptional. Copulation is a strongly motivated behavior, and complete suppression after eight conditioning trials may be atypical.

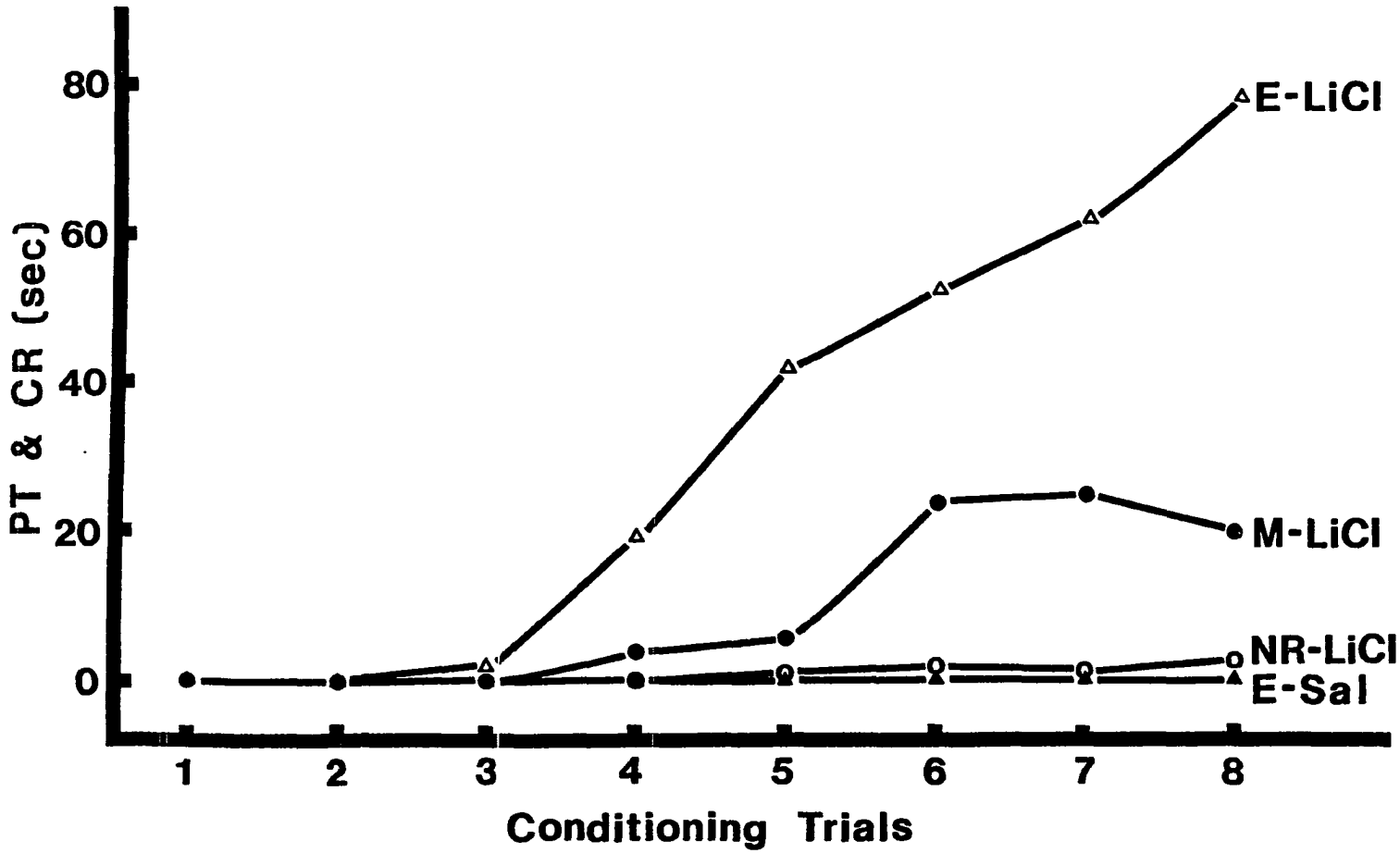
Experimental animals that ejaculated during the post-conditioning copulatory test had fewer intromissions than control animals. The mean number of intromissions preceding ejaculation for rats in Group M-LiCl (3.6) and Group NR-LiCl (5.2) were significantly less than the mean (9.3) for rats in Group E-Sal (t=2.92, df=13, p<.05 and t=2.28, df=14, p<.05,

respectively). Although the mean number of intromissions for rats in Group E-LiCl (5.8) was not significantly different from the means for the other experimental groups, it was also not significantly different from the mean for Group E-Sal. A similar decrease in the number of intromissions required to attain ejaculation has been reported by Peters et al. (1985) in the CIA paradigm.

Over the course of the experiment, rats that received LiCl injections generally gained less weight than rats that received saline injections. Body weight gains were significantly less for rats in Groups E-LiCl and E-Noncon compared with the weight gained by rats in Group E-Sal ($p<.05$). This decrease in body weight gain is often seen with repeated administration of LiCl (Peters et al., 1985), but since all rats that received noncontingent LiCl injections ejaculated during the post-conditioning copulatory test, the lower body weight gain was not a significant factor in the suppression of copulatory behavior demonstrated by rats in Group E-LiCl.

As in Experiment 2, animals that received an injection of LiCl immediately following each exposure to a stimulus animal gradually began to display paw treading and/or chin rubbing after a few conditioning trials (Figure 3). By the

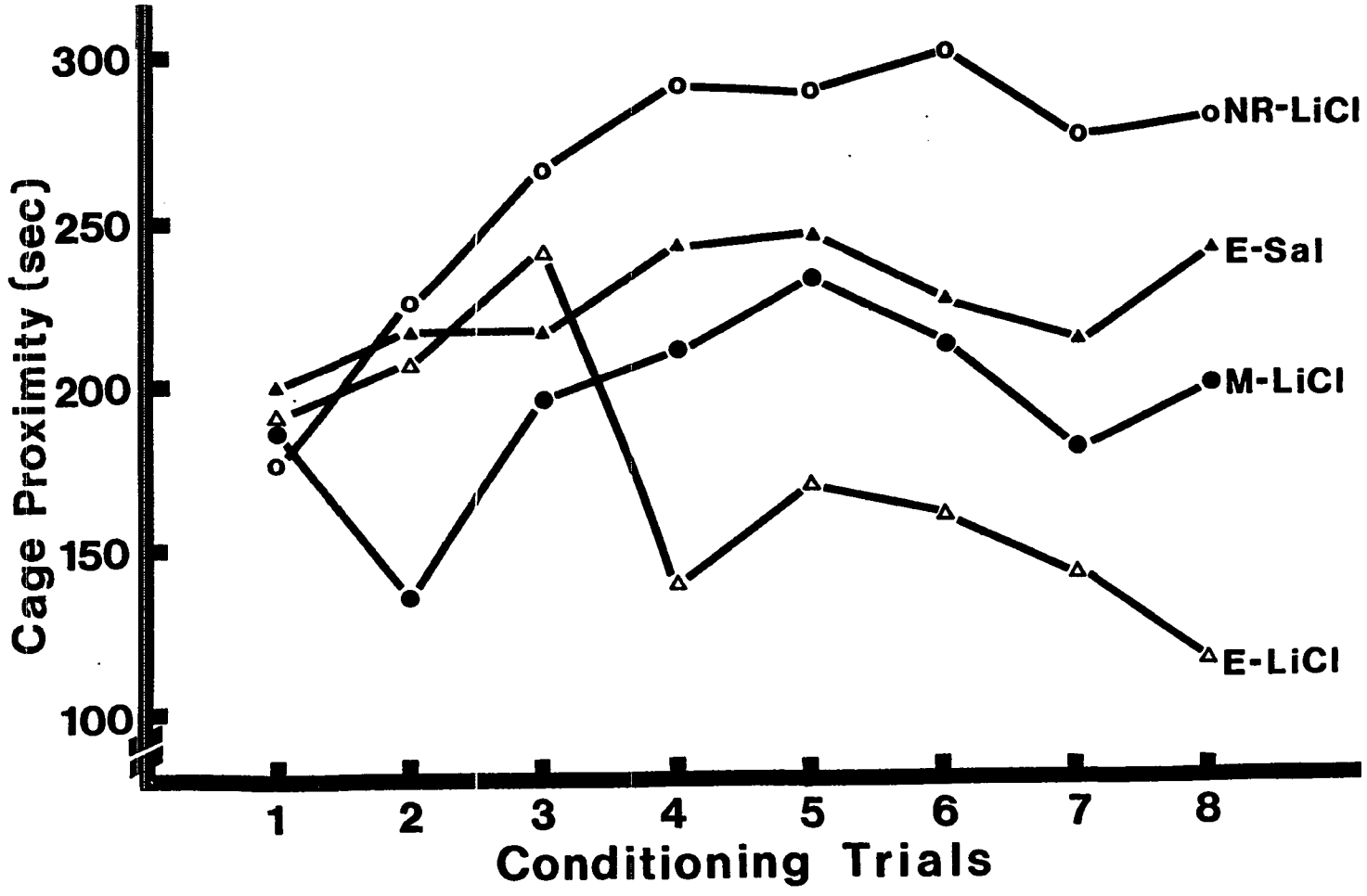
Figure 3. Mean paw treading (PT) and chin rubbing (CR) by experimental groups during conditioning trials in Experiment 3


80
60
40
20
0
PT & CR (sec)
E-LiCl
M-LiCl
NR-LiCl
E-Sal
1
2
3
4
5
6
7
8
Conditioning Trials

last conditioning trial, all rats in Groups E-LiCl and M-LiCl, but only 50% of the rats in Group NR-LiCl, had displayed paw treading and/or chin rubbing during at least one conditioning trial. The mean duration of paw treading and/or chin rubbing displayed by Group E-LiCl (78.5 sec) was significantly greater than that of Group M-LiCl (20.2 sec) which was, in turn, significantly greater than that of Group NR-LiCl (2.7 sec) (t=5.28, df=18, p<.001 and t=4.23, df=18, p<.001, respectively). When subsequently given the opportunity to copulate with an estrous female, all rats in Groups E-LiCl and M-LiCl, but only half the rats in Group NR-LiCl, engaged in paw treading or chin rubbing. There was no significant correlation between the presence or absence of paw treading and/or chin rubbing and the probability of ejaculation during the post-conditioning copulatory test for rats in Group NR-LiCl. No control animals displayed paw treading or chin rubbing at any time during the experiment.

There were no initial group differences (Trial 1) for measures of cage proximity (Figure 4). Originally, all groups preferred the side of the chamber that contained the appropriate stimulus (estrous female rat, male rat or no rat) behind the hardware cloth partition. Over trials, however, significant group differences developed. On the last conditioning trial,

Figure 4. Mean time spent on the side of the chamber with the hardware cloth partition (cage proximity) for groups during conditioning trials in Experiment 3


300
250
200
150
100
Cage Proximity (sec)
NR-LiCl
E-Sal
M-LiCl
E-LiCl
1
2
3
4
5
6
7
8
Conditioning Trials

rats in Group NR-LiCl spent significantly ($p<.05$) more time than any other group on the side of the chamber containing the hardware partition. Casual observations suggested that these rats climbed the partition more often than rats in other groups.

During the last few conditioning trials, rats in Group E-LiCl spent less and less time on the side of the chamber containing the inaccessible estrous female. By the last conditioning session, the mean cage proximity score for rats in Group E-LiCl was significantly ($p<.05$) less than the mean scores for any other group.

In Experiment 2, rats in Group M-LiCl spent more time on the side of the chamber containing the stimulus rat than animals in Group E-Sal. In contrast, the rats in Group M-LiCl in the present experiment spent approximately the same amount of time near the stimulus animal as did rats in Group E-Sal. Two factors may be responsible for this difference in location preference. First, albino rats rather than hooded rats were used as stimulus males in Experiment 3. Second, placement of the stimulus males behind hardware cloth partitions rather than in retaining cages did not permit the experimental rats to assume a dominant position.

EXPERIMENT 4

The majority of odor aversion research has involved pairing biologically irrelevant odors (e.g., peppermint) with illness. A change in response rate (e.g., water consumption) in the presence of that odor has served as an index of the strength of the association. In Experiments 1-3, biologically relevant odor cues were present in the chamber during conditioning trials for all groups. As discussed above, female rats secrete chemical signals which attract males. Male rats also produce chemical signals that appear to be androgen dependent (Nyby, 1983). Even odors from stressed rats can influence activity levels in other male rats (e.g., Mackay-Sim & Laing, 1981). For most groups, a mixture of these odors was present during conditioning trials in various concentrations. The purpose of Experiment 4 was to determine if sexually-active male rats exposed to a biologically irrelevant novel odor (almond extract) followed by LiCl injections would show decrements in subsequent copulatory behavior in the presence of that odor. Biologically irrelevant stimuli (e.g., lights, tones) paired with shock suppress ongoing behavior in the CER paradigm (Estes & Skinner, 1941).

Method

Subjects

This experiment was run concurrently with Experiment 3. Rats of the same strain and age were used as in that experiment.

Apparatus

The nine compartments as modified for Experiment 3 were used for pre- and post-conditioning copulation tests. In a separate room, three operant chambers (Lehigh Valley Electronics) enclosed within sound-attenuating shells (51 x 34 x 28 cm) were used for conditioning sessions. Each operant chamber (30.5 x 21 x 19 cm) had two stainless steel sides, two Plexiglas sides, a Plexiglas ceiling, and a grid floor. Five min before the first animal was introduced to the operant chamber, a petri dish (9 cm diameter) that contained approximately 10 ml of almond extract (Tone's 40% alcohol) was placed within each stainless steel shell in an area that was visually-isolated from the operant chamber. Ventilation fans and house lights were not activated during the experiment.

Procedure

Eight conditioning sessions were conducted at 3-4 day intervals during the middle third of the dark cycle. During a conditioning session, each male rat was placed inside an operant chamber for 300 sec and then received a 20 ml/kg ip

injection of either .3 M LiCl (n=8) or .3 M saline (n=8). Four days after the last conditioning trial, the male rats were tested for copulatory activity with a receptive female as in Experiment 2. Two petri dishes containing almond extract (described above) were placed in the small section of each chamber behind the hardware cloth partition during the post-conditioning copulation test. To avoid introduction of almond odors during copulatory tests of Experiment 3, copulatory tests of this experiment were conducted after those of Experiment 3.

Results and Discussion

There were no significant differences between groups for any measures prior to conditioning.

When given the opportunity to copulate after the series of conditioning trials, only 3 of the 8 rats that had received LiCl ejaculated, as compared to 6 of 8 rats that had received saline. Although this lower proportion of ejaculation for experimental animals compared to that of controls was not significant ($p=.14$), there were significant decrements in other aspects of copulatory behavior observed post-conditioning. The mean latency to first intromission was significantly ($p<.05$) greater for animals that had received LiCl rather than saline (645 and 296, respectively). Analysis of mount frequency data yielded the same pattern of results. Therefore, sexually-active male rats that received LiCl paired with almond extract showed some decrements in copulatory behavior in the presence

of that odor.

All male rats that received a LiCl injection immediately after each conditioning trial displayed paw treading and/or chin rubbing during subsequent pairings with estrous females. It was impossible to determine if these males were paw treading or chin rubbing during the conditioning trials because the operant chambers were enclosed in the stainless steel shells. Animals that received saline injections did not display paw treading or chin rubbing during the copulation test.

After several conditioning sessions, it was observed that some of the male rats were secreting copious amounts of saliva as they were taken from the conditioning chamber to be injected. With more careful observation on later trials, it was noted that only males that received LiCl injections exhibited this strong salivary response. Subsequent research in this laboratory (Koch, 1985) has demonstrated similar secretion of saliva by juvenile male rats that had received LiCl injections paired with exposure to an estrous female. Salivation is a cephalic response that readily conditions to arbitrary stimuli (Pavlov, 1902/1910; Powley, 1977). Although excessive secretion of saliva was not observed in Experiments 1-3, this response may have gone unnoticed during conditioning trials and copulatory tests due to the dim red lighting conditions.

GENERAL DISCUSSION

Comparable suppression of copulatory behaviors was observed in male rats following LiCl-paired exposure to inaccessible estrous female rats, nonestrous female rats, male rats, or to the test chamber itself. Rats that received LiCl injections paired with a novel odor (almond) also displayed copulatory decrements when later paired with a receptive female in the presence of that odor.

Several interpretations of these data are possible. First, animals within various groups may associate the LiCl-induced illness with the most salient cues of the conditioning situation. The most salient cues may be different for each group. In the estrous condition (Group E-LiCl), these cues may be the unique cues associated with estrus. In the nonestrous (Group NE-LiCl) and male rat (Group M-LiCl) conditions, the most salient cues may be characteristics unique to nonestrous females and males, respectively. In the no rat condition (Group NR-LiCl), these cues may be the static cues of the environment. If these salient cues are present during the post-conditioning copulation test, or if generalization occurs to other similar cues available during the test session, then comparable amounts of suppression would be expected. Second, the static cues of the environment

that were common for all groups in Experiments 2 and 3 may mediate the suppression of copulatory behaviors. If the static cues of the environment were more familiar to male rats prior to conditioning trials (Nakaya, 1982), then graded suppressions of copulatory behavior may have been associated with the various stimulus conditions. Finally, associations formed with potent odor cues may be sufficient to mediate conditioned suppression of copulatory behaviors, since exposure to LiCl-paired almond odor in an environment with distinctly different static cues from those present during conditioning also leads to copulatory decrements.

Although comparable suppression of copulatory behaviors was observed for all experimental groups in Experiments 2 and 3, other behavioral measures reflected significant group differences. Rats in Group M-LiCl had copulatory decrements comparable to those of rats in Group E-LiCl, yet differed significantly in the amount of time spent near the stimulus animals during conditioning trials. Toward the end of Experiment 2, rats in Group M-LiCl spent the majority of each trial in close proximity to the male conspecific enclosed in the retaining cage, while rats in Group E-LiCl preferred the side of the chamber away from the estrous female.

When the chambers were modified with hardware cloth partitions in Experiment 3, rats in Group M-LiCl showed no greater preference for the side of the chamber that contained the stimulus animal than control animals. Rats in Group E-LiCl, however, continued to avoid the estrous female contained behind the hardware cloth partition. Therefore, cage proximity scores revealed significant group differences that were not reflected in subsequent copulatory tests.

Groups also displayed differential amounts of paw treading and chin rubbing during conditioning and post-conditioning copulation tests. Group E-LiCl displayed the most paw treading and chin rubbing, and Group M-LiCl displayed more of these behaviors than Group NR-LiCl. Rats that received saline or noncontingent LiCl injections following each exposure to an inaccessible estrous female did not engage in these agitated behaviors.

Paw treading and chin rubbing are part of a typical response sequence to ingestion of very bitter quinine (Teitelbaum & Epstein, 1962) or subsequent ingestion of sapid solutions that have been paired with LiCl (Berridge, Grill, & Norgren, 1981; Garcia et al., 1973; Garcia, Hankins, & Rusiniak, 1974; Grill & Norgren, 1978). Some evidence indicates that paw treading and chin rubbing may be specific

to aversions induced by LiCl. Pelchat, Grill, Rozin, & Jacobs (1983) paired sucrose solution with either LiCl, shock, or lactose (which produces lower gastrointestinal discomfort). Only rats exposed to sucrose that had been paired with LiCl showed any aversive responses (e.g., chin rubbing). Parker (1982) reported that equally strong flavor aversions to saccharin were formed in a single pairing with LiCl and amphetamine, but chin rubbing was displayed only by rats that received saccharin solution that had been paired with LiCl. After three conditioning trials, chin rubbing was still primarily limited to those rats that had received LiCl.

More recently, Parker, Hills, and Jensen (1984) compared the conditioned responses elicited by LiCl- or amphetamine-paired contextual cues of a test chamber. While both drug conditions suppressed grooming activities as unconditioned and conditioned responses, some differences in other activity measures emerged between the two groups. The amount of rearing and line crossing suggested drug-opposite conditioned responses. Even with three conditioning trials, chin rubbing was not observed. Parker et al. (1984) concluded that chin rubbing was probably specific to situations in which flavors serve as the CS. The prevalent chin rubbing observed in the CIA paradigm (Peters, 1983; Peters et al., 1985) and

the present series of experiments indicates that this response can occur within several different conditioning situations. Of course, it could be argued that anogenital sniffing and licking and penile grooming by the male rat during the copulatory sequence provides an opportunity for flavor aversions to form in the CIA paradigm (Peters, 1983). No such contact, however, was possible during the conditioning trials with an inaccessible female in the present experiments. Yet, all male rats in Group E-LiCl eventually displayed chin rubbing.

The most convincing evidence for the ubiquity of paw treading and chin rubbing in LiCl-induced aversive conditioning is provided by rats in Group NR-LiCl. These male rats started to engage in paw treading and chin rubbing during later conditioning trials. This suggests that chin rubbing can occur when LiCl is paired with the exteroceptive cues of the test chamber. The absence of chin rubbing noted by Parker and her colleagues may have been due to the limited number of pairings between LiCl and the contextual cues of the chamber.

Data from this series of experiments demonstrate that associations formed between LiCl and cues other than flavors will elicit paw treading and chin rubbing. As discussed above, the most salient cues of the conditioning situation may

vary across groups. Differential paw treading and chin rubbing may reflect the relative salience of cues that serve as potential conditioned stimuli in each experimental condition.

In summary, multiple pairings of LiCl-induced illness with various stimulus conditions (estrous and nonestrous female rats, male rats, contextual cues of the chamber, almond odor) support comparable suppression of subsequent copulatory behaviors in male rats. Group differences were evident, however, in the differential display of paw treading and chin rubbing, as well as the amount of time spent near the inaccessible stimulus animals during conditioning trials.

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