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Scopolamine Inhibition of Female Sexual Behavior in Rhesus Monkeys (*Macaca mulatta*)

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LYNCH, C. S., T. E. RUPPEL, R. N. DOMINGUE AND G. L. PONTHIER. *Scopolamine inhibition of female sexual behavior in rhesus monkeys* (Macaca mulatta). PHARMACOL BIOCHEM BEHAV **63**(4) 655–661, 1999—Previous research supports the activational role of central cholinergic mechanisms in rodent female sexual behavior. This experiment examined if similar central cholinergic mechanisms facilitate female rhesus monkey (*Macaca mulatta*) sexual behavior. Eight ovariectomized female rhesus monkeys received daily estradiol benzoate priming (5 μg/kg, SC). After 13–16 days of estrogen priming, animals were injected intravenously with either the cholinergic antagonist, scopolamine (0.70 mg/kg), or saline vehicle (1 ml/kg). Results indicate that the female proceptive behaviors of noncontact presentations significantly decreased 15–45 min after scopolamine injection. Scopolamine inhibition was sustained up to 75 min only after 15 days of estrogen priming. Scopolamine did not significantly reduce other female sexual behaviors. Additionally, significant decreases in the number of mounts and intromissions, but not hip touches, were displayed by males exposed to scopolamine-treated females. This research suggests the possibility of a central cholinergic mechanism regulating female sexual behavior in rhesus monkeys. However, the general nature and duration of the cholinergic regulation of primate female sexual behavior differs substantially when compared to rodent behavior. © 1999 Elsevier Science Inc.

Scopolamine Rhesus monkeys Acetylcholine Female sexual behavior

CHOLINERGIC mechanisms have been implicated in the regulation of female rodent receptive sexual responses, such as lordosis (10) and solicitations (13). In intact, cycling female rats, sexual behavior is dependent on the presence of estrogen, and is significantly enhanced by the presence of progesterone (7). The display of lordosis and solicitations can be affected through pharmacological manipulations of estrogen-dependent, central cholinergic mechanisms (12).

Recent manipulations of central cholinergic mechanisms by administration of cholinergic agonists and antagonists in intact and hormonally primed, ovariectomized female rats have reliably supported an activational role for central cholinergic mechanisms in the regulation of rodent female sexual behavior. For example, administration of the cholinergic antagonists, scopolamine or hemicholinium-3, decreased female sexual behaviors in intact proestrous–estrous and hormone primed ovariectomized female rats (9,13,19). Conversely, infusion of the cholinergic agonists, physostigmine, facilitated lordosis responding in intact female rats, but only during proestrus when endogenous estrogen levels are elevated (20). However, physostigmine did induce lordosis during middiestrus and diestrus II if females were primed with free estradiol (21). This study further suggests that endogenous estrogen levels at diestrus are too low to prime cholinergic mechanisms involved in lordosis, and elevations in estrogen levels above diestrous titers are sufficient to facilitate the cholinergic regulation of female sexual behavior. Furthermore, scopolamine inhibition of lordosis was found to vary relative to the dose and duration of estrogen priming (17,22). These results support the estrogen dependency of the cholinergic regulation of rodent female sexual behavior.

The possibility of central cholinergic regulation of the rhesus monkey sexual behavior has not been investigated. However, previous clinical research on human schizophrenic patients has reported that infusion of acetylcholine directly into the septum resulted in increased electroencephalographic activity accompanied by reports of intense sexual pleasure by the patient (16). This finding suggests the possibility that central cholinergic regulation of sexual behavior is not limited to rodent sexual behavior, and may be evident in primates.

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The steroid regulation of female sexual behavior in rhesus monkeys has been proposed. Periovulatory increases in female sexual behavior in rhesus monkeys in pair test situations have been reported (14,15,23–25). However, while some report periovulatory increases in initiation of proximity and solicitation (11,28), others report no relationship between the hormonal condition of the female and the occurrence of presentations in the pair test situation (18,24,26). Therefore, while there appears to be evidence for the hormonal regulation of rhesus female sexual behavior, this regulation appears to be highly varied in the pair test situation. The periovulatory increase of rhesus female sexual behavior in more naturalistic settings has been reliably demonstrated (33,34). Collectively, these studies and others examining the influence of spatial constraints on sexual behavior (30) may indicate that the space for social interaction may influence and/or interfere with hormonally regulated events, especially in the tight constraints of the pair test situation. Nevertheless, these findings do provide support for the hormonal regulation of sexual behavior in female rhesus monkeys.

Based on these studies, it is suggested that high levels of endogenous estrogen increase female sexual behavior in rhesus monkeys. Because previous rodent research has reported similar findings, it is possible that similar central cholinergic mechanisms that are responsible for regulating female receptive and proceptive rodent behavior may likewise be involved in rhesus monkey sexual behavior. If this is true, then female rhesus sexual behaviors may be reduced by administration of cholinergic antagonists, such as scopolamine. To determine the role of cholinergic mechanisms upon female rhesus monkey sexual behavior, male–female sexual interactions were measured before and after administration of a cholinergic antagonist, scopolamine, to ovariectomized female rhesus monkeys primed for 13 days with high levels of estradiol benzoate (5 μg/kg) daily. If the cholinergic regulation of proceptive or receptive behaviors in rhesus monkeys is similar to rodents, then it is expected that these female sexual behaviors will significantly decrease after intravenous administration of the cholinergic antagonist.

METHOD

Animals

Eight ovariectomized adult female rhesus monkeys between 8–13 years of age were used in this experiment. However, one female was dropped from the study due to problems with intravenous injections of the cholinergic agent on the first day of testing. Four intact male rhesus monkeys between 8–13 years of age were used as stimulus males during behavioral testing. Previous reports suggest that no significant differences in female solicitation patterns were apparent for rhesus females ranging in ages from 8–26 years (27). All animals were reared to adulthood at the New Iberia Research Center, Louisiana. All female rhesus monkeys had at least one offspring, and ranged in weight from 5 to 12 kg. Both the stimulus males and the females were sexually experienced. Testing was performed in two treatment rooms each housing four females and two males. Female monkeys were housed separately in squeeze cages, four squeeze cages per testing room, in a temperature-controlled environment. All eight female rhesus monkeys were exposed to 4 weeks of pole and collar training prior to behavioral testing. Three days before scopolamine infusion, four male monkeys were removed from their social groups and placed in four stud cages, two cages per testing room. Both males and females had access to water ad lib, and were fed twice daily, once in the morning and once after testing.

Pole and Collar Training

During the testing procedure, females were restrained for intravenous injection by means of a specialized restraint chair (Primate Products, Redwood City, CA). All female animals were exposed to 4 weeks of pole and collar training prior to behavioral testing under direct supervision by the veterinary staff at New Iberia Research Center. This pole and collar method was recommended as a humane, safe, and effective method for moving and restraining animals during drug infusion. In week 1 of pole and collar training, two poles (approximately 2 m long) were inserted into each squeeze cage and secured to a restraint collar attached to the neck of the female rhesus. In week 2, the animals were removed from their cages and walked in the vicinity of the testing room via two 4-m guiding poles. In week 3, the animals were led to the restraint chair by the guiding poles and restrained until animal resistance ceased. Finally, in week 4 the animals were led to the restraint chair, restrained, and lightly touched on the arms by the experimenters to desensitize the animals for future venous injections. This training schedule was adopted in an attempt to reduce stress to the females that may interfere with their sexual performance during the behavioral tests.

Animal Preparation

Ovariectomies were conducted by Dr. Hasselschwert, resident veterinarian, and her support clinical staff at New Iberia Research Center. Prior to ovariectomy, each female received Ketamine as a preanesthetic. Anesthesia during surgery was maintained with isoflurane. A single 1.57-cm midline incision allowed for removal of the ovaries. Lack of menstruation was noted during subsequent monitoring of menstrual cyclicity after the completion of the project, suggesting that ovariectomies did result in a substantial reduction in gonadal steroid production.

Animals were allowed 2 weeks after ovariectomy for recovery before estrogen priming was initiated. At this time, each female received daily injections of 5 μg/kg, SC, estradiol benzoate (Sigma Chem. Co., St. Louis, MO) for 16 days at 1500 h. This dose and estradiol benzoate priming schedule are equivalent to the amount of endogenous estrogen around ovulation, and was chosen to maximize solicitation behaviors by the female, and thus, elicit male copulation attempts (29).

Behavioral Measures

The complexity of the male–female interaction of rhesus monkeys is quite elaborate, with as many as 42 distinguishable sexual behavior parameters (33). Although there exists an extensive repertoire of behaviors that can occur during a typical mating session, certain behaviors predominate during the copulatory sequence. Parsimoniously, the following predominant rhesus monkey female sexual behaviors that have been previously defined (3,32,33) were measured: present, intromission, mounts, proximity, back proximity, grooming, crouching, and hip touch.

Testing Procedure

All tests occurred between 1230 and 1500 h during the summer months, and were performed in strict accordance to National Institute of Health procedure for testing of laboratory animals. The procedures used were reviewed and approved by the USL IACUC (Institutional Animal Care and Use Committee) before initiation.

Estrogen priming described above and behavioral testing occurred in two 4-week phases, separated by a 2-week period.

Because of the short-lived actions of cholinergic agents, such as scopolamine (i.e., maximum effectiveness is usually 15–45 min after administration), a typical pair-testing situation was used despite its limitations. Pair testing, in this case, allowed for immediate access to the female for cholinergic manipulation, as well as immediate return of the female to the test situation.

During phase 1, behavioral testing of each female occurred daily over 4 days, 21 h after the 13th, 14th, 15th, and 16th estradiol benzoate injection. Behavioral tests were conducted in a divided stud cage (37.80 × 11.22 × 10.63 cm). To begin, the female was escorted to the divided stud cage that housed a stimulus male. The divider was left in place to allow for a 30-min habituation time. After 30 min, the divider was removed and the female was allowed contact with the stimulus male for a 30-min behavioral pretest.

After 30 min, the female was removed, escorted to a restraining chair, restrained, and injected intravenously in the saphenous vein with either 0.70 mg/kg scopolamine hydrobromide (Sigma Chem. Co., St. Louis, MO) or saline vehicle (1 ml/kg). Previous research concerning scopolamine administration to rhesus monkeys used intravenous dosages ranging from 1.0–1.78 mg/kg (1). Due to the lack of previous research concerning scopolamine administration and rhesus monkey sexual behavior, this scopolamine dosage was determined to be effective through previous pilot research with two ovariectomized females at New Iberia Research Center.

Fifteen minutes following venous injection, the female was reintroduced to the stimulus male in the stud cage for a 60-min behavioral test. After 60 min, the female was removed from the stud cage and returned to her home cage. Behavioral data was video-recorded and scored at a later date. Estradiol benzoate injection followed behavioral testing on the first 3 days of behavioral testing. Following phase 1, each animal was allowed a 2-week rest period without injections or manipulations. During phase 2, 16-day estradiol benzoate priming and 4-day behavioral testing was repeated in a similar manner as that described above during phase 1.

The schedule of injections followed a repeated-measures ABAB/BABA matched-design procedure, with scopolamine injection occurring during the A conditions and saline injection occurring during the B conditions. Therefore, animals assigned to the ABAB procedure received scopolamine on the first and third day of behavioral testing, whereas animals assigned to the BABA procedure received scopolamine on the second and fourth day of behavioral testing. During phase 1, testing was conducted across 4 weeks, with two females assigned to the ABAB procedure during the first week, another two females assigned to the BABA procedure during the second week, another two females assigned to the ABAB procedure during the third week, and the last two females assigned to the BABA procedure during the fourth week. During phase 2, injection procedure assignments were reversed such that each animal that was assigned to the ABAB procedure during phase 1 was assigned to the BABA procedure during phase 2, and those animals that were assigned to the BABA procedure during phase 1 were assigned to the ABAB procedure during phase 2.

Data Analysis

All videotaped behaviors were scored by one observer. VCR time coding of videotapes was used for calculation of duration measures (i.e., proximity, back proximity, or grooming). Discrete measures (i.e., presents, intromissions, mounts, hip-touches, crouches) were counted. Because seven animals were tested in eight sessions (ABAB, BABA) with three repeated measures (PRE, POST-1, POST-2) within each session, 168 measurements in all were analyzed and compared for each duration and discrete dependent variable.

A one-way analysis of variance (ANOVA) over repeated measures was used to evaluate the effect of cholinergic treatment (i.e., scopolamine or saline) upon female rhesus monkey proceptive and receptive sexual behaviors before drug infusion (PRE), 15–45 min after drug infusion (POST-1), and 45–75 min after drug infusion (POST-2) for all 4 days of drug treatment. Independent comparisons determined drug effects at each repeated measure. Independent comparisons, followed by Fishers Protected LSD post hoc comparisons, were also used to examine changes across repeated testing in each drug-treated group. Finally, independent ANOVAS were used to examine drug effects at each day of testing. Note that alternative nonparametric and regression analyses conducted are not reported here, as they did not enhance the interpretation of the current results.

RESULTS

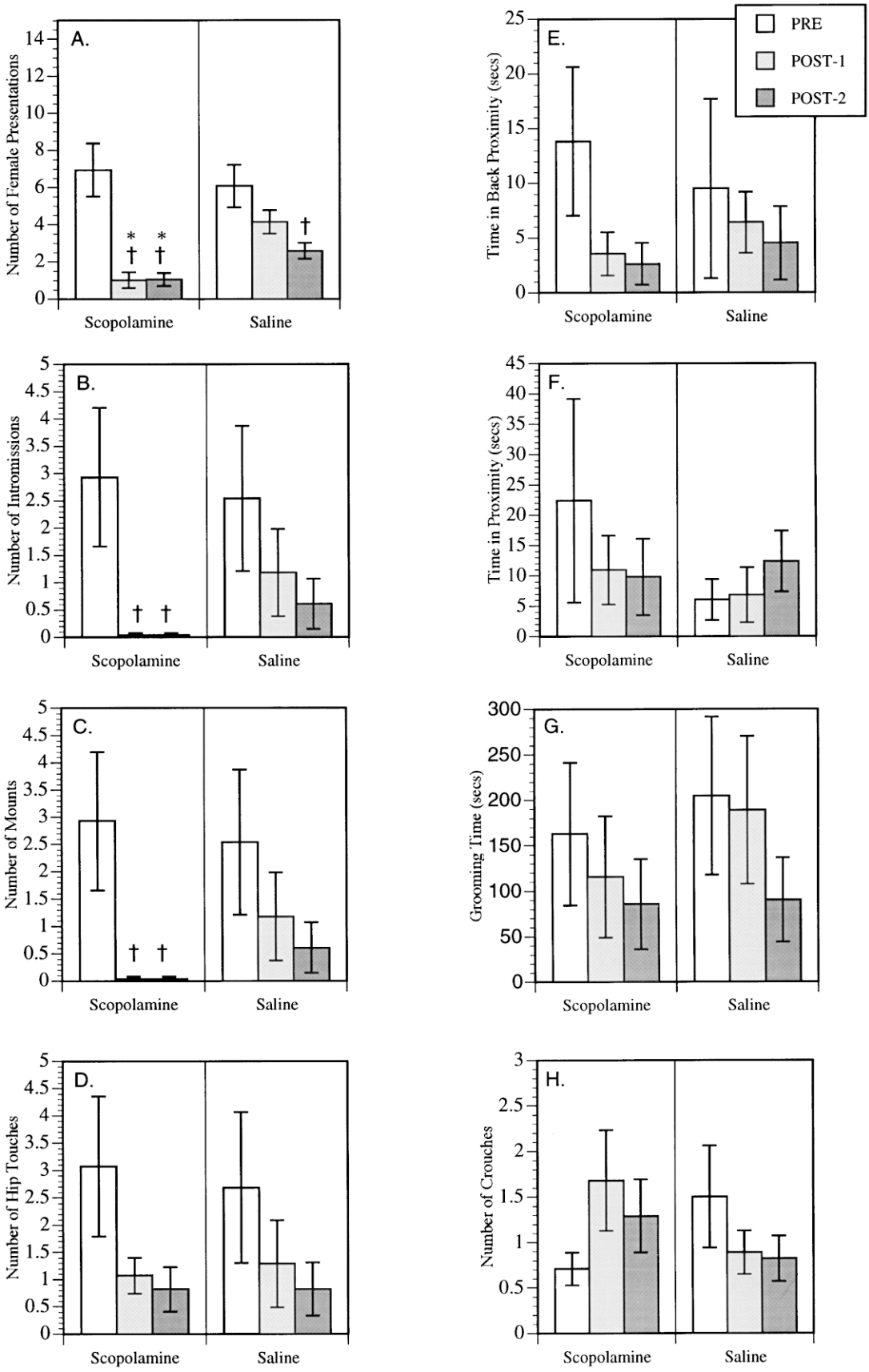
Scopolamine vs. Saline

Scopolamine treatment compared to saline treatment reduced overall female presentations $F(2,108) = 19.86$, $p = 0.0001$ (see Fig. 1). The remaining four measures of female sexual behaviors (i.e., time in back proximity, time in proximity to male, grooming time, and number of crouches) were highly varied and not statistically significant (see Fig. 1). No significant differences across drug treatments were found in male sexual behavior (i.e., number of intromissions, mounts, and hip touches) (see Fig. 1).

Female presentations. Independent comparisons of treatment effects on female presentations indicated no significant differences between the scopolamine-treated and saline-treated females during PRE. This suggests that sexual behavior patterns were equivalent before drug administration. However, independent comparisons of female presentations at POST-1 and POST-2 analyzed across treatment days and at each day indicated significant drug effects.

Females treated with scopolamine ($n = 7$) displayed significantly fewer presentations after drug infusion across all testing days when compared to females treated with saline ($n = 7$), $F(2,108) = 19.86$, $p = 0.0001$ (see Fig. 1, graph A). Independent comparisons of drug effects at POST-1 indicated that mean female presentations were significantly reduced after scopolamine treatment when compared to presentations after saline treatment, $F(1,55) = 22.86$, $p = 0.0001$. The significant decrease in female presentations after scopolamine treatment continued into POST-2, $F(1, 55) = 11.78$, $p = 0.0012$, suggesting that the inhibitory effect of scopolamine on female presentations continued for 45–75 min after drug infusion.

Drug effects on presentations were also found to differ across days of treatment. Significantly fewer female presentations were observed for the females treated with scopolamine after 13 days, $F, (2, 24) = 6.32$, $p = 0.0063$, 15 days, $F(2, 24) = 6.08$, $p = 0.0073$, and 16 days, $F(2, 24) = 5.32$, $p = 0.0123$, of estradiol benzoate priming. Independent comparisons of drug effects at POST-1 indicated that female presentations were significantly reduced by scopolamine after 13 days, $F(1, 13) = 1.92$, $p = 0.0028$, 15 days, $F(1, 13) = 6.92$, $p = 0.0219$, and 16 days, $F(1, 13) = 7.24$, $p = 0.0196$, of estradiol benzoate priming. Therefore, treatment with a cholinergic antagonist decreased female proceptive behavior on 3 of the 4 days of treatment. Despite variation across days, these results may


A.
Number of Female Presentations
Scopolamine
Saline
B.
Number of Intromissions
C.
Number of Mounts
D.
Number of Hip Touches
E.
Time in Back Proximity (secs)
PRE
POST-1
POST-2
F.
Time in Proximity (secs)
G.
Grooming Time (secs)
H.
Number of Crouches

suggest the cholinergic regulation of female rhesus monkey proceptive behavior.

Independent comparisons of drug effects at POST-2 indicated that mean female presentations were significantly reduced by scopolamine after 15 days of estradiol benzoate priming only, $F(1, 13) = 14.00$, $p = 0.0028$. This indicates that the scopolamine-induced decrease in female presentations lasted for up to 75 min after drug administration only on the third day of treatment. Unlike previous research using rodents, this current finding suggests that scopolamine effects in rhesus monkeys may not be limited to 45 min. Furthermore, because this sustained effect was only observed on one day of behavioral testing, this may indicate that estrogen priming of cholinergic mechanisms differs across days.

Scopolamine Effects Across Tests: Pretest vs. POST-1 vs. POST-2

Independent comparisons across repeated measures of scopolamine-treated females indicated significant decreases in female presentations ($p = 0.0001$) (see Fig. 1, graph A). These decreases occurred at both POST-1 ($p < 0.05$) and POST-2 ($p < 0.05$) after scopolamine treatment. However, independent comparisons of saline-treated females also indicated a significant decrease in presentations at POST-2 ($p < 0.05$) after saline treatment. As mentioned before, analysis of drug effects at POST-2 indicated that presentations in the scopolamine-treated females were significantly less than presentations in the saline-treated females. Therefore, scopolamine-induced decreases in presentations are considered to occur during the POST-2, despite the general decline in presentations observed during this phase.

Independent comparisons across repeated measures of scopolamine-treated females also indicated significant decreases in the male sexual behaviors of intromissions ($p = 0.0076$) and mounting ($p = 0.0076$) at POST-1 ($p < 0.05$) and POST-2 ($p < 0.05$) after scopolamine treatment (see Fig. 1, graphs B and C). Note that in all cases, mounts and intromissions were equivalent, suggesting that all mounts resulted in intromissions.

Scopolamine Effects Across Days of Estradiol Benzoate Priming

The means for scopolamine-treated females were analyzed across days to further determine if scopolamine treatment varied significantly by day. There were no significant differences in scopolamine-induced female presentations across days. This suggests that the decreases in presentations, intromissions, and mounts by scopolamine were consistent across testing days. Therefore, there was no additive effect of repeated scopolamine treatment on female presentations. Furthermore, this may suggest that variability in female presentations across days occurred independent of cholinergic mechanisms.

DISCUSSION

The results of this experiment indicate that cholinergic mechanisms may regulate certain components of female sexual behavior in rhesus monkeys. Intravenous infusion of the cholinergic antagonist, scopolamine, significantly reduced female presentations compared to saline controls. Scopolamine did not significantly alter other female sexual behaviors, such as back proximity, proximity to male, grooming, or crouches.

Scopolamine administration to females also decreased male responsiveness to the females, as indicated by a significant decrease in the number of mounts and intromissions. However, decreases in the number of hip touches after scopolamine were not significant, suggesting that not all hip touches resulted in copulation after scopolamine treatment. Nevertheless, the persistence of hip touching after scopolamine treatment may suggest that males were still motivated to initiate interaction with drug-altered females. It was observed that when hip-touched, the drug-altered females often time interrupted the copulatory sequence by moving away. Interestingly, grooming also continued after scopolamine administration, further suggesting that the scopolamine-treated females were still motivated to socially interact.

Although there were significant decreases in female presentations and male mounts and intromissions after scopolamine, there were also general declines in female and male sexual behavior after saline as well. This general decline in both female and male sexual behavior would indicate that experimental manipulation alone may have interfered with the sexual interactions. This is understandable, considering that the female was removed from the test cage, restrained, and injected intravenously. Nevertheless, scopolamine reduced these sexual behaviors to a significantly greater degree than that seen after saline injection. Therefore, despite the interruption in the sexual behavior created by the experimental manipulation and the restriction of the pair-testing situation used, scopolamine effects were still evident.

The current results that reveal that scopolamine significantly disrupted female presentations in estrogen-treated rhesus monkeys are consistent with previous research that has reported that scopolamine consistently reduced the incidences of lordosis, solicitive behavior, and mate preference in hormone-primed female rodents (8,9,13). Although these female sexual behaviors do differ substantially across species, these results do indicate, however, that at least certain sexual behaviors in rhesus monkeys may be cholinergically regulated. However, the fact that scopolamine had no significant effect upon other female sexual behaviors does not necessarily suggest that other female sexual behaviors are not regulated by the same cholinergic mechanisms. Alternatively, the dose of estrogen and or scopolamine may have been inadequate to produce an effect upon the other sexual behaviors measured in this study. Also, the lack of a scopolamine inhibition of other female sexual behaviors measured in this experi-

FIG. 1. Mean number of presentations (A), number of intromissions (B), number of mounts (C), number of hip touches (D), time in back proximity (E), time in proximity to male (F), time in affiliative grooming (G), and number of crouches (H) (±SEM) representing female and male sexual behaviors before (PRE), 15–45 min after (POST-1), and 45–75 min after (POST-2) intravenous infusion of either scopolamine (0.70 mg/kg) or saline vehicle across all 4 days of scopolamine treatment ($n = 7$). Each animal had received daily SC injections of estradiol benzoate (5 μg/kg) for 13 days before the first day of behavioral testing and throughout behavioral testing. The mean number of presentations was significantly less after scopolamine vs. saline (*$p = 0.0001$). The mean number of mounts and intromissions was less after scopolamine treatment compared to before scopolamine treatment (†$p = 0.0076$).

ment may be due to the dimensions of the behavioral testing space and the lack of freedom available to the female. Previous research has shown that when female rhesus monkeys are given greater freedom to control heterosexual interactions, female proceptive sexual behaviors increase (6,28,30,31). Therefore, female control of the pacing of sexual interactions appears to be a factor that should be included in future research.

Previous research has reported that the inhibitory effect of scopolamine on female rodent proceptive and receptive behavior was dependent upon the level of endogenous estrogen (13,17,22). The current results reveal that scopolamine significantly disrupted female presentations for a prolonged period after 15 days of estrogen priming. Although this experiment suggests that endogenous levels of estrogen were sufficient to prime cholinergic mechanisms after 13 days in the rhesus monkey, estrogen priming of cholinergic mechanisms may be maximal after 15 days of estrogen treatment.

Although this study reported that some monkey sexual behaviors may be under central cholinergic regulation, more research in this area is necessary using varied doses of estrogen and or varied doses of cholinergic agonists and/or antagonists before the cholinergic regulation of primate sexual behavior can be substantiated. Also, because scopolamine has been found to impair memory task performance in monkeys (1,2,4,5), it is possible that scopolamine inhibition of female presentations could be regulated indirectly by alternative central cholinergic mechanisms, such as those involved in learning and memory. These factors must be explored as well. However, the cholinergic regulation of other primate female sexual behaviors may become more evident by examining the scopolamine inhibition of rhesus sexual behavior under less restrictive conditions or within various social settings.

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