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Dopaminergic Drugs in the Medial Preoptic Area and Nucleus Accumbens: Effects on Motor Activity, Sexual Motivation, and Sexual Performance

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MOSES, J., J. A. LOUCKS, H. L. WATSON, L. MATUSZEWICH AND E. M. HULL. *Dopaminergic drugs in the medial preoptic area and nucleus accumbens: Effects on motor activity, sexual motivation, and sexual performance.* PHARMACOL BIOCHEM BEHAV 51(4) 681-686, 1995.—In two experiments, dopamine agonists and/or antagonists were injected into the medial preoptic area (MPOA) or the nucleus accumbens (NAcc) of male rats. The animals were then tested in an X-maze with four goal boxes, which contained a receptive female, a male, or were empty. In Experiment 1, the D_1 antagonist SCH-23390 and the D_2 antagonist raclopride in the MPOA decreased the percentage of trials on which the female's chamber was chosen, a measure of sexual motivation. Raclopride also decreased the number of animals that copulated after choosing the female's chamber. The 10-μg dose of the D_3/D_2 agonist quinelorane increased the latency to reach the female's chamber, slowed the onset of copulation, and decreased the number of intromissions preceding an ejaculation. In Experiment 2, 1- and 5-μg doses of quinelorane and of the mixed D_1/D_2 agonist apomorphine were injected bilaterally into the NAcc. Both doses of quinelorane increased the number of times that the subject did not select a chamber within 60 s. No drug in the NAcc affected specifically sexual motivation or performance. The results are consistent with differential influence of the MPOA and the NAcc on motor activity, sexual motivation, and sexual performance.

Medial preoptic area (MPOA) Nucleus accumbens (NAcc) Dopamine Apomorphine Quinelorane SCH-23390 Raclopride Sexual behavior D_1 and D_2 receptors Rats

DOPAMINE (DA) activity in the medial preoptic area (MPOA) appears to facilitate several aspects of copulation. Microinjection of the DA agonist apomorphine into the MPOA increased copulatory rate and the number of ejaculations per test (12); it also increased the number of ex copula penile reflexes (erections and anteroflexions, or "flips") (25). On the other hand, microinjections of the DA antagonist *cis*-flupenthixol reduced the number of males that initiated copulation and slowed the rate of those that did (24); it also decreased penile reflexes and sexual motivation (choice of the female in an X-maze) (29). Motor activity was not affected (24,29).

Stimulation of the two major families of DA receptors in the MPOA differentially affects sexual behavior. [Although at least five subtypes of DA receptors have been cloned, the D_1 and D_5 subtypes are included in the D_1 family, whereas the D_2, D_3, and D_4 subtypes constitute the D_2 family (5). We refer here to any of the variants within the two families.] Stimulation of D_1 receptors speeded the rate of copulation and increased the number of ejaculations (20); it also increased the number of ex copula penile reflexes (16). These effects are similar to those of low doses (0.2-1 μg) of apomorphine (12,25). On the other hand, a relatively high dose of the D_3/D_2 agonist quinelorane (10 μg) delayed and slowed copulation (13), decreased the number of ex copula penile reflexes, but increased ex copula seminal emissions (1). Thus, stimulation

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of D_1 receptors in the MPOA may facilitate the early stage of copulation, whereas stimulation of receptors in the D_2 family may shift to the ejaculatory phase.

The mesolimbic DA tract has been implicated in virtually all types of motivated behaviors, including feeding, copulation, drug self-administration, and electrical self-stimulation (3,8,9,19,21,23,27,28,30). However, the mesolimbic tract may be more important for sensorimotor activation than for specifically sexual motivation (3,18). Decreasing mesolimbic activity, by stimulating autoreceptors in the VTA, delayed and slowed copulation (14), and also increased the latency to reach all chambers of an X-maze (15). However, it did not decrease the percentage of trials on which the male selected the female's chamber. Furthermore, in videotaped copulation tests this treatment increased the number of misdirected or incomplete mounts and decreased the number of active behaviors (walking, grooming, rearing, etc.) (15). Therefore, the mesolimbic tract may be more important for general activation or interaction with the environment than with specifically sexual behavior.

Studies using systemically administered drugs have suggested that D_1 and D_2 families of receptors have synergistic effects on numerous behaviors that are thought to be regulated by the mesolimbic and/or nigrostriatal DA tracts (6). The present experiments were conducted to clarify further the roles of D_1 and D_2 families of receptors in the MPOA and the NAcc in the consummatory vs. motivational aspects of male sexual behavior. Animals were tested in an X-maze, which contained a receptive female in one of the four goal boxes, to dissociate motor activation (latency to reach any chamber and the number of trials on which the male failed to move from the choice area) from specifically sexual motivation (percent of trials on which the male chose the female's goal box). Copulatory performance was assessed on those trials on which the male chose the female's chamber.

METHOD

Subjects

Forty male Long-Evans (300–350 g Harlan Sprague-Dawley/Blue Spruce) rats were divided into two groups of 20. Subjects were singly housed in clear plastic cages in a temperature- and humidity-controlled environment on a 14L : 10D cycle (lights off at 1100 h). Food and water were available ad lib.

Surgical Procedure

Subjects were anesthetized with ketamine hydrochloride (50 mg/kg) and xylazine hydrochloride (4 mg/kg), and were implanted with intracranial cannulae according to the procedure of Hull et al. (12). In Experiment 1, a single cannula was aimed to end 1 mm above the MPOA (AP 2.4, ML 0.2, and DV − 7.0 mm from bregma) (26). In Experiment 2, bilateral cannulae were aimed to end 1 mm above the NAcc (AP 4.0, ML 1.4 and DV − 8.2 mm from bregma) (26).

Drug delivery immediately before testing was accomplished by removing the obturator, placing an injection cannula attached to PE-20 polyethylene tubing within the guide cannula, and, with the aid of a Harvard infusion pump, administering drug or vehicle at a rate of 1 μl per min. The injection cannula protruded 1 mm below the level of the guide cannula. The injection cannula remained in place for 30 s after drug delivery and was then removed and replaced by the obturator. In Experiment 2, drug or vehicle was infused into one cannula and, after a 30-s pause, into the other.

Materials

X-Maze devices were constructed of plywood and painted white. These mazes were a plus-shaped design with small chambers situated off to the side at the end of each of the four arms. Each arm, excluding the chamber, was 15.24 cm wide and extended 30.48 cm from a 15.24 × 15.24 cm central hub. Chambers were 30.48 × 30.48 cm. The chamber designated to be that of the female was marked with a 15 cm high "X" in black electrical tape on the wall at the end of the arm, so as to be visible to a rat in the center of the maze. A piece of black electrical tape was stretched across the floor of the maze even with the near end of each chamber; crossing this line with both forepaws was recorded as a choice of that chamber. Objects in the chambers were out of sight of a rat placed in the center and were separated from the arms of the maze by a removeable, clear Plexiglas barrier.

Data were collected on a network of four IBM-compatible computers utilizing a data collection program written by Stephen Yeoh.

Drugs

Drugs were dissolved in a solution of 0.2% ascorbic acid and water immediately prior to testing. The mixed D_1/D_2 agonist apomorphine was purchased from Sigma Chemical Company. The D_3/D_2 agonist quinelorane was donated by Dr. Mark Foreman, Eli Lily and Company (Indianapolis, IN). The D_1 antagonist SCH-23390 was donated by Dr. Allen Barnett, Schering corporation (Bloomfield, NJ). The D_2 antagonist raclopride was a gift of Dr. Sven Ahlenius (Astra Pharmaceuticals, Sodertalje, Sweden).

Procedure

Preoperative conditioning consisted of training sessions every 3 days in the X-maze. In the first training session the subject was allowed 30 min to explore the maze without the Plexiglas barriers or other rats. Then an estrogen-primed, receptive female was put into the chamber marked with the "X," and the subject was allowed 30 min to copulate with her. On subsequent training sessions a receptive female was placed into the female chamber and a stud male was placed into the chamber directly opposite that of the female. The experimental subject was placed into the female's chamber, allowed one intromission, and then placed into the center of the maze. The direction in which the male was faced when placed into the center was alternated from trial to trial. To gain access to any chamber the subject had to place two feet over the black electrical tape separating the arms from the chambers within 60 s. The Plexiglas barrier was raised and the subject either entered the chamber of his own volition or was gently pushed in. If the selected chamber was other than the female's chamber, the subject was retained within the chamber for 30 s, removed, and placed into the center of the maze again. If the subject selected the female's chamber, he was allowed a maximum of 5 min to perform an intromission or ejaculation, after which he was removed from the chamber and placed into the center of the maze again (in the case of an intromission) or the test was concluded (in the case of an ejaculation). If the male did not perform an intromission or an ejaculation in 5 min, he was raised out of the chamber and placed into the center again. Three trials in which the male entered the female's chamber but did not perform an intromission ended the test. If the subject did not select a chamber within the allotted 60 s on 10 occasions, the test was concluded.

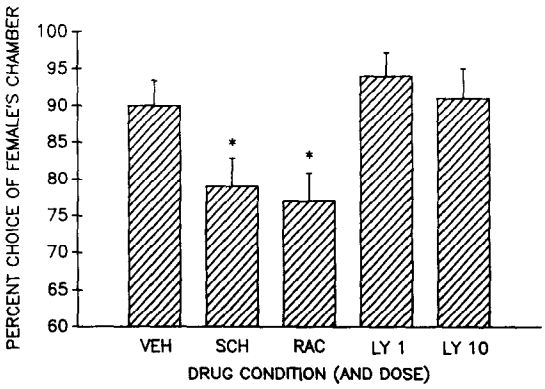

FIG. 1. Effects of SCH-23390 (SCH, 10 μg), raclopride (RAC, 10 μg), and quinelorane (LY 1, 1 μg; LY 10, 10 μg) injected into the MPOA on the percent choice of a female's chamber. Both SCH-23390 and raclopride decreased the percent choice of the female's chamber. VEH, vehicle. *$p < 0.05$.

Conditioning and testing were carried out under dim red light. X-Mazes were always placed in the same configuration with respect to room features to ensure that external cues were held constant. After a subject achieved ejaculation, he was removed and all arms and chambers of the X-maze were wiped down with a weak soap and water solution in preparation for the next test. Testing was scheduled once a week and ran from 1300 through 1600 h.

Preoperative conditioning was concluded when each subject achieved the criterion of selecting the female's chamber on 70% of all trials in which they chose a chamber. At this point, subjects underwent surgical implantation of cannulae. After a 7-day recovery period, subjects were given three postoperative conditioning trials over a period of 2 weeks or until they again chose the female's chamber on 70% of the trials on which they chose a chamber. A week later testing began, using the same protocol with one exception; after an initial intromission with a receptive female, drug and/or vehicle was injected, and the subject was immediately placed into the center of the maze to resume testing.

In Experiment 1, 1 or 10 μg of the D_3/D_2 agonist quinelorane (LY-163502) (4), 10 μg of the D_2 antagonist raclopride (11), 10 μg of the D_1 antagonist SCH-23390 (17), or vehicle was microinjected into the MPOA. In Experiment 2, 1 or 5 μg per side of the D_2 agonist quinelorane, 1 or 5 μg per side of the mixed D_1/D_2 agonist apomorphine, or vehicle was microinjected into the NAcc. All animals within each experiment received all treatments in counterbalanced order.

Histology

Following the experiment, subjects were anesthetized and decapitated, after which their brains were removed and frozen in a Reichert-Jung Cryocut 1800 cryostat. Sections (40 μm) were cut, mounted on slides, stained with cresyl violet, and examined with a projection magnifier. Only those animals with histologically verifiable cannulae in the MPOA ($N = 17$, in Experiment 1) or the NAcc ($N = 16$, in Experiment 2) were included in data analysis. We have previously reported that dye injections of 0.5 μl are confined to a volume approximately 0.5 mm in radius (12).

Statistical Analysis

Data were analyzed by one-way repeated-measures analyses of variance (ANOVA), followed by Newman-Keuls comparisons among groups. These results are presented as means + SEs. For several measures data from only those subjects that committed a particular action were analyzed, using ANOVAs for independent groups (for example, number of intromissions preceding ejaculation only for animals that ejaculated). The number of males not copulating after reaching the female's chamber was analyzed by Cochran's Q-test, followed by McNemar's paired comparisons.

RESULTS

Experiment 1

Both the D_1 (SCH-23390) and the D_2 (raclopride) antagonists, microinjected into the MPOA, decreased the percentage of trials on which the female's chamber was chosen, $F(4, 64) = 6.35, p < 0.001$ (Fig. 1). Raclopride, compared to all other treatments, increased the number of males that did not copulate on any of the three trials in which they chose the female's

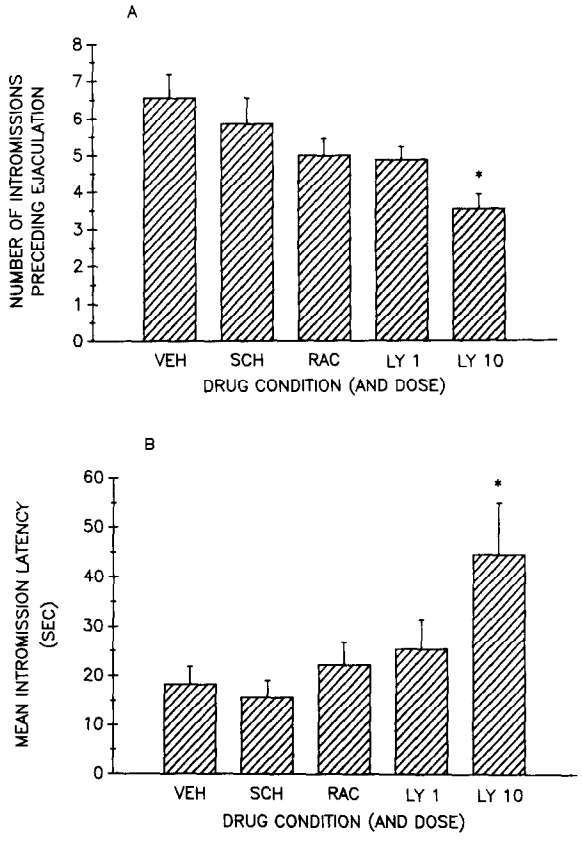

FIG. 2. (A) Effects of SCH-23390 (SCH, 10 μg), raclopride (RAC, 10 μg), and quinelorane (LY 1, 1 μg; LY 10, 10 μg) injected into the MPOA on the number of intromissions preceding ejaculation. The 10-μg dose of quinelorane reduced the number of intromissions necessary to achieve ejaculation. (B) Effects of SCH-23390 (SCH, 10 μg), raclopride (RAC, 10 μg), and quinelorane (LY 1, 1 μg; LY 10, 10 μg) injected into the MPOA on the mean intromission latency (measured from the time when the male stepped over a line, signaling a choice of the female's chamber). The 10-μg dose of quinelorane increased intromission latency. VEH, vehicle. *$p < 0.05$.

chamber [vehicle, 1; SCH-2330, 1; raclopride, 7; 1 μg quinelorane, 0; 10 μg quinelorane, 2; $Q(4) = 15.4$, $p < 0.005$]. A similar comparison of the number of males that failed to copulate on any one trial revealed a significant difference only between raclopride and the 1-μg dose of quinelorane, which produced a slight facilitation of copulation [vehicle, 4; SCH-23390, 6; raclopride, 10; 1 μg quinelorane, 1; 10 μg quinelorane, 6; $Q(4) = 12.71$, $p < 0.01$]. The 10-μg dose of the D_3/D_2 agonist quinelorane decreased the number of intromissions preceding ejaculation in animals that did ejaculate, $F(4, 63) = 4.55$, $p < 0.005$ (Fig. 2A), and slowed the onset of copulation, as reflected by an increased latency to intromit, $F(4, 63) = 3.3$, $p < 0.025$ (Fig. 2B).

There were few adverse effects of these dopaminergic drugs on general motor activities. No condition affected failure to select a chamber within the allotted 60 s. The 10-μg dose of quinelorane significantly increased the latency to reach the female's chamber, $F(4, 64) = 5.37$, $p < 0.001$ (Fig. 3). A similar trend towards increased latency to reach all other chambers was not statistically significant, in part because many animals failed to choose any chamber other than the female's, and in part because of the variability of the latencies of those that did.

Experiment 2

No drug microinjected into the NAcc affected the percentage of trials on which the male selected the female's chamber compared to vehicle condition. Similarly, there were no effects on various copulatory measures, including intromission frequency, intromission latency, and the number of males not copulating after entering the female's chamber.

However, both doses of quinelorane increased the number of times that the male did not make a chamber selection, $F(4, 60) = 10.46$, $p < 0.001$ (Fig. 4A). These instances of not selecting a chamber were not spread throughout the experimental session but were clustered at the beginning of the session. Thus, both doses of quinelorane increased the number of trials it took to select the female's chamber for the first time, $F(4, 60) = 6.22$, $p < 0.001$ (Fig. 4B).

DISCUSSION

In Experiment 1, microinjections of the D_1 and D_2 antagonists, SCH-23390 and raclopride, into the MPOA decreased the percentage of trials on which the male selected the female's chamber. This finding suggests that D_1 and D_2 receptors in the MPOA act synergistically to promote sexual motivation. The two families of receptors may also act together to disinhibit (decrease the latency of) genital reflexes, but may act with different thresholds to promote erections, via D_1 stimulation, and then to shift autonomic balance to favor ejaculation, via high threshold D_2 stimulation (16).

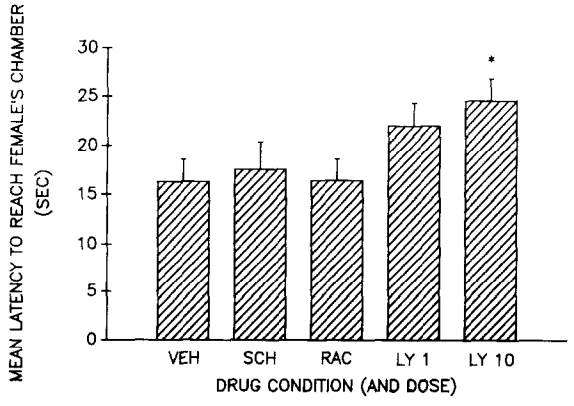

FIG. 3. Effects of SCH-23390 (SCH, 10 μg), raclopride (RAC, 10 μg), and quinelorane (LY 1, 1 μg; LY 10, 10 μg) injected into the MPOA on mean latency to reach the female's chamber. The 10-μg dose of quinelorane increased the latency to reach the female's chamber. VEH, vehicle. $*p < 0.05$.

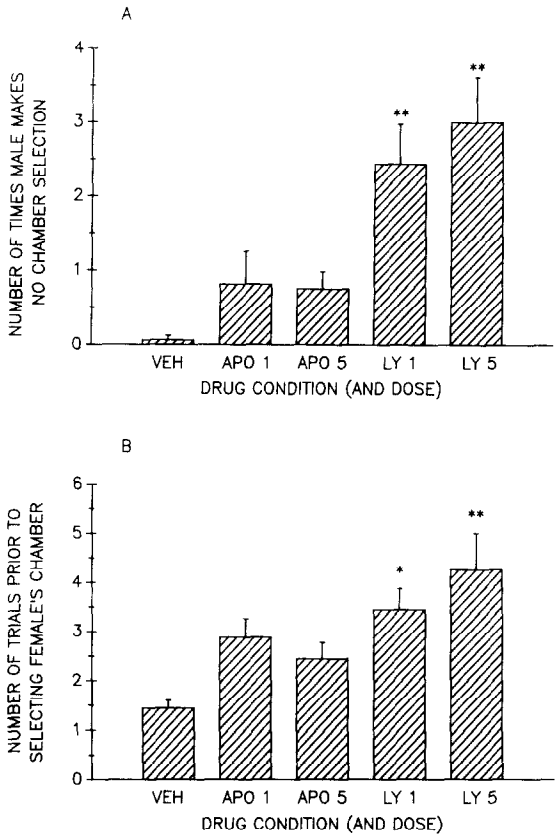

FIG. 4. (A) Effects of apomorphine (APO 1, 1 μg; APO 5, 5 μg), and quinelorane (LY 1, 1 μg; LY 5, 5 μg) injected bilaterally into the NAcc on the number of times that the male made no chamber selection. Both doses of quinelorane increased the number of instances in which the male did not make a chamber selection. (B) effects of apomorphine (APO 1, 1 μg; APO 5, 5 μg) and quinelorane (LY 1, 1 μg; LY 5, 5 μg) injected into the NAcc on the number of trials before the male selected the female's chamber. Both doses of quinelorane increased the number of trials prior to selection of the female's chamber. VEH, vehicle. $*p < 0.05$, $**p < 0.01$.

On the other hand, only the D_2 antagonist raclopride increased the number of animals that failed to copulate on all three trials on which they chose the female's chamber. Animals that did copulate were allowed as many trials as necessary to achieve an ejaculation; however, the test was ended after three 5-min periods in which the male failed to copulate after choosing the female's chamber. The number of males that failed to copulate on any one or more trials was increased by raclopride only in comparison with the 1-μg dose of quinelorane. Neither the slight impairment by raclopride nor the slight facilitation by quinelorane was significantly different from vehicle.

The effects of the 10-μg dose of quinelorane on copulatory

performance in Experiment 1 are consistent with a previous report that the same treatment increased the latency to intromit and decreased the number of intromissions necessary to achieve an ejaculation (13). The difference between the slight facilitative effect of the 1-μg dose on ability to copulate after reaching the female's chamber is in contrast with the effects of the 10-μg dose, which delayed the onset of copulation, but, once the male began to copulate, enhanced his ejaculatory ability. These data emphasize the dose dependence of effects of agonists of the D_2 family, as noted previously (1,10,13,16).

These copulatory effects were not due to a general drug-induced motor deficiency. Neither the number of times that the male did not select a chamber within the allotted time nor the latency to reach chambers other than that of the female was affected by any drug manipulation. In another measure of motor activity, only the 10-μg dose of quinelorane had an effect on the latency to reach the female's chamber, increasing the latency compared to the vehicle condition. This will be discussed below.

In Experiment 2 there were no effects of any drug on motivation to engage in copulation or on various copulatory measures. On the other hand, quinelorane did increase the number of times that the male did not make a chamber selection. These results are similar to those of a previous report in which apomorphine in the VTA, which would have stimulated autoreceptors and thereby decreased activity of the mesolimbic tract, slowed running speed to chambers in the X-maze, but had no effect on the percent choice of the female's chamber (15). Taken together, these results suggest that the mesolimbic DA tract has less to do with specifically sexual motivation than with the motor activational aspects and/or sensorimotor integration of copulation.

In light of this suggestion, it is interesting to compare the behavior of rats with quinelorane in the NAcc, which displayed an increase in the number of times that they did not select a chamber, with the behavior of rats with quinelorane in the MPOA, which displayed an increased latency to reach the female's chamber. Although these behaviors were not quantified, the observers noted that rats receiving quinelorane in the NAcc remained immobile in the center of the maze for the first few trials. This is similar to a finding of Mogenson and Wu (22) that the D_3/D_2 agonist quinpirole in the NAcc produced a dose-dependent reduction of exploratory locomotion; administration of the D_1 agonist SKF-38393 had no effect. On the other hand, when the 10-μg dose of quinelorane was injected into the MPOA in Experiment 1, rats spent time exploring the X-maze and avoided stepping over the line that would have signalled a chamber selection. This result agrees with a recent finding (7) that the 10-μg dose of quinelorane in the MPOA increased walking and rearing, while delaying the onset of copulation, in a videotaped copulation study. These competing behaviors may have increased the latency to reach the female's chamber in Experiment 1 as well. Similarly, the trend towards increased latency to reach other chambers is consistent with this interpretation. Thus, the increased latencies would reflect, not a general motor retardation, but rather, enhanced exploration.

Everitt (8) has suggested that the motivational aspect of copulation is controlled by the mesolimbic DA tract whereas the consummatory portion is mediated by the MPOA. The results of the present experiments suggest otherwise. Specifically, dopaminergic drugs in the MPOA affected not only the consummatory behaviors of copulation (mounts, intromissions, and ejaculations), but influenced motivation as well, decreasing the percent choice of the female's chamber. The influence of dopaminergic agents in a primary terminal area of the mesolimbic DA tract, the NAcc, on the other hand, was limited to disruptions in motor activity.

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