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Apomorphine Facilitates Male Sexual Behavior of Rhesus Monkeys[1]

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POMERANTZ, S. M. *Apomorphine facilitates male sexual behavior of rhesus monkeys.* PHARMACOL BIOCHEM BEHAV **35**(3) 659–664, 1990.—In the present study, a novel sexual behavior paradigm was used to study the effects of the dopamine agonist, apomorphine, on male sexual behavior of rhesus monkeys. In Experiment 1, the effects of apomorphine treatment were assessed by observing the behavioral responses of male rhesus to a sexually receptive female monkey that they could see, hear, and smell, but could not physically contact. Apomorphine treatment produced a spectrum of behavioral effects that differed depending on the dose of drug administered. Low doses of apomorphine (25–100 μg/kg) stimulated yawning, moderate doses (50–200 μg/kg) facilitated male sexual responses associated with the genitals including penile erection and masturbation, and high doses (>200 μg/kg) elicited stereotypic behavior. Experiment 2 examined whether the behavioral responses of male monkeys to apomorphine treatment were influenced by the stimulus female. Apomorphine treatment facilitated penile erections in tests in which a stimulus female was present, but did not facilitate erections in tests in which she was absent. In sum, these experiments provide preliminary evidence that dopaminergic mechanisms may play a role in the regulation of male sexual behavior of rhesus monkeys.

Apomorphine Dopamine Male sex behavior Penile erection Rhesus monkeys Primates

RESEARCH with rats suggests that dopaminergic activity may play a role in regulating male sexual behavior. Specifically, drugs which increase dopaminergic activity by stimulating either dopamine synthesis or postsynaptic dopamine receptor sties have been found to facilitate male sexual behavior (1, 2, 8, 10, 16, 18, 19, 28), whereas drugs that decrease dopaminergic activity by inhibiting either dopamine synthesis or blocking postsynaptic receptor sites have been found to reduce male sexual behavior (1, 16, 28). Although a great deal is known regarding the mechanism of action of dopamine in regulating male rat sexual behavior, very little is known regarding dopaminergic regulation of male sexual behavior in other species including primates. In studies conducted on rhesus monkeys, administration of the dopamine agonist, apomorphine, did not reliably influence male copulatory performance (6, 7, 22); however, a reduction of male sexual behavior was observed following administration of the dopamine antagonist, sulpiride (7).

Recently it has been reported that apomorphine stimulated the occurrence of penile erections in both normal and impotent men (12,14). Previous studies evaluating the effects of apomorphine on sexual behavior of rhesus monkeys have concentrated on copulatory measures of male sexual behavior and paid little attention to possible effects that these compounds might have on other noncopulatory measures such as penile erection. Therefore, the present study was designed to evaluate the effects of apomorphine on various noncopulatory measures of male sexual behavior. In order to accomplish this aim a novel testing paradigm was developed in which male rhesus monkeys were tested under conditions in which they were exposed to a sexually receptive female that they could see, hear, and smell, but could not physically contact. Under these testing conditions penile erections, courtship behavior, and masturbatory behaviors of male rhesus monkeys were able to be evaluated.

METHOD

Subjects

Sexually experienced male rhesus monkeys that were 8–12 years of age and born in breeding facilities in the U.S. were used as experimental subjects. Eight males were used in Experiment 1. In Experiment 2, seven males used in Experiment 1 and two additional males not used previously served as subjects. A pool of six adult female rhesus monkeys served as stimulus females, with three of these females serving as stimulus females with two different males each. Females were treated with estradiol cypionate (500 μg/week IM). This hormonal regimen maintains blood levels of estradiol around 300 pg/ml while reliably stimulating female sexual behavior (4).

Monkeys were individually housed in rooms that were temperature (18–21°C) and light controlled (12:12 light:dark with lights on at 0700 hr). They were fed Purina Monkey Chow supplemented with fresh fruit. Water was available ad lib.

Apparatus

A wire mesh cage with a clear Lexan front and stainless steel partition dividing the cage into two identical compartments (0.9 ×

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0.8 × 0.85 m) was used as a testing cage. The floor of the cage was 0.75 m above the floor of the room. During the experiment, males lived on one side of the cage and were tested on the other side of the cage. A clear Lexan transport cage (0.75 × 0.40 × 0.70 m) with wheels mounted on the bottom was used to present the stimulus female to the males.

Experiment 1—Procedure

Males were moved into the testing cage the day before the experiment began. In the experiment, males were transported in the testing cage to an empty experimental room. They were then removed briefly (<2 min) from the testing cage, weighed, injected (IM) with either apomorphine or 1 mM ascorbic acid vehicle in a counterbalanced fashion, and then returned to the testing cage in the compartment opposite to the one in which they were previously housed. Each monkey was run through a range of apomorphine doses (25, 50, 100, 200 and 400 μg/kg) using a Latin Square design. Ten minutes following apomorphine or vehicle injection, a sexual stimulus female was placed in the transport cage and wheeled into the experimental room so that she was situated approximately 0.5 m in front of the testing cage. An observer sat 1 m from the transport cage and scored the male's behavior for the next fifteen minutes. The 15-min test was divided into 10-sec blocks, and each block in which a behavior was observed was recorded as one occurrence of that behavior. The following sexual behaviors were scored: purse-lip courtship gesture (23), penile erection, and masturbation. Penile erections were classified according to three grades of intensity: Grade 1—the glans penis visibly protruded from the penile sheath; grade 2—the glans penis and shaft of the penis largely extended, but not fully erect; and grade 3—penis fully erect and oriented at less than a 90° angle from the male's trunk. Although capable of exhibiting a single sustained penile erection, the monkeys never exhibited such a response in this testing situation. Rather, monkeys tended to exhibit multiple erections that varied in duration. Additionally, during the course of an erection the intensity often varied; therefore, for each 10-sec period, a monkey received a score for the highest intensity of erection exhibited during that period. Nonsexual behaviors were also scored including yawning and stereotypic behavior. After the 15-min test was concluded the stimulus female was returned to her home cage and the experimental male was transferred back to the testing cage compartment in which he was originally housed prior to the test. Males were maintained in the testing cage until the experiment was completed. Testing was conducted Monday through Friday between 1400 hr and 1730 hr.

Experiment 2—Procedure

Males were treated and tested on four consecutive days. On alternate days males received either 100 μg/kg apomorphine or ascorbic acid vehicle injection. Ten minutes following treatment, either an empty transport cage or a transport cage containing a stimulus female was placed in front of the male's cage and behavior scored for the next fifteen minutes. Testing conditions were counterbalanced such that half the males were tested with the female first and half were tested with an empty transport cage first.

Data Analysis

In Experiment 1, one-way analysis of variance (ANOVA) tests were conducted to determine whether repeated testing of the monkeys influenced their behavior in vehicle tests. Since no effects of repeated testing were found for any of the behaviors being assessed, for each behavior the males' mean score in vehicle tests was used in subsequent analyses aimed at evaluating the effects of apomorphine. For these analyses, repeated measures one-way ANOVA tests were conducted. Analyses yielding significant overall effects were followed by post hoc comparisons using the Duncan multiple range test (30). In Experiment 2, behavior was analyzed using repeated measures two-way ANOVA tests, with the effects of drug treatment (apomorphine vs. vehicle) and testing condition (stimulus female present or absent) being analyzed.

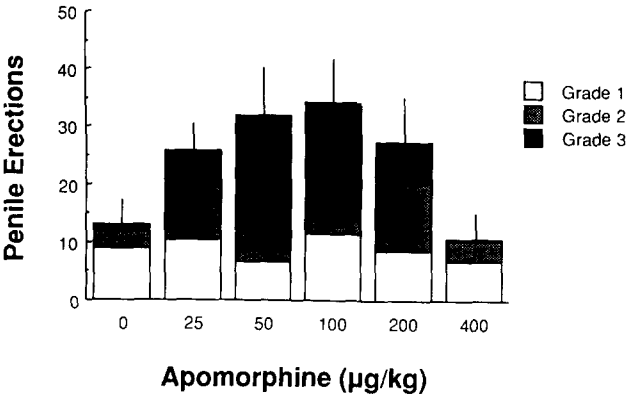

FIG. 1. Mean ± SEM number of 10-sec periods in which male rhesus monkeys (N = 8) exhibited grade 1, grade 2 and grade 3 penile erections following administration of varying doses of apomorphine (25–400 μg/kg) or 1 mM ascorbic acid vehicle.

RESULTS

Experiment 1

As shown in Fig. 1, apomorphine produced a dose-dependent stimulation of penile erection. The effect of apomorphine on the total sum of all three grades of penile erection was significant, $F(5,35) = 4.03$, $p < 0.01$. Further analysis revealed that apomorphine significantly influenced performance of grade 2 and 3 erections, $F(5,35) = 4.11$, $p < 0.01$, but not grade 1 erections ($F < 1.0$). Compared to vehicle treatment, the facilitation of penile erection by apomorphine was statistically reliable at 50, 100 and 200 μg/kg apomorphine ($p < 0.05$). At 400 μg/kg apomorphine, however, a significant decline in penile erections was observed ($p < 0.05$) such that monkeys were performing at a level that was not found to differ reliably from their performance under vehicle conditions. Two monkeys failed to exhibit any penile erections following treatment with 400 μg/kg apomorphine. These were the only two tests in the experiment in which no penile erections were observed.

Figure 2 depicts the masturbatory behavior of the monkeys. A reliable increase in genital masturbation was observed following apomorphine treatment, $F(5,35) = 2.52$, $p < 0.05$. The frequency of masturbatory behavior in monkeys administered 100 μg/kg apomorphine was significantly higher than that observed in monkeys administered vehicle or 25, 200, or 400 μg/kg apomorphine ($p < 0.05$). Six of the eight monkeys tested exhibited an apomorphine-dependent increase in masturbatory behavior. The remaining two monkeys failed to exhibit masturbation under any of the treatment conditions. Masturbation proceeded to an ejaculation in two instances, both of which occurred when the monkeys received 100 μg/kg apomorphine.

The effect of apomorphine on purse-lip courtship gestures is

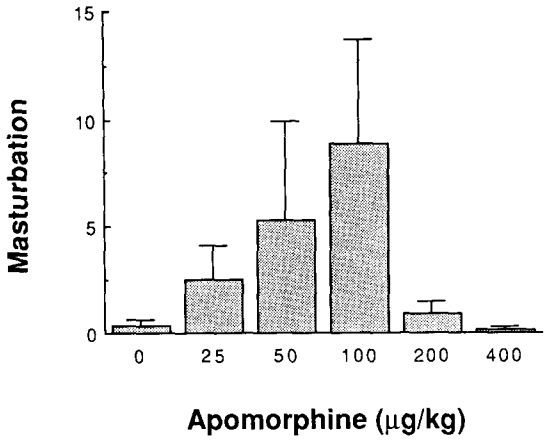

FIG. 2. Mean ± SEM number of 10-sec periods in which male rhesus monkeys (N = 8) exhibited masturbation following administration of apomorphine or 1 mM ascorbic acid vehicle.

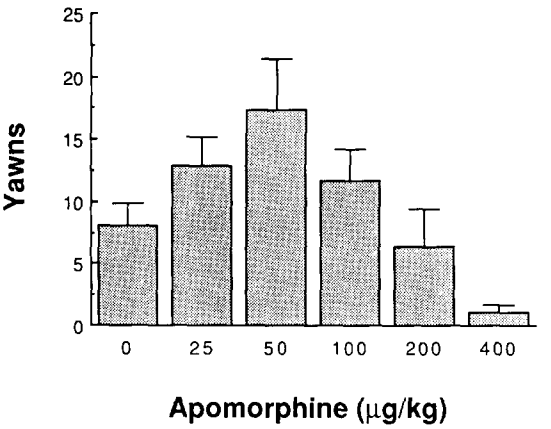

FIG. 4. Mean ± SEM number of 10-sec periods in which male rhesus monkeys (N = 8) exhibited yawning following administration of apomorphine or 1 mM ascorbic acid vehicle.

shown in Fig. 3. At least one purse-lip gesture was exhibited in every test. An increase in courtship behavior was observed following treatment with 100 and 200 μg/kg apomorphine; however, this increase was not statistically reliable ($F<1.0$).

As shown in Fig. 4, apomorphine produced a biphasic effect on yawning, $F(5,35)=7.12$, $p<0.001$. Compared to vehicle-based performance, yawning was significantly increased in monkeys treated with 50 μg/kg apomorphine ($p<0.01$) and was significantly decreased in monkeys treated with 400 μg/kg apomorphine ($p<0.01$). Two monkeys failed to yawn at 200 μg/kg apomorphine and three monkeys failed to yawn following treatment with 400 μg/kg apomorphine. In all other tests at least one yawning response was observed.

Figure 5 shows that apomorphine produced a dose-dependent increase in stereotypic behavior, $F(5,35)=9.34$, $p<0.001$. The predominant behavioral stereotypy being exhibited under these conditions was one in which the males gnawed and fingered a chain that was attached to the cage for protracted periods of time. During this period they would orient away from the stimulus female. It should be noted that locomotor stereotypies were not observed at the dosages of apomorphine used in this experiment. Compared to vehicle performance the induction of stereotypic behavior was statistically reliable at 200 μg/kg apomorphine ($p<0.05$), with a further increase being observed at 400 μg/kg apomorphine. Consistent with these findings, stereotypic behavior was observed in only 25% of the monkeys administered doses of apomorphine less than 100 μg/kg, whereas stereotypy was observed in 37.5%, 75%, and 87.5% of the monkeys administered 100, 200 and 400 μg/kg apomorphine, respectively.

Experiment 2

The effect of manipulating both drug treatment and social testing conditions on behavior of rhesus monkeys is shown in Table 1. The presence of the stimulus female reliably stimulated grade 1 penile responses regardless of whether or not apomorphine was administered, $F(1,8)=8.54$, $p<0.05$. Apomorphine failed to influence this penile response ($F<1.0$) and the interaction of treatment and testing conditions was not significant ($F<1.0$). In contrast, performance of both grade 2, $F(1,8)=41.6$, $p<0.001$, and grade 3, $F(1,8)=5.84$, $p<0.05$, penile erections was signif-

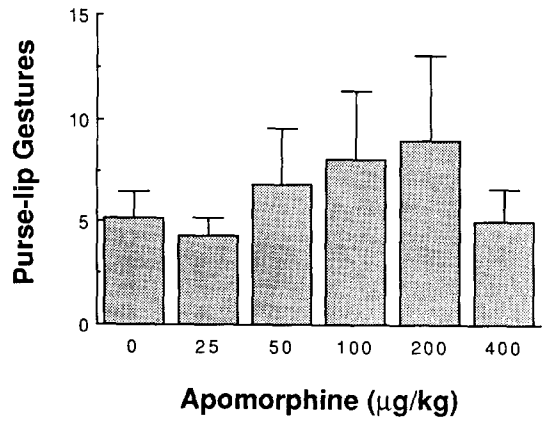

FIG. 3. Mean ± SEM number of 10-sec periods in which male rhesus monkeys (N = 8) exhibited courtship purse-lip gestures following administration of apomorphine or 1 mM ascorbic acid vehicle.

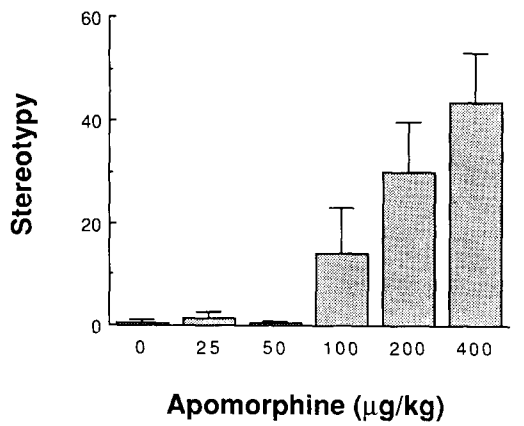

FIG. 5. Mean ± SEM number of 10-sec periods in which male rhesus monkeys (N = 8) exhibited stereotypic behavior following administration of apomorphine or 1 mM ascorbic acid vehicle.

TABLE 1

EFFECT OF FEMALE PRESENCE/ABSENCE AND APOMORPHINE/VEHICLE TREATMENT ON BEHAVIOR OF MALE RHESUS MONKEYS

	Female Present		Female Absent	
Behavior*	Apomorphine	Vehicle	Apomorphine	Vehicle
Penile Erection				
Grade 1	12.0 ± 3.0	10.5 ± 2.9	3.3 ± 1.4	2.3 ± 1.2
Grade 2	14.4 ± 2.0	2.2 ± 0.8	1.4 ± 1.0	0.1 ± 0.1
Grade 3	9.9 ± 4.5	0.6 ± 0.5	0.7 ± 0.7	0.1 ± 0.1
Purse-Lip Gesture	9.5 ± 3.2	6.6 ± 1.8	0.3 ± 0.3	0.1 ± 0.1
Yawn	12.3 ± 2.7	7.8 ± 1.9	12.4 ± 3.7	9.5 ± 3.3

*Values represent mean ± SEM.

icantly influenced by a drug treatment × social testing condition interaction. These grades of penile erections were most prominently exhibited in tests in which apomorphine was administered and the stimulus female was present. Under other treatment and social testing conditions grade 2 and grade 3 penile erections seldom occurred.

In the absence of the stimulus female, only one of the nine males exhibited purse-lip gestures. By contrast, in the presence of the stimulus female all the males under both vehicle and apomorphine treatment exhibited courtship purse-lip gestures. Similar to Experiment 1, in tests in which the stimulus female was present, apomorphine treatment was not found to significantly influence courtship behavior performance, $F(1,8)=2.78$, $p>0.05$. Masturbation was not observed in any of the monkeys following vehicle treatment in tests in which the stimulus female was absent. Two of the nine males masturbated following apomorphine treatment in the absence of the stimulus female; whereas, in the presence of the stimulus female, three males masturbated following vehicle administration, and six males masturbated following apomorphine treatment. Mean ± SEM number of 10-sec periods with masturbation among responding males was 2.5 ± 0.5 following apomorphine in tests without the stimulus female, 1.1 ± 0.8 following vehicle treatment in tests with the stimulus female present, and 11.8 ± 6.0 following apomorphine in tests with the stimulus female present.

The effects of drug treatment and social testing conditions on yawning were also examined (see Table 1). Although yawning was increased following apomorphine treatment in tests with either the stimulus female present or absent, this effect did not quite reach statistical significance, $F(1,8)=4.41$, $p<0.07$. It should be noted that in Experiment 1, only the 50 μg/kg dosage of apomorphine and not the 100 μg/kg dose of apomorphine produced a statistically reliable increase in yawning over vehicle levels. Yawning was not influenced by social testing condition ($F<1.0$) and the interaction of treatment and testing conditions was not significant ($F<1.0$).

DISCUSSION

In order to assess neurochemical influences regulating noncopulatory aspects of rhesus male sexual behavior, a novel testing paradigm was developed in which male rhesus monkeys were tested under conditions in which they were exposed to a sexually receptive female monkey that they could see, hear, and smell, but could not physically contact. Under these testing conditions, several measures of male sexual behavior were able to be monitored following drug treatment, including penile erection, courtship behavior, and masturbatory behavior. The present study utilized this paradigm to evaluate the effects of the mixed D1/D2 receptor agonist, apomorphine.

Apomorphine treatment produced a spectrum of behavioral effects that differed depending on the dose of drug administered. Low doses of apomorphine facilitated male sexual responses associated with the genitals, including penile erection and masturbation. These doses also stimulated yawning. At higher doses of apomorphine, sexual responses declined and stereotypic behavior was elicited.

Apomorphine has been reported to stimulate both penile erections and yawning in other species including rats (3, 9, 20, 27) and humans (12–14). Thus, the finding that rhesus monkeys also respond in a similar fashion to apomorphine administration lends further species generality to the behavioral action of this compound. Since dosages of apomorphine that facilitate penile erections and yawning are substantially lower than dosages that induce stereotypic behavior, it has been widely suggested that apomorphine acts presynaptically on autoreceptors to elicit the former behavioral responses and postsynaptically to elicit the latter behavioral responses (9, 13, 27, 31). However, a number of studies conducted in rats argue against this hypothesis. First, (+)-3-PPP, a pre- and postsynaptic dopamine receptor agonist, facilitated penile erections and yawning; whereas, (−)-3-PPP, a presynaptic dopamine receptor agonist and postsynaptic dopamine receptor antagonist failed to influence these behaviors (9, 17, 26). Secondly, recent studies have demonstrated that direct intracerebral application of apomorphine into the paraventricular nucleus and medial preoptic area facilitated penile erection and yawning (17,21). In light of these findings, it has been proposed that the biphasic effects of systemically administered apomorphine on penile erections and yawning may reflect differential stimulation of anatomically separate populations of dopamine receptors (17,20). Low doses of apomorphine may preferentially gain access to and stimulate postsynaptic dopaminergic receptors in the medial preoptic area and hypothalamus that facilitate sexual behavior (11,17) and yawning (17). At higher dosages, apomorphine may additionally gain access to and stimulate other neural sites (e.g., striatum) that promote behavior stereotypies and interfere with sexual behavior performance.

Several studies have addressed whether systemically administered apomorphine is acting centrally or peripherally to affect penile erections. In both rats (3, 9, 20) and humans (15) prior treatment with domperidone, a dopamine antagonist that does not cross the blood-brain barrier, failed to prevent apomorphine from stimulating penile erections. In contrast, treatment with haloperidol or sulpiride, dopamine antagonists that act both centrally and peripherally, blocked penile erections that were induced by systemically administered apomorphine (3, 9, 20). Similar experiments need to be conducted on rhesus monkeys. Nevertheless, the observation that apomorphine was effective in facilitating penile erections when the stimulus female was present, but not when she was absent, indicates apomorphine may alter sexual behavior by influencing the central processing of sociosexual information. An effect of social testing conditions on apomorphine-stimulated erections has not been reported in studies conducted in rats and humans. However, in the human studies it is important to stress that the subjects were fully aware that they were participating in an erectile response experiment. Therefore, it seems reasonable to postulate that the knowledge of the sexual nature of the experiment may have resulted in some subjects generating sexual images that could potentially influence the ability of apomorphine to facilitate penile erections.

Apomorphine significantly stimulated masturbation in the mon-

keys. Combining the results of both experiments in which 100 μg/kg apomorphine was administered revealed that masturbation occurred in 12 of the 17 tests. In 3 of the 12 tests in which masturbation occurred, the monkeys masturbated to ejaculation. In general, erections were not elicited as a result of masturbatory behavior. Rather, in those tests in which masturbation occurred, the animals began to masturbate only after they achieved at least a grade 2 erection. Thus, it appears that 100 μg/kg apomorphine increased male sexual arousal, resulting in more complete erections and masturbatory behavior which occasionally proceeded to ejaculation. Ejaculations were not observed at other dosages of apomorphine or following vehicle injections. Although there have not been any reports of masturbatory behavior following apomorphine in either rats or humans, apomorphine has been found to stimulate seminal emission (20) in rats.

Apomorphine treatment failed to significantly stimulate male courtship behavior of the monkeys. This finding is in marked contrast to the capacity of apomorphine to potentiate other measures of male sexual arousal such as penile erection and masturbation. Although different sexual behaviors may be differentially sensitive to dopaminergic stimulation, it is possible that the testing conditions being utilized did not provide an environment in which a significant drug effect on courtship behaviors could emerge. Since courtship purse-lip gestures in macaque species generally serve as an affiliative signal produced while males are at a distance from the female (29), the close proximity of the stimulus female to the male in the present studies may have reduced the need for the male to exhibit these behaviors. Thus, male courtship performance may have reached an asymptote under vehicle conditions. Further testing will have to evaluate this possibility by determining whether courtship behaviors are affected by increasing the distance between the experimental male and stimulus female.

High dosages of apomorphine elicited excessive gnawing, licking and fingering of a metal clip attached to the cage. This finding replicates similar reports of high doses of apomorphine producing oral hyperkinesia in several different nonhuman primate species including rhesus monkeys (5, 24, 25). These other studies did not evaluate the effects of these dosages of apomorphine on sexual phenomena or yawning; however, in the present study, dosages of apomorphine that produced oral hyperkinesia also led to a decline in penile erections and yawning. Although the biphasic effect of apomorphine on penile erection may be a result of behavioral stereotypies interfering with sexual effects of this compound, recent data in the rat have demonstrated that apomorphine administered directly into the lumbosacral subarachnoid space inhibited penile reflexes (21). This finding suggests that apomorphine may have contrasting effects on behavior depending on its ability to gain access to different neural sites at which dopamine acts to promote or inhibit sexual behavior.

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