THE INFLUENCE OF ESTROGEN AND ANDROGEN ON THE SEXUAL BEHAVIOR OF FEMALE RHESUS MONKEYS

by

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INTRODUCTION

The fluctuations in sexual activity that characterize the ovarian cycles of infraprimate mammals are not found in all primates. Sexual receptivity appears to follow an evolutionary trend from strict dependence on a hormonal state in rodents to a relaxation of this hormonal control and more dependence on other stimulus conditions in higher species (Beach, 1948; Ford and Beach, 1951). In a recent review, Rowell (1972) found no typical relationship between copulatory frequency and the menstrual cycle in primates. For primate species, then, hormones may play a role less prominent than certain social, developmental, and experiential factors. Among the complex array of conditions which stimulate sexual interaction between pairs of monkeys, however, hormonal influences should not be completely discounted.

Studies with intact macaques indicate that although mounting and intromission by the male can occur at any time during the female's menstrual cycle, rhythmic fluctuations sometimes characterize the copulatory behavior of a pair of monkeys (Ball and Hartman, 1935; Carpenter, 1942a and b; Michael, Herbert, and Welegalla, 1967a). Ejaculation occurs most frequently during the late follicular phase, reaching a peak near ovulation in pig-tailed (Bullock, Paris, Resko, and Goy, 1968; Goldfoot, 1971; Eaton, 1973) and rhesus macaques (Phoenix, Goy, Resko, and Koering, 1968; Michael and Zumpe, 1970a). In fact, when rhythms have been observed, most copulatory behavior takes place during the follicular and ovulatory phases of the ovarian cycle (Ball and Hartman, 1935; Carpenter, 1942a and b; Michael et al., 1967a; Michael and Welegalla, 1968; Michael and Zumpe, 1970a).

It should be noted, however, that in these studies of copulation it is usually the male behaviors (often ejaculation) that are measured and these may not be indicative of all sexual interaction. In a recent study with Macaca nemistrina, systemic levels of estradiol and progesterone were measured during the menstrual cycle of intact females while their sexual behavior with males was being tested (Eaton and Resko, 1974). Despite marked cyclic variation in the hormone levels there was no such cyclicity in female sexual behaviors.

In most recent studies of female sexual interaction, hormonal influences on behavior have been examined from two perspectives: effects on female attractiveness, defined as the sexual stimulus value of the female for the male, and effects on female receptivity, defined as the female's willingness to copulate. This distinction has been useful since the effects on attractiveness and receptivity are not always correlated. In fact, a third category of female sexual behaviors has been recognized for some time but has seldom been studied separately. The behaviors have been called "incitement," "solicitation," "invitation," and "courtship," and usually they are included in discussions of female receptivity. Beach, however, has recently suggested (Beach, 1975) that these behaviors be classified as "proceptive" and that they be distinquished from receptive behavior.

Beach's schema thus proposes 3 female qualities which determine her sexual interactions: attractivity, receptivity, and proceptivity. Attractivity is defined as the female's value as a sexual stimulus and is measured by male behaviors, e.g., mounting attempts, mounts, intro-

missions, and ejaculations. Receptivity is defined as the female's willingness to receive the male in copulation and is measured only by those female responses to male stimuli which are necessary and sufficient to allow intravaginal ejaculation. Usually these responses are postural adjustments. For example, the lordosis response of a female rodent when a male attempts to mount is a receptive behavior. In the monkey, receptivity is measured by female "presents" in response to male mount invitations ("contacts"). Proceptivity in contrast, is that behavior which the female displays to initiate or stimulate sexual interaction with a male. In the monkey proceptivity is indicated by the female's approaching and maintaining proximity to the male and by those responses which invite the male to mount (e.g., assuming the present posture before being contacted by the male). It should be noted here that proceptive behavior is not reserved to primates but has been observed in many species. For example, female rats in estrus perform ear-wiggling and "hopping and darting" responses in the presence of a male which probably serve to stimulate his sexual behavior.

Work with ovariectomized rhesus females and hormone replacement studies have shown that ovarian hormones play a role in female attractivity, receptivity and proceptivity. Ovariectomy resulted in a dramatic decrease in the copulatory behavior of pairs of rhesus monkeys (Ball, 1936; Michael and Saayman, 1967; Michael et al., 1967a; Michael and Welegalla, 1968; Zumpe and Michael, 1968; Michael and Zumpe, 1970b; Zumpe and Michael, 1970). After ovariectomy mounting activity and ejaculation by the male declined (Michael et al., 1967a; Michael and Welegalla, 1968), as did female mount invitations (Michael and Zumpe,

1970b). Male refusals of female invitations increased (Michael and Zumpe, 1970b), but female mount refusals did not change consistently after ovariectomy (Zumpe and Michael, 1968).

The administration of estrogen to ovariectomized females reverses these behavioral effects. Exogenous estrogen stimulated male mounting and ejaculation and thus enhanced attractivity, increased female mount invitations and thus elevated proceptivity, and reduced refusals in both sexes and thus increased receptivity and attractivity. (Ball, 1936; Michael et al., 1967a; Michael and Welegalla, 1968; Trimble and Herbert, 1968; Zumpe and Michael, 1968, 1970). Progesterone administration to ovariectomized, estrogen-treated monkeys, on the other hand, inhibited all measures of copulatory behavior in both sexes (Ball, 1941; Michael, Saayman, and Zumpe, 1967b), an indication that progesterone reduces attractivity, receptivity and proceptivity in female rhesus monkeys. This is in contrast to its facilitatory effects on sexual behavior in rodents but is consistent with the decline in sexual interaction which sometimes characterizes the luteal phase of the menstrual cycle of the intact female rhesus.

Androgens also have been reported to play an important role in regulating sexual interaction in female rhesus. The removal of adrenal androgens from ovariectomized, estrogen-treated females by adrenalectomy or administration of dexamethasone has been reported to produce a decrease in female sexual invitations and an increase in female mount refusals (Herbert, 1970; Everitt and Herbert, 1971; Everitt, Herbert, and Hamar, 1972). Subsequent administration of exogenous testosterone or androstenedione reversed these behavioral results (Herbert, 1970;

Everitt and Herbert, 1971; Everitt et al., 1972; Dixson, Everitt, Herbert, Rugman, and Scruton, 1973) These results indicate that a lack of testosterone leads to diminished female proceptivity and receptivity. No effects of androgens on attractivity have been reported.

The display of sexual behavior by the female monkey depends upon social as well as hormonal stimulation. Complex social interactions, related partly to dominance relationships and personal preferences, appear to regulate sexual behaviors as surely as do hormones in both natural troops and in laboratory groups. The importance of these social variables is especially evident when one is attempting to evaluate the meaning of the female "present" response, a common receptive and proceptive behavior.

The receptive present occurs in response to the male's contact and as such is an acceptance of his invitation to copulate. The value of female acceptance as an indicator of receptivity is limited by the behavior of the male. If the male seldom solicits the female, she obviously has little opportunity either to accept or to reject his invitations. A more accurate indicator of receptivity therefore is the ratio between female acceptances and male invitations. By definition, receptivity cannot be determined unless the male offers stimuli to which the female can respond.

The present posture is proceptive when it occurs before the male has contacted the female. A low number of proceptive presents (or other invitations), however do not necessarily indicate a low level of proceptivity. For example, if in the first few moments after being introduced the male mounts and ejaculates, the female invite rate would be

zero because she had no opportunity to invite the male to mount. If, on the other hand, the male had been slower to ejaculate and had paused several times between mounts, an invite rate of zero would be more likely to indicate a female with low interest in sexual interaction.

The present posture can also be used as a submissive or polite gesture to ward off aggressive encounters. This potential ambiguity in the female responses that are used to measure receptivity and proceptivity cannot be eliminated from the pair test. In this study, therefore, the behavior of the female was observed before it became confounded by the presence of the male in a pair test. This was done by using a testing situation which allowed the female to control the male's access to the test cage and thus to herself. Her release of a male into the test cage thus indicated the female's sexual proceptivity.

This type of operant release response has been used before in tests of sexual behavior with intact pig-tailed macaques (Eaton, 1973; Eaton and Resko, 1974) and with rhesus females (Michael, Zumpe, Keverne, and Bonsall, 1972). In these tests, releasing frequency did not change across the pig-tailed female's menstrual cycles, nor did measures of those females' receptivity and proceptivity show any cyclicity. In rhesus females, however, hormonal effects on releasing were reported.

The female role in sexual interactions is commonly characterized as passive, that of the male as active. When the behavior of the pair is closely examined however, such clear-cut distinctions are not valid. This study provides additional information on the nature of the female role in initiating and modulating sexual interactions and identifies related hormonal states.

MATERIALS AND METHODS

Subjects: Nine ovariectomized adult female and 8 adult male rhesus monkeys were used. All except one laboratory-born female were feral animals and had been in the laboratory at least 3 years. The females had been ovariectomized at least 18 months before the study began. The animals were housed in a common room in individual wire mesh cages.

Apparatus: The test cage, constructed of wire mesh with a clear Plexiglas front, measured 1.81 x 0.71 x 1.22 m. Small transfer cages were attached at each side. Animals had access to the test cage from the transfer cages through pneumatically operated guillotine doors of wire mesh. The animals had visual, auditory, and olfactory contact with each other while still in the transfer cages. The door to the female's transfer cage was operated by the observer from a desk console, the male's by a red plexiglass panel measuring 8.5 x 12.0 cm on one wall of the test cage. The panel was illuminated from behind and could be pressed; when this happened the light went out and the male's door opened. This door could be closed from the observer's console.

The observer sat at a table approximately 2 m in front of the test cage in clear view of the animals. The testing room was separate from the animals' common living room and was further isolated by sound-proofing.

Training of Females: Several months before testing, the females were taught the operant panel press response in order to gain access to a preferred food (raisins, fruit-flavored cereal, bananas, or oranges) in

the male's transfer cage. Training continued until the females pressed the panel within 5 minutes after entering the cage on ten consecutive trials.

Testing Procedure: A male and a female were brought to the test room in separate transfer cages, which were then attached to the test cage. The experimenter then allowed the female to enter the test cage and started a timer. The panel was illuminated and the female could press it to allow the male to enter the cage. The female's pre-release behavior was recorded. If she did not release the male in 10 minutes, the test was terminated; she was returned to her transfer cage, and the male was replaced by another. If the female did release the male, the latency of release was recorded, and a pair test was conducted during which the behavioral interaction of the pair was recorded. This test continued for 10 minutes or until the male ejaculated. After the pair test, both animals were returned to their transfer cages, and the male was replaced by another. This procedure was repeated until the female had been tested with all 8 males.

The order of male appearance was rotated for each test and at least one day intervened between tests. All females had the opportunity to release all males under each hormone condition. Each female received one day of testing during each hormone treatment, and four weeks elapsed between each of her test days.

The following behaviors were recorded:

Female only:

A. Before release of the male

1. Present: The female stands with her legs rigid and extended, tail deviated from the perineum, and her perineum toward the male.

2. Invitation

a. hand slap: While seated near the male, the female rapidly lifts one hand, extends her arm, and slaps her hand on the floor in front of her.

b. head duck: While seated near the male, the female quickly lowers her head in relation to her shoulders.

c. head bob: While seated near the male, the female quickly moves her head upwards.

3. Fear grimace: The female retracts her lips to expose clenched teeth.

4. Proximity response (prox): The female approaches and sits within one foot of the male's door.

5. Release latency: The time that elapses from the entry of the female into the test cage until she presses the panel.

B. During the pair test

1. Present: The same posture as in A_1, but differentiated by whether it

a. Was not immediately preceded by a male contact.

b. Was made in response to a male contact.

2. Invitation: Same gestures as in A_2.

3. Fear grimace: Same expression as in A_3.

Male Only: during the pair test

1. Erection: The glans and shaft of the penis are fully visible.

2. Contact: The male places his hands on the female's lower back or hips either

a. Without any previous female invitation or present, or

b. In response to a female invitation or present.

3. Mount: The male grasps the female's hips with his hands and clasp her ankles or calves with his feet.

4. Latency to first mount: The time that elapses from the release of the male until he mounts.

5. Intromission: The male inserts his erect penis into the vagina.

6. Latency to first intromission: The time that elapses from the release of the male until intromission.

7. Pelvic thrusts: Rhythmic pelvic movements that are executed during intromission.

8. Ejaculation: A pause after rapid pelvic thrusting is accompanied by spasmodic muscular contractions in the thighs, vertical jerking movements of the tail, and seminal emission.

9. Latency to ejaculation: The time that elapses from the release of the male until ejaculation.

Both Male and Female

1. Proximity response (prox): One animal approaches and sits within one foot of the seated partner.
2. Groom: One animal manually picks through the fur of the partner, sometimes lip smacking during the process.
3. Yawn: One animal opens his mouth wide to expose the teeth and wrinkle the skin on the back of the head and neck.
4. Rejecting jerk: Quick spasmodic jerks, resembling a shiver, seize the whole body or upper torso and head. An annoyance response.
5. Threat: One animal stares at his partner and accompanies this gesture by a gape and flip of the ears, head movement, forward lunge, or vocalization; sometimes hitting or grabbing at the partner is included.
6. Aggression: One animal vigorously bites his partner.

From these measures, the following scores were derived:

1. Female acceptance ratio: The proportion of male mount initiations accepted by the female (♀ presents to contact/♂ initiated contacts) This measure is comparable to the lordosis ratio frequently used in studies of female rodent estrus.
2. Male acceptance ratio: The proportion of female mount initiations accepted by the male (♂ contacts to presents and invitations/ ♀ initiated presents and invitations)

3. Percent of mounts initiated by the female ([♀ initiated mounts/ total mounts] x 100)
4. Mean number of thrusts per intromission (total thrusts/total intromissions)

Hormonal Manipulation: The order of hormone treatment at one month intervals was estrogen (EB-1), testosterone (TP) estrogen (EB-2), no hormones (NORX), and dexamethasone plus estrogen (DXEB). The estrogen treatment was used twice to check on possible novelty effects during the first test condition (when females were permitting access to a male rhesus for the first time) and to determine whether a higher dose would have a greater behavioral effect.

Hormones were administered as follows:

1. EB-1: Estradiol benzoate (Progynon, Schering), 10 μg, was injected intramuscularly (IM) daily in alternate (left and right) legs for 10 days before testing, i.e., the female was tested on her tenth injection day.
2. TP: Testosterone propionate (Perandren, Ciba), 1 mg, was injected IM daily in alternate legs for 10 days before testing.
3. EB-2: Estradiol benzoate was injected as in (1), except that the daily dosage was 20 mg and treatment continued for 12 days before testing.
4. NORX: Sesame oil, 0.5 ml, was injected IM daily for 12 days before testing.
5. DXEB: In addition to estradiol benzoate, 10 μg per day for 12 days, dexamethasone sodium phosphate (Decadron, Merck, Sharpe, and Dohme), 0.5 mg per kg body weight, was injected daily in 2 equal doses for

12 days before testing. This dosage has been reported to suppress corticoid production but not to alter serum concentrations of sodium, potassium, or chloride, the 24-hour urinary excretion of sodium and potassium, or the hematocrit in ovariectomized rhesus females (Everitt and Herbert, 1969a).

Data Analyses: Since the length of the pair tests varied depending on the males' latencies to ejaculate, all frequency scores were converted to rates (occurrences per minute). A mean score for each female behavior under each hormone condition was computed for every female from her scores with the eight males, and a mean score for each male behavior was computed for every male from his scores with the nine females. It should be noted that since the females did not always release all the males, the number of pair tests during each hormone treatment varied. The mean scores for each hormone treatment were compared with those for each other treatment with a single factor analysis of variance for repeated measures and t-tests. Latency measures were compared with the Friedman 2-way analysis of variance and Wilcoxon T-tests. The .05 level of probability for a 2-tailed test was used as the level of statistical significance.

RESULTS

Behavior under the two estradiol conditions (EB-1 and EB-2) was compared with t-tests; since no significant differences were found for any behavior (Table 1), the data from these two treatments were combined and are referred to as treatment EB.

Pre-release behavior:

Female pre-release behaviors occurred infrequently, and the rates did not vary significantly during the hormone treatment conditions. Pre-release present, invite, and prox showed similar trends, however: the highest rates occurred during EB and TP treatments, the lowest rates during NORX and DXEB treatments (Table 2).

Female releasing behavior:

One female (1339) did not begin releasing males until the third treatment (EB-2), after which she released some males each test day. All other females released some males during all treatments. The reason for 1339's idiosyncratic behavior was not apparent, and her releasing data were dropped from the analysis.

The percentage of tests on which a release occurred was not significantly different during treatments EB (86%), TP (91%), and NORX (74%) but dropped to 64% during treatment DXEB (Fig. 1). This level is significantly lower than that during EB and TP treatment ($F = 4.192$, $df = 3/21$, $p < .05$).

Release latencies were highly variable, and no significant differences appeared between the means of any treatment conditions. Because of the wide variability in this measure, latencies were also analysed with Wilcoxon T-tests for each female individually. Three of the eight females showed no differences between treatments. One female had significantly longer latencies during NORX than during any other condition ($p < .02$). Four females had the longest latencies during DXEB, significantly longer than during EB and TP in 3 cases ($p < .05$) and than

during EB, TP, and NORX in 1 case ($p = .01$). Thus no consistent hormonal effect on release latency was demonstrated: the most common result was that the longest latency to release a male occurred during DXEB treatment, but this was observed in only half the females.

Pair-test behavior:

The total number of pair tests to occur during EB treatment was 117; during TP treatment, 58; during NORX treatment, 53; and during DXEB treatment, 46.

Female behavior: The female present rate was not affected by any of the hormone treatments ($F = 0.733$, $df = 3/24$, $p > .05$). However, the other form of female sex initiating behavior, the invite, did change during treatment. The rate was significantly higher under treatments EB and TP than NORX and DXEB ($F = 4.73$, $df = 3/24$, $p < .05$) (Table 3). Thus the 2 forms of female initiating were not equally affected by the hormonal state of the female.

Female prox followed a pattern quite similar to that of female inviting, the highest rate occurring during EB and TP treatments and the lowest during NORX and DXEB treatment ($F = 7.286$, $df = 3/24$, $p < .01$). For none of these behaviors were the rates significantly different between EB and TP treatments nor between NORX and DXEB treatments (Table 3).

When the male initiated a mount, the females were equally ready to cooperate by appropriate postural adjustments under all hormonal conditions tested here; that is, the female acceptance ratio remained high throughout the study (Table 3). The lowest ratio (.62) occurred during

treatment NORX, but this was not a significant drop from the ratio during treatments EB (.80), TP (.82) or DXEB (.81) ($F = 1.992$, $df = 3/24$ $p > .05$).

The percentage of male mounts that were preceded by female initiating behavior did not vary significantly with hormone treatment ($F = 1.105$, $df = 3/24$, $p > .05$), but females initiated the highest percentage of male mounts under TP and the lowest percentage under DXEB treatment (Fig. 2). During all treatments, the females initiated less than half the male mounts.

Female behaviors not patently sexual, i.e., grooming, rejecting jerks, threats and aggression, were infrequent, and were not significantly affected by hormone treatment (Table 4). The female fear grimace rate, however, was significantly higher during treatments NORX and TP than during treatment EB ($F = 4.50$, $df = 3/24$, $p < .05$), but male threats were also most frequent under these treatments, not, however, to the point of statistical significance. The only male antagonistic behavior to vary significantly with treatment was the male rejecting jerk which occurred at a higher rate during TP treatment than during other treatments ($F = 4.268$, $df = 3/21$, $p < .05$) (Table 5).

Female yawns occurred only rarely during treatments EB, NORX, and DXEB (mean rate = .00/min in all cases), but the rate during treatment TP (.07/min) was significantly higher ($F = 6.50$, $df = 3/24$, $p < .01$). Still, this female yawning rate was far below the overall mean rate for males (.61/min) (Table 6).

Male behavior: Male sexual behavior was strongly affected by the hormonal status of the female partner. Rates of contacting, mounting, and intromission (Fig. 3) and percent of tests with erections and ejaculations (Fig. 4) were all at the highest levels during treatment EB. During all other treatments, the levels of these behaviors were significantly lower than the EB level. The scores during treatments TP, NORX, and DXEB did not differ significantly from each other except for erections, which occurred significantly more often during TP treatment than during NORX or DXEB treatment. The male acceptance ratio was also significantly higher during EB than during any other treatment ($F = 3.99$, $df = 3/21$, $p > .05$) (Fig. 5).

Latency measures also indicate optimal male sexual performance during treatment EB. Mean latencies to first mount, first intromission, and ejaculation were shortest during EB treatment but for latency to first intromission, the differences were not statistically significant ($X^2_r = 5.10$, $df = 3$, $p > .05$). The latency to first mount was significantly shorter during treatment EB than during any other treatment ($X^2_r = 9.038$, $df = 3$, $p < .05$). Male latency to ejaculate during treatment EB was significantly shorter than during treatment NORX and DXEB ($X^2_r = 11.738$, $df = 3$, $p < .01$). None of these latency measures showed any significant differences between treatments TP, NORX, and DXEB (Fig. 6).

The mean number of pelvic thrusts per intromission did not vary significantly with treatment ($F = 2.248$, $df = 3/21$, $p > .05$). Once a

male achieved intromission, he made about the same number of pelvic thrusts (mean = 7.26) regardless of the hormonal condition of his female partners.

Male social behaivor, such as grooming and proxing, occurred only infrequently and was not influenced by the hormone manipulation of the females (Table 4). Male antagonistic behavior was discussed above in connection with female fear grimaces. The rates of rejecting jerks, threats, and aggression are given in Table 5.

DISCUSSION

The current hypothesis that in primates female attractiveness is controlled by estrogen and female receptivity is controlled by androgen (Herbert, 1970) is not supported by the results of this study. Instead, these data indicate that both estrogen and androgen are important determinants of female attractiveness and proceptivity but not of female receptivity.

It is apparent from this study that androgens did contribute to female attractiveness. Blocking the adrenal androgen output of these females with dexamethasone diminished their sexual attractivity despite the estrogen they received during treatment DXEB. Since other adrenal steroids besides androgens were also suppressed, this study does not demonstrate that androgens are the key blocked hormones. However, Everitt and Herbert (1971) found that testosterone could reverse the effect of dexamethasone on sexual behavior, whereas cortisol and progesterone were ineffective.

The infrequency of male sexual behavior during DXEB treatment cannot be explained simply by accompanying low levels of female receptivity as has been done by others (Everitt and Herbert, 1969, 1971; Herbert, 1970). Though female invitations were low during this time, the present rate and the female acceptance ratio did not drop significantly from those during other treatments. Thus male interest was not diminished because of an increase in female refusals. Furthermore, those aspects of male behavior not necessarily dependent on female receptivity were depressed during the DXEB tests: the percent of tests with erections, the contacting rate, and the male acceptance ratio were all lower during DXEB than during EB treatment. These data are not in agreement with those reported by Everitt and Herbert (1971) and Everitt et al. (1972), which indicated that the male acceptance ratio was not affected by dexamethasone treatment or adrenalectomy of females.

Testosterone alone, however, does not produce an attractive female rhesus monkey; estrogen is also required. The sexual behavior of the males was low during TP and NORX treatment. Females in the NORX condition had no estrogen, but they may have had some adrenal testosterone. Resko (1971) measured 0.5 ng testosterone per ml of plasma in ovariectomized female rhesuses. In the TP condition, they had exogenous testosterone in addition to that produced by the adrenal. Whatever the blood levels may have been, neither of these amounts of testosterone rendered the females attractive to the males. Trimble and Herbert (1968) similarly found that ovariectomized females receiving only testosterone were not sexually attractive to males.

Only during EB treatment did the behavior of the males indicate that the females were attractive to them. During this treatment the females had adrenal testosterone in addition to exogenous estrogen, and evidently this combination heightened the females' attractiveness. Neither estrogen alone (treatment DXEB) nor testosterone alone (treatments TP and NORX) was sufficient to stimulate male sexual activity, but together they produced attractive females.

The importance of testosterone in making females attractive was so pronounced in this study that is is surprising that others (Everitt and Herbert, 1971; Everitt et al., 1972) failed to report it. The discrepancy may be due to the fact that throughout these other studies a female was paired with the same male whereas in the present experiment each female was paired with eight different males. There is some indication that in other species (Macaca nemestrina) the relation found between hormones and behavior may have been influenced by the method of pairing (cf. Eaton and Resko, 1974). Since social environment and partner preference undoubtedly have profound effects on primate behavior, the relative importance of such procedural variations should be determined.

Female proceptivity was also influenced by estrogen and androgen. Not all proceptive behaviors however, showed equivalent patterns of hormonal effects: presenting and releasing behaviors did not vary as much as proxing and inviting. Nonetheless, the rates for all proceptive behaviors were equivalent during EB and TP treatments and were never higher than during these treatments. Thus exogenous testosterone and estrogen were equally effective in producing proceptive females.

Trimble and Herbert (1968) likewise found testosterone to be as effective as estrogen in restoring "receptivity" (a term which in their study included proceptivity) in ovariectomized rhesus females.

EB treatment was seen to provide the females with a combination of estrogen and androgen. Additionally, the levels of circulating testosterone induced during treatment TP may result in some peripheral conversion of testosterone to estrogen; thus this treatment also would produce females with both estrogen and androgen. That such a conversion can occur has been shown in an ovariectomized rhesus female injected with testosterone (Greton, .05 mg/kg/day for 14 days) who had elevated plasma levels of estradiol (69.7 pg/ml plasma) not unlike those of intact females during the early follicular phase of the menstrual cycle (R.M. Brenner, personal communication, 1974) Thus, treatments EB and TP, because of adrenal androgen output and peripheral conversion of testosterone to estradiol respectively, may be considered conditions of estradiol and testosterone, and the combination of both hormones led to the highest levels of female proceptivity.

The low levels of male sexual behavior during TP treatment do not rule out the conversion of testosterone to estradiol. In fact, the levels of all male sex behaviors were slightly higher during this treatment than during NORX treatment. The failure to activate male behavior completely was probably due to the lower levels of estrogen from the peripheral conversion of testosterone than from the systemic injections of estradiol. Of course, the minimum amounts of these hormones required to activate a particular aspect of sexuality are not

known. There is no a priori reason to expect proceptivity and attractiveness to be affected to the same degree by a particular combination of estrogen and testosterone.

When either estrogen or androgen was lacking in the female, the levels of proceptivity were reduced. During NORX treatment, the females had adrenal androgens but their lack of significant amounts of estrogen (ovariectomized rhesus have 0-20 pg estradiol per ml plasma) led to reduced rates of inviting and proxing. The levels of releasing and presenting, however, were not significantly affected. Michael and Zumpe (1970b) also reported that the decrease in the total number of female sexual initiations after ovariectomy was due entirely to a decline in inviting behavior since the number of presents remained unchanged. It may be that invitations are more sensitive indicators than presents of variations in female proceptivity. Low levels of proceptivity were also apparent during DXEB treatment, when females had estradiol but lacked androgen because of the suppression of adrenal output. Thus neither androgen alone (treatment NORX) nor estrogen alone (treatment DXEB) produced proceptive females.

The fact that the present response did not vary to the same extent as the other proceptive behaviors may be because the present can be a submissive gesture as well as a sexual invitation. The rate of another submissive gesture, the fear grimace, was lower during EB treatment than during the other treatments, and male antagonism was generally higher during treatments TP, NORX, and DXEB. Thus during the latter two treatments when the rate of invitations and proxs shows proceptivity to be low, the

level of male antagonistic behavior may have prevented the present response from declining to similarly low levels.

The release response varied somewhat more like the inviting and proxing responses, but the hormonal effects were not so marked. The lack of either estrogen or testosterone caused the releasing of males by females to decline, but the change was significant only when testosterone was suppressed. Thus the release response may be more dependent on androgen than on estrogen. Since estrogen administration had no significant effect on releasing, it is not surprising that Eaton and Resko (1974) found no change in releasing behavior by pig-tailed monkey females during the estrogen peak of their menstrual cycle.

Even though hormone treatment did not cause releasing to vary as dramatically as proxing and inviting, the same general pattern was evident. Female behaviors not obviously sexual (e.g., grooming and threats) did not show any similar variation during the hormonal manipulations. Thus the release response, which allows social and sexual interaction between the pair, probably reflects the sexual interest of the female rather than any social deprivation. However, an underlying constant requirement for social stimulation could partially obscure the effect of hormones on female proceptivity as it is revealed by a release response.

As measured in this study by the female acceptance ratio, female sexual receptivity was unaffected by the manipulations of estrogen and testosterone. Trimble and Herbert (1968) also found that the administration of estrogen or testosterone to ovariectomized females did not

affect their already high level of acceptance of male mounting. Removal of adrenal androgens, however, by dexamethasone treatment (Everitt and Herbert, 1971) or adrenalectomy (Everitt et al., 1972) was reported to reduce the female acceptance ratio and to increase female refusals; but it should be noted that in both studies half the females failed to show the effect. Thus, unlike their effects on female proceptivity and attractiveness, estrogen and testosterone exert no clear control over female receptivity. If there is an emancipation of sexual behavior from hormonal control in primates as compared to rodents, it is especially evident in female receptivity.

Yawning is testosterone-dependent in both the male and the female rhesus. Normally it is a male behavior, and is only rarely displayed by females. Castration eliminates the behavior in males, and testosterone replacement restores it (Phoenix, Slob and Goy, 1973). In the present study, females similarly responded to exogenous testosterone with an increased rate of yawning. However, the rate of female yawning induced by testosterone is lower than that of the normal male or of the testosterone-treated castrated male.

SUMMARY AND CONCLUSIONS

The interaction of pairs of male and ovariectomized female rhesus monkeys was observed while the hormonal state of the females was experimentally manipulated; and the behavior was analyzed with respect to female attractiveness, value as a sexual stimulus for a male; receptivity, willingness to receive a male in copulation; and proceptivity, interest

in initiating sexual interaction with a male. The hormonal conditions of the females included a combination of estradiol and adrenal androgen (treatment EB), a combination of testosterone, adrenal androgen, and estradiol as a conversion product of testosterone metabolism (treatment TP), adrenal androgen alone (treatment NORX), and estradiol alone (treatment DXEB).

The effects of these hormones on the qualities of female sexuality were as follows:

1. Female attractiveness: A combination of estrogen and androgen was required for the females to be sexually attractive to the males. This was achieved during treatment EB. Though treatment TP also provided a combination of these hormones, the amounts of estradiol during this treatment were evidently insufficient to fully stimulate male interest. Neither endogenous androgens in the absence of estradiol nor estradiol in the absence of adrenal activity produced attractive females.
2. Female proceptivity: During both hormone treatments which provided the females with combinations of estrogen and androgen they displayed high levels of proceptive behavior. Thus, as with attractiveness, both hormones were needed to activate proceptivity, but the threshold concentration of estradiol required was lower in the case of proceptivity. Females were not proceptive when they had either estrogen alone or androgen alone.
3. Female receptivity: Receptivity was not affected by the hormone treatments; rather, it remained high throughout this study. This facet of female rhesus sexual behavior thus demonstrated a freedom

from hormonal control. Proceptivity and attractiveness in female rhesus, though not as strictly regulated by the female's hormonal condition as they are in rodents, did show some hormonal dependency.

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Table 1. Mean scores for several sexual behaviors during two estradiol treatments of the females. None of the differences are statistically significant, $p > .05$.

Behavior	EB-1	EB-2
Female release (% of tests)	89.00	82.75
Female present rate	.23	.19
Female invite rate	.14	.09
Female acceptance ratio	.82	.78
Male contact rate	1.56	1.96
Male mount rate	1.73	1.82
Male ejaculation (% of tests)	53.11	65.75
Male latency to ejaculation (minutes)	2.76	3.66
Male acceptance ratio	.51	.61

Table 2. Rates of female behavior before release of the male (mean ± S.E. for 9 females with 8 males). None of the differences are significant, $p > .05$.

Behavior	Female Treatment			
	EB	TP	NORX	DXEB
Pre-release present	.28 ± .09	.54 ± .26	.09 ± .03	.03 ± .01
Pre-release invite	.04 ± .02	.06 ± .03	0	.01 ± .01
Pre-release prox	.91 ± .76	2.19 ± 1.80	.59 ± .31	.23 ± .09
Pre-release fear grimace	.06 ± .03	.09 ± .08	.07 ± .07	.02 ± .02

Table 3. Rates of female sexual behavior and the female acceptance ratio after release of the male by the female (mean ± S.E. for 9 females).

Behavior	Female Treatment				F-test
	EB	TP	NORX	DXEB	p value
Present	.21 ± .05	.23 ± .06	.19 ± .07	.14 ± .05	NS
Invite	.12 ± .03	.18 ± .05	.03 ± .01*	.06 ± .05*	< .05
Prox	.17 ± .03	.25 ± .06	.08 ± .02*	.07 ± .02*	< .05
Acceptance Ratio	.80 ± .05	.82 ± .08	.62 ± .09	.81 ± .10	NS

*Significantly different from EB and from TP.

Table 4. Rates of 5 social behaviors (mean ± S.E. for 9 females and 8 males after release of the male by the female). None of the differences are significant, $p > .05$.

Behavior	Female Treatment			
	EB	TP	NORX	DXEB
Female groom	.02 ± .01	.03 ± .02	0	0
Male groom	.01 ± .004	.01 ± .01	0	0
Male prox	.05 ± .02	.03 ± .01	.03 ± .02	.03 ± .01
Female rejecting jerk	.03 ± .01	.02 ± .01	.02 ± .01	.01 ± .01
Female threat	.11 ± .04	.07 ± .06	.03 ± .02	.03 ± .02

Table 5. Rates of male antagonistic behaviors and female fear grimace. (mean ± S.E. for 8 males and 9 females after release of the male by the female.)

Behavior	Female Treatment				F-test
	EB	TP	NORX	DXEB	p value
Male rejecting jerk	.04 ± .01●	.15 ± .03	.06 ± .02●	.06 ± .03●	< .05
Male threat	.03 ± .02	.10 ± .03	.11 ± .04	.11 ± .05	NS
Male aggression	0	0	.01 ± .01	.01 ± .01	NS
Female fear grimace	.05 ± .02	.15 ± .05*	.15 ± .04*	.10 ± .04	< .05

* Significantly different from EB

● Significantly different from TP

Table 6. Yawning rate (mean ± S.E. for 9 females and 8 males after release of the male by the female).

Behavior	Female Treatment				F-test
	EB	TP	NORX	DXEB	p value
Female yawn	0*	.07 ± .03	0*	0*	< .05
Male yawn	.50 ± .13	.69 ± .20	.62 ± .20	.55 ± .18	NS

* Significantly different from TP.

Figure 1. Percentage of tests on which the female released the male (mean ± S.E. for 8 females).

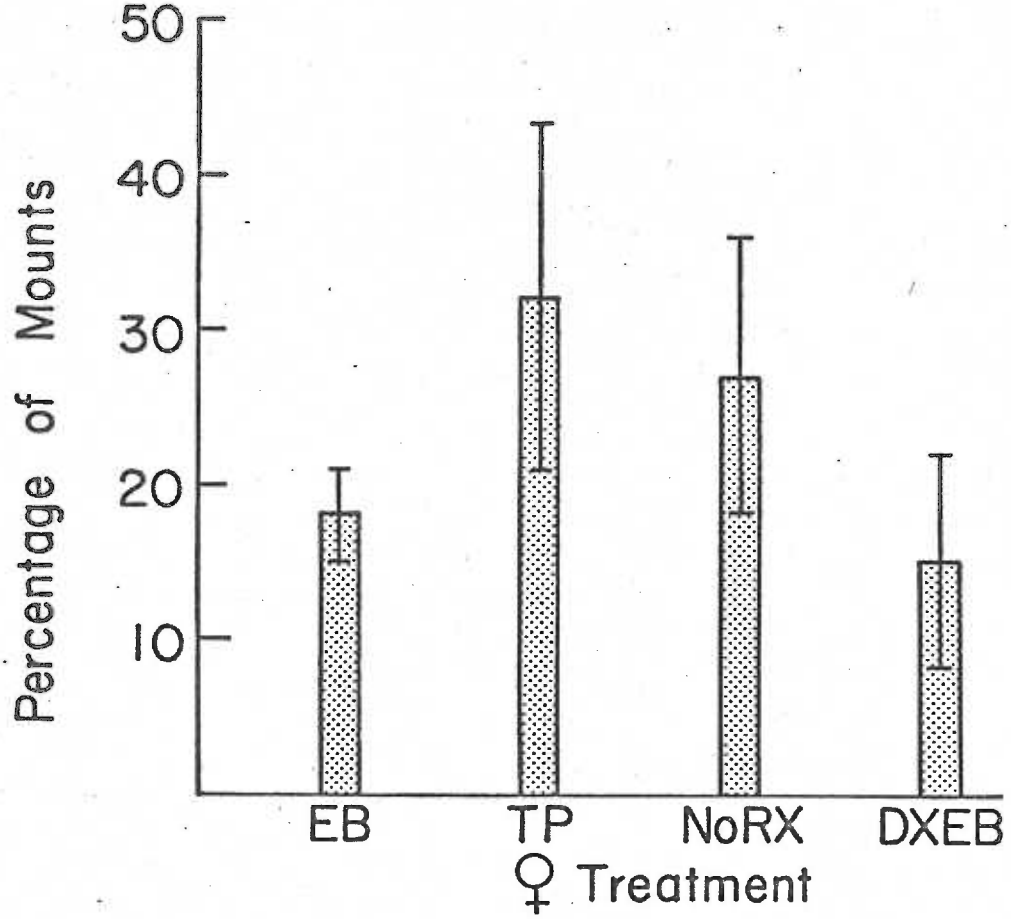
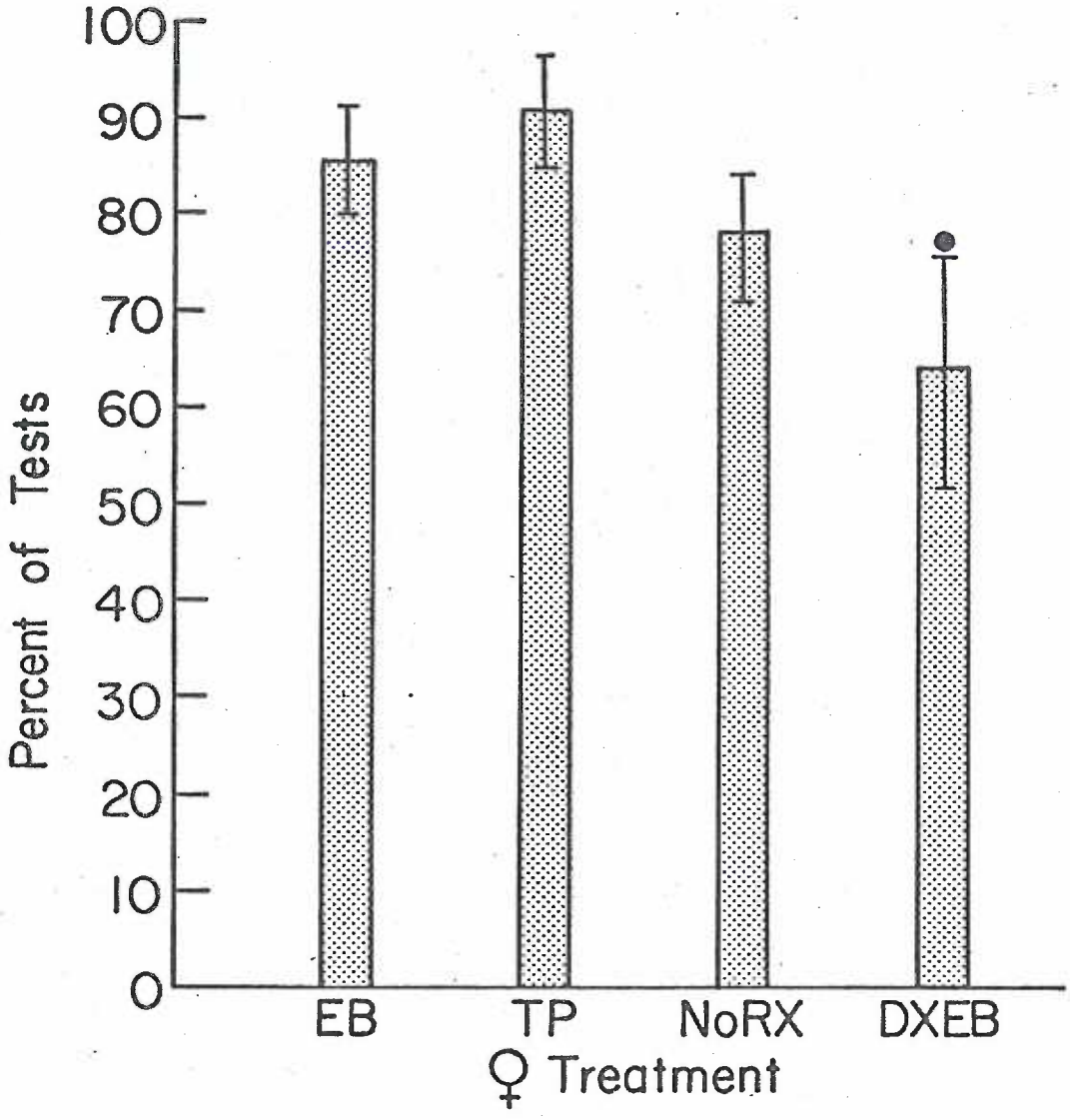
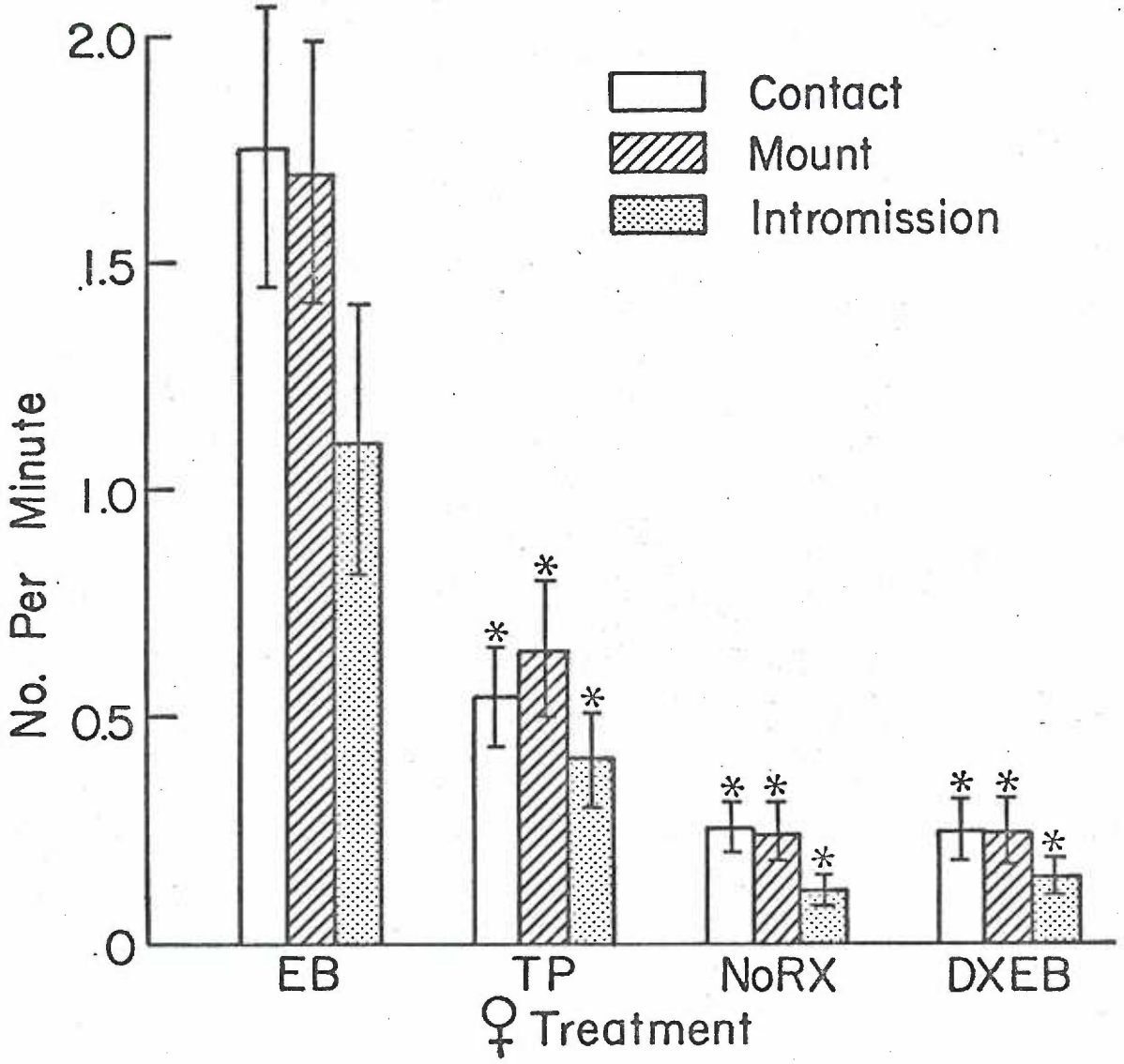

50
40
30
20
10
Percentage of Mounts
EB
TP
NoRX
DXEB
♀ Treatment

Figure 2. Percentage of male mounts initiated by the female during the pair test (mean ± S.E. for 9 females after release of the male by the female). None of the differences are statistically significant, $p > .05$.



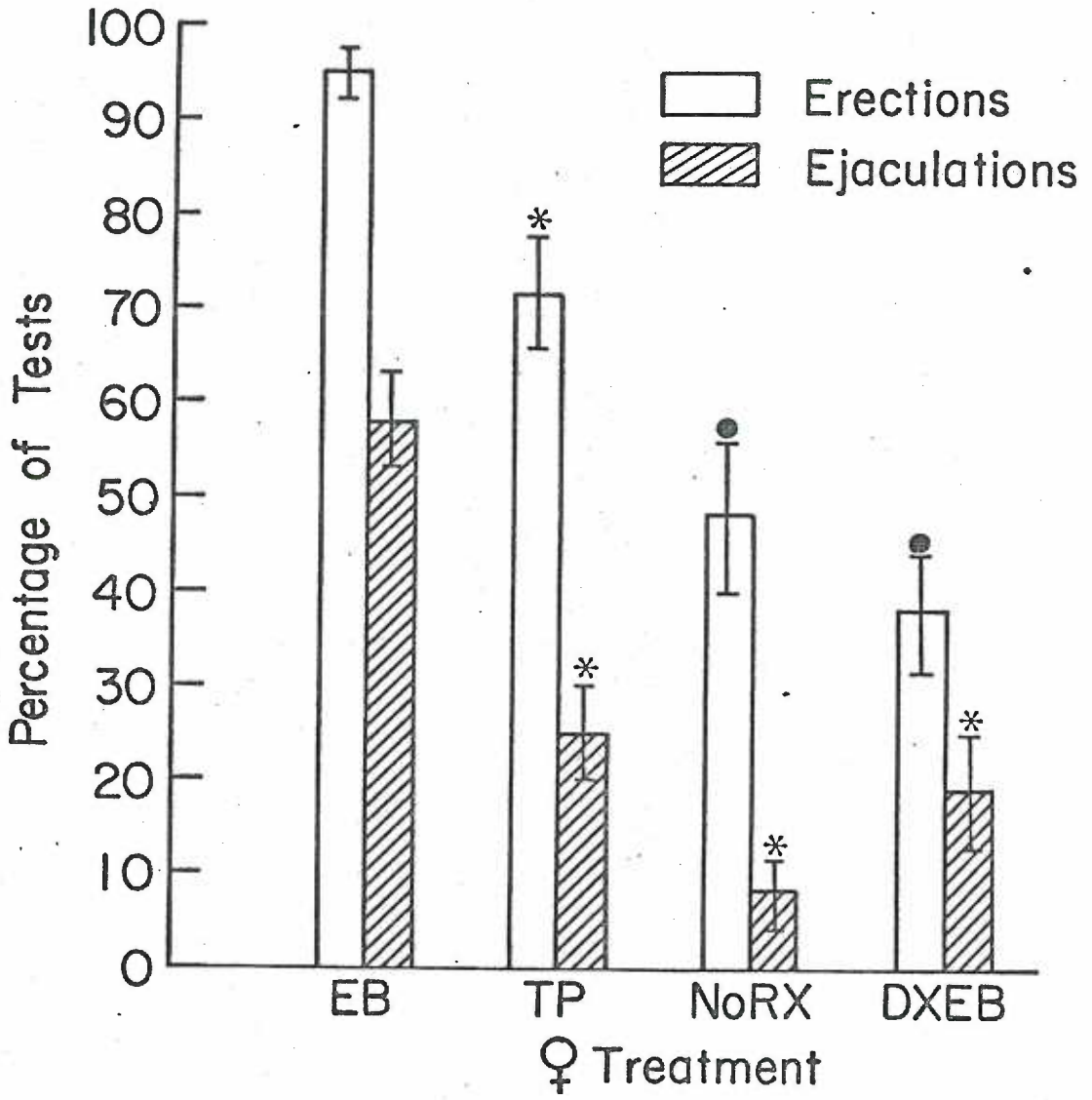
●: Significantly different from EB and from TP

Figure 3. Rates of contacting, mounting, and intromitting during the pair test (mean ± S.E. for 8 males after release by the female). $F = 12.43$, 12.78, and 5.43 respectively; $df = 3/21$; $p < .01$ in all cases.



*: Significantly different from EB

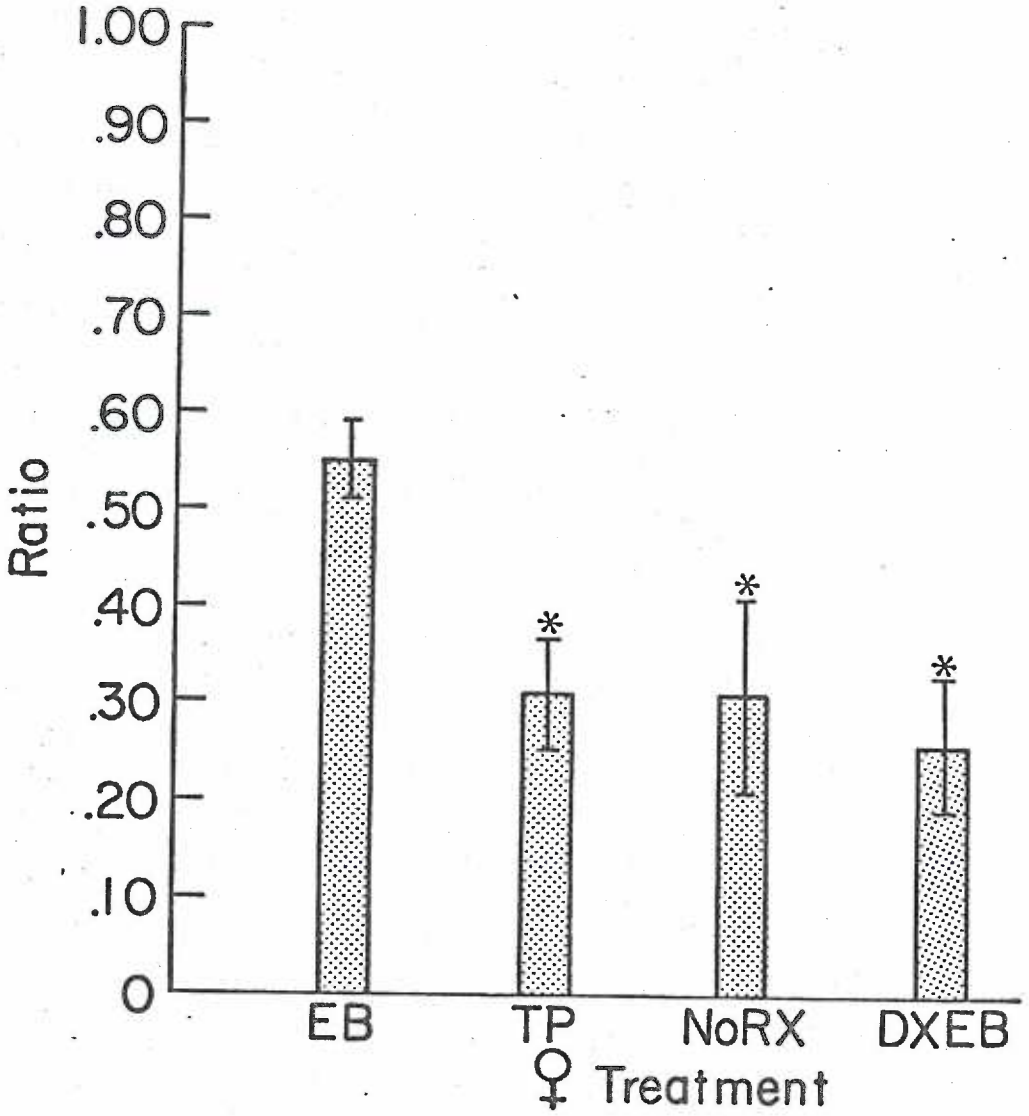
Figure 4. Percentage of pair tests on which erections and ejaculations occurred (mean ± S.E. for 8 males for release by the female). $F = 17.95$ and 16.83 respectively; $df = 3/21$; $p < .01$ in both cases.



●: Significantly different from EB and from TP

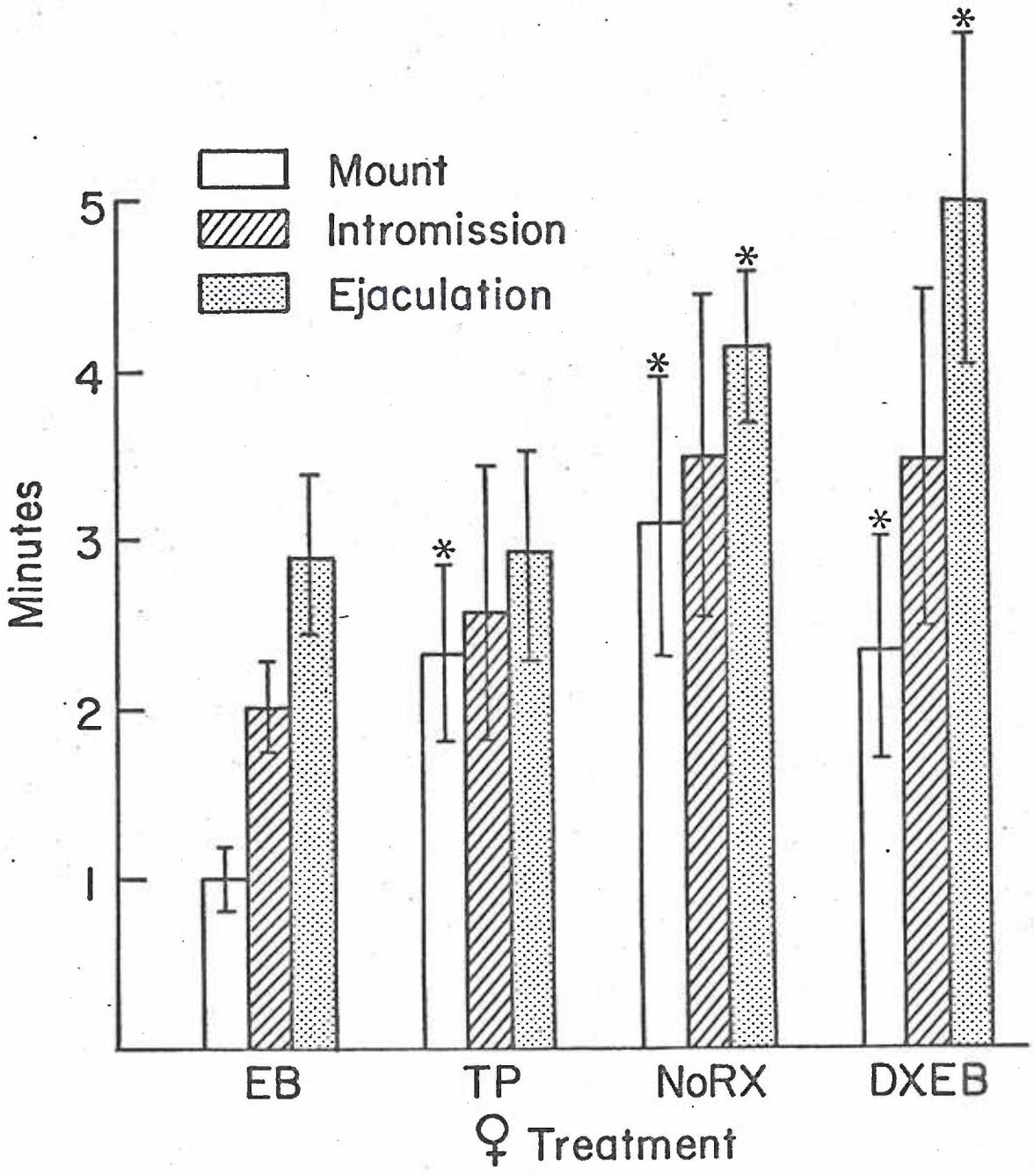
*: Significantly different from EB

Figure 5. Male acceptance ratio (mean ± S.E. for 8 males after release by the female).



*: Significantly different from EB

Figure 6. Latency to the first occurrence of a mount, intromission, and ejaculation during the pair test (mean ± S.E. for 8 males after release by the female).



*: Significantly different from EB