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Expression of Adult Female Patterns of Sexual Behavior by Male, Female, and Pseudohermaphroditic Female Rhesus Monkeys[1]

STEVEN M. POMERANTZ,[2] MARC M. ROY, JANICE E. THORNTON, and ROBERT W. GOY

Wisconsin Regional Primate Research Center
and the Neuroscience Training Program
University of Wisconsin
1223 Capitol Court
Madison, Wisconsin 53715-1299

ABSTRACT

Gonadally intact pseudohermaphroditic female and normal female and neonatally castrated male rhesus monkeys were given estrogen treatment as adults and evaluated for attractivity, proceptivity, and receptivity during tests with a tethered stud male. Pseudohermaphrodites were produced by injecting their mothers during pregnancy with either testosterone propionate (TP) or dihydrotestosterone propionate (DHTP).

Castrated males had reliably lower attractivity than normal females on all indicator responses shown by the tethered males. Additionally, castrated males showed reliably fewer proceptive responses on 4 of 5 measures than normal females. Receptivity could not be assessed in this situation for castrated males, because tethered males never contacted them unless the castrated males were displaying presentation.

No reliable differences were observed between pseudohermaphrodites produced by prenatal treatments with TP or DHTP. Pseudohermaphrodites generally showed reliably less attractivity and proceptivity than normal females and reliably more of these traits than castrated males. Attractivity scores for pseudohermaphrodites were not different from those for normal females until proximity to the tethered male was established. Receptivity was not different in pseudohermaphrodites compared with normal females.

Results indicate prenatal androgenization and its developmental sequelae lead to a defeminization in adulthood which, in this testing situation, was principally manifested by a deficiency in the performance of proceptive behaviors. Additionally, defeminization in rhesus monkeys, unlike that demonstrated in rodents, does not depend upon actions of an aromatizable androgen.

INTRODUCTION

In studies of rodents, it is widely recognized that testicular hormones, particularly testosterone (T), act during a critical period of perinatal development to both masculinize and defeminize later adult sexual behavior (for review see Baum, 1979; Goy and McEwen, 1980). Although studies of rhesus monkeys have demonstrated that androgens during prenatal development are critical for the differentiation and expression of masculine behavior traits (Goy, 1964, 1968, 1978, 1981; Goy and Resko, 1972; Eaton et al., 1973), several studies have failed to detect any deficits in the expression of feminine behavior traits that are attributable to androgen action during prenatal development (Goy, 1978; Phoenix et al., 1983). Nevertheless, only recently has the female-typical sexual behavior of male and female rhesus monkeys been systematically evaluated during standardized pair tests (Thornton and Goy, 1985). In that study, when castrated males and spayed females were treated with estradiol benzoate, sex differences in the expression of female-typical sexual responses emerged, but behavioral differences were not observed when the animals were tested without exogenous estrogen. The extent to which prenatal androgen exposure contributed to these sex differences remained unclear, however. When comparisons of female sexual behavior were made between female rhesus monkeys treated prenatally with androgens (female pseudohermaphrodites) and control females, pseudo-

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hermaphroditic females were found to differ from control females in the same ways that neonatally castrated males differed from control females; however, most of these comparisons were not statistically reliable.

In the present study, we attempted to evaluate further the effects of androgen exposure during prenatal development of rhesus monkeys on the performance of adult patterns of female sexual behavior. In contrast to previous studies in which the monkeys were observed in a typical pair-test cage environment (Phoenix et al., 1983; Thornton, 1983), we studied their behavior while they were in a large room with a tethered stimulus stud male. Previously, the tethered male procedure was found to be a useful technique for evaluating sexual behavior of female rhesus monkeys in the laboratory (Pomerantz and Goy, 1983). We felt the use of the tethering procedure in the present study would allow experimental monkeys greater control over sociosexual interactions with a stimulus stud male and, thus, enable us to more directly assess their expression of feminine patterns of sexual behavior.

MATERIALS AND METHODS

Subjects

The subjects were 29 6–9-yr-old rhesus monkeys (*Macaca mulatta*) born at the Wisconsin Regional Primate Research Center. The monkeys were divided into 4 experimental groups: 1) *testosterone propionate (TP)-treated female pseudohermaphrodites* (n = 8)—females born to mothers that, beginning approximately postconception day 42, were injected i.m. with 10–15 mg/day TP for 54–55 days (n = 6) or 5 mg/day TP for 75 and 80 days (n = 2); 2) *5α-dihydrotestosterone propionate (DHTP)-treated female pseudohermaphrodites* (n = 8)—females born to mothers that, beginning approximately postconception day 42, were injected i.m. with 10–15 mg/day DHTP for 55–60 days (n = 6) or 5 mg/day DHTP for 79 days (n = 2); 3) *castrated males* (n = 6)—males castrated within the first month after birth; and 4) *control females* (n = 7)—females from untreated pregnancies. Control females and pseudohermaphrodites were gonadally intact throughout these experiments. Genital virilization of the female pseudohermaphrodites was extensive, with a well-formed penis (similar to that observed in neonatally castrated males) that was infantile in size due to the lack of testosterone stimulation after birth. Vaginal orifices were obliterated and scrota of variable size were conspicuous. A more complete description of genital virilization has been published (Goy, 1981). One control female was subsequently dropped from the experiment on the basis of her failure to adapt to the testing situation. During all tests, she would cling to the top corner of the testing pen, constantly remaining at maximum distance from the tethered male. This behavior was observed only rarely in other monkeys, and no other experimental monkey showed this behavior to this extent.

Prior to the present experiment, monkeys were reared in social mother-infant groups during the first year of life. At approximately 1 yr of age the monkeys were weaned and housed in groups for the next 3 yr, except for 50–60 days each year when they were individually housed and tested for 0.5 h daily with their natal peers (Goy and Wallen, 1979). When the monkeys were 4.5 yr old they were housed individually or in groups depending on available space. One year prior to the present study, 5 TP-treated female pseudohermaphrodites, 5 DHTP-treated female pseudohermaphrodites, 6 castrated males, and 4 intact females were studied by Thornton and Goy (1985).

Two vasectomized sexually experienced males approximately 12–13 yr old served as stimulus males. Stimulus males were adapted to the tethering procedure (Pomerantz and Goy, 1983) prior to initiation of tests with the experimental subjects.

All monkeys were individually housed. The rooms where the animals were kept were maintained at a constant day/night length (11L:13D) and a constant temperature (21–22°C). Animals were fed Purina Monkey Chow supplemented with fresh fruit. Water was available ad libitum.

Apparatus

Stimulus males were tethered and behavior tests conducted in a wire-mesh pen 2.8 × 1.9 × 1.9 m high, illustrated in Fig. 1. It should be noted that this pen was larger than the cage used in our previous study (Pomerantz and Goy, 1983). Stimulus males wore a leather harness (Pomerantz and Goy, 1983) to which was attached one end of a 91-cm flexible stainless-steel tether (Spalding Medical Products, Arroyo Grande, CA). The other end of the tether was attached to a feed-through swivel (Model 310, Spalding Medical Products) mounted on top of an open-front "tethering cage" (1.6 × 0.7 × 0.8 m) that was situated at one end of the test pen. The tethering arrangement permitted the males full freedom of movement inside the tethering cage, and in addition enabled the males to move on the platform in front of or climb on top of the tethering cage. Harnessing and tethering of the stimulus males was performed with the males awake. Stimulus males were not tethered for more than 5 days consecutively, after which the tether and harness were removed. At least 3 days intervened before the male was tethered again.

Procedure

Prior to testing, all experimental monkeys were implanted s.c. under Ketamine anesthesia (10 mg/kg) with two 5-cm Silastic capsules (0.335 cm I.D., 0.465 cm O.D.) containing estradiol-17β (E_2). This hormonal regimen maintained blood levels of E_2 around 200 pg/ml, which approximates average levels close to the time of ovulation in rhesus monkeys (Goy and Resko, 1972). Behavior tests commenced 1 wk after implantation of the estradiol capsules. Experimental monkeys received 3 tests/wk for 2 wk. A different stimulus male was used each week with the order of the presentation of the males being counterbalanced. Behavior tests were 20–30 min in duration and were started by introducing the experimental animal into the pen at the end opposite to the tethered male. Tests were

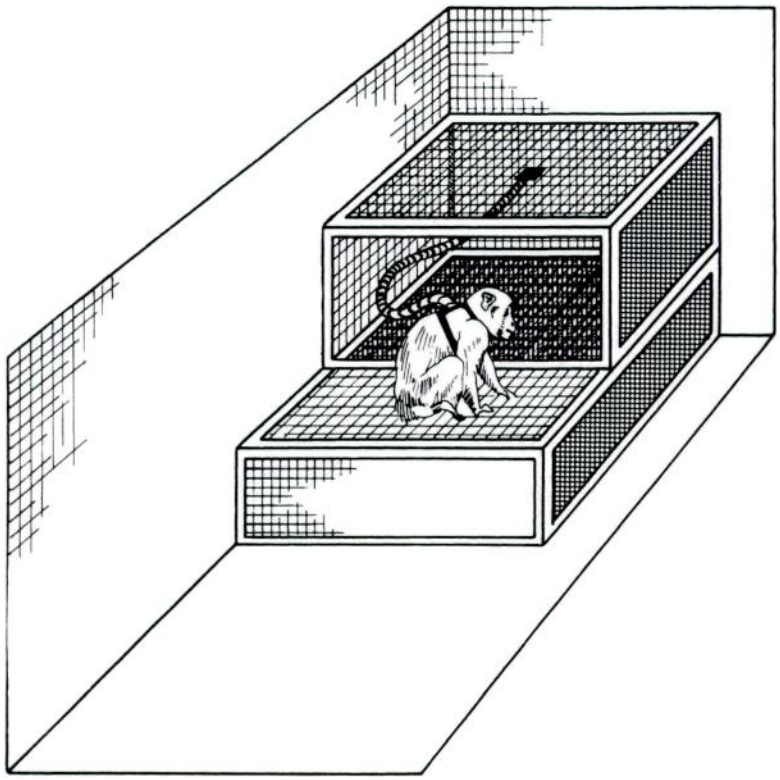

FIG. 1. Schematic representation of wire mesh pen in which behavior tests were conducted with "tethering cage"; stimulus tethered male is also depicted.

ended when any of the following criteria were met: 1) 20 min without copulation or without ejaculation if the first double foot-clasp mount occurred in the first 10 min of test; 2) no ejaculation within 10 min of first double foot-clasp mount, if this mount occurred after the first 10 min of test; or 3) first ejaculation.

Behavior tests were observed by two experimenters through a one-way glass mirror outside the room containing the test pen. One experimenter dictated behavioral events to another, who recorded the behavior on a checklist divided into 15-s intervals. The recorded behaviors of experimental animals were for the most part similar to the female behaviors used previously (Pomerantz and Goy, 1983) and included:

Approach: Experimental animal walk directed toward and stopping within an arm's length of the stimulus male.

Proximity: Experimental animal seated within an arm's length (<0.6 m) of the stimulus male. This measure was not scored during bouts of grooming.

Solicit: This category included "head bob/duck" (Michael and Zumpe, 1970), hand slap or "sporadic arm reflex" (Carpenter, 1942; Czaja and Bielert, 1975), glance (Pomerantz and Goy, 1983), and sidle (Pomerantz and Goy, 1983) responses by the experimental animal.

Presentation: Rigid posture with orientation of the perineum toward the stimulus male and varying degrees of tail deviation (Michael and Zumpe, 1970). A distinction was made between presentations immediately following a contact by the stimulus male and spontaneous pressentations (Wallen and Goy, 1977). Spontaneous presentations were further subdivided into those that the tethered male could and could not contact.

Maximum Distance: Experimental animal stationary within 0.3 m of the opposite end of the test pen from where the stimulus male was tethered.

Recorded sexual behaviors of the tethered male included contact, mount, intromission, and ejaculation. Also, instances of male purse-lip display directed toward the experimental animal were scored. This behavior has been recognized previously as a possible courtship gesture in rhesus monkeys (Pomerantz and Goy, 1983). It involves a rapid pursing and pouting of the lips that is often accompanied by bobbing of the head, widening of the eyes, and pulling back of the ears. In pig-tailed macaques a similar display has been defined and referred to variously as the "jaw thrust" (Kaufman and Rosenblum, 1966) and "protruded-lips face" (van Hoof, 1967).

Derived Behavioral Measures

The following measures were calculated from the raw data: *approach latency*, time in seconds from introduction of an experimental animal to the first approach; *mount latency*, time in seconds from introduction of an experimental animal to the first double foot-clasp mount by the stimulus male; *ejaculation latency*, time in seconds from introduction of an experimental animal to first ejaculation; *female typical acceptance score* (Wallen and Goy, 1977), proportion of contacts by the stimulus male (prior to a presentation) to which the experimental animal responded with a presentation; and *male acceptance score*, proportion of spontaneous presentations by the experimental animal (which the tethered male could contact) that resulted in a contact by the stimulus male. For each test, percentages of 15-s intervals during which the experimental monkey was in proximity to the stimulus male or at maximum distance from the stimulus male were calculated. Also, the rates (no./min) at which the experimental animals exhibited approaches, solicits, and presentations and the stimulus male exhibited purse-lip displays, contacts, and mounts were calculated. By expressing these behaviors in terms of percentage scores or rates, monkeys that were in tests of unequal time duration could be compared. Similarly, percentages of 15-s intervals and rates during which behaviors were exhibited were calculated for the interval of the approach latency, the interval from first approach to the end of the test, and the interval of the mount latency.

Data Analysis

In order to provide a framework for analyzing the data, the behavioral measures that were used in the experiment were classified as being an index of attractivity, proceptivity, or receptivity (Table 1). For each behavioral measure, each experimental monkey was assigned a score equal to the combined mean of their 3 tests with each of the 2 stimulus males. Comparisons of the behaviors of the experimental groups were made using the behavior scores during the ejaculation latency if ejaculation occurred, or during the entire test session if no ejaculation occurred. Comparisons of behavior were also made for the periods of time corresponding to the approach latency, first approach to end of test, and mount latency. Animals that did not receive a mount were assigned a score for a particular behavior equal to their score for the entire test. Nonparametric tests were used in analyzing the data. Kruskal-Wallis one-way analysis of variance (ANOVA) tests (Siegel, 1956) were conducted to test for overall group differences in behavior. Analyses yielding significant overall effects were followed by one-tailed paired-comparison tests using the Mann-Whitney U test (Siegel, 1956).

Since the behavior of the monkeys did not vary statistically between the two stimulus tethered males, the data presented represent the combined mean behavior scores with both stimulus males. Testosterone propionate and DHTP female pseudohermaphrodites did not differ statistically on any measure (their data are depicted separately in subsequent tables and figures) and were combined for statistical comparison to control females and castrated males. Additionally, female pseudohermaphrodites receiving 5 mg/kg TP or DHTP for 75–80 days did not differ statistically from female pseudohermaphrodites receiving 10–15 mg/kg TP or DHTP for 55–60 days on any measure of behavior; thus, these groups were combined during the statistical analyses.

RESULTS

Attractivity Measures

Behavior exhibited by the tethered males toward the experimental monkeys during the test sessions provided an indirect assessment of the attractiveness of the experimental monkeys (Fig. 2). Overall comparisons of these 4 measures of attractiveness revealed significant main effects (Kruskall-Wallis ANOVA, $P<0.001$ to $P<0.05$) among experimental groups for every measure. Selected contrasts demonstrated that castrated males differed reliably (Mann-Whitney U test, $P<0.001$ to $P<0.01$) from control females on every measure of attractivity.

TABLE 1. Classification of behavior measures.

	Behavioral measure
Attractivity	Stimulus male purse-lip rate
	Stimulus male contact rate
	Stimulus male mount rate
	Stimulus male acceptance score
Proceptivity	Experimental subject approach rate
	Experimental subject solicitation rate
	Experimental subject spontaneous presentation rate
	Experimental subject proximity score
	Experimental subject maximum distance score (negatively related)
Receptivity	Experimental subject female-typical acceptance score

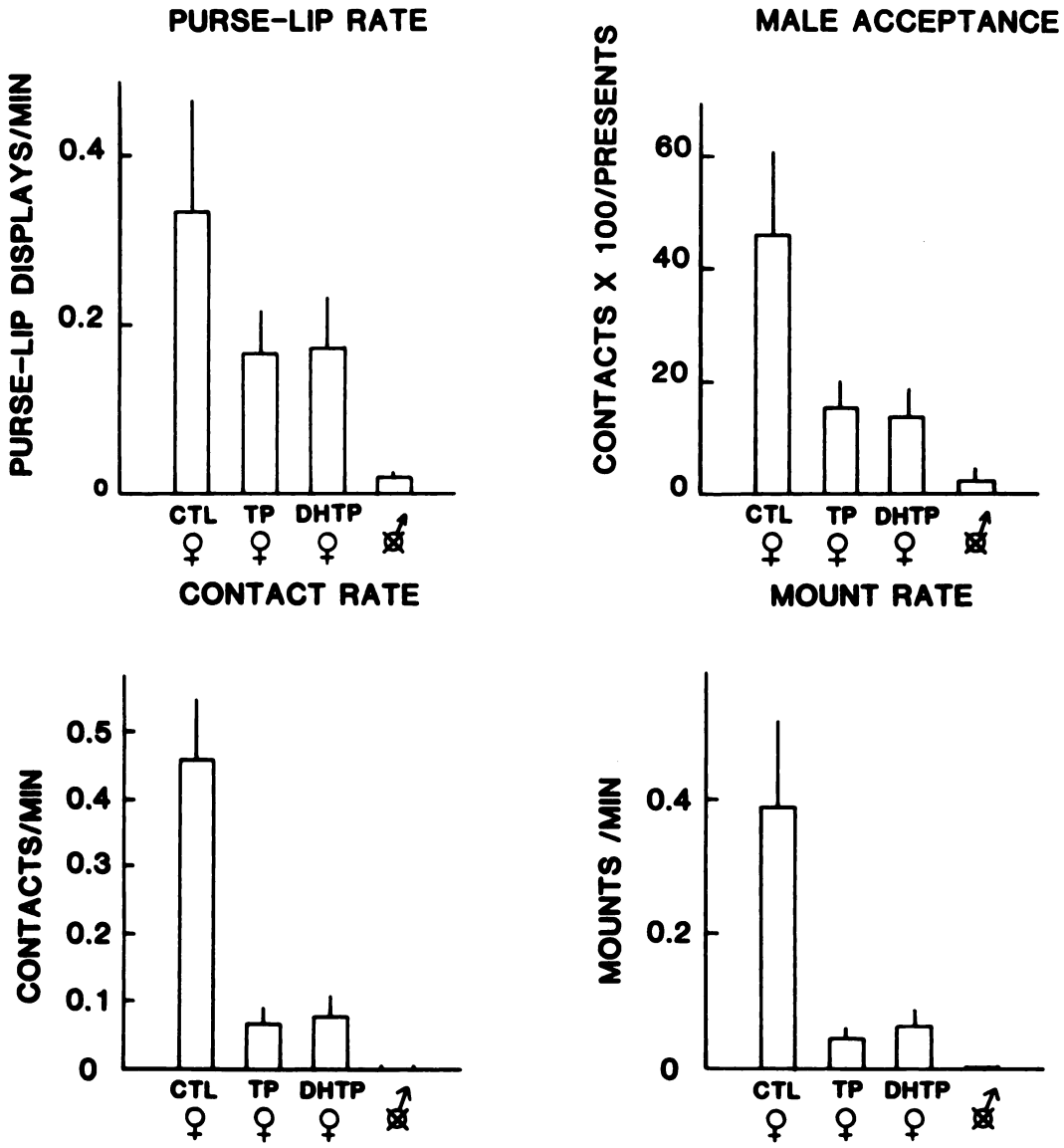

FIG. 2. Mean (± SEM) sexual behavior scores exhibited by the tethered male toward control females (n = 6), TP female pseudohermaphrodites (n = 8), DHTP female pseudohermaphrodites (n = 8), and castrated males (n = 6).

Female pseudohermaphrodites differed statistically ($P<0.05$) from castrated males on all 4 measures of attractivity and from control females on 3 of 4 measures—contact rate, mount rate, and male acceptance score. Analysis of the percentage of tests in which the tethered male exhibited mounting behavior revealed a statistically significant difference among the groups (χ^2_3 = 31.9, $P<0.001$), with the tethered males mounting control females in 22 of 36 tests (61%), TP female pseudohermaphrodites in 12 of 48 tests (25%), DHTP female pseudohermaphrodites in 11 of 48 tests (23%), and castrated males in 1 of 36 tests (3%). Further analysis showed that the tethered males mounted the female pseudohermaphrodites in reliably fewer tests than control females (χ^2_1 = 19.0, $P<0.001$), but in reliably more tests than castrated males (χ^2_1 = 5.8, $P<0.05$).

The display of purse-lip gestures by the tethered male prior to and after each experi-

mental subject's first approach provided an additional useful measure of attractiveness of the experimental subjects. In our testing situation, this facial display functioned in large part as a distance signal communicating an interest in positive affiliation. Its initial display during a test tended to occur within a few seconds of the experimental animal's introduction into the test pen. The tethered male exhibited this gesture prior to the experimental subjects' first approach in 24 of 36 tests (67%) with control females, 64 of 96 tests (67%) with female pseudohermaphrodites, and only 6 of 36 tests (17%) with castrated males. The overall difference among groups on this measure was statistically significant ($\chi^2_2 = 28.1$, $P<0.001$). When the purse-lip rate prior to the first approach was used to compare the experimental groups (Table 2), a similar group difference ($P<0.001$) was detected. It should be noted that the failure of the castrated males to elicit purse-lip responses was not due to there being insufficient time for the tethered male to purse-lip prior to the castrated males' first approach. Rather, if at all, the converse was true, with the approach latency of the castrated males being slightly longer than that for the other groups ($P<0.10$). When purse-lip rate was analyzed for the time period following the first approach until the end of the test, a somewhat different picture emerged. Although overall differences among the means were again statistically significant ($P<0.01$), in selected contrasts, pseudohermaphrodites received reliably fewer purse-lip gestures than control females ($P<0.05$), and they received reliably more than castrated males ($P<0.01$). Additional analyses of group differences in contact and mount rates following the first approach produced results that were identical to those found when the rates of these behaviors were compared over the entire test as reported above.

Proceptivity Measures

Proceptive behaviors, as measured by approach rate, solicitation rate, spontaneous presentation rate, and proximity score (Fig. 3), were found to vary significantly among the groups ($P<0.01$ to $P<0.05$). For all of these

TABLE 2. Mean (± SEM) approach latency and attractivity scores before and after first approach in four groups of rhesus monkeys.

Measure	Control females	TP female pseudohermaphrodites	DHTP female pseudohermaphrodites	Castrated males
Approach latency (s)	46.5 ± 16.5	73.5 ± 34.5	82.5 ± 24.0	121.5 ± 39.0
Purse-lip rate before first approach[a] (#/min)	0.75 ± 0.19[b]	0.88 ± 0.15	0.94 ± 0.19	0.10 ± 0.08[e]
Purse-lip rate after first approach[a] (#/min)	0.32 ± 0.14[bc]	0.10 ± 0.04	0.12 ± 0.04	0.01 ± 0.00[e]
Contact rate after first approach[a] (#/min)	0.22 ± 0.13[bd]	0.08 ± 0.02	0.09 ± 0.04	0.00 ± 0.00[e]
Mount rate after first approach[a] (#/min)	0.19 ± 0.12[bd]	0.06 ± 0.02	0.07 ± 0.03	0.00 ± 0.00[e]

[a] Kruskall-Wallis one-way ANOVA ($P<0.01$).

[b] Control females vs. castrated males (Mann-Whitney U Test, $P<0.01$).

[c] Control females vs. TP and DHTP female pseudohermaphrodites (Mann-Whitney U Test, $P<0.05$).

[d] Control females vs. TP and DHTP female pseudohermaphrodites (Mann-Whitney U Test, $P<0.01$).

[e] Castrated males vs. TP and DHTP female pseudohermaphrodites (Mann-Whitney U Test, $P<0.01$).

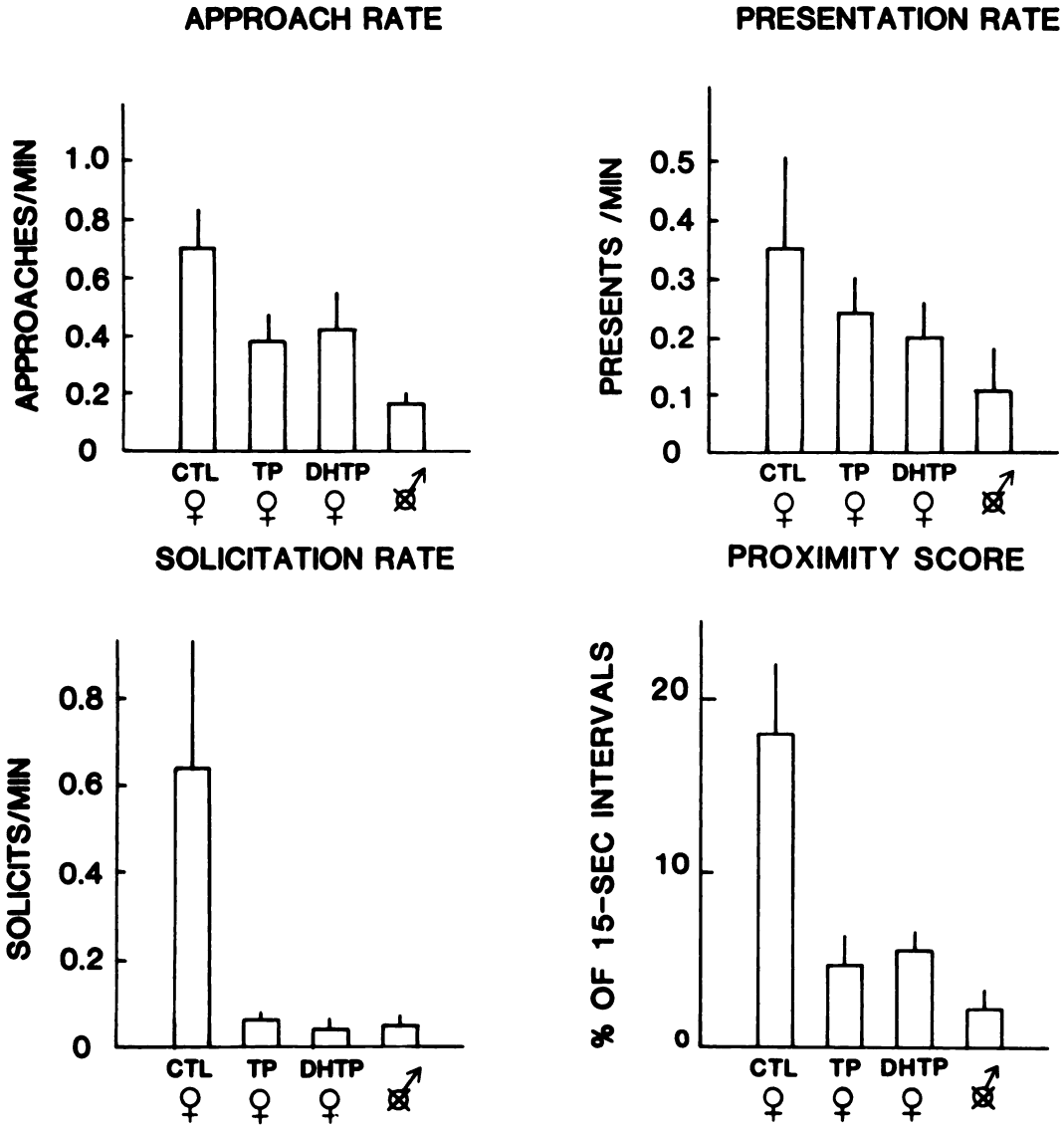

FIG. 3. Mean (± SEM) proceptive behavior scores exhibited by control females, TP female pseudohermaphrodites, DHTP female pseudohermaphrodites, and castrated males toward the tethered male.

proceptive behavior measures, the scores of castrated males were statistically less than control females ($P<0.001$ to $P<0.01$). Female pseudohermaphrodites differed reliably ($P<0.01$ to $P<0.05$) from control females on approach rate, solicitation rate, and proximity score but not spontaneous presentation rates, and from castrated males on approach rate, spontaneous presentation rate, and proximity score but not solicitation rate. No reliable group differences ($P>0.05$) in maximum distance score were observed, with the mean percentage (± SEM) of 15-s intervals during which the monkeys were at maximum distance from the tethered male being 17.7 ± 5.5 for control females, 27.3 ± 5.0 for female pseudohermaphrodites, and 29.3 ± 9.3 for castrated males.

In an attempt to separate out differences in proceptive behavior that might simply reflect differences in copulatory activity, measures of proceptive behavior were calculated for the period of time corresponding to the mount latency (Fig. 4). Comparisons of the proceptive behavior scores revealed statistically significant

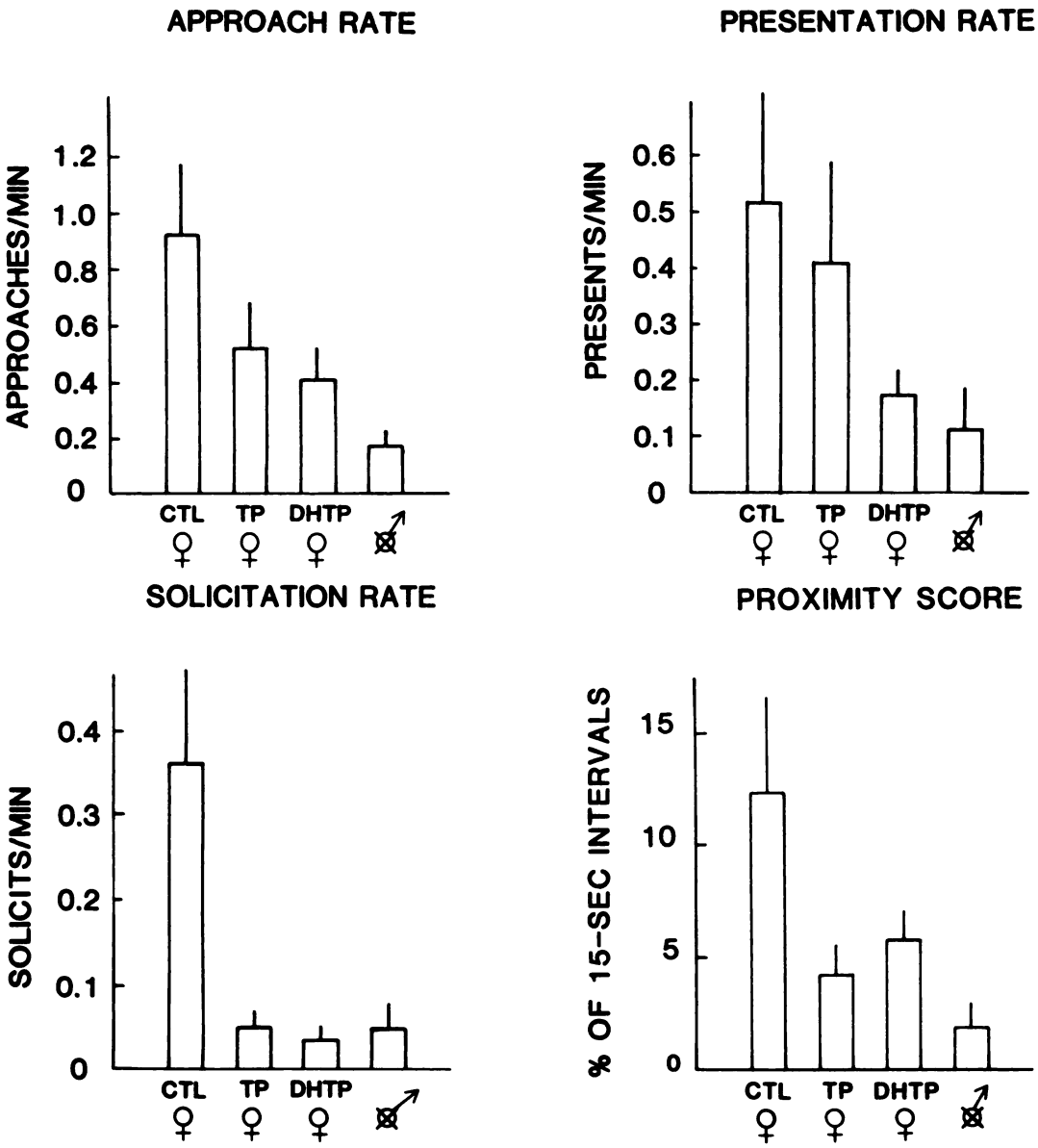

FIG. 4. Mean (± SEM) proceptive behavior scores during the mount latency exhibited by control females, TP female pseudohermaphrodites, DHTP female pseudohermaphrodites, and castrated males toward the tethered male.

differences among the groups ($P<0.001$ to $P<0.05$) that were similar in magnitude and direction to those observed when scores for the entire test session were used. Additionally, proceptive responses of the monkeys were compared for the period of time following the first approach. Results of these analyses also yielded differences among all groups similar to those found when other periods were analyzed (data not shown).

Receptivity Measures

Receptivity scores of the experimental monkeys as measured by the female-typical acceptance scores are presented in Fig. 5. Castrated males did not contribute data to this measure, since they were never contacted by the tethered male unless they had previously presented to him. Among the other experimental groups no statistically significant

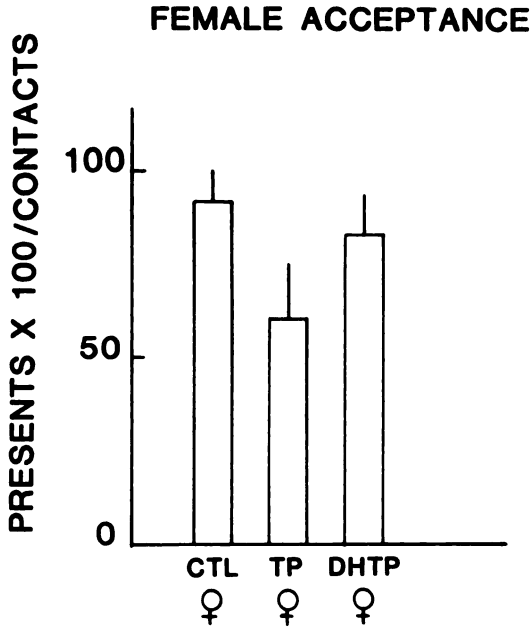

FIG. 5. Mean (± SEM) female-typical acceptance scores exhibited by control females, TP female pseudohermaphrodites, and DHTP female pseudohermaphrodites.

differences on this behavioral measure were observed.

The display of threats and/or aggression by the tethered males did not contribute in any way to the differential scores of the experimental groups for attractivity, proceptivity, and receptivity. In fact, threat and aggression was shown by only one tethered male on one test when paired with a DHTP pseudohermaphrodite. That aggressive encounter terminated a brief series of mounts by the pseudohermaphrodite. We found no instance of threat gestures utilized as a distance signal communicating hostility and functioning to prevent the approach of an experimental subject.

DISCUSSION

In the present study, during tests with a tethered male partner, the existence of clear sex differences in female sexual behavior of adult rhesus monkeys was established. Although our tests did not effectively evaluate sex differences in receptivity, castrated male monkeys treated with estrogen showed deficits on behavioral indices of attractivity and proceptivity compared to females. Furthermore, support for the hypothesis that these sex differences in female sexual behavior were in large part a result of prenatal androgen exposure was demonstrated by the finding that female rhesus monkeys administered androgens prenatally (female pseudohermaphrodites) and tested as adults also exhibited deficits in both attractive and proceptive components of female sexual behavior.

Although differences in female sexual behavior among the experimental groups may in large part be a function of exposure to androgen prenatally, the extent to which such variation is attributable to reduction of attractivity or to defeminization of proceptivity or to both combined is unclear. The use of the tethered male testing procedure as a means of effecting greater independence in the measurement of attractivity and proceptivity was only partially successful, and averages for the experimental animals' proceptive responses covaried with averages for attractivity measures derived from the stimulus males' behavior.

Nevertheless, several strategies were adopted in the analysis of the data that we hoped would enable us to render measures of proceptivity and attractivity more independent of one another. Analysis of purse-lip gestures by the tethered male, prior to the first approach of the experimental monkey, provided a useful index of each monkey's attractiveness irrespective of its display of proceptive behavior. It also enabled us to distinguish between attractivity at a distance as opposed to attractivity in proximity to the tethered male. In this analysis, the tethered males easily discriminated castrated males from both normal and pseudohermaphroditic females despite the circumstance of equal estrogen treatment. The tethered male differentially displayed the purse-lip response such that this gesture was more often than not given to both normal and pseudohermaphroditic females within the first few seconds following their introduction into the test pen and rarely displayed to castrated males.

Although one might argue that the difference in attractivity observed between castrated males and female pseudohermaphrodites was a consequence of the castrated males being exposed to androgens in a different fashion (e.g., for a longer period of time in utero) than female pseudohermaphrodites, we are more inclined to attribute this difference in attractivity to the expression of a genetic sex difference in body morphology. Male rhesus monkeys, regardless of their testicular status, attain longer

bodies than females or pseudohermaphrodites, and this difference in body length is easily discriminable at a distance. Somatometric measures obtained in collaboration with Dr. J. W. Kemnitz at the end of the present study showed that body lengths (crown-heel) differed significantly ($F_{2,20}$) = 14.22, $P<0.001$) among neonatally castrated males (85.1 ± 1.1 cm), pseudohermaphrodites (78.5 ± 0.8 cm), and females (78.0 ± 1.4 cm); however, neonatally castrated males did not differ reliably from gonadally intact males (88.7 ± 1.6 cm). Thus, in terms of this measure of attractiveness-at-a-distance, castrated males were much less attractive than either females or pseudohermaphrodites, but the basis for their lower attractiveness probably was not attributable to their endocrine history.

Females and pseudohermaphrodites did not differ in attractiveness-at-a-distance. However, tethered males discriminated in favor of the females in measures of attractiveness once proximity was established by showing lower purse-lip, contact, and mount rates to female pseudohermaphrodites than to normal females. It could be argued that such deficits arose from the fact that these female pseudohermaphrodites do not possess a vagina. Nevertheless, the lack of a vagina did not prevent a male from executing intromissions with female pseudohermaphrodites. In the present study, tethered males obtained anal intromissions with several pseudohermaphrodites and achieved an ejaculation with one of the TP female pseudohermaphrodites. Thornton (1983) reported similar observations of a male ejaculating on a number of occasions with female pseudohermaphrodites (both TP and DHTP treated) as well as with a castrated male. In none of these cases were there behavioral indications that partners experienced any discomfort from the anal intromissions. However, possible resolution of any effect that the absence of a vagina has on female attractiveness of rhesus monkeys might be accomplished with surgical reconstruction of the vagina and successful adaptation by the monkey to it (Phoenix et al., 1984).

An alternative explanation for the findings of the reduced male interest in female pseudohermaphrodites is that the female pseudohermaphrodites exhibited reduced levels of proceptive behavior when compared to normal females. Deficits among pseudohermaphrodites were observed for approach, proximity, and soliciting behaviors. Clearly, these deficits in behavior could have resulted in the tethered male having both less opportunity and a lowered motivation to direct sexual behaviors to female pseudohermaphrodites.

The observation of reduced proceptive behavior among female pseudohermaphrodites is also extremely interesting in its own right, since it is evidence in support of the hypothesis that prenatal androgen has a defeminizing influence on female proceptive behavior. To eliminate any possible influence that copulation had on the performance of proceptive behavior, the behavior was analyzed prior to the first mount. Using such an analysis female pseudohermaphrodites were still found to be deficient in their expression of proceptive behavior when compared to normal females. Additionally, since most measures of proceptive behavior depend by definition on responses made in proximity to the tethered male, in order to prevent the possibility of disproportionately weighting the behavior of animals that were reluctant to first approach the tethered male, behavior was analyzed after the first approach. Again, female pseudohermaphrodites were found to be deficient in their expression of proceptive behavior. It is our contention that these consistent findings of defeminization among both female pseudohermaphrodites and castrated males in different analyses lend further support to the hypothesis that prenatal androgen exposure has a defeminizing influence on adult proceptive behavior.

Differences in proceptive behavior found between the female pseudohermaphrodites and castrated males are easily attributable to differences in prenatal androgen exposure or differences in endocrine histories alone. Truly comparable assessments of proceptive behavior of these groups was not possible, since prior to their exhibition of proceptive behavior, while they were still at a distance from the tethered male, the monkeys from these two groups were differentially attractive to the tethered male. Clearly the possibility exists that the tethered male's communication of differential interest could contribute to the experimental animals' display of proceptive responses.

Readers should bear in mind a circumstance that limits the generalizability of our findings on proceptive behaviors. Our data were obtained from subjects treated with exogenous estradiol alone. Recently Feder and Goy (1983) suggested that high concentrations of steroids at particular early stages of development might

act to "switch" female proceptive behaviors to a greater activational dependence upon androgens in adulthood. It has been proposed that androgens contribute to rhesus proceptive responses for normal females (Everitt and Herbert, 1975; Baum et al., 1977; Wallen and Goy, 1977), and the possibility should be considered that pseudohermaphroditic female rhesus as well as male rhesus monkeys have a greater requirement for androgenic activation of proceptivity than normal females. If this were shown to be the case, then the deficits we have shown would have to be interpreted as merely deficits in response to estrogen alone, and combinations of estrogens plus androgens might yield different results.

In the present study it was not possible to evaluate whether the receptive behavior of castrated males was defeminized. Previously, it was reported that castrated males exhibited deficits in receptive behavior relative to castrated females (Thornton and Goy, 1985) in tests conducted in a pair-test cage environment, suggesting that endogenous prenatal androgens may have a defeminizing influence on expression of receptive behavior by genotypic males. Nevertheless, further testing of this hypothesis both in the present study and in studies in which the pair-test cage environment was used (Phoenix et al., 1983; Thornton, 1983) revealed no reliable differences in female-typical acceptance scores between female pseudohermaphrodites and control females. Thus, the evidence for rhesus monkeys favors the view that mechanisms governing receptivity are somehow protected against defeminization. In this respect, the receptivity mechanisms resemble those governing ovarian function (Goy and Resko, 1972) and positive feedback of estrogen on gonadotropin output (Steiner et al., 1976).

In most species studied, exposure to androgen during specific developmental stages causes defeminization of both proceptive and receptive components of feminine sexual behavior (dog: Beach et al., 1977; rat: Fadem and Barfield, 1981; pig: Ford, 1983; hamster: Johnson and Teifer, 1972). In rhesus monkeys, in contrast, defeminization of proceptive behavior is not necessarily accompanied by defeminization of receptive behavior. To our knowledge, the only other species in which a similar dissociation of proceptive and receptive components of female sexual behavior occurs is the ferret (Baum et al., 1985).

Female pseudohermaphroditic rhesus monkeys, whether produced through exposure to TP or to DHTP prenatally, behaved similarly in adulthood on tests of female sexual behavior in this study. This result compares favorably to the behavior of these animals as infants and juveniles, in which both TP and DHTP female pseudohermaphrodites exhibited similar masculinization of protosexual mounting behavior and play behavior (Goy, 1978, 1981). These results further demonstrate that sexual differentiation of behavior in rhesus monkeys by androgens does not appear to depend on aromatization of androgens to estrogens, and in this respect distinguish the mechanism of androgen action on sexual differentiation in the rhesus monkey from that in species such as the rat and hamster, in which aromatization of androgens to estrogens is necessary for sexual differentiation to occur (Baum, 1979).

The findings of the present study generally differ from those of Phoenix et al. (1983) and Thornton and Goy (1985). The Phoenix et al. study failed to find any deficits in proceptive behavior of female pseudohermaphrodites, while the Thornton and Goy study found a deficit that was limited to soliciting behavior. In our opinion, methodologic factors may account for the differences in results. Both of those studies tested the monkeys in a small space with unrestrained stimulus males. The persuasive argument has been advanced that the conditions imposed by this testing environment are not conducive to the full expression of female behavior (Pomerantz and Goy, 1983; Wallen, 1982). In general, by using the tethered male procedure, we feel we were able to more effectively limit the stimulus male's influence on the behavior of the experimental animals. In so doing, the effect of prenatal androgen exposure on defeminization of female proceptive behavior was more readily apparent.

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