ABSTRACT

THE EFFECTS OF EARLY CASTRATION AND TESTOSTERONE PROPIONATE TREATMENT ON THE DEVELOPMENT AND DISPLAY OF BEHAVIOR PATTERNS BY MALE RHEUSS MONKEYS (*MACACA MULATTA*)

By

Craig F. Bielert

The aim of this thesis was an evaluation of the role gonadal hormones play in the development and display of social and sexual behavior patterns by male rhesus monkeys. Consideration was also given to the role social factors may play in moderating the frequency of certain hormone stimulated behavior patterns.

The development of male rhesus monkeys castrated on either day of birth or at three months of age, was compared to the development of similarly reared intact males. During the first two years of life, castrates resembled the intact males in their display of dimorphic behavior patterns which significantly distinguish intact males from females. During the first two years of life there was no evidence of deficient masculine behavior development on the part of the castrate males. In order to assess the effects of increased postpubertal gonadal hormone levels comparisons were made between castrates and intact males for the first four years

of life. Two behavior patterns, erection and yawning markedly increased postpubertally for intact males; similar increases were not observed for castrates. Intact and castrate males did not differ in the measure of brief contact and rough and tumble play suggesting that the decline in this behavior occurs independently of the gonadal events of puberty. Both castrates and intact males exhibited mounts, intromissions, and ejaculatory responses. Gonadal status appeared to affect the level of aggression exhibited during periods of social instability with intact males exhibiting higher levels at such times than the castrates. In order to assess the activational potential of the major male gonadal hormone, testosterone, testosterone propionate injections were given to several groups of castrate male rhesus of two age classes: 1) fourteen and one-half months; 2) fifty months. The effects of androgen were assessed under social as well as in pair test situations. Results of the testosterone treatment period were compared to the prehormone test period. For the social group testing castrates differed from intact males in erections, yawning, groom solicitations, and genital examinations received. No increases in mounting or aggression were obtained. The group of older castrates increased in the measures of yawn, erection, and auto-genital manipulation after testosterone treatment. Though the older castrates exhibited higher prehormone treatment levels of mounting and aggression than the younger

castrates, these measures failed to increase during the testosterone treatment period. During pair testing young castrates increased their levels of approach, contact, and mount while under testosterone treatment. These measures differed significantly between castrates and intact males during the TP treatment period, but not the prehormone treatment period. Two young castrates exhibited intromission while receiving testosterone therapy and one of these two also displayed ejaculation. The old castrates also increased their sexual behavior scores, but varied individually.

In another experiment the mating behavior of adult intact and castrate males which were raised with peers were compared. These two groups were also compared to a group of adult intact wild-caught males. Laboratory-reared males had a lower percentage of responders for several measures of sexual behavior. The castrate group had the smallest number of responders. Contact and mount frequencies of the intact laboratory-reared males were significantly lower than those of the wild-caught males. Female stimulus partners behaved differently with the three groups of males and measures of proximity and spontaneous were at low frequencies during tests with castrates. A dominance paradigm was followed in order to categorize the pair tests as one in which the male was dominant to the female or one in which the female was dominant to the male. The dominance interactions between the pair were shown to affect the level with which certain male and female sexual behavior patterns were shown. Testosterone injections modified the dominance relations between the adult castrate males and their stimulus female partners.

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By

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"For you have learned. One school is finished, and the time has come for another to begin."

Richard Bach, Jonathan Livingston Seagull

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INTRODUCTION

Many nonhuman primate species exhibit physiological, social and behavioral similarities with man. These similarities make certain primates appropriate for use as models in the examination of human biomedical problems. One area of research in which the rhesus monkey (Macaca mulatta) has been extensively employed is that of sexual behavior. The rhesus appears sensitive to many of the same general social and endocrine factors that affect humans. Experimental manipulation of humans is impossible, and for this reason clinical cases and observations on unusual syndromes become an important source of basic information from which relevant hypotheses are generated. A critical examination of hypotheses relevant to a particular clinical condition does require experimentation and it is in this regard that data from nonhuman primate experiments take on a very important role. These data allow one to assess the relative merits of a particular hypothesis as generated by work with the monkey and as it may be pertinent to the human.

The concern of this thesis was the fashion in which gonadal hormones affect the behavior of male rhesus monkeys. It is hoped that the projects carried out with these monkeys may aid in the understanding of the fashion in which gonadal hormones influence human behavior. It is with this in mind that a review will now be given to the experimental data which are already in the literature and may be relevant to a consideration of the ways in which gonadal hormones affect behavior in a wide variety of species.

For several years data have accumulated which are consistent with the hypothesis that hormones of testicular origin can permanently alter mammalian behavior patterns if present at the appropriate period during embryological development. In 1959 workers from the laboratory of Dr. W.C. Young published a paper dealing with the organizing action of prenatally administered testosterone propionate on the tissues which mediate mating behavior in the female guinea pig (Phoenix, Goy, Gerall and Young, 1959). It was in this paper that attention was first drawn to the effects which early gonadal hormone exposure might have on a sexually dimorphic behavior, although the possibility of behavioral modification had been suggested by earlier work (Dantachakoff, 1938a, b, c; Raynaud, 1938; Wilson, Young, and Hamilton, 1940). Following publication of the work on the guinea pig similar effects in behavioral modification were reported for the rat (Harris and Levine, 1965). Experiments assessing the effects of hormonal manipulation on the mating behavior of the genetic female have also been carried out with the mouse (Edwards and Burge, 1971), the Syrian golden hamster (Swanson and Crossley, 1971), and the dog (Beach and Kuehn, 1970; Beach, Kuehn, Sprague, and Anisko, 1972). Many excellent reviews have come out on the general topic area and they offer a breadth of interpretation (Valenstein, 1968; Whalen, 1968; Beach, 1971;

Brain, 1971; Gorski, 1971; Money and Ehrhardt, 1971; Davidson and Levine, 1972; Money and Ehrhardt, 1972a; Goy and Goldfoot, 1973; Steinbeck and Neumann, 1973).

In general, the hypothesis as it currently stands is that fetal gonadal hormones act as inducers if present during embryological development. In other words, nervous system tissue is permanently modifiable if appropriate hormonal exposure occurs during the period of neural organization. The period of neural organization and hormone sensitivity is neonatal in some species such as the hamster (Eaton, 1970; Carter, Clemens, and Hoekema, 1972), while for the rat it appears to include both uterine and postparturient periods (Gerall and Ward, 1966; Gerall, Hendricks, Johnson, and Bounds, 1967; Stern, 1969). For the guinea pig and rhesus monkey this sensitive period occurs during the time period <u>in utero</u> (Goy, Bridson and Young, 1964; Resko, 1970). The genetic sex of the individual appears irrelevant to behavioral modification; neural tissues of females as well as males appear equally modifiable, although genetic sex may yet be shown to exert some type of limitation in this regard. For the species studied, it is only the genetic male which is exposed to a high concentration of gonadal hormone during early development; the fetal ovaries show little secretory activity (Resko, Feder, and Goy, 1968; Resko, 1970; Resko, Malley, Begley, and Hess, 1973). There has however, been the suggestion that the ovary may serve in a potentiating capacity for the female (Gerall, 1973; Gerall, Dunlap and Hendricks, 1973), but this potentiation phenomenon doesn't appear to involve any central nervous system alteration.

Experimental manipulations of gonadal hormones have been determined by the sex of the individual animal as well as by the nature of the species typical gestation for that particular animal. Genetic females can be exposed to hormones by means of direct injection, hormone implantation, or indirectly while *in utero* through injections of their mothers. The genetic male's hormonal environment can also be manipulated at several levels (Jost, 1971/72). One experimental approach is through interference with the glandular processes of hormone synthesis and release. A second and perhaps the most common manipulative technique is by castration. A third level at which hormone action can be manipulated in the genetic male is through interference with hormone receptors, hormone conversion, and gross cellular activity. It should be remembered that no matter what the sex of the individual or the manipulation employed the effects are to a great degree dependent upon ongoing developmental processes. Not all behavioral patterns exhibit the same period of sensitivity (Coniglio, Paup, and Clemens, 1973). During a particular behavioral pattern's period of sensitivity small manipulations of the hormonal environment can result in radical modification, however by starting at a later period somewhat similar changes may be induced by increasing the hormone do se level (Goy et al., 1964). Demonstrations of the limits of this physiological sensitivity have frequently utilized the rat. Ward (1972) has shown that by stressing pregnant female rats a decrease in mounting by the male offspring can be detected In addition, Clemens and Coniglio (1971) have shown that the number of males present _in utero_ and their relative proximity to their female siblings appear related to the frequency of mounting eventually shown by these females. Partly because of the unidirectional nature of developmental processes, there are time periods past which no amount of hormonal exposure will result in behavioral modification.

Hormones during postnatal periods have what has been described as an activational action on behavior patterns, and the activational action of gonadal hormones on mating as well as social behaviors has been well reviewed (Guhl, 1961; Young 1961; Hart, 1974). Work on the hormonal activation of sex behavior has dealt with the problem through two experimental approaches: a) developmental studies of mating behavior; b) manipulations of gonadal condition in animals which have already exhibited complete mating behavior. For both males and females the elimination of gonadal hormones will result in the deterioration and decline of the complete mating pattern. Males as well as females gonadectomized prepuberally may also fail to develop the complete mating pattern. Complete mating behavior can be restored in gonadectomized males and females of numerous species, through the administration of hormones of the appropriate variety and concentration. The hormone itself, however, remains passive in terms of its affect on mating behavior; hormones don't have the capacity to alter the specific pattern shown or increase the maximal response rate though their level may affect certain measures of response within narrow limits (Grunt and Young, 1953; Peretz, 1968). It appears that it is experiential (Lehrman, 1962; 1971) as well as genetic factors (Valenstein, Riss and Young, 1954; Goy and Young, 1957; Goy and Jakway, 1962) which are critical in determining the behavioral responses which hormonal stimulation may elicit.

It is largely as a result of the work which has gone on with rodent species that it has come to be accepted that gonadal hormones can affect behavior patterns in two different and distinct fashions. These two actions have been categorized as "organization" and "activational"; and can be described and distinguished as follows.

1. The organizational action of gonadal hormones for those mammalian species in which it has been investigated is of protracted duration and limited to fetal and larval stages. Effects of hormonal action of this type are persistent and may or may not require adult sex hormone levels for their exhibition.

2. The activational action of gonadal hormones may be limited in one direction by an age boundary. Effects of hormonal action of this type are transient or tonic depending upon the presence of the appropriate hormonal substrate and its level.

Though the preponderance of research dealing with the effects of gonadal hormone on sexual behavior has utilized nonprimate species, there are data on the rhesus monkey (*Macaca mulatta*) in this regard as well as clinical literature on the human. A recent review (Luttge, 1971) dealt very broadly with the topic for both males and females. The remainder of this literature review will focus on the male and the female pseudohermaphrodite and the affects which gonadal hormones have on their behavior.

The psychological literature contains numerous references to the importance which genetic sex plays in determining behavioral response. Dr. Harry Harlow and his associates at the University of Wisconsin were the first to demonstrate in a conclusive fashion that for the rhesus monkey these behavioral differences can emerge in a situation devoid of maternal intervention. Dr. Leonard Rosenblum (1961) published work on young surrogate reared rhesus monkeys which were allowed only peer contact showing that under these conditions young male and female rhesus exhibited dimorphic patterns of play, sex and aggression. Work carried out by Drs. William Young, Robert Goy and Charles Phoenix at the Oregon Regional Primate Research Center corroborated these findings. These researchers have enumerated five separate patterns of social interaction in which, (in terms of frequency of occurrence), juvenile males differ significantly from juvenile females. The patterns have been descriptively named: a) threat b) play initiation c) rough and tumble play; d) pursuit play; and e) mounting behavior. Under the peer rearing conditions employed, males differed quantitatively from females at levels of from 5x to 10x depending upon the behavior pattern examined (Young, Goy and Phoenix, 1964; Phoenix, Goy and Resko, 1968; Goy, 1968, 1970; Goy andPhoenix, 1971; Goy and Resko, 1972). A sixth begavior pattern, that of presenting, was not found to be dimorphic under these rearing conditions. This is an interesting observation in light of the fact that presenting is the posture which is most analogous to that of the lordotic posture exhibited by receptive female rodents. In rodents, this behavioral pattern is exhibited dimorphically and its display may be affected by early hormone exposure.

In more recent work carried out at the Wisconsin Regional Primate Research Center by Dr. Goy and his colleagues, a rearing condition has been utilized in which adult females are housed with their infants in small social groups. Sex dimorphisms consistent with those previously observed have again been documented (Goy and Goldfoot, 1974). It may, in fact, be the case that under this social rearing condition, situations are such that they maximize the reinforcement which mothers may provide for those behavior patterns which are biologically determined. It is known that mother-infant interaction is important to the rhesus (Harlow and Harlow, 1969) and others have documented marked differences in mother-infant interaction which are related to the sex of the infant for the pigtail macaque (Jensen, Bobbitt, and Gordon, 1968). The biological nature of sex differences in behavior for the rhesus has received further support from the work of Dr. Gene Sackett who has examined isolate reared rhesus monkeys and has found sex to be an important variable for a wide variety of measures including locomotor behavior, exploration time, and self-directed behavior (Sackett, 1972).

The literature on humans also contains documentation of sex differences in motor and facial patterns for infant play (Brindley, Clarke, Hutt, Robinson, and Wethli, 1973). These differences appear to be culturally modifiable but hold up to the cross cultural test of biological validity (Blurton-Jones and Konner, 1973). The sex differences between young boys and girls are not limited to measures of play alone (Hutt, 1972). Differences exist in the tendency of a child to leave its mother, the frequency of returns to mother, and the interval of these returns. Genetic sex also affects the choice of play objects. In a study of exploratory behavior carried out by Hutt (1970) a novel "play object" was presented to young nursery school children. Fewer girls than boys approached the object and the treatment of the object also differed for the sexes. Young girls tended to treat the play object in a very conventional and utilitarian fashion, while young boys tended to be creative and innovative in terms of their employment of the object in their play interaction.

The theory of the organizational action of gonadal hormones on behavior has been recently extended to the rhesus. Drs. Goy and Phoenix have demonstrated that it is possible through early androgen exposure to modify the exhibition of dimorphic behavior patterns by the genetic female rhesus monkey. Pregnant female rhesus were given daily injections of testosterone propionate from about day 40 to day 110 of gestation. The injection dosages varied as did the duration of treatment; complete details on the manipulations can be found in Goy (1970). The genetic female infants of mothers so treated exhibited marked anatomical masculinization at the time of birth. This masculinization was in good accord with that which Wells and Van Wagenen (1954) had obtained. The young pseudohermaphrodites had well developed penes and scrotum with no vestiges of vaginae. The young pseudohermpahrodites also had secondary male sex organs as well as functional ovaries. Menarche for these females was retarded from that of normal females, however (Goy, 1970; Goy and Phoenix, 1971; Goy and Resko, 1972). Once menarche had occurred, ovulatory ovarian cycles were documented (Goy and Resko, 1972). The behavioral development of these pseudohermaphrodites was characteristic of that of the genetic male. In all behavior categories for which sex differences had been described the pseudohermaphrodites failed to differ from the males. Furthermore, even in the mother-infant rearing condition, a social setting under which rapid development of mounting behavior occurs in genetic males, the pseudohermaphrodites followed the developmental path which was typical of genetic males raised under this condition. It appears clear from this work that the hypothesis of hormonal organization, which was formulated from research on rodent mating behavior, is validly extendable to the primate and to the rich social repertoire of these animals.

Additional support for the extension of the original theory comes from human clinical literature (as reviewed by Money and Ehrhardt, 1972b). There is evidence from cases of progestin-induced hermaphroditism as well as from cases of the andrenogenital syndrome which suggest that early exposure to androgenic substances will modify both the anatomy and the behavior of genetic female humans (Ehrhardt and Money, 1967; Ehrhardt, Evers, and Money, 1968). It should be added that the modifications of this hormonal exposure in the human are consistent with those of the rhesus. These individuals possess a penis and scrotum as well as functional ovaries. Further as was the case for the rhesus, there is evidence of delayed menarche for these girls (Jones and Verkauf, 1971). It has been reported that the young girls which received such early androgen exposure exhibited marked tomboyism in their play patterns. This has been suggested to be analogous to the rough and tumble play pattern which male and pseudohermaphrodite rhesus monkeys exhibit. These young girls also exhibited toy preferences which were of a more masculine character. In marked contrast to these propensities, young males afflicted with the syndrome of androgen insensitivity show very little masculine behavior although in rare cases some degree of anatomical masculinization may have occurred (Money, 1972, 1973; Money and Ehrhardt, 1972b).

It appears that data from both the rhesus monkey and the human are consistent with the hypothesis that early hormone action in the primate can be characterized as organizational in regard to its effects on behavior patterns which can normally be classed as dimorphic. Rodent sexual behavior, though frequently employed as an endpoint in examinations of the organizational action of gonadal hormones on behavior fails in these species to appear until puberty and cannot really be considered hormone-independent, may not be the best test of the theory on the organization action of gonadal hormones on behavioral patterns _per se_. In addition to the work on the rhesus monkey work with the effects of early gonadal hormones on the urinary postures of the dog has added convincing evidence that hormone independent behavior patterns can be permanently altered (Beach, 1970, 1974; Sprague and Anisko, 1973). The best evidence for the theory of hormonal organization of behavior, however still remains the experimental work on the rhesus for the rich social repertoire of this species offers an unrivalled potential.

Though early reports exist on the effects of castration and subsequent androgen therapy on the sexual behavior of nonhuman primates (Thorek, 1924; Zuckerman and Parkes, 1938, 1939; Clark, 1945), these reports are far from complete or systematic. Field reports following the effects of prepuberal castration in the rhesus also exist (Sade, 1968; Wilson and Vessey, 1968; Loy, 1971), but an assessment of the reported decline in mating behavior is difficult to make. In recent years, however, the effects of castration in the adult male rhesus monkey have been systematically examined under laboratory conditions (Michael, 1972; Michael, Wilson and Plant, 1973; Phoenix, Slob, and Goy, 1973; Michael and Wilson, 1974).

Following castration, peripheral androgen levels drop significantly within hours (Resko and Phoenix, 1972; Michael _et_ _al_., 1973). The sexual behavior of the castrated animals shows a decline over time, but the rate of decline seems highly individualistic. In addition to sexual behavior, a marked decline in frequency of occurrence is observed for yawning and spontaneous erection. It appears that the rate of decline for intromission and mounting may diverge markedly in some animals with a significant decrease in mounting rate occurring only over a very extended period.

Treatments with testosterone propionate have been shown to be effective in the restoration of precastration levels of sexual behavior (Michael, 1972; Michael _et_ _al_., 1973; Phoenix, 1973; Phoenix _et_ _al_., 1973; Michael and Wilson, 1974). Testosterone was equally effective in the restoration of yawning (Phoenix, 1973; Phoenix _et_ _al_., 1973), a behavior pattern which has been suggested to be androgen stimulated (Goy and Resko, 1972). Dihydrotestosterone propionate has also been shown to be capable of restoring sexual behavior as well as yawning (Phoenix, 1973, 1974). It appears that age may affect the decline in sexual behavior as well as the effectiveness of testosterone as a replacement therapy (Michael, 1972; Michael _et_ _al_., 1973). The results which have been reported for the castrate talapoin are consistent with those which have been reported for the rhesus (Dixson, Everitt, Herbert, Rugman, and Scruton, 1973). The castrate talapoin study is interesting in that it clearly demonstrated that social position can modify the expression of androgen-stimulated sexual behavior.

The activational potential which testosterone has for male primate sexual behavior is certainly clear from the data previously mentioned for the rhesus. An interesting sidelight in this regard comes from work on ovariectomized female pseudohermaphrodites. Recently it was demonstrated that adult pseudohermaphroditic rhesus which had been ovariectomized and given testosterone propionate treatments can exhibit the complete male sexual pattern, including ejaculation (Eaton, Goy and Phoenix, 1973). This observation extends the data which had already been obtained from work on rats and guinea pigs (Goy, Phoenix and Meidinger, 1967; Whalen and Robertson, 1968) and demonstrates the level of sexual behavior modification which can be achieved through the organizational action of gonadal hormones.

The human clinical literature on the effects of castration was reviewed by Tauber (1940). By and large the data from the human is of the case observation variety (Daniels and Tauber, 1941; Miller, Hubert, and Hamilton, 1938; Feinier and Rothman, 1937), and often includes observations on individuals afflicted with syndromes such as Klinefelter's syndrome (Beumont, Bancroft, Beardwood, and Russell, 1972). Even with the paucity of human data on the role of gonadal hormones in sexual behavior expression the human appears consistent with the rhesus in many regards. Following castration peripheral testosterone values in most cases have declined rapidly by ten days post operation (Sciarra, Sorcini, DiSilverio, and Gagliardi, 1973). Spontaneous erections for castrates become infrequent for both man (Tauber, 1940) and the rhesus (Michael and Wilson, 1974) though they do still occur. In this regard, it appears that sexual performance declines even though some capability for erection is maintained. Miller _et al_. (1938) reported that their subjects described intercourse as "arduous work" partially with reference to the difficulty they encountered in maintaining an erection. Michael and Wilson (1974) have suggested that erectile capability may be a critical factor in the maintenance of rhesus sexual behavior. Though the individual differences in level of sex behavior and the occurrence of spontaneous erection were not thought to be related to adrenal androgens (Hamilton, 1943) recent work utilizing radioimmunoassay has suggested that the adrenal may be responsible for low levels of testosterone peripherally in at least some cases (Sciarra _et al_., 1973). Work employing the antiandrogen cyproterone acetate has also resulted in data consistent with the proposition that gonadal hormones are critical to the full expression of primate sexual behavior (Michael, Plant, and Wilson, 1973; Morse, Leach, Rawley, and Heller, 1973). Cyproterone acetate treatments result in depressed peripheral testosterone levels and concurrent decreases in sexual behavior. Cessation of drug treatment is followed by recovery of sexual drive as well as resumption of normal testicular function and testosterone titer. There is some reason to believe that for the monkey complete behavioral restoration may not occur (Michael, Plant and Wilson, 1973) but reversability for the human has been documented (Cooper, Ismail, Phanjoo, and Love, 1972).

Testosterone propionate appears capable of restoring erection capability (Hamilton, 1937 a, b; Miller _et_ _al_., 1938) and has been said to increase libido (Daniels and Tauber, 1941; Beumont _et_ _al_., 1972). An interesting observation in this regard is that certain cases of human impotence are accompanied by significantly lower urinary testosterone levels than controls, suggesting decreased production as a possible factor for the condition (Cooper, Ismail, Smith and Loraine, 1970). It would appear that testosterone is in some way necessary for the sexual behavior of the male primate. One effect of testosterone may be the maintenance of penile integrity, since it has recently been demonstrated that penile feedback of some variety is necessary for the maintenance of the complete mating pattern in the male rhesus (Herbert, 1973). It might be important to comment in this regard that the penile sensory systems for both the male rhesus and the human have certain anatomical similarities such as the presence of complicated claw-like nerve endings and a high incidence of typical genital corpuscles (Malinovsky and Sommerova, 1972 a, b).

There are, however, certain data which are inconsistent with a functionally significant role for testosterone and male sexual behavior. There is a report for humans which suggests that even prepuberal levels of testosterone are sufficient for an active sex life (Raboch and Starka, 1973).

It also appears clear that testosterone level *per se* and sexual vigor are not closely related. Failure had been reported for clinical improvement of chronically impotent men despite a doubling of endogenous testosterone levels through the use of clomiphene (Cooper, Ismail, Harding and Love, 1972). In a full year study of sexual behavior and testosterone level for a group of eight rhesus monkeys, Plant (1974) failed to find any consistent relation between hormone level and sex performance though inconsistencies were reported.

As previously mentioned, castrate humans have difficulty in maintaining an erection. Erections do, however, occur (Hamilton, 1943). Human infants are also capable of spontaneous erection (Halverson, 1940; Korner, 1969). In the case of infants this behavior may be at least indirectly related to the testosterone levels during this period (Forest, Cathiard, and Bertrand, 1973).

It is well documented for the rhesus (Hines, 1942; Goy, 1966; Phoenix, Goy and Young, 1967; Goy, 1968) as well as for some other primate species (*Cercopithecus aethiops*, Struhsaker, 1967; *Macaca radiata*, Rahaman and Parthasarathy, 1969; *Macaca fuscata*, Hanby and Brown, 1974; *Papio cynocephalus*, Anthoney , 1968; *Pan troglodytes*, van Lawick-Goodall, 1968) that young males exhibit mounting attempts, pelvic thrusting and erections. The occurrence of intromissions has been reported for juvenile chimpanzees (van Lawick-Goodall, 1968) as well as for baboons (Hall and DeVore, 1965; Kümmer, 1968). Documentation of the testosterone levels for animals of these ages for species other than the rhesus are lacking. In the case of the rhesus, peripheral testosterone values don't reach an appreciable level until the age of about 2 yrs. and 10 mos. (Resko, 1967). Puberty, as measured by mating tests and testicular biopsies, has been reported to occur in laboratory male rhesus at ages of 2 yrs. 11 mos. (van Wagenan and Simpson, 1954) to 3 yrs. 6 mos. (Hartman, 1932). Reports on free ranging male rhesus suggest that puberty has taken place by 3 yrs., 6 mos. (Conaway and Sade, 1965). The data are consistent with the hypothesis that the high androgen levels which accompany puberty aren't necessary for the development of appropriate patterns of mature mounting in the primate. Further evidence of a minimal role for gonadal hormones in early male sexual development comes from data on the development of young castrate male rhesus. These young monkeys were frequently observed to develop erections as well as to exhibit mounting at levels equivalent to those of similarly aged intact males (Goy, 1966, 1968; Phoenix, et al., 1967); however, no reports have appeared on the occurrence of intromissions or the ejaculatory pattern for prepuberally castrated rhesus. In fact, certain reports from the literature suggest a critical role for the pubertal production of androgen in this regard. Loy and Loy (1974) in a recent paper on two year-old male rhesus stated, "In no instance was a series mounting observed to end in the motor pattern characteristic of ejaculation (Loy, 1971) or in the female clutching reaction (Zumpe and Michael, 1968). No female was seen with a vaginal plug of coagulated semen. These results were not surprising, since Conaway and Sade (1965) reported that free-ranging rhesus males on Cayo Santiago do not reach maturity until about three and one-half years of age." One recent study has followed the development of the intromission pattern and ejaculation and correlated the onset of these behaviors with physiological changes characteristic of puberty (Michael and Wilson, 1973). This study might be taken as suggestive evidence that pubertal hormone levels are necessary for the occurrence of the intromission and ejaculatory responses characteristic of adult sexual behavior (Bielert and Goy, 1973).

The activational action of gonadal hormones has also been examined through the manipulation of sexually immature animals. These attempts have been carried out in order to assess the role which chronological age may play in determining the effects of hormonal action on behavior. In this regard, the experimental induction of precocious sexual behavior through exogenous testosterone propionate treatments has been achieved in the rat and the guinea pig. Beach (1942), following up some work done by Stone (1940), was able to stimulate complete male sexual behavior from his experimental animals thirty days in advance of his control animals. Beach stated that although it was generally accepted that copulatory behavior would not be shown before puberty, thebehavioral system for copulation was well organized and capable of functioning before this time. Further, the gonadal hormone wasn't an active organizer, it merely lowered a threshold for the behavior pattern. Precocious sexual behavior in the guinea pig was elicited through exogenous TP treatment but the difference between the experimental and controls was only 3-6 days (Riss, Valenstein, Sinks and Young, 1955; Gerall, 1958; 1963).

A clinical condition known as "pubertus praecox" exists in the human and has profound consequences. For example, "we find in the records that Salamis, the son of Euthmenes, grew to 4'6" in his third year; he walked slowly and had a bass voice, and was carried off by a sudden attack of paralysis when he turned three." (Pliny, Natural History). Experimentation on this condition has been done and numerous studies are available on the neuroendocrine basis for precocious ovulation and spermatogenesis. An adequate review of the area is Donovan and van der Werff ten Bosch (1965). The psychological ramifications of precocious puberty are little known, although Money and co-workers have reported data on the psychosexual state of some two dozen cases of idiopathic sexual precocity (Money and Alexander, 1969; Money and Walker, 1971). This work has suggested that the psychosexual development of boys that were studied was clearly not correlated with the precocious appearance of the gonadal hormone. The body became sexually mature first and the intellectual and psychological maturity followed. The boys exhibited a tendency to high I.Q. early occurrence of the capacity for frankly sexual imagery in dreams and daydreams, and early establishment of the capacity for erotic and sexual arousal in relation to visual imagery and visual perception as well as tactile sensation. At present, no study has attempted through hormonal manipulation to induce sexual behavior in prepuberal rhesus monkeys.

The activational action which gonadal hormones might have on social behaviors other than those related to sex has been a topic of considerable research effort. Field reports have documented increases in aggressive interaction for free-ranging rhesus during the mating season (Kaufman, 1965; Southwick, Beq, and Siddiqi, 1965; Vandenbergh and Vessey, 1968). The suggestion has been made that since recrudescence of the testis has occurred by this time (Sade, 1964), these increases in aggression may be androgen-related (Wilson and Boelkins, 1970). Relevant to these observations are the reports that individual male's peripheral androgen levels are correlated with their social positions as well as with their levels of aggression (Rose, Holaday, and Bernstein, 1971), and that in humans testosterone level may correlate with aggression (Persky, Smith, and Basu, 1971). Further work has suggested that social interactions connected with defeat may depress peripheral androgen levels (Rose, Gordon, and Bernstein, 1972). Numerous laboratory studies (Clark and Birch, 1945; Birch and Clark, 1946; Mirsky, 1955; Kling, 1968; Green, Whalen, Rutley, and Battie, 1972; Joslyn, 1973) have attempted to answer questions about how androgens might affect social interactions in group situations. By and large, these attempts have been unsuccessful in altering social interactions (Mirsky

1955; Kling, 1968; Green et al., 1972) but a recent study has reported social change when young females were given daily androgen injections (Joslyn, 1973).

In the light of the preceding literature review, it seems clear that the rhesus monkey is an ideal animal with which to pursue certain basic questions about gonadal hormones and their effects on male primate behavior patterns. The thesis project which was carried out attempted to gain basic data on the following questions:

1) How does neonatal castration affect the development of social and sexual behavior patterns in the male rhesus?

2) Can the action of testosterone be considered activational in terms of its effects on the social and sexual behavior patterns of the male rhesus?

3) To what extent does an individual's social position as well as his experiential state determine the behavioral effects of testosterone stimulation?

This thesis will present the data from three seperate experimental evaluations of behavior by castrate and intact male rhesus monkeys. These evaluations will be presented as sections 2, 3, and 4. These sections will be presented as discrete units with their own introductions, results, and discussions. It is hoped that each of these sections can be published in a seperate paper sometime in the future.

Section 2. Longitudinal comparisons of the social and sexual development of prepuberally castrated and intact laboratory-reared male rhesus (Macaca mulatta).

2.1 INTRODUCTION

The rhesus monkey (Macaca mulatta) is a comparatively long-lived animal and shares with many primates, including man, a period of extended social development preceding adolescence. The contributions gonadal hormones may make to male primate behavior patterns are most frequently associated with the behavioral changes of puberty, but early hormone exposure also has been shown to have profound consequences (Goy and Phoenix, 1971; Goy and Resko, 1972; Money, 1972, 1973). In a recent review of the literature on the role of gonadal hormones in the sexual behavior of the rhesus and the human (Luttge, 1971), it was stated that, ". . . the effects of castration in both species should be further examined [p. 83]." Since then, several papers have come out on the role of gonadal hormones in adult male rhesus sexual behavior (Michael, 1972; Resko and Phoenix, 1972; Michael, Wilson, and Plant, 1973; Phoenix, 1973; Phoenix, Slob, and Goy, 1973; Michael and Wilson, 1974). Reports also exist on the effects of prepuberal castration in the rhesus (Goy and Dodsworth, 1962; Wilson and Vessey, 1968; Phoenix *et al.*, 1967; Goy, 1968; Phoenix, 1973), but no study has yet attempted to deal in a longitudinal fashion with the effects which prepuberal castration may have on the rhesus.

A longitudinal study which extends through puberty allows the assessment of both the "organizational" and "activational" actions of the gonadal hormones (Beach, 1970; Goy and Goldfoot, 1973) and may help in the determination of gonadally dependent and gonadally independent behavior patterns. As the literature stands today it is primarily from work primates and canids that dimorphic behavior patterns have been described which appear to be hormonally independent (Young, Goy, and Phoenix, 1964; Beach, 1970, 1974; Goy and Phoenix, 1971; Goy and Resko, 1972; Sprague and Anisko, 1973). A recent report (Michael and Wilson, 1973) has documented changes in sexual behavior of male rhesus at puberty, but the tests were "pair" sex tests, and few data were offered on social behaviors other than those normally associated with mating. Evaluation of behavioral changes which occur within a constant social grouping over several years may add important dimensions to our understanding of behavioral events associated with puberty in the male primate.

2.2 METHODS

Subjects. The animals selected for this analysis were all born of wild-caught female rhesus who were part of the Oregon Regional Primate Research Center's breeding colony. Experimental animals lived with their mothers until the age of three months, at which time they were separated and caged individually. Social peer groups were made up of similarly aged animals, once a peer group was assembled its membership remained constant, barring death. The sex composition and size of the peer groups varied, but for this analysis a matching was made between castrate and intact groups in terms of the total number of animals in the group and the ratio of genetic males to genetic females. Table 2.1 lists the animals and groups used in this analysis.

All castrations were carried out either the day of birth (day 1) or at approximately three months of age. The castrations were carried out under general anaesthesia with a subumbilical incision in a fashion consistent with sterile surgical practice.

Rearing procedures and observations. Within controllable limits, all groups were treated similarly. Following the designation of a group of animals born roughly within the span of one month as a social peer group, all animals remained caged individually. Beginning when the mean age of the animals designated as a peer group was 3 months, daily one-half hour group tests were carried out five days a week for 100 test days during the first year of life. During a group test the entire peer group was assembled and released into a small testing room 8 x 7 x 5 ft. which contained a stainless steel ramp and platform. Individual animals were scored on a rotating basis by one observer for five minutes per animal. During the same testing period, a second observer kept a record of the occurrence of a wide variety of sociosexual behaviors, noting the interaction and the animals involved.

Following the 100-day test run, animals remained caged individually. These same social groups were again brought together for social test runs when the mean age of the animals in a group reached 12, 24, and 36 and 48 months. For these later test runs, the groups were tested five days a week for a total of 50 test days. The same scoring procedures that had been used during the first year of social testing were used on these later runs. On the later test runs, the animals were tested in a slightly larger testing room 10 x 7 x 6 ft. Animal care and maintenance procedures remained relatively constant for all groups across all the runs and no extraneous manipulations were carried out on the animals of any of the groups. At various times and for varying periods of duration, the social groups were given opportunities for 24 hour continuous living experience. The duration and occurrence of these constant living periods are as follows: group 38: one month between runs 2 and 3, four months between runs 4 and 5; group 41: two months between runs 2 and 3, one month between runs 4 and 5; group 43: four months between runs 2 and 3, one month between runs 4 and 5; group 36: one month between runs 2 and 3, one month between runs 4 and 5; group 30: three months between runs 1 and 2, three months between runs 2 and 3, one month between runs 3 and 4; group 37: one month between runs 2 and 3.

Data analysis. Data from all groups were used when available. Group 41 was a group which was of the composition listed in Table 2.1 only for social test runs numbers 3, 4, and 5. Originally, group 41 had been composed of animals #2321, 2329, 2324, 2320 and another castrate and second intact female. The castrate and second intact female died after the end of run 2. Female 2344 was added to group 41 prior to social test run 3; she was of similar age and had received similar social testing and early rearing. Some data for males #1638, 1558, and 1618 and females #1642 and 1551 were incomplete for the first social run and in consideration of the behaviors for which this was the case, it was necessary to omit these animals from the repeated measures analysis of variance. All figures carry notations as to the numbers of animals used in the final analyses. When males 1636, 1558 and 1618 were omitted from an analysis, females #1642 and 1551 were also deleted. For purposes of the repeated measure design, only the first 50 test days of the 100-day social test run number 1 were used in the comparisons. All analyses of variance considered three factors: 1) sex or condition; 2) year of test run; and 3) blocks of tests within thesocial test run. When comparisons of means between sex or condition within years were made, the Newman-Kuels test (Winer, 1962) was employed. The minimal level of statistical significance acceptable throughout this paper is $p < .05$.

Table 2.1

Social peer groups of castrate and intact male rhesus.

Group #	38	37	41	30	43	36
Animal No. and Sex	2574[a] ●	2557 ♂	2321[b] ●	1636 ♂	4859[b] ●	2354 ♂
	2576[a] ●	2552 ♂	2329[b] ●	1558 ♂	4861[b] ●	2356 ♂
	2577 ♀	2555 ♂	2324[b] ●	1618 ♂	4874[b] ●	2358 ♂
	2580 ♀	2539 ♀	2320 ♀	1642 ♀	4863[b] ●	2359 ♂
	2575 ♀	2569 ♀	2344 ♀	1551 ♀	4868 ♀	2362 ♀
		2551 ♀			4857 ♀	2369 ♀

[a] castration on day of birth (day 1)

[b] castration at 3 months of age

Definitions

There were eighteen separate behavior categories on the 30=minute or group score sheet; the five minute or individual score sheet had a total of 29 categories. For purposes of this paper, only the behaviors to be discussed will be defined.

Behaviors scored for thirty minutes per trial:

Yawn. Hyperextension of the mandible and retraction of the lips, exposing all of the teeth. The expression closely resembles that of the yawn stereotypic of human beings.

Aggression. A vigorous biting of a portion of the body of another animal. Head and body shaking may accompany this contact; bleeding and laceration sometimes result from this interaction.

Erection. Engorgement and subsequent turgidity of the penis sufficient to permit extension of theglans beyond the prepuce. This turgidity may or may not be accompanied by penis flips. Erection was scored when noticed such as during grooming bouts or as associated with some mount attempts as well as in seemingly unprovoked circumstances.

Single foot or double foot clasp mount. An erect stance associated with coitus in the monkey, in which the hands are placed on the partner's hips, perineum or back. One or both feet of the male clasp one or both legs of the partner. Pelvic thrusting may occur.

Disoriented mount. An erect stance in which the hands are placed on the partner's back or head and appropriate hindquarter orientation is lacking, with thrusting directed either to the partner's side or head.

Deficient mount. A stance in which full hind leg extension is never achieved and which thus is carried out in a crouched posture.

Gape. A facial expression characterized by full jaw opening without teeth exposure. Brow contraction is not evident nor is mandible extension. This expression is often associated with play initiation.

Box. A brief open-mouth contact with another animal in which the point of contact becomes the focus of either the head or body's movements.

Brief contact play. A vigorous upper torso involvement with another animal. The forelimbs and mouth are the principle contact areas with the hind limbs often involved in position or equilibrium maintenance.

Rough and tumble play. A vigorous whole body involvement with another animal in a complex and varied manner including components of biting, wrestling or tugging.

Pursuit play. Vigorous chasing of another animal of sufficient duration or complexity to make the involvement recognizable and not random.

Groom. A stereotyped sorting or brushing aside of the fur of another animal. This behavior pattern may involve one or two hands and is often accompanied by lip smacking.

Groom receive. A quiet and relaxed response to social grooming. The groomee may exhibit changes of posture or limb movement as if to accomodate the grooming partner.

Groom solicit. A sustained presentation of head, throat, chest or side to another animal. Another posture considered a solicitation is the direct elevation of the hindquarters with accompanying tail deviation and collapse of the front quarters to a point of apparent rest on the cage floor.

2.3 RESULTS

Tables 2.2, 2.3 and 2.4 give the results for the analyses of variance which were carried out. The tables give the analyses as they pertain to social runs numbers 1, 2 and 3 for males, prepuberally castrated males and females, and social runs 1, 2, 3, 4, and 5 for males and castrate males alone. The analyses for thebehavior categories of yawn, groom, groom received, and groom solicit were carried out for males, prepuberally castrated males and females for social runs 1, 2, 3, 4, and 5.

Figure 2.1 presents a composite array of those data for the behavior categories of gape, box, brief contact and rough and tumble play, and pursuit play. For all of these behaviors, the analysis of variance revealed significant effects of sex, year and block (Table 2.2). Post hoc comparisons, employing the Newman-Kuels tests, were made for a consideration of the effect of sex or condition; males were compared to females, males were compared to castrates, and castrates were compared

Table 2.2 Results for the three way analysis of variance for repeated measures comparing males, castrate males, and females across their first three social testing runs.

Table 2.2

Behavioral Pattern	A. Sex & Condition	B. Year of Testing	C. Block of Test Run	Interactions
Gape	$p < .005$	$p < .001$	$p < .005$	AB n.s. BC** AC n.s. ABC*
Box	$p < .001$	$p < .001$	$p < .001$	AB n.s. BC** AC n.s. ABC*
Brief contact and Rough & tumble play	$p < .005$	$p < .001$	$p < .005$	AB* BC** AC n.s. ABC*
Pursuit play	$p < .005$	$p < .001$	$p < .025$	AB n.s. BC** AC n.s. ABC n.s.
Aggression	$p < .05$	$p < .001$	n.s.	AB n.s. BC n.s. AC n.s. ABC n.s.
Disoriented & Deficient mounts	$p < .025$	$p < .025$	n.s.	AB* BC* AC n.s. ABC n.s.
Single & double foot clasp mounts	n.s.	$p < .025$	n.s.	AB n.s. BC n.s. AC n.s. ABC n.s.

*$p < .05$

**$p < .01$

Table 2.3 Results for the three way analysis of variance for repeated measures comparing prepuberally castrated and intact males across their first five social runs.

Table 2.3

Behavioral Pattern	A. Condition	B. Year of Testing	C. Block of Testing	Interactions
Brief contact & rough and tumble play:	n.s.	$p < .001$	n.s.	A B n.s. B C ** A C n.s. A B C n.s.
Aggression	n.s.	$p < .005$	$p < .001$	A B n.s. B C ** A C ** A B C **
Erection	$p < .05$	$p < .05$	n.s.	A B * B C n.s. A C n.s. A B C **
Disoriented and deficient mounts	n.s.	$p < .05$	n.s.	A B n.s. B C n.s. A C n.s. A B C n.s.
Single and double foot clasp mounts	n.s.	$p < .025$	n.s.	A B n.s. B C n.s. A C n.s. A B C n.s.

* $p < .05$
** $p < .01$

Table 2.4 Results for the three way analysis of variance for repeated measures comparing males, castrate males, and females across their first five social testing runs.

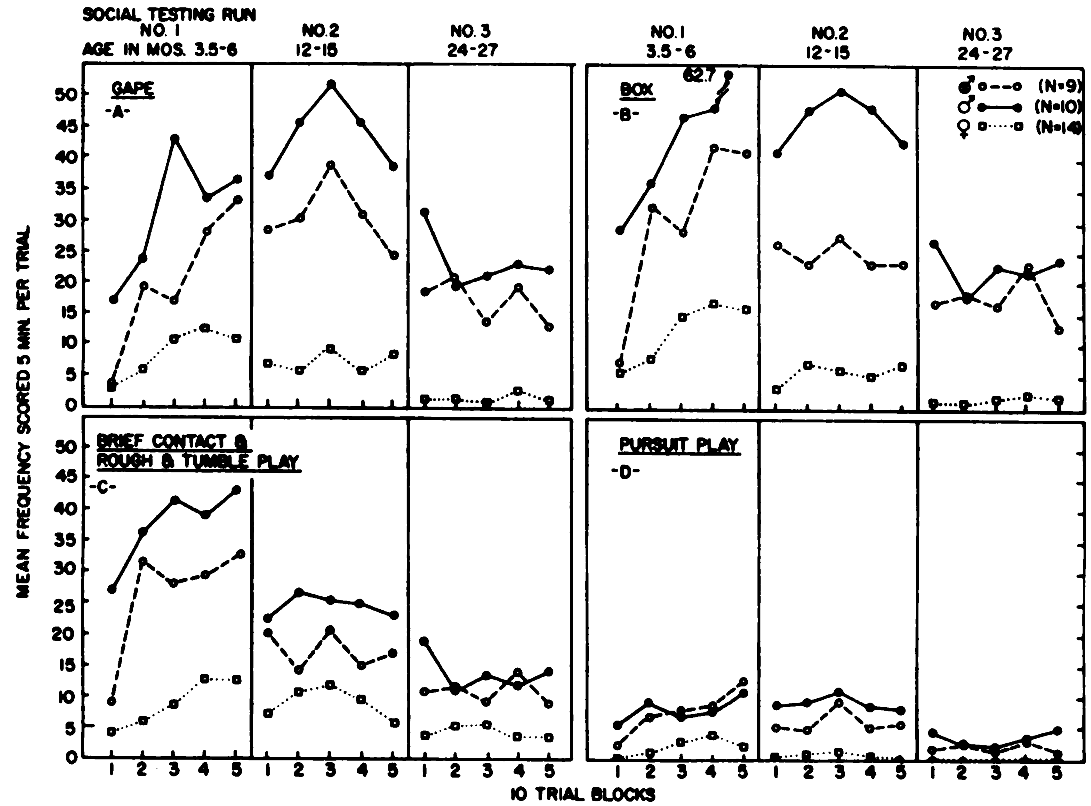
Table 2.4

Behavioral Pattern	A. Sex and Condition	B. Year of Testing	C. Block of Test Run	Interactions
Yawn	$p < .001$	$p < .025$	n.s.	AB* BC** AC n.s. ABC**
Groom	n.s.	$p < .05$	n.s.	AB n.s. BC** AC n.s. ABC n.s.
Groom Receive	n.s.	$p < .001$	$p < .01$	AB n.s. BC** AC n.s. ABC n.s.
Groom Solicit	n.s.	n.s.	n.s.	AB n.s. BC** AC n.s. ABC**

* $p < .05$

** $p < .01$

Figure 2.1 Dimorphic behavior patterns for male, castrate male and female hesus during their first three social testing runs. A) the category of gape; B) the category of box; C) the category of brief contact and rough and tumble play; D) the category of pursuit play

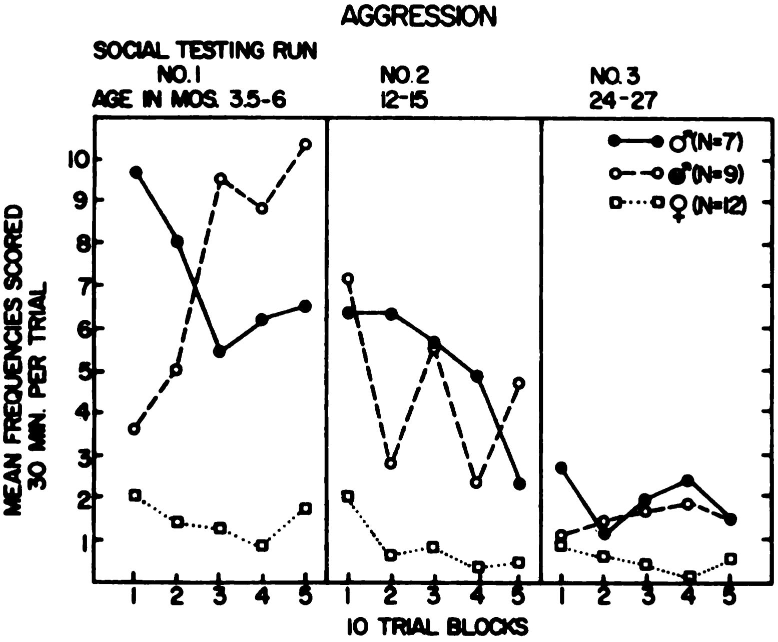

SOCIAL TESTING RUN
NO. 1
AGE IN MOS. 3.5-6
NO.2
12-15
NO. 3
24-27
NO.1
3.5-6
NO.2
12-15
NO.3
24-27
GAPE
-A-
BOX
-B-
62.7
BRIEF CONTACT &
ROUGH & TUMBLE PLAY
-C-
PURSUIT PLAY
-D-
♂ o--o (N=9)
♂ ●—● (N=10)
♀ □····□ (N=14)
MEAN FREQUENCY SCORED 5 MIN. PER TRIAL
0
5
10
15
20
25
30
35
40
45
50
1
2
3
4
5
10 TRIAL BLOCKS

to females. For all four of these behavior patterns, statistically higher frequencies displayed by males on at least one of three social runs examined. During the test run in which the animals were aged from 3.5 - 6 months, differences between the sexes were obtained for the measure of gape, box and brief contact and rough and tumble play. For the category of pursuit play, there were differences in mean frequency for the two sexes with males showing higher frequencies than females as reference to Figure 2.1 (d) illustrates, but these differences failed to reach significance. No differences were statistically significant for any of these four behavior patterns in the comparisons made between males and castrates. During the second test run when the animals were aged from 12-15 months, statistical differences were attained for the behavior frequencies of pursuit play, gape, and box on the comparison between males and females, but brief contact and rough and tumble play did not differ significantly between the sexes for this period of social testing, although reference to Figure 2.1 (c) makes it clear that the mean frequency with which males and females exhibited these play patterns was different. For the behavioral patterns for which sex differences had been statistically verified, no differences were obtained between males and prepuberally castrated males. For the behavioral category of gape, a statistically reliable difference did exist between castrates and females for the second testing period. For all four of the behavior patterns illustrated in Figure 2.1, no statistical differences for sex or condition were confirmed for the social testing run which was carried out when the animals were between 24-27 months of age. It is clear even during this run, however, that there were differences in the mean frequencies with which these behaviors were exhibited with the females consistently being the lowest level performers.

The frequency of aggressive behavior was highest during the first social testing run and declined over subsequent testing periods (Figure 2.2). The effect of years was revealed to be significant by the analysis of variance, (Table 2.2). Analysis of variance also revealed a significant effect of sex or condition but post-hoc comparisons failed to establish any differences between any of the groups for any of the test runs. Females, however, consistently achieved the lowest mean frequency across all three social test runs.

The frequency with which disoriented and deficient mounts occurred was high during the beginning of the first social testing run, but subsequently the mounting of the single or double foot clasp variety (Figure 2.3). Analysis of variance reflected this through a significant interaction of condition or sex and year. Though the analysis of variance revealed significant effects of sex or condition and years on the measure of disoriented and deficient mounts, only an effect of years was revealed for the single and double foot clasp mount category. The post-hoc analysis for the deficient and dis-

Figure 2.2 Aggression by male, castrate male and female rhesus for their first three social testing runs


AGGRESSION
SOCIAL TESTING RUN
NO. 1
AGE IN MOS. 3.5-6
NO. 2
12-15
NO. 3
24-27
●—● ♂ (N=7)
○- -○ ♂ (N=9)
□····□ ♀ (N=12)
MEAN FREQUENCIES SCORED
30 MIN. PER TRIAL
1
2
3
4
5
6
7
8
9
10
10 TRIAL BLOCKS
1
2
3
4
5

oriented mount category failed to substantiate a difference between males and castrates, or females although females exhibited the lowest level of response (Figure 2.3).

The levels of play declined significantly from the first year across the next four social runs (Figure 2.4).

The castrates did not differ significantly from intact males across all five years in terms of the frequency of aggression which they displayed, but social runs did have a significant effect across the five runs followed for these two groups, and aggression declined during the first three social runs and then showed some increases (Figure 2.5). This increase was particularly noticeable during the first block of runs four and five for intact males and a significant interaction for condition, year and block was revealed (Table 2.3).

The occurrence of erection was significantly affected by both condition and year of testing (Figure 2.6). Unpaired $\underline{t}$ tests (Winer, 1962) on the data for the castrates and intacts for all five social test runs, revealed no differences between the two groups for the social testing at 3.5 - 6 months of age ($\underline{t} = 1.51$, df = 14, 1-tailed test). However, one of the castrates, 2321, was markedly different from the eight others in frequency of erection during the first 10-day block of test run one; when he was excluded from a second analysis, there was a significant difference between the intact males and the castrates during the first social run ($t = 2.25$, $p < .025$, df = 13, 1-tailed $\underline{t}$ test). No

Figure 2.3 Mounts by male, castrate male and female rhesus for their first three social testing runs.

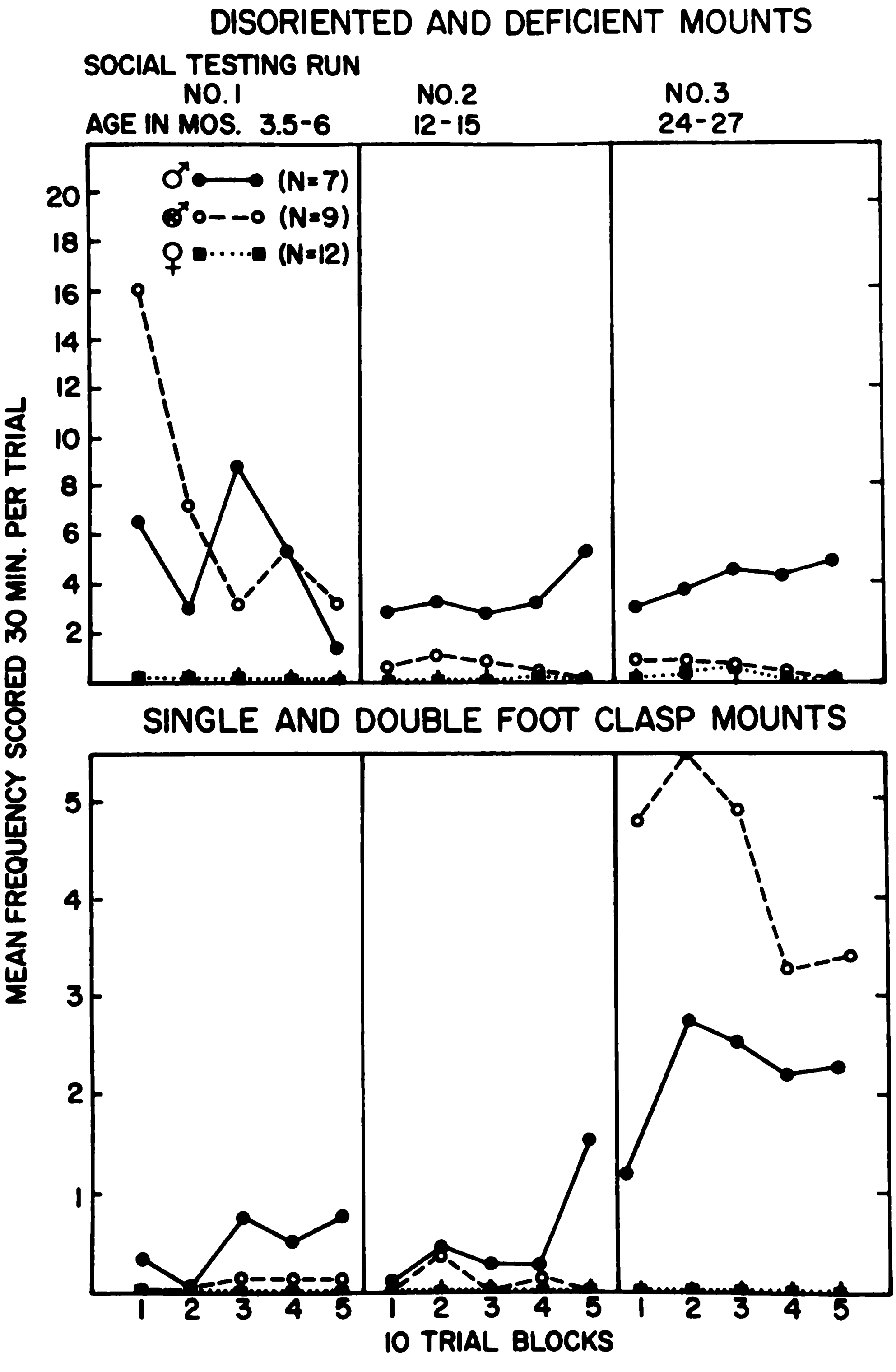

DISORIENTED AND DEFICIENT MOUNTS
SOCIAL TESTING RUN
NO. 1
NO. 2
NO. 3
AGE IN MOS. 3.5-6
12-15
24-27
♂ ●——● (N=7)
⊗♂ o– –o (N=9)
♀ ■·····■ (N=12)
MEAN FREQUENCY SCORED 30 MIN. PER TRIAL
20
18
16
14
12
10
8
6
4
2
SINGLE AND DOUBLE FOOT CLASP MOUNTS
5
4
3
2
1
1 2 3 4 5 1 2 3 4 5 1 2 3 4 5
10 TRIAL BLOCKS

Figure 2.4 Brief contact play and rough and tumble play by prepuberally castrated and intact male rhesus for their first five social testing runs.

BRIEF CONTACT PLAY AND ROUGH AND TUMBLE PLAY

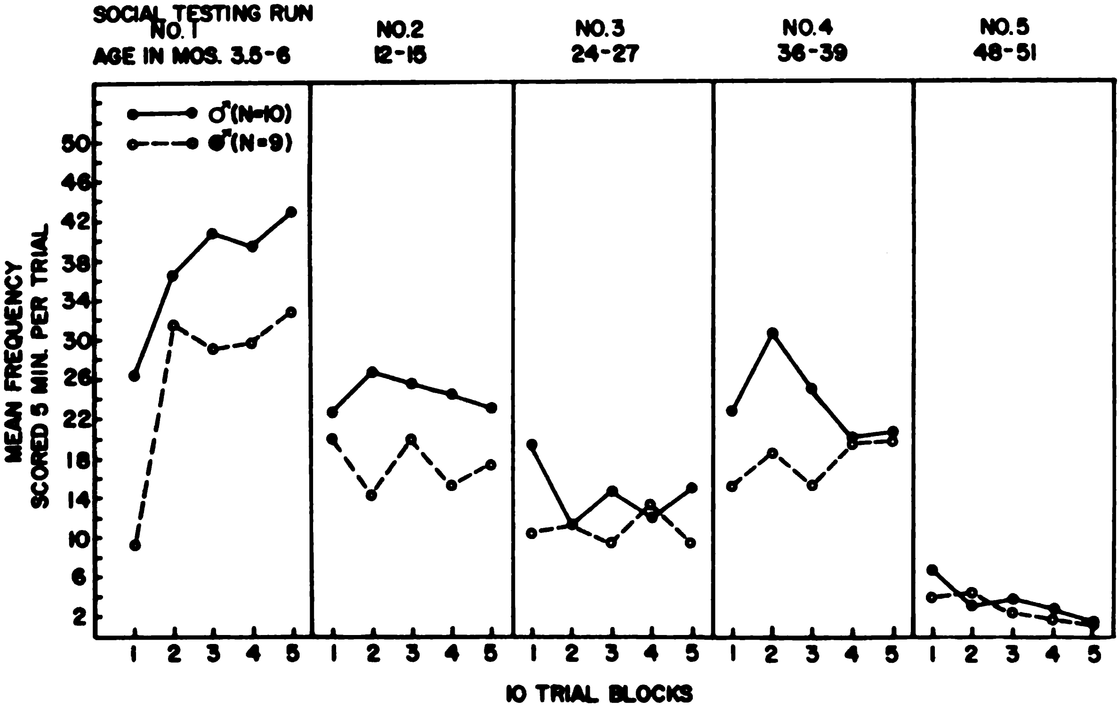


Figure 2.5 Aggression by prepuberally castrated and intact male rhesus for their first five social testing runs.

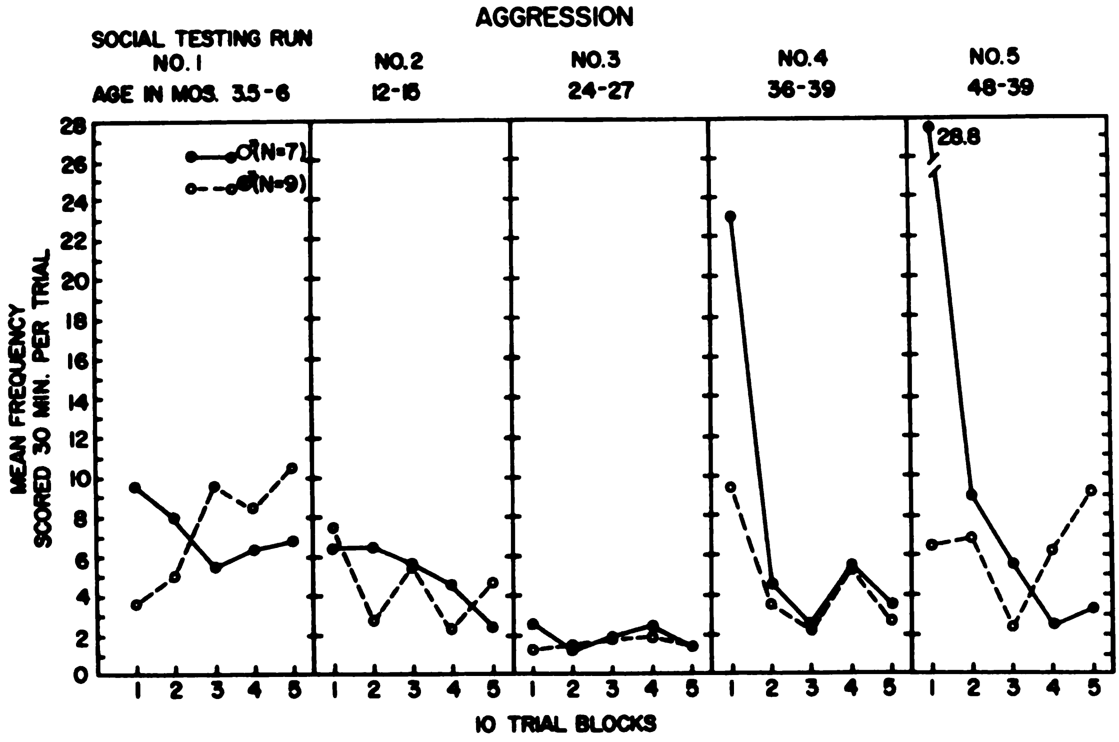
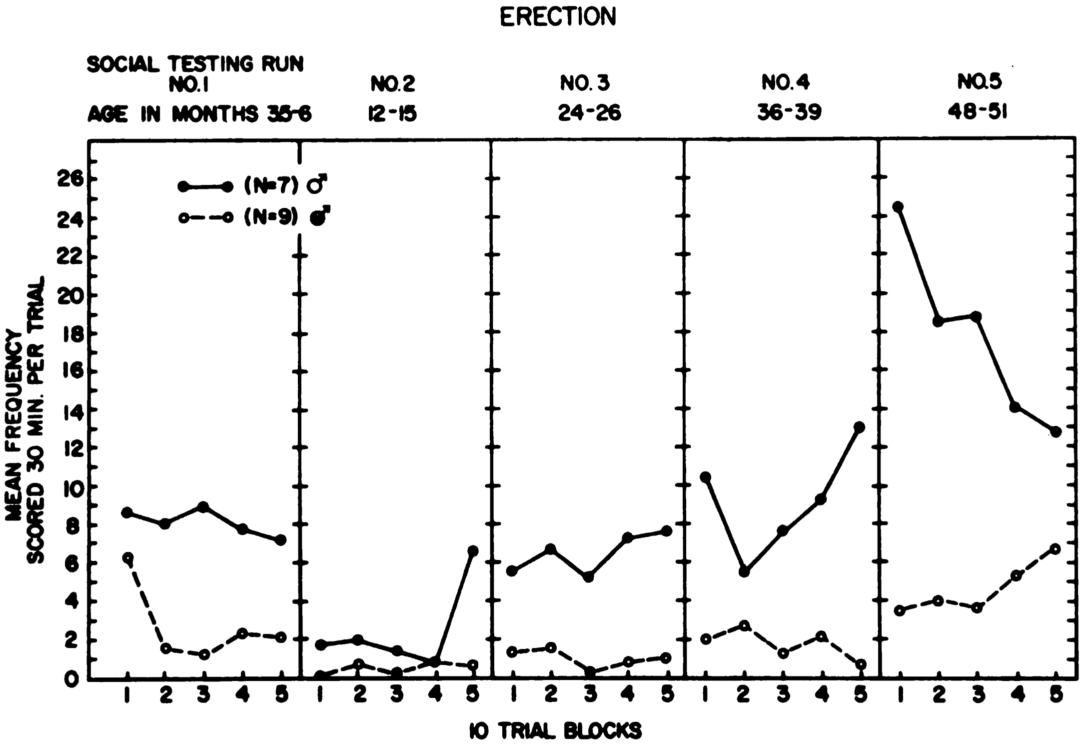

AGGRESSION
SOCIAL TESTING RUN
NO. 1
AGE IN MOS. 3.5-6
NO. 2
12-15
NO. 3
24-27
NO. 4
36-39
NO. 5
48-39
♂ (N=7)
♀ (N=9)
28.8
MEAN FREQUENCY SCORED 30 MIN. PER TRIAL
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
1 2 3 4 5
10 TRIAL BLOCKS

Figure 2.6 Erections by prepuberally castrated and intact male rhesus for their first five social testing runs.


ERECTION
SOCIAL TESTING RUN
NO.1
NO.2
NO.3
NO.4
NO.5
AGE IN MONTHS 3.5-6
12-15
24-26
36-39
48-51
(N=7) ♂
(N=9) ♂
MEAN FREQUENCY
SCORED 30 MIN. PER TRIAL
0
2
4
6
8
10
12
14
16
18
20
22
24
26
1 2 3 4 5
1 2 3 4 5
1 2 3 4 5
1 2 3 4 5
1 2 3 4 5
10 TRIAL BLOCKS

difference between the two groups for social test run two was revealed (*t* = 1.27, df = 14, 1-tailed *t* test). Differences were significant for the two groups of males on social runs three, four and five (three: $t = 2.27$, $p < .025$; four: *t* = 2.01, $p < .05$; five: *t* = 2.52, $p < .025$; for all runs, df = 14, 1-tailed *t* test).

For both disoriented and deficient and single and double foot clasp mounts there was no statistical difference between the castrates and the intacts (Figure 2.7). For both categories, years was revealed to be a significant variable. However, the trends for these two mount categories were opposite to each other: the disoriented and deficient mount category showed a decrease from the first social run on, while there were increases in the frequency of single and double foot clasp mounts for social test runs numbers three, four, and five.

There were no effects of sex or condition for measures of groom, groom receive and groom solicits (Figure 2.8, Table 2.4). However, for the measures of groom and groom receive, there was a significant increase across years. In addition, for the measure of groom receive a significant effect of test blocks was also found.

There was a significant and dramatic increase in the frequency with which intact males displayed yawning during the fifth social run (Figure 2.9). The yawning frequency during this run declined and this decline was reflected in a significant interaction between year and block (Table 2.4).

Figure 2.7 Mounting behavior by prepuberally castrated and intact male rhesus monkeys for their first five social testing runs.

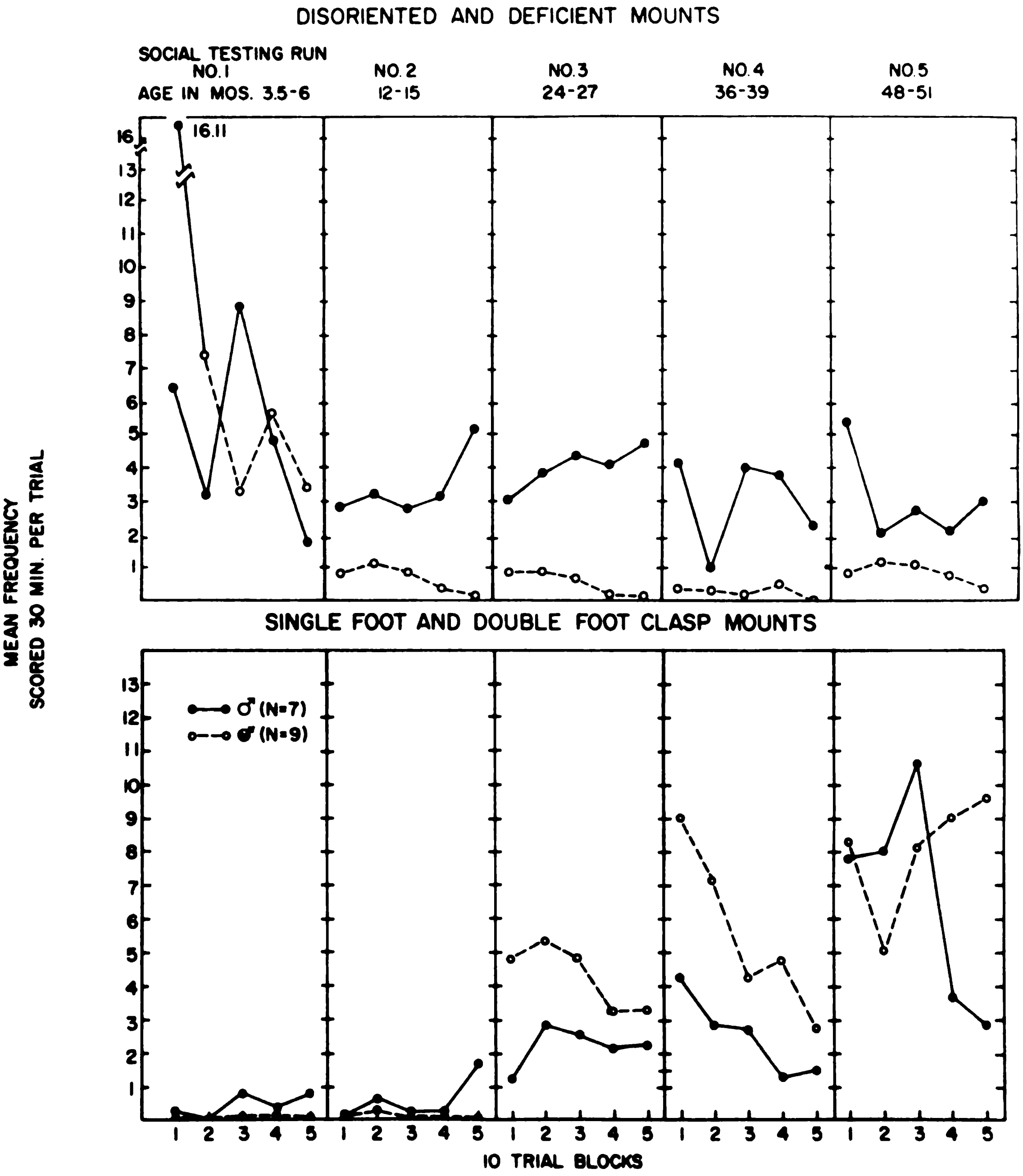

DISORIENTED AND DEFICIENT MOUNTS
SOCIAL TESTING RUN
NO. 1
AGE IN MOS. 3.5-6
NO. 2
12-15
NO. 3
24-27
NO. 4
36-39
NO. 5
48-51
16.11
16
13
12
11
10
9
8
7
6
5
4
3
2
1
MEAN FREQUENCY
SCORED 30 MIN. PER TRIAL
SINGLE FOOT AND DOUBLE FOOT CLASP MOUNTS
♂ (N=7)
♀ (N=9)
1 2 3 4 5
10 TRIAL BLOCKS

Figure 2.8 Measures of grooming behavior for male, castrate male, and female rhesus for their first five social testing runs

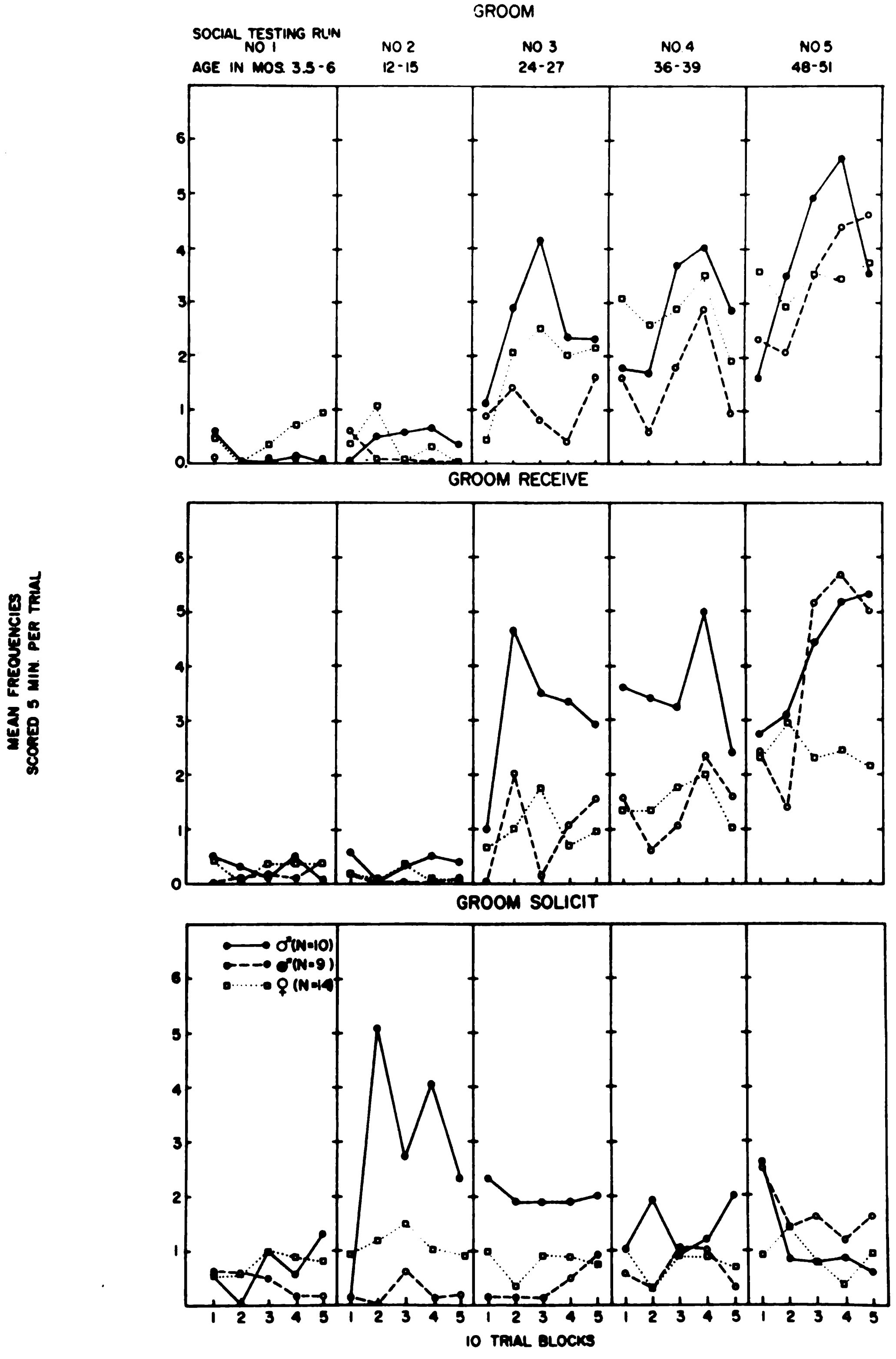
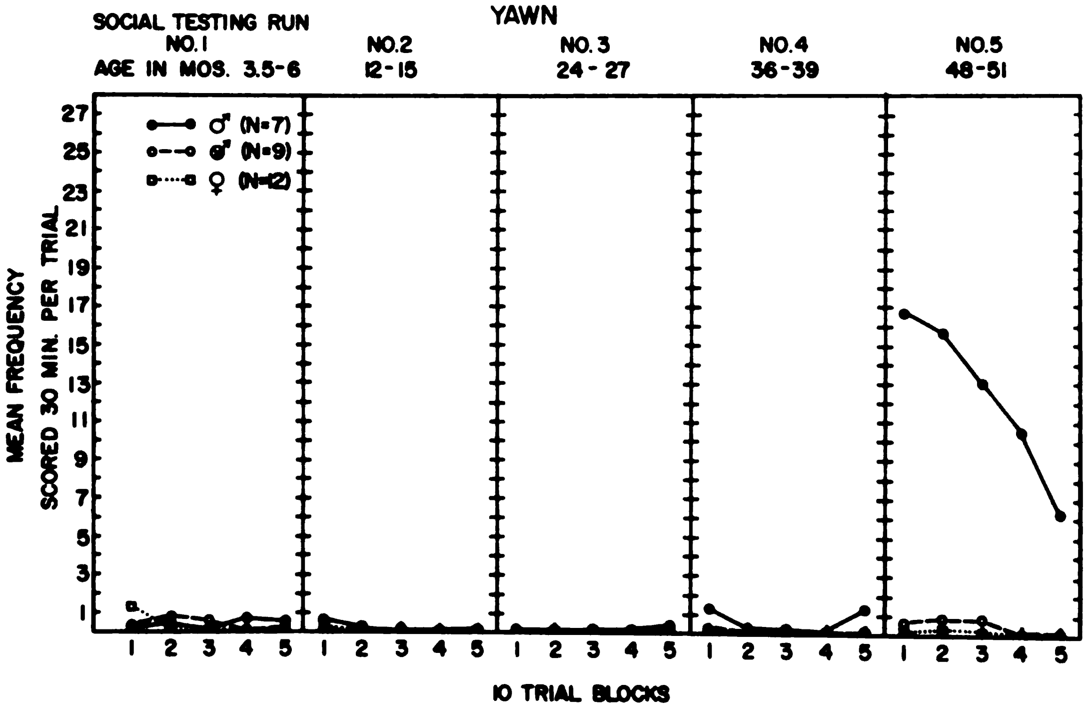

GROOM
SOCIAL TESTING RUN NO 1
NO 2
NO 3
NO 4
NO 5
AGE IN MOS. 3.5-6
12-15
24-27
36-39
48-51
GROOM RECEIVE
GROOM SOLICIT
♂(N=10)
♂(N=9)
♀ (N=14)
MEAN FREQUENCIES
SCORED 5 MIN. PER TRIAL
0
1
2
3
4
5
6
1 2 3 4 5
10 TRIAL BLOCKS

Figure 2.9 Yawning by male, castrate male, and female rhesus for their first five social testing runs.


YAWN
SOCIAL TESTING RUN
NO. 1
AGE IN MOS. 3.5-6
NO. 2
12-15
NO. 3
24-27
NO. 4
36-39
NO. 5
48-51
♂ (N=7)
♂ (N=9)
♀ (N=12)
MEAN FREQUENCY
SCORED 30 MIN. PER TRIAL
27
25
23
21
19
17
15
13
11
9
7
5
3
1
1 2 3 4 5
10 TRIAL BLOCKS

The fact that it was only the intact males which yawned during run five was reflected in a significant interaction for year and condition. Prior to run five, yawning was infrequently shown by any group of animals. The frequency with which females yawned was low for all five of the social runs and a similar situation existed for the castrate males.

2.4 DISCUSSION

The sex differences for thebehavior patterns of box, gape, brief contact and rough and tumble play, pursuit play, and mounting behavior are consistent with data which have been previously reported (Goy, 1968, 1970; Goy and Phoenix, 1971). The lack of statistically significant differences between the castrate and intact males for these behavior patterns during the first three social runs suggests that gonadal hormones during this time period play little role in thedisplay of these behaviors. Further support for this position comes from a recent study (Joslyn, 1973) in which young female rhesus monkeys reared in a fashion similar to that described in this study were given testosterone injections in an attempt to modify the frequency with which these females exhibited the dimorphic behavior patterns already enumerated. The androgen treatments were ineffective in the modification of the frequencies with which these females exhibited any of these five patterns of social interactions (Joslyn, 1973).

Data from the present study and those collected on genetic female monkeys whose mothers were androgen-treated while pregnant (such androgen treatments were effective in the modification of the frequencies with which these females exhibited these patterns of social interaction) are consistent with the hypothesis that prenatal gonadal hormone exposure in this species modifies the expression of dimorphic behavior patterns in a direction characteristic of that of the genetic male. The display of the behavior patterns described for the castrate males in this study appears to be independent of concurrent gonadal hormone stimulation and in this regard clearly differentiates the behaviors of box, gape, brief contact and rough and tumble play, pursuit play, and mounting behavior from those dimorphic patterns studied frequently in the rodents (Whalen, 1971). Recently, evidence similar to that which has been obtained with monkeys has been reported for the urination postures of dogs (Beach, 1970, 1974). These postures are exhibited dimorphically by both males and prepuberally castrated males. In addition, genetic females which have been exposed to androgen while _in utero_ exhibit the pattern typical of the male. The data from male castrate and female pseudohermaphrodite dogs in terms of the onset of this behavior pattern make it clear that this behavior is independent of concurrent gonadal hormone stimulation. At the moment, the hormone-independent dimorphic behaviors of the dog and the rhesus appear to be the best evidence for the permanent behavioral changes which early hormone exposure can induce.

Measures of groom, groom solicit and groom receive failed to substantiate a sex difference for these behavior patterns. Age affected the display of these patterns. In this regard the data agree with studies which have found that the grooming performed by female rhesus increases with age (Lindburg, 1973) and that the frequency of grooming by males increased as they grew older (Miller, Kling, and Dicks, 1972). The rearing and testing procedures followed in the present study may well have affected the measures of the grooming behavior in this study. Although the animals failed to show much grooming prior to the third social run, it has been reported that if infant rhesus are reared with their mothers in small groups of four or five females and an adult male, grooming may appear by 3 weeks of age (Hinde, Rowell, and Spencer-Both, 1964).

It is difficult to say a great deal about a possible sex difference in grooming behavior. Studies of adults have suggested that females are more avid groomers than males (Lindburg, 1973), but Hinde and Spencer-Booth (1967) reported no sex differences for the first 2-½ years of life. A recent review (Sparks, 1967) brought together data suggesting that factors such as age, sex, class, dominance status, and kinship affect the patterns of grooming behavior shown by several primate species. Consequently broad generalizations will not be attempted from this study.

One of the major goals of this study was an examination of the activational action which gonadal hormones play in the modification of social and sexual behavior patterns of intact male rhesus. It is clear that the high levels of gonadal hormones associated with puberty in the male rhesus and present from about the age of 3 years on are unnecessary for the dramatic decline in play behavior which occurred under our social testing conditions. It would appear that social development may be the critical factor moderating the frequency with which male rhesus exhibit patterns of play behavior. Other studies have also documented a dramatic prepuberal decline in play behavior by young males (Hansen, 1966; Hinde and Spencer-Booth, 1967; Ruppenthal, Harlow, Eisele, Harlow and Suomi, 1974). Certainly adult male monkeys do play and when placed in certain situations this play may occur at fairly high levels (Redican and Mitchell, 1974) and the absence of play initiators may have been what accounted for the steady decline in play in our groups. The lack of difference in the play behavior of castrates and intacts cannot be taken as evidence against the effect which gonadal hormones may have on play behavior. Gonadal hormones may interact with social development and exert an influence on play behavior. It has been reported that four-year-old male rhesus play twice as much as eight-year-old male rhesus, and this could be a reflection of an effect of lengthy exposure to gonadal hormones (Kaufman, 1967). It does not, however, appear that the decline over time in this behavior is causally related to the endocrine activity characteristic of puberty.

The occurrence of erection in intact males was much more frequent than in castrates suggesting that even low androgen levels may affect this response. There are data from the human which suggest that from the time of birth to approximately three months of age, serum testosterone levels are rising (Forest, Cathiard, and Bertrand, 1973). From the time of three months of age, peripheral testosterone levels show a decline and remain fairly low until puberty. It appears from the data on erection that the gonadal hormone pattern for the rhesus may be similar to that of man. It is well documented that castration affects the occurrence of erection in the rhesus and that subsequent androgen therapy can restore this behavior pattern (Michael and Wilson, 1974). In view of this the decline in the occurrence of spontaneous erection during the period of the first social testing run could be suggested to reflect a similar decline in circulating testosterone from the age of about three and one-half months on. The occurrence of erection by castrates remains low from the time of social test run one on, and this appears consistent with a lack of gonadal hormone activity on the part of these animals. The frequency with which intact males exhibited this behavior increased on runs three, four, and five from a low level during run two. It should be remembered that erection is sometimes noticed during grooming as well as occasionally prior to a mount.

However, castrates did not differ from intact males for either of these behavioral categories, and thus it is difficult to ascribe differences in the occurrence of erection to a social factor or to social behavior differences such as frequencies of grooming or mounting by the intact males.

Occurrence of erection in male rhesus monkeys may be an extremely sensitive index of hormonal state. Recent work on testosterone levels of group living rhesus has revealed a correlation between testosterone level and social rank (Rose, Holaday and Bernstein, 1971). Field reports on baboons and vervets have documented a high frequency of erection in adult males and have suggested a social communication function for this display (Wickler, 1969, 1972). Consequently social position may regulate, through peripheral androgen levels, the occurrence of erection.

Yawning is a sexually dimorphic behavior pattern in adult rhesus monkeys. Yawning is reduced by castration but can be restored with androgen treatment (Phoenix, 1973; Phoenix, Slob and Goy, 1973; Phoenix, 1974) and females will yawn if given exogenous testosterone (Goy and Resko, 1972; Eaton, Goy and Phoenix, 1973). It is very reasonable, then, that the intact males were the only animals to exhibit this behavior at a high level and that the appearance of this behavior pattern was during a postpubertal social testing run.

To the extent that yawning has been considered a dominance display for baboons (Hall and Devore, 1965) its occurrence may also be modulated through peripheral androgen levels in a fashion similar to that previously suggested for erection. However, it is important to mention that social factors _per se_ are not sufficient to stimulate frequent occurrence of this behavior in male rhesus;for castrates, although they occupied social positions superior to the females of their groups and equivalent to those occupied by the intact males in their groups failed to exhibit yawning frequencies equivalent to intact males postpubertally.

Mounting behavior for both intact and castrated males was very similar both in terms of frequency and development. Both groups exhibited mounting during all five of the social runs and both showed a gradual shift from immature mounts to single and double foot clasp mounts characteristic of adult mating behavior (Bielert and Goy, 1973). It doesn't appear that gonadal hormone activation is critical to the occurrence and development of the mature mounting pattern in rhesus (Phoenix, 1973).

Although mounting may not be radically affected by castration, the occurrence of intromission definitely is (Michael, Wilson, and Plant, 1973). Intact and castrate animals in the present study displayed intromission, although with the social rearing condition under which they were followed, only about 30% of each group achieved intromissions. Three intact males (1636, 1558 and 1618) started showing intromissions during social run number five. Male 1558 displayed only one intromission; male 1618 exhibited a total of nine, and male 1636 had a total of 129 intromissions during the 50-day test period.

Male 1636 was also observed to ejaculate a total of nine times. Starting in social run number four, castrates 4859, 4861 and 4874 began to exhibit intromission; castrate 4859 exhibited one, and castrates 4861, and 4874 each exhibited a total of three. Castrates 4859 and 4861 also exhibited the ejaculatory response pattern during this test run. During social run five, the same three castrates again displayed intromissions. Castrate 4874 who had exhibited a total of three intromissions during run four, exhibited a total of eighteen intromissions during run five and this same castrate exhibited the ejaculatory response pattern a total of four times. The castrates were never seen to ejaculate seminal fluid, nor were their female partners ever observed with a plug of coagulated seminal fluids. The accessory sex glands of rhesus require androgen for their maintenance (Zuckerman and Parkes, 1938; Zuckerman and Sandys, 1939) and castrate rhesus fail to exhibit seminal emission (Phoenix and Jensen, 1973). The ejaculatory response which the castrates exhibited was indistinguishable from that of an intact male. The observation of this response in castrates is apparently the first to be reported for prepuberally castrated males. The occurrence of ejaculatory behavior can be taken as evidence for a certain degree of hormone independence in the sexual behavior of male primates. Apparently the potential for the display of complete mating behavior is present in these nonhuman primates even in males which have only received prenatal androgen exposure. The critical nature of such exposure is confirmed by the observation of ejaculation in female hermaphrodite rhesus under testosterone stimulation (Eaton, Goy and Phoenix, 1973).

The fact that one of the three intact males in the present study intromissions displayed at a level far above that of any of the castrates could suggest a positive effect for gonadal hormones on the display of this measure of male sexual behavior. In this regard, it would appear that the role of androgen in rhesus monkey sexual behavior may be that of a behavioral potentiator. Its effects may be mediated through a variety of paths or systems, and interactions may well exist between them. As an example, the effects may be mediated through the maintenance of the penis or the nerves servicing it, for it has been shown that integrity of penile feedback is critical to the display of sexual behavior in the male rhesus (Herbert, 1973). The effects of androgen may also be expressed through the male's general demeanor and behavioral attitude. There is recent evidence suggesting that the interaction of male-female rhesus pairs is altered by castration of the male partner (Michael and Wilson, 1974). A third possibility is that the effects of testosterone may be mediated through visual or olfactory cues to the female. Data from two species have suggested that the sex skin color of the male is androgen dependent (Zuckerman and Parkes, 1938, 1939; Vandenbergh, 1965; Dixson and Herbert, 1974). At the moment however, it is impossible, to determine how cues as skin color might affect the interaction between a rhesus pair. Although androgen is certainly of biologically critical importance to male primate reproduction, its importance for male sexual behavior patterns may be truly unique in regard to the degree of independence which may exist for the development and display of mating behavior. The observation of the ejaculatory response pattern in prepuberally castrated rhesus may have a human analog in the occurrence of the orgasm far in advance of the time of puberty when gonadal hormone concentrations show a dramatic rise (cited as general knowledge by Bermant and Davidson, 1974).

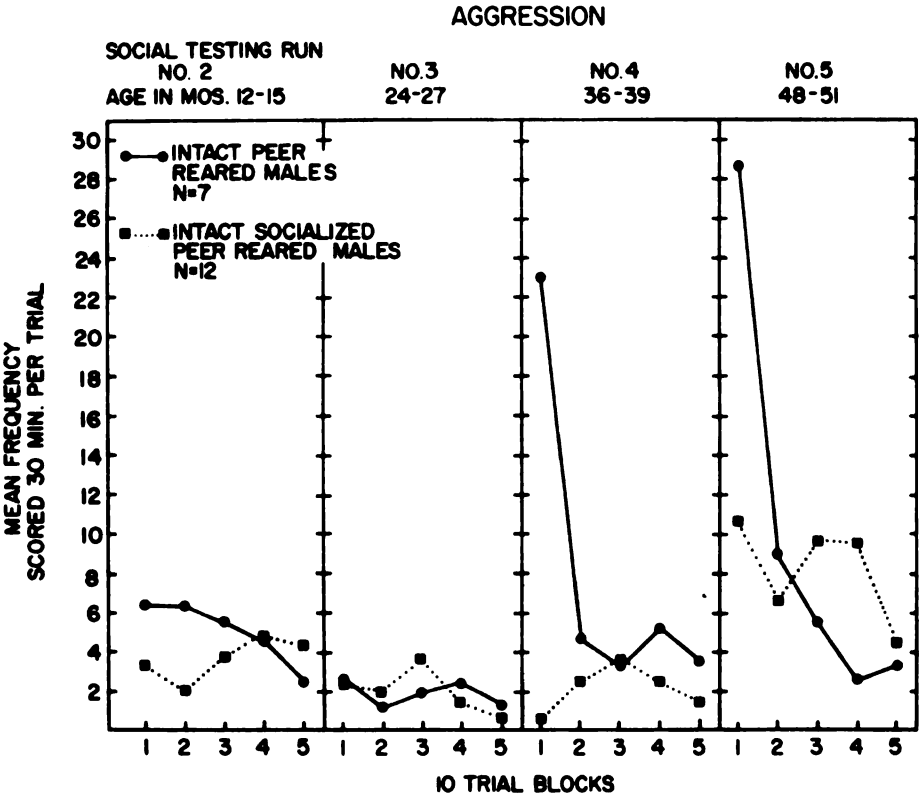
A very interesting contrast existed for intact males and castrates in regard to the level of aggression exhibited in the first block of ten tests during social runs four and five. It has been reported for several age groups and species of primates that the period of time immediately following a group formation is characterized by high levels of aggression (Bernstein and Mason, 1963; Bernstein, 1964; Bernstein and Draper, 1964; Bernstein, 1969). The high level of aggression during block one of test runs four and five is consistent with these reports for at this time the animals of the social groups were being reunited after a period of single cage housing. A comparison of the levels of aggression during this period by the intact males and the castrates indicates that gonadal hormones may have had an influence on the frequency of aggressive interactions which occurred during this period, for these monkeys.

Attempts at the manipulation of social position through hormonal means in a group situation have by and large (Mirsky,

1955; Green, Whalen, Rutley and Battie, 1972) been unsuccessful. This may partly be due to the fact that alliances and allegiances exist in monkey social groups and result in what has been described as a dependent social rank phenomenon (Kawai, 1965; Varley and Symmes, 1966). The existence of social inertia may be a critical factor resulting in failure of androgen manipulation to alter the social structure of a group social inertia has been suggested where males remain dominant in a troop even after injury or disability (Southwick and Siddiqi, 1967). However, one study stands in marked contrast to the others (Joslyn, 1973). In this study, androgen injections to young female rhesus resulted in an upward shift of their positions in the dominance hierarchy of their group. An important factor contributing to the success of this project may have been the experimental design which was employed. Androgen injections were begun while the group was in a daily social testing run and these injections were continued following the end of the social testing, at which time the animals were singly caged. After several months, the group was reunited and the females who were continuing to receive androgen injections were observed to have shifted in their hierarchy positions. These shifts occurred at a time of social disorder and it may be the case that androgen's effects on social position are most pronounced at such a time. An unstable social situation maximizes the probable occurrence of aggression and androgen may well affect the intensity of this particular behavior pattern, and through this means, exert an effect on an individual's dominance position. An important consideration in the androgen-aggressive behavior interaction is that of early experience and the effects which the early social environment may have on the propensity to display aggressive behavior. Early social restriction has pronounced effects on measures of agonistic behavior for the monkey (Harlow and Harlow, 1965). Because there was reason to believe that the rearing condition of the males in this study may have had an effect on their display of certain behavior patterns such as mounting (Goy and Goldfoot, 1973; Goy, Wallen, and Goldfoot, 1974), a further examination of aggressive behavior was carried out. Although the social experience of the groups of intacts and castrates compared in this study was very similar, groups 30 and 43 received more constant living experience than the others. Group 30 received several more months of social exposure than the two other intact groups; this group is one which has been described as "socialized" because of this fact (Goy and Goldfoot, 1973). Using additional data collected in a fashion exactly like those already described in the methods section for intact groups nos. 28, 29, and 32, which also have been termed socialized (Goy, Wallen, and Goldfoot, 1974) an analysis of variance was carried out on the data for aggression from social test runs two, three, four and five. The males of groups 36 and 37 (the nonsocialized animals) were compared to the males of groups 28, 29, 30, and 32 (the socialized animals). The duration

And occurrence of these constant living periods for the animals of the additional three groups are as follows: group 28: six months between runs 2 and 3; group 19: five months between runs 2 and 3; group 32: five months between runs 1 and 2, two months between runs 2 and 3. The data are illustrated in Figure 2.10. The analyses of variance failed to reveal a statistically significant difference between the socialized and nonsocialized groups, although there was a statistically significant effect for both years and block, and, in addition, there were statistically significant interactions between social experience and block, year and block, and social experience, year, and block. A check of Figure 2.10 verifies the fact that the level of aggression which was exhibited in block 1 of runs four and five was different for these two groups. The socialized males failed to exhibit the high levels of aggression shown postpubertally by the nonsocialized males during these periods of social instability. Although many explanations could be offered, two seem very reasonable. One explanation involves the social interaction network which may exist in socialized groups. It could be that the allegiances and alliances which exist between the animals of such a group contribute a moderating effect on the agonistic behavior shown during periods of social instability. A second interpretation, somewhat related to the first, is that of the effect which behavioral maturation within a socialized environment may have on aggressive behavior. In consideration of this second interpretation, data from studies which have examined the interaction between testosterone levels and aggression in humans is offered.

Figure 2.10 Aggression shown by intact peer-reared and intact socialized peer-reared males during four social testing runs.


AGGRESSION
SOCIAL TESTING RUN
NO. 2
AGE IN MOS. 12-15
NO.3
24-27
NO.4
36-39
NO.5
48-51
MEAN FREQUENCY SCORED 30 MIN. PER TRIAL
INTACT PEER REARED MALES N=7
INTACT SOCIALIZED PEER REARED MALES N=12
30
28
26
24
22
20
18
16
14
12
10
8
6
4
2
1 2 3 4 5 1 2 3 4 5 1 2 3 4 5 1 2 3 4 5
10 TRIAL BLOCKS

Persky, Smith and Basu (1971) reported a correlation between a psychological measurement of aggression and testosterone level in adult males. This study suggested that a relation did exist between aggression and testosterone level in their sample. Recent work (Meyer-Bahlburg, Boon, Sharman and Edwards, 1974) has failed to replicate this correlation and has suggested that the Persky _et al_. study may have been influenced by the blood sampling procedure. Work which has been carried out with a criminal population also failed to find a correlation between testosterone and aggressive behavior when a broad population examination was done, but did find a meaningful relationship between these two measures when a subsample was critically examined (Kreuz and Rose, 1972). In this paper a hypothesis was presented that within a population that is predisposed by virtue of social factors to develop antisocial behavior, levels of testosterone may be an important additional factor in placing individuals at risk to commit more aggressive crimes in adolescence. The data from the groups of monkeys examined in this study seem in some regards consistent with the hypothesis proposed by Kreuz and Rose, for it appears that a relationship between intensity of aggressive behavior and postpubertal testosterone levels may exist for those animals which for some reason exhibit a propensity for that behavior during periods of social instability such as at the start of a social run.

Section 3: TESTOSTERONE TREATMENTS OF CASTRATE MALE RHESUS OF VARYING AGES IN GROUP AND PAIR TESTING SITUATIONS

3.1 INTRODUCTION

Male rhesus monkeys are dependent upon gonadal hormones for the display of species typical sexual behavior (Michael, 1972, Michael, Wilson and Plant, 1973, Phoenix, Slob and Goy, 1973, Michael and Wilson, 1974). Adult levels of androgen production normally begin about the age of three years as suggested by the physiological changes associated with puberty begin. Puberty as measured by mating tests and testicular biopsies has been reported to occur in laboratory reared male rhesus between the ages of 2 years 11 months (van Wagenen and Simpson, 1954) to 3 years 6 months (Hartman, 1943). Reports on free-ranging male rhesus utilizing only testicular biopsy suggest that puberty has taken place by 3 years 6 months of age (Conaway and Sade, 1965). Measurement of gonadal hormones in laboratory housed rhesus indicate that peripheral testosterone remain low until the age of about 2 years 10 months (Resko, 1967). Mature mating behavior seems tied to the events of puberty for reports on rhesus followed on Cayo Santiago have failed to record frequent sexual behavior by males of an age less than 5 years. It is well known, however, that males one, two and three years old are capable of exhibiting the mature mounting pattern, i.e. a double foot clasp mount (Goy and Goldfoot, 1974). In the free-ranging troop situation it may be that young males though fully capable of mating at the time of puberty, are prevented from doing so by older males (Koford, 1963). A recent laboratory study on pubertal rhesus has documented the fact that under pair testing situations, in which conspecific interference is eliminated, males of pubertal age exhibit complete mating behavior (Michael and Wilson, 1973). Another explanation of the low level of sexual behavior on the part of pubertal males is that related to an incomplete development of secondary male sexual characteristics (Harlow, Joslyn, Senko and Dopp, 1966).

Age affects the level at which certain components of the typical mating pattern are displayed with young males exhibiting more mounts prior to ejaculation (Michael and Wilson, 1973). Observations on complete mating behavior by pubertal laboratory primates tested in a pair situation have been reported by Rosenblum and Nadler (1971) for bonnet macaques. Pertinent data has also come from enclosure group studies. Hanby and Brown (1974) have followed the mating behavior shown by young Japanese macaques studied in a large coral and report that prepuberal males exhibited the mature mating pattern with the exception of the intromission and ejaculation components. It would appear that the development of the mounting component of mature mating behavior for several species of primates occurs at an age far in advance of that for physiological puberty. In birds and rodents it has been possible by administration of exogenous testosterone to elicit prepuberal sexual behavior (Hamilton, 1938; Stone, 1940; Beach, 1942; Noble and Zitrin, 1942; Riss, Valenstein, Sinks, and Young 1955; Gerall, 1958, 1963). As of yet, no attempt has been made to examine the induction of precocious sexual behavior in any primate species. However, a clinical condition, "pubertus praecox", is well documented for the human and its consequences are profound, "we find in the records that Salamis, the son of Euthmenes, grew to 4'6" in his third year, he walked slowly and had a bass voice, and was carried off by a sudden attack of paralysis when he turned three" (Pliny, Natural History). The psychological ramifications of this syndrome are little known, although Dr. John Money and co-workers at The Johns Hopkins University have reported data on the psychosexual state of some two dozen cases of idiopathic sexual precocity (Money and Alexander, 1969; Money and Walker, 1971). Their work has suggested that in boys psychosexual development was clearly not an automatic by-product of the precocious appearance of gonadal hormones. The body became sexually mature first and intellectual and psychological maturity followed. However, in comparison to similarly aged controls the boys exhibited a tendency to high I.Q., early occurrence of the capacity for frank sexual imagery in dreams and daydreams, and early establishment of the capacity for erotic and sexual arousal in relation to visual imagery and visual perception as well as tactile sensation.

In consideration of human clinical data it is important to note that these boys were limited by social and parental pressures to a peer group environment and that the girls with which they had contact were at a fairly immature psychosexual stage themselves. It would appear that social factors *per se* may have had an inhibitory effect on the sexual behavior of these boys and it is open to speculation as to whether they might have, under conditions free of social constraint, exhibited some form or attempts at appropriate sexual behavior.

Attempts have been made to alter the social hierarchy and social interactions in established primate groups through exogenous hormonal manipulation (Mirsky, 1955; Green, Whalen, Rutley, and Battie, 1972; Joslyn, 1973). By and large these attempts have been unsuccessful; however, one study did report success in the manipulation of dominance through exogenous testosterone treatment of genetic females tested in a group situation (Joslyn, 1973), and under pair testing situations testosterone has been shown effective in the modification of social status for apes (Clark and Birch, 1945, Birch and Clark, 1946).

In light of the scarcity of information on the activation testosterone might have on sexual behavior in young male primates as well as its possible effects on the social interactions within a group, a series of manipulations was carried out in which castrate male rhesus of two different age classes were observed while receiving testosterone propionate injections. The behavior of these animals was measured in a social group testing situation and later these animals were tested under a pair testing situation with estrogen-primed stimulus females.

3.2 METHODS FOR PART I: TESTOSTERONE STIMULATION AND GROUP TESTING.

Subjects and treatments. The animals used were all born in the laboratory of wild-caught mothers who were members of either the Wisconsin Regional Primate Research Center Breeding Colony or the Oregon Regional Primate Research Center Breeding Colony. A total of ten castrates comprise the experimental subject pool for these studies. Pertinent data on these animals are given in Table 3.1. Castrations were performed under general anesthesia by way of a subumbilical incision. The operations were carried out in a fashion consistent with routine sterile surgery practice. Castrates received testosterone (1 mg/day/kg) in a corn oil (Mazola) solution. This dosage has been shown to be effective in the restoration of sexual behavior in the adult male rhesus castrate (Phoenix, Slob and Goy, 1973). Intact males were given corn oil injections of a volume adjusted to that of .05 cc/kg/day as a control procedure for the injections which the castrates received.

Rearing procedures and social testing: All groups received similar social rearing. Oregon group 43's early rearing was identical to that of the younger groups for the first two years of life. All animals as infants were allowed

Table 3.1

Social peer groups of castrate male rhesus.

Group #	Animal #	Sex & Condition	Birth Date	Castration	Social Position Pretreatment	Social Position Treatment
Oregon 43	4859	castrate male	3-21-69	3-21-69	2	2
	4861	castrate male	3-19-69	3-19-69	3	3
	4874	castrate male	3-11-69	3-11-69	1	1
	4863	castrate male	3-17-69	3-17-69	4	4
	4868	intact female	3-15-69		5	5
	4857	intact female	3-21-69		6	6
Wisconsin 1	S-18	intact female	10-2-71		2	2
	S-24	castrate male	10-11-71	1-14-72	3	3
	S-29	intact female	10-16-71		4	4
	S-31	castrate male	10-18-71	1-14-72	1	1
	S-39	intact male	10-29-71		5	5
Wisconsin 2	S-45	castrate male	11-13-71	3-2-72	4	1
	S-47	intact male	11-21-71		5	2
	S-49	intact female	11-22-71		1	4
	S-55	castrate male	12-22-71	3-2-72	6	3
	S-56	intact female	12-30-71		3	5
	S-57	intact male	12-30-71		2	6

Table 3.1 (continued)

Group #	Animal #	Sex & Condition	Birth Date	Castration	Social Position Pretreatment	Social Position Treatment
Wisconsin 3	S-70	castrate male	3-16-72	3-16-72	5	5
	S-71	intact male	3-20-72		3	3
	S-72	intact female	3-22-72		6	6
	S-75	intact female	4-4-72		2	2
	S-77	intact male	4-7-72		1	1
	S-78	castrate male	4-7-72	4-7-72	4	4

to live with their mothers until the age of 3 months at which time they were separated from them weaned and caged individually. Social groups were originally formed of animals born roughly within the span of one month and once a peer group had been set up its membership remained constant. Daily one-half hour group tests were carried out during the first year of life. For a session of daily testing all the animals of a group were removed from their home cages and released into a small testing room containing a stainless steel ramp and platform. Individual animals were scored on a rotating basis by one observer for 5 minutes per animal. During the same testing period, a second observer kept a record on the occurrence of a number of sociosexual behaviors, noting the behavioral category and animals involved. This second observer scored the entire group for the full one-half hour test session. Following the 100-day test run, the animals remained caged individually for a period of time. All the anmmals of a group were given opportunities for 24 hour continuous living experience sometime following the end of their 100-day test run. During this constant living period, the group was released into a large cage and there they remained until one month prior to their next social run at which time they were again caged individually. Following their first test run Wisconsin groups 1, 2 and 3 received 3 months of constant living experience; the older Oregon group had received 4 ½ months of such exposure following but not until the finish of its second social testing run. The animals of all three Wisconsin groups were again tested for their social behavior as a group when the mean age of the animals in the group reached 12 months. The groups were tested 5 days a week for a total of 50 test days. Group 43 received social testingwhen the group members mean age reached 24, 36 and finally 48 months of age. In between these test runs the animals of this group received periods of single cage housing as well as constant living experience. The 50-day test run when the younger groups were 12 months of age and when the older group was 48 months of age constituted what will be called the pretreatment baseline test period. All castrates were started on daily testosterone propionate injections at the end of this pretreatment period and the intact males were started on similar daily injections of corn oil. All groups were followed for a 50-day test run treatment period. Following this treatment period, all injections ceased, and testing was continued for an additional period of 50 test days. Data from this last 50-day testing period was only available for Wisconsin groups 1 and 2. For the two other groups testing was discontinued sometime during what would have been the post-treatment test period; for group Wisconsin 3 this followed thedeath of female S-75 and castrate S-70 from shigellosis and Oregon 43 was discontinued due to severe aggression between the two females of the group which left female 4857 physically debilitated.

Social hierarchy positions were determined by use of a constructed fear grimace matrix. A matrix is constructed by plotting an animal against those group members he fear grimaces to with alpha being the animal of a group which never exhibits fear grimaces to any group member.

Definitions. There were eighteen separate behavior categories which were scored for their occurrence during the thirty minute social testing period. In addition, a total of twenty-one behavioral categories were scored for their occurrence during the five minute period in which each animal received focal animal scoring treatment. For purposes of this discussion, only the behaviors to be discussed will be defined.

Those behaviors scored for one-half hour included:

Disoriented mount: An erect stance in which the hands are placed on the partner's back or head and appropriate hindquarters orientation is lacking with thrusting being directed either to the partner's side or head.

Deficient mount: A stance in which full hind leg extension is never achieved and which thus is carried out in a crouched posture. Thrusting movements must accompany the mount.

No foot-clasp mount: A hind-quarter oriented stance behind another animal in which the hands are placed on the partner's hips, perineum, or back. No clasping by the hind feet occurs. Thrusting movements must accompany the mount.

Single or double foot clasp mount: An erect stance associated with coitus in the monkey, in which the hands are placed on the partner's hips, perineum, or back. One or both feet of the actor clasp one or both legs of the partner. Pelvic thrusting may or may not accompany these mounts.

Intromission: Penile insertion in thevagina, recognized by deep and regular pelvic thrusting.

Ejaculatory response pattern: A recognizable behavioral state characterized by full-body tenseness, immobility, and slight quivering of the flanks.

Present: A posture in which the hind quarters are raised and oriented towards another animal, while the front legs are generally rigid or slightly flexed. The behavior is not scored if more than one animal could have been the receiver of the social movement.

Erection: Engorgement and subsequent turgidity of the penis sufficient to permit extension of the glans beyond the prepuce. This turgidity may or may not be accompanied by penis flips. Erection was scored when obvious such as during grooming bouts, after or preceding occasional mounting attempts as well as under situations of seemingly unproved circumstances.

Yawn: Hyperextension of the mandible and retraction of the lips, exposing all of the teeth. The expression closely resembles that of the stereotypic of human beings.

Aggression: A vigorous biting of a portion of the body of another animal. Head and body shaking may accompany this contact; bleeding and laceration sometimes result from this interaction.

Fear Grimace: A stereotyped submissive facial expression in which the lips are fully retracted to expose the teeth.

Those behaviors scored for only 5 minutes per test period include:

Groom: A stereotypical sorting or brushing aside of the fur of another animal. This behavior pattern may involve one or two hands and is often accompanied by lip-smacking.

Groom receive: A quiet and relaxed response to social grooming. The groomer may exhibit changes of posture or limb movement as if to accommodate the grooming partner.

Groom solicit: A sustained body presentation limited in this study to one of two postures. 1) a prone display of the entire or nearly entire ventral body surface; 2) a seated posture in which the legs are slightly spread and the head is tilted back in a fashion to extend the neck. A reference to Figures 3.1 and 3.2 will make this behavioral category somewhat clearer.

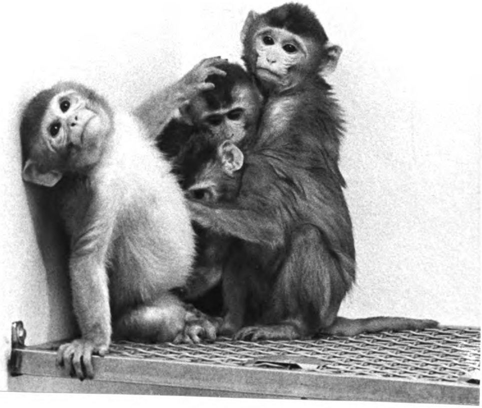
Autogenital manipulation: A manipulation of the genitals with the front or hind feet in the case of males.

Genital manipulation received: The acceptance of genital examination or manipulation by another animal. This manipulation may be manual or oral in nature.

Weights and measurements: The animals of Wisconsin groups 1, 2, and 3 were periodically weighed. On a weighing day all

Figure 3.1 Castrate S-55 exhibiting the prone body display described as groom solicit while under testosterone propionate therapy

Figure 3.2 Castrate S-55 exhibiting the seated body presentation described as groom solicit while under testosterone propionate therapy.



of the animals of a specific group were removed from their home cages by means of a transport cage which was then placed on the scale for weight determination. During the treatment period the weights were used to adjust the testosterone propionate injections for thecastrates and the oil injections for the intacts. This same procedure was followed for the animals of Oregon 43 during their treatment period. Measurements were also taken on the penis size of the young castrates and intacts. These measurements were done with calipers as well as a flexible plastic measuring tape.

3.3 RESULTS FOR PART I

Physiological Measures:

By the second week after the start of injections the castrates weighed significantly more than their pre-treatment weight (Figure 3.2) (Mann-Whitney U test; u = 4, $p < .026$). The testosterone treatments resulted in a pronounced reddening of the sex skin of the young castrates. This effect has been reported previously for other castrate rhesus (Zuckerman and Parkes, 1938; Vandenbergh, 1965). During the period of treatment the penes of the castrates responded with rapid growth, (Table 3.2.) By day 40 from the start of testosterone propionate treatment the penes of all castrates had shown some response to the stimulation. The blanks in Table 3.2 reflect penile development stages of marked immaturity. In such stages the glans is often completely contained by a prepuce which is tightly adherent in the coronal area. Similar juvenile penile

Figure 3.3 Weight gains by young male rhesus monkeys prior to, during, and following an experimental treatment period.

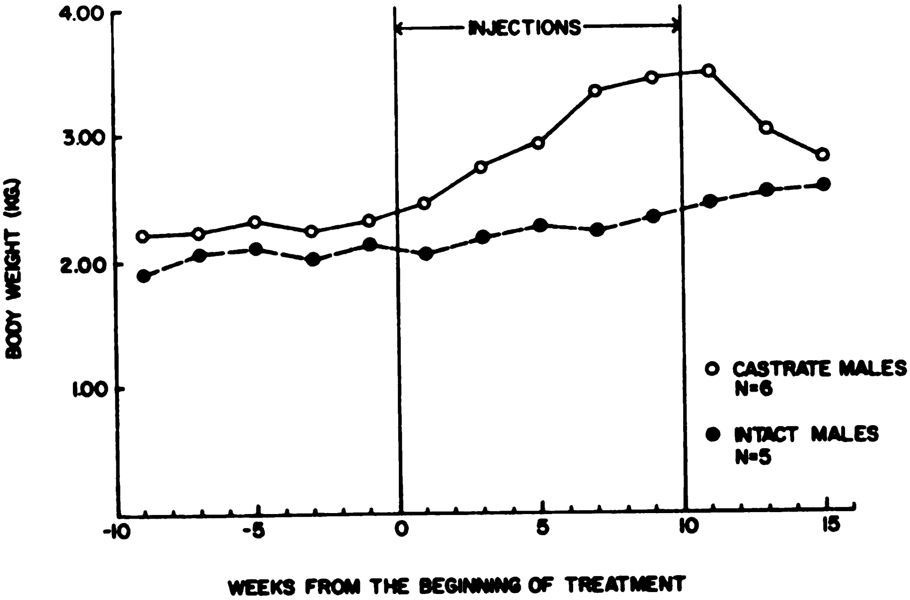

4.00
3.00
2.00
1.00
BODY WEIGHT (KG)
INJECTIONS
○ CASTRATE MALES N=6
● INTACT MALES N=5
-10
-5
0
5
10
15
WEEKS FROM THE BEGINNING OF TREATMENT

Table 3.2 Penis measurements for young male rhesus prior to and during an experimental treatment period.

Table 3.2

Castrate Animal Number	Measurement	Pre- B	Day 40 post TP	Day 75 post TP	Intact Animal Number	Measurement	Pre B	Day 40 post oil	Day 75 post oil
S-24	A	1.5	1.5	1.5	S-39	A	1.5	1.5	1.5
	B	1.0	1.9	2.3		B	---	---	---
	C	0.6	1.0	1.0		C	---	0.5	0.5
S-31	A	1.5	1.5	1.5	S-47	A	1.5	1.5	1.5
	B	0.7	2.5	3.0		B	---	---	---
	C	0.5	1.0	1.2		C	0.5	0.5	0.6
S-45	A	---	1.5	1.5	S-57	A	1.5	1.5	1.5
	B	---	0.5	2.5		B	---	---	---
	C	---	0.7	0.7		C	0.3	0.3	0.3
S-55	A	1.5	1.5	1.6	S-71	A	1.5	1.5	1.5
	B	---	---	2.8		B	0.1	0.1	0.1
	C	0.2	1.0	1.0		C	0.5	0.5	0.5
S-70	A	---	1.5	1.5	S-77	A	1.5	1.5	1.5
	B	---	2.0	2.4		B	---	---	---
	C	---	1.0	1.5		C	0.2	0.2	0.2
S-78	A	---	1.0	1.5					
	B	---	2.4	3.0					
	C	---	0.5	1.0					

A. Circumference of penile shaft behind glans in cm.

B. Distance of glans from prepuce in cm.

C. Distance of opening of urethra from end of glans in cm.

development conditions have been reported for young talapoin (Dixson and Herbert, 1974).

Behavioral Measures:

Prior to the start of daily injections there was only one behavior category for which intact males and castrates differed, that behavior category was the brief contact & rough and tumble play category Table 3.3. Other work has suggested that castrates do not differ from intact males on this play behavior category and the difference in this study may have been related to the specific animals involved and the age of these animals at the time of the study (Bielert, unpublished data).

Brief contact & rough and tumble play have been described as sex dimorphic and in this regard a statistical comparison between the castrates and the females in their social groups was carried out. The females exhibited brief contact and rough and tumble play at a frequency of 3.6 ± 1.3 and differed from the castrate at a significant level (t test, df = 11 $p < .005$).

During the period of treatment the young castrates were shown to differ from intact males on a total of six behavioral measures. For these six behaviors castrates also showed statistically significant differences from their pretreatment testing period. Only one behavior category that of brief contact and rough and tumble play differed in a similar fashion for the intact control males. It should be added here that females exhibited these play behaviors at a frequency of 8.9 ± 2.1 during the treatment period, but castrates remained statistically different from them (t test, df = 11 $p < .025$).

Table 3.3 Behaviors of young male rhesus prior to and during an experimental treatment period. All behaviors tested in the upper half of the table were scored for a one half hour period each test session; the behaviors listed in the lower half of the table were scored for a five minute period and test session. Means are for fifty day test periods.

Table 3.3

	Before Injections		During Injections	
Behavior:	♂	♂̸	♂	♂̸
Disoriented & deficient mounts:	5.5 ± 3.9	2.1 ± 1.2	3.2 ± 1.1	2.3 ± 1.4
No foot clasp mounts:	2.0 ± 1.0	0.3 ± 0.2	1.8 ± 1.7	0.2 ± 0.1
Single or double foot clasp mounts:	0.2 ± 0.1	0.8 ± 0.7	0.4 ± 0.2	0.6 ± 0.4
Presents:	4.0 ± 1.7	6.9 ± 3.1	6.2 ± 3.1	8.1 ± 3.9
Erections:	0.8 ± 0.4	1.5 ± 0.7	1.2 ± 0.5	25.3 ± 9.3[‡][*]
Yawns:	0.6 ± 0.5	1.2 ± 0.7	0.4 ± 0.4	36.9 ± 8.9[‡][*]
Aggression:	0.7 ± 0.3	0.3 ± 0.2	1.1 ± 0.3	0.7 ± 0.3
Brief contact & rough & tumble play:	21.4 ± 1.9	12.9 ± 2.5[*]	32.6 ± 1.7[†]	19.7 ± 3.8[‡][*]
Groom:	0.0 ± 0.0	0.3 ± 0.2	0.4 ± 0.1	0.8 ± 0.4
Groom solicits:	0.1 ± 0.0	0.5 ± 0.4	0.1 ± 0.0	5.7 ± 2.5[‡][*]
Groom receive:	0.0 ± 0.0	0.2 ± 0.1	0.2 ± 0.1	1.4 ± 0.5[‡][*]
Autogenital manipulation:	0.5 ± 0.5	1.0 ± 1.0	0.0 ± 0.0	0.2 ± 0.1
Genital manipulation received:	0.9 ± 0.2	1.8 ± 0.7	1.3 ± 0.6	5.9 ± 1.3[‡][*]

Mean ± S. E.

[*] Significant difference (using the t test, $p < .05$) between castrates and intacts.

[†] Significant difference (using the t test for matched pairs, $p < .05$) before and after oil injections to intact males.

[‡] Significant difference (using the t test for matched pairs, $p < .05$) before and after TP injections to castrates.

No increases in aggression or for any measure of mounting were seen during the treatment period. However, erection and genital manipulation received did increase during the period of testosterone administration. One of the more conspicuous changes was groom-solicit. Frequently a castrate would solicit and then receive grooming and or genital manipulation from another animal. Sometimes an erection would occur during this period of social interaction, often however, an erection was evident at the time of the solicitation. Figures 3.1 and 3.2 show S-55 exhibiting this solicitation posture in its two forms. Erections and yawning often occurred during the grooming periods but both of these behaviors also occurred in situations seemingly independent of any social stimulation. The castrates themselves devoted very little attention to their own genitalia and no increases in the incidence of autogenital manipulation were obtained nor were any incidents of masturbation observed during testosterone treatment.

For the older group of castrates six behavior categories showed changes in frequency during the treatment period, (Table 3.4). As had been the case for the younger castrates there were no increases in mounting or in aggression. In fact aggression decreased significantly in frequency during the treatment period.

Two behaviors, erection and autogenital manipulation, showed statistically significant increases during the testosterone injection period. The measure of genital manipulation received was not affected by the testosterone treatment.

Table 3.4 Behaviors of adult neonatally castrated male rhesus prior to and during a testosterone propionate therapy period. All behaviors listed in the upper half of the table were scored for a one half hour period each test session; the behaviors listed in the lower half of the table were scored for a five minute period each test session. Means are for fifty day test periods.

Table 3.4

Behavior:	Before TP	During TP
Single or double foot clasp mounts:	6.4 ± 2.1	4.7 ± 1.0
Presents:	9.3 ± 1.9	4.2 ± 1.4*
Erections:	3.9 ± 1.9	33.3 ± 9.1*
Yawns:	0.5 ± 0.3	58.1 ± 13.8*
Aggression:	3.3 ± 0.7	0.7 ± 0.3*
Brief contact & rough & tumble play:	3.1 ± 1.9	0.1 ± 0.1
Groom	4.5 ± 1.3	3.7 ± 1.6*
Groom solicits:	1.1 ± 0.8	0.7 ± 0.2
Groom received:	6.4 ± 0.6	8.7 ± 3.1
Autogenital manipulation:	2.1 ± 1.2	5.3 ± 2.1*
Genital manipulation received:	0.6 ± 0.2	1.4 ± 0.6

Mean ± S. E.

*Significant difference (using *t* test for matched pairs, $p < .05$) before and during TP administration.

Autogenital manipulations by these animals were occasionally of a masturbatory nature and ejaculations by way of masturbation occurred 16 times for 4874 and once for 4859. Figure 3.4 is of 4874 during a period of autogenital manipulation. Castrate 4863 exhibited two ejaculations with female 4868 during the period of testosterone therapy; however, prior to testosterone therapy he had exhibited the ejaculatory response pattern four times with this same partner. During the period of testosterone administration the castrates did expel visible quantities of seminal fluid. No groom solicit increases were noticed for these older castrates; and there were decreases in grooming by these animals.

Table 3.5 presents a pretreatment test run behavior comparison for the young animals and the older castrates. Frequencies for certain sex behavior categories differed markedly between these two age classes of males. In terms of mounting behavior the older castrates were showing almost exclusively the mature mount pattern. The younger males occasionally showed mature mounts, i.e. single or double foot clasp mounts, but the ratio of mature mounts to immature mounts was only about .45 on the average. The older castrates were also showing a higher incidence of erection. Aggression was also higher for the older males. Play by the older castrates was infrequent but grooming occurred at a fairly high frequency. These differences in social interaction appear strictly developmentally related and gonadal hormone independent.

Figure 3.4 Castrate male 4874 showing autogenital manipulation while under testosterone propionate therapy.

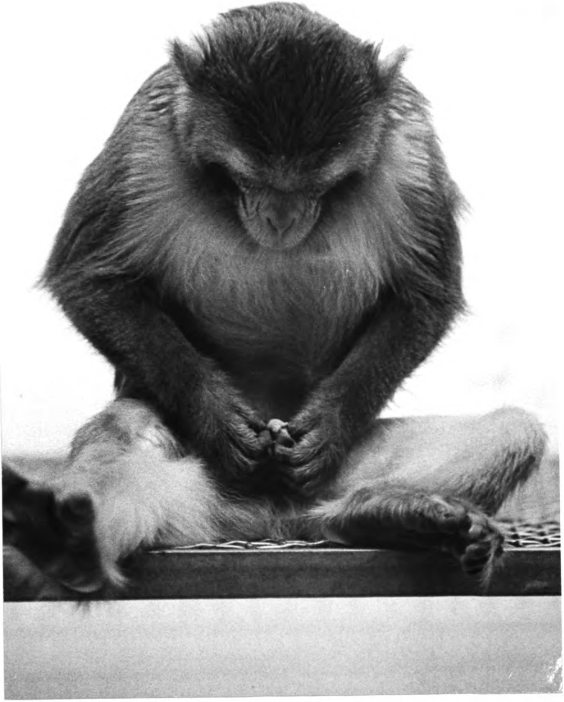


Table 3.5 Behaviors for young male, young castrate male, and adult neonatally castrated male rhesus during a fifty day test period. All behaviors listed in the upper half of the table were scored for a one-half hour period each test session; the behaviors listed in the lower half of the table were scored for a five minute period each test session.

Table 3.5

Behavior:	Young ♂ and ⚦	Old ⚦
Disoriented & deficient mounts:	3.7 ± 1.9	0.5 ± 0.5
No foot clasp mounts:	1.1 ± 0.5	0.0 ± 0.0
Single or double foot clasp mounts:	0.5 ± 0.4	6.4 ± 2.1*
Presents:	5.6 ± 1.8	9.3 ± 1.9
Erections:	1.2 ± 0.4	3.9 ± 1.9*
Yawns:	0.9 ± 0.4	0.5 ± 0.3
Aggression:	0.5 ± 0.2	3.3 ± 0.7*
Brief contact & rough & tumble play:	12.9 ± 2.5[1]	3.1 ± 1.9*
Groom:	0.2 ± 0.1	4.5 ± 1.3*
Groom solicits:	0.5 ± 0.3	1.1 ± 0.8
Groom received:	0.1 ± 0.1	6.4 ± 0.6*
Autogenital manipulation:	0.8 ± 0.5	2.1 ± 1.2
Genital manipulation received:	1.4 ± 0.4	0.6 ± 0.2

Mean ± S. E.

[1] Mean here is for young castrates only, since young castrates differed significantly from young intact males.

*Significant difference (using *t* test, $p < .05$) between old and young males and old castrates.

In only one group, Wisconsin 2, was there a change of social hierarchy during the period of testosterone treatment. Table 3.6 summarizes data on dominance shifts. The occurrence of this social order shift allowed a consideration of the fashion in which social position exerts an effect on the display of certain behavior patterns which appeared testosterone stimulated. In Wisconsin 2 the two castrate males S-45 and S-55 rose in the dominance hierarchy from positions 4 and 6 to positions 1 and 3, respectively. This occurred on day 39 of social testing during the period of treatment. Table 3.6 presents the frequency data from the six behaviors for which testosterone treatment values differed from those of the pre-test period. Erection and yawn were the two behavior patterns which exhibited the most marked effects. It should be mentioned in this regard that the values for the ten-day period preceding the dominance shift were very typical of those shown during other ten-day testing blocks as reference to table 3.6 substantiates.

The data for the four castrates that were followed through a 50-day post-treatment test run are presented in Table 3.7. Brief contact & rough and tumble play showed no difference across the comparisons for the pre-treatment, treatment, and post-treatment period. This was also the case for the measure of groom solicit, but the pattern of changes for these two behaviors was dissimilar. In the case of play there was an increase in the level from the pre-treatment

Table 3.6 Behavior scores for two castrate rhesus prior to and following a dominance shift during testosterone treatment.

Table 3.6

	Castrate S-45			Castrate S-55		
Behavior:	A	B	C	A	B	C
Erection	2.3	3.0	21.0	45.0	59.0	131.0
Yawn	54.5	88.0	105.0	4.5	6.0	40.0
Brief Contact & Rough & Tumble Play	32.3	26.0	17.0	10.5	9.0	6.0
Groom Solicit	5.3	3.0	5.0	17.0	15.0	21.0
Groom Received	1.5	1.0	0.0	3.3	3.0	0.0
Genital manipulation Received	8.5	7.0	4.0	8.5	10.0	9.0

A = the mean frequency for ten-day test blocks prior to dominance shift

B = the absolute frequency for the ten-day test block prior to dominance shift

C = the absolute frequency for the ten-day test block following dominance shift

Table 3.7 Behavior scores for young castrate male rhesus prior to, during, and after testosterone propionate treatment. Means are for fifty day test periods.

Table 3.7

Behavior	Animal No.	Pre ℞	℞	Post ℞	
	♂				
Erection:	S-24	0.4	14.0	3.6	Pre ℞ vs. ℞*
	S-31	3.2	43.4	13.4	℞ vs. Post℞ *
	S-45	0.0	6.0	1.6	
	S-55	3.8	62.2	16.8	
	$\bar{X}$	1.9	31.4	8.9	
Yawn:	S-24	0.0	22.8	1.6	Pre ℞ vs. ℞*
	S-31	4.0	42.4	4.6	℞ vs. Post ℞*
	S-45	0.0	64.6	7.8	
	S-55	0.0	11.6	2.8	
	$\bar{X}$	1.0	35.3	4.2	
Brief Contact & Rough and Tumble Play:	S-24	12.8	25.2	27.4	Pre ℞ vs. ℞ n.s.
	S-31	13.8	26.2	26.8	℞ vs. Post ℞ n.s.
	S-45	20.0	29.2	29.4	
	S-55	16.6	9.6	9.0	
	$\bar{X}$	15.8	22.5	23.1	
Groom Solicit:	S-24	0.0	1.0	1.2	Pre ℞ vs. ℞ n.s.
	S-31	0.0	4.6	4.6	℞ vs. Post ℞ n.s.
	S-45	0.6	5.2	0.4	
	S-55	2.4	17.8	1.6	
	$\bar{X}$	0.7	7.1	1.9	
Groom Receive:	S-24	0.0	1.0	1.0	Pre ℞ vs. ℞*
	S-31	0.0	3.2	2.4	℞ vs. Post ℞ n.s.
	S-45	0.8	1.2	0.0	
	S-55	0.2	2.6	0.0	
	$\bar{X}$	0.3	2.0	0.9	
Genital Manipulation Received:	S-24	2.0	3.6	1.4	Pre ℞ vs. ℞**
	S-31	1.0	8.4	2.8	℞ vs. Post ℞***
	S-45	4.8	7.6	0.0	
	S-55	2.4	8.6	3.0	
	$\bar{X}$	2.5	7.1	1.8	

*Significant difference (using *t* test for matched pairs, $p < .05$).

**Significant difference (using *t* test for matched pairs, $p < .025$).

***Significant difference (Using *t* test for matched pairs, $p < .001$).

period during the time of testosterone injections and the level of play continued at this level during the post-treatment period. In contrast to play the groom solicit measure showed an increase during the treatment period followed by a decline during the period of testosterone withdrawal.

3.4 METHODS FOR PART II: TESTOSTERONE STIMULATION AND PAIR TESTING

Subject and treatments: The same group of males used in Part I of this series of experiments was used in Part II. In addition, a total of eight females were used in Part 2. Five of these females were used as partners for the young males and castrates. All of these five were from the social groups Wisconsin 1, 2 and 3. These females were given subcutaneous silastic tubing implants of crystalline estradiol. The procedure employed for the making of these implants and their placement was similar to that which has been described (Karsch, Dierschke, Weick, Yamaji, Hotchkiss, and Knobil, 1973). In the case of these young females the exposed estrogen packed silastic tubing was a length of approximately 1.5 cm. No testing was carried out with the females until two weeks following estradiol implantation. For the older castrates a total of three females were employed as stimulus animals. One of the females, 4868, was familiar to the castrates, a second female, 4875, had been similarly reared and was similarly aged to 4868 but was an unfamiliar partner to the males of this study; the third femlae, 1559, had been wild-caught and a member of the Wisconsin Regional Primate Research Center Breeding Colony for 2 years but was estimated to be of similar age to the other females. These females received implants of an estrogen packed silastic tubing with an exposure length of approximately 3 cm. They also received a two week post-operative period prior to the beginning of behavioral testing. When the pretesting of all the males had finished they were put on a daily testosterone injection regime of 1 mg/kg/day. The young intact males received daily corn oil injections of .05 cc/kg/day. The animals received at least one month of such injections prior to retesting with the females.

Testing: At a mean age of 2.1 years, which was at least 195 days following previous androgen treatment, the young castrate and intact males were given pretreatment sex tests with the familiar and unfamiliar estrogen=implanted stimulus females. At a mean age of 5.1 years, which was 86 days following previous androgen treatment, the castrates of group 43 were given pretreatment sex tests with their estrogen implanted stimulus female partners. All pair tests were of twenty minutes duration and were carried out in a balanced fashion. No male received more than one test a day. The tests were conducted in a large bare test room which contained a stainless steel ramp and platform. A test began with the introduction of the female into the test room which already held the male. Two observers scored the pair's interactions utilizing a scoring inventory which included a large variety of both male and female behaviors.

Defnintions: In addition to scoring no foot clasp mounts, single foot clasp mounts, double foot clasp mounts, intromissions, ejaculations, yawns, erections and female presents, the following behavioral measures were scored.

Approach: A directed walk at a moderate to fast rate towards the partner. Approaches may or may not be followed by a contact of the other animal.

Contact: A light touching of the partner's perineum, back, hindquarters, or hips with one or both hands.

Purselip: A facial expression in which the ears are drawn back as well as the brows and scalp while the chin is thrust forward and the lips puckered and rhythmically smacked.

Threat: Any of the following behaviors or combinations of these behaviors which contain obvious and direct orientation towards the partner.

Contact threat: Brief bouts of gentle to moderate biting, shaking or slapping. Distinguished from aggression by degree of intensity.

Body lunge: A sudden body thrust with an intense and directed stare. May be followed by an aggressive interaction or cage shaking.

Charge: A directed pursuit of another animal which may be accompanied by woofing vocalization and followed by body contact.

3.5 RESULTS FOR PART II

Table 3.8 presents the behavioral data for the young castrates and males on their pretreatment and treatment testings. Only one measure, that of female present, differed significantly between the groups during the period of pretreatment testing. By the end of the first series of testosterone treatment tests the castrates differed from the intact males on the measures of purselip, and yawn. The measures of approach, contact, mount, intromission, and erection had higher means for the castrates, but the differences failed to reach a level of statistical significance. The castrates differed from the intacts at the time of the second testing during treatment, for measures of approach, contact, mount, erection, purselip, and yawn.

By the first series of androgen treatment sex tests for the castrates the measures of approach and contact differed significantly from the pretreatment testing when matched pair _t_ tests were carried out ($p < .005$ for approach and $p < .05$ for contact). Two castrates S-31 and S-78 showed intromissions during the first and second treatment testings. In addition, during both the first and second treatment test series, castrate S-78 ejaculated. Examination of the female partner on these occassions revealed evidence of seminal emission.

The results for the older castrates were very individualistic. Three castrates 4859, 4875, and 4861 all showed approaches,

Table 3.8 Sex behavior scores for young male and young castrate male rhesus prior to and during experimental treatment. The scores represent means for a total of five fifteen minute pair tests with young estrogen primed stimulus females.

Table 3.8

	Pretreatment			Treatment Test #1			Treatment Test #2		
Behavior:	Male	Castrate		Male	Castrate		Male	Castrate	
Approach	1.5	1.8	n.s.	1.9	4.4	n.s.	1.0	5.0	**
Contact	3.1	1.0	n.s.	1.5	3.2	n.s.	.8	4.4	*
Mount	1.0	0.8	n.s.	1.2	2.4	n.s.	0.7	3.7	*
Intromission	0.0	.2		0.0	0.8		0.0	0.5	
Purselip	.2	.8	n.s.	.1	2.0	*	.1	2.2	**
Yawn	0.0	0.0	n.s.	0.0	2.5	*	0.0	5.4	***
Erection	0.5	1.9	n.s.	0.2	1.8	n.s.	0.0	3.3	**
Threat	0.0	1.7	n.s.	0.0	0.2	n.s.	0.2	0.9	n.s.
Female Present	0.7	2.9	*	0.7	5.0	*	1.0	5.4	*

* Significant difference (using the t test, $p < .05$) between castrates and intact males.

** Significant difference (using t test, $p < .01$) between castrates and intact males.

*** Significant difference (using the t test, $p < .001$) between castrates and intact males.

contacts, and mounts of their female partners during their pretreatment testing; in addition 4874 displayed an intromission. Following treatment, all four castrates displayed higher frequencies of approach, contact, and mount, and 4874 showed an increase in intromissions. Erections, yawns, and purselip were also displayed at higher frequencies during the first series of treatment test. In this regard no yawns or purselips, were seen during the pretest period and only one male (4874) had any erections. No consistent trend was apparent for measures of threat and aggression. The second round of pair tests was very similar to the first for all measures. No ejaculations were seen by any of the castrates during the period of androgen treatment, however, masturbation incidents occurred for two castrates, 4859 and 4874.

3.6 DISCUSSION

In contrast to several previous studies (Mirsky, 1955; Green _et_ _al_., 1972) clear behavioral differences were obtained between castrates and intacts while under testosterone treatment and in the group testing situation. The behaviors of erection, yawn, groom solicit, groom receive, and genital manipulation all increased in frequency during the period of testosterone stimulation. The castrates also exhibited behavioral changes under the pair testing condition and the behaviors which increased in frequency included approach, contact, mount, purselip, yawn and erection.

The concern of this study was with behavior and not dominance interactions within the group and because of this a contrast to those studies which were directed towards an examination of dominance hierarchy changes may be inappropriate for the data reported on social behavior in the previous studies were limited. In only one of the four social groups examined in this study was there a shift, using fear grimace matrix, in dominance order during the period of testosterone treatment. A similar occurrence was reported by Joslyn (1973) in which androgen injections were given to young females which were reared in a fashion similar to the castrates of this study and for which a dominance shift was reported during the treatment period. In the present study for two of the three groups no dominance changes occurred, but the dominance positions of the castrates were high to begin with in these groups. In a third group, Wisconsin 3, the castrates occupied low dominance positions. Possibly a shift might have occurred in Wisconsin 3 as a result of the testosterone treatments. Castrate S-78 did attempt to assert himself with male S-77 but these attempts were rebuffed by S-77 acting in unison with female S-75. It would appear that dependent rank is an important factor which may well affect the outcome of studies which have attempted to manipulate dominance through hormonal manipulation (Kawai, 1965; Varley and Symmes, 1966). In this regard, attention might be drawn to male S-47. Prior to the start of the treatment period, S-47 occupied the fifth social rank position in his group. His preferred play partner was castrate S-45. During the treatment period a dominance shift occurred in this group and male S-47 moved to the second rank position. This male had received only oil during the entire treatment and his shift is probably best explained by a dependent rank process. It would appear that within a group setting social factors may well interact in a fashion to offset any influence gonadal hormones may play in the determination of a social hierarchy position.

Although some studies (Rose, Holaday, and Bernstein, 1971; Rose, Gordon, and Bernstein, 1972) have suggested a relationship between testosterone and aggression for primates, the causality of the relation appears questionable (Eaton and Resko, 1974). No increases in aggression were seen in any of the groups of this study. In fact a further analysis was carried out on two motor components frequently associated with rhesus agonistic behavior, the "woof threat", and the "ear flip". And again no increases were found for these measures when the pretreatment period was compared to the treatment period. One study has been carried out in which increases in aggression were reported to accompany androgen administration (Trimble and Herbert, 1968). This study employed adult ovariectomized female rhesus and similar increases have not been reported in studies which have utilized adult castrate male rhesus (Phoenix, Slob, and Goy, 1973; Michael and Wilson, 1974). It is at least possible that the physiological variables affecting the display of aggressive behavior for the two sexes are different. Consistent with this interpretation are several studies which have dealt with central nervous system control of aggression. Kling (1974) reported that female rhesus monkeys, when given amygdaloid nucleus lesions increased their levelsx of aggression while males which received the same lesion failed to show such increases. Work on cats (Inselman-Temkin and Flynn, 1973) utilizing central nervous system stimulation for the elicitation of attack has suggested that the neural substrates critical to this behavior in males and females respond differently to hormone priming. It would appear possible to suggest that aggressive behavior is mediated through different neural networks in the two sexes and that the effects which testosterone have on this behavior are closely related to those neural and physiological substrates critical to its expression. Work carried out on genetic female rhesus monkeys which were exposed to testosterone *in utero* (Goy and Phoenix, 1971) indicates that testosterone may well have an influence on the level of aggression exhibited by adult rhesus monkeys, but its effects on aggression are achieved by early hormone exposure and one intimately related to situational circumstances as well as individual behavioral propensities (Bielert, unpublished data).

The social and individual behavior categories which were affected by testosterone treatments in the group testing situation were different for the two age groups of castrates.

In the case of the three groups of young castrates, the most noticeable changes were for those behaviors concerned with grooming. The appearance of thebody display described as a groom solicitation was an unexpected outcome in this study. A number of observations on several species (Sparks, 1969) have documented the findings that grooming sessions are frequently associated with sexual interaction and may be influenced by endocrine factors (Michael and Herbert, 1963). Data from the present study suggests that for males the groom solicitation may have a degree of testosterone dependence. In this regard it may be that groom solicitation postures are age related and that the older castrates in our study employed solicitation postures other than the two which were scored under the taxomony employed in this study. In contrast to an interpretation of age dependency, it could be suggested that the behavior response seen under this testing situation by the young castrates was idiosyncratic and related to the specific animals and their rearing background. There is at least suggestive evidence that such is not the case.

Kling (1968) has reported that when a group of young 2 year old males were given testosterone treatment and pair tested with other young males, "the most consistent effect of testosterone . . . was the increase in grooming behavior", though it is impossible to tell from the report if this increase was related to an increase in groom solicitation. Further evidence for a role of testosterone allogrooming comes from Trimble and Herbert (1968); they reported that when adult ovariectomized female rhesus were given androgen "there was an overall increase in the mean number of grooming invitations offered by the female while they were receiving the three doses of testosterone compared with the series in which they were not treated". In addition, Michael and Wilson (1974) have reported that female grooming of a constant male partner decreased following castration of the male. It would appear that the effect of testosterone on groom solicitation and the display of grooming by rhesus is clear but is probably partly determined by the individual animal involved and his age.

The finding that the young castrates exhibited yawning at higher frequencies under testosterone treatment may be interpreted to mean that the neural substates critical to this response were fully responsive to androgen stimulation. It has been suggested that yawning is a testosterone stimulated behavior pattern for both sexes (Goy and Resko, 1972) and further data consistent with this position has been offered by Eaton and associates (Eaton et al., 1973). It is clear that this behavior pattern normally makes its appearance postpuberally in intact males (Bielert, unpublished data). Data following the dominance shift in group Wisconsin 2 make it clear that social factors play a role in the display of yawning. Though yawning is rarely shown by females it can be displayed at high levels under social conditions where the dominance relationship between a heterosexual pair is dominated by the female (Bielert, unpublished data).

The occurrence of erections differed significantly between the two groups of castrates prior to testosterone therapy. In both groups erection frequency was significantly increased by androgen treatment. One explanation for the pretreatment difference might be that of social behavior profile differences. As has been previously mentioned the older group spent more time in grooming sessions. Frequently during these sessions erections were noted and it may have been through the increased grooming activity that the erection scores for the two ages differed. Though the occurrence of erection was clearly testosterone related it appears that this behavior pattern is also influenced by social factors. Following the dominance shift in Group 2 both castrates showed increases in the frequency of this behavior pattern. The testosterone dose for these two castrates remained constant throughout the period of treatment and thus appears unrelated to the frequency shifts. It has been suggested that erection has a social signal value (Wickler, 1969, 1972). In this regard, it may well be that social position affects peripheral testosterone levels and through this mechanism the occurrence of erection but it also appears that social position *per se* is also capable of affecting the display of this particular behavior pattern.

One of the most dramatic differences between the two groups was the sudden appearance of autogenital manipulation in the group of older castrates during the period of testosterone treatment and its absence during the treatment period of the younger groups. To the extent that this behavior may be termed sexual it would appear that the younger castrates were insensitive to testosterone's affects on its display. The fact that the erections occurred for both groups under androgen treatment may be taken as evidence for responsiveness of the peripheral and neural tissues. If the absence of increased autogenital manipulation for the young castrates cannot be attributed to physiological insensitivity it may be attributable to behavioral immaturity. It may be that one year old laboratory-reared male rhesus are still sexually immature in regard to their autoerotic behavior patterns and that social experience *per se* is a critical factor in the effectiveness of testosterone in altering this particular sex behavior pattern.

The failure of mounting behavior to increase during testosterone stimulation during the period of social testing is difficult to explain since mounting behavior was occurring in all of the groups though its display did differ for the two age groups with the older castrates exhibiting almost exclusively the mature mount pattern which characterizes adult rhesus sexual behavior (Bielert and Goy, 1973). It may be that social interactions were an inhibitory factor in this regard for dominance does appear to affect the individual sexual behavior pattern components displayed by both males (Perachio, Alexander, Marr, 1973) and females (Herbert, 1967; Goldfoot, 1971).

It was with this consideration in mind that the pair tests were conducted. Under the pair testing situation all testosterone treated males did show increases in mounts during the period of treatment. These increases were particularly noteworthy in the case of the young castrates. An important consideration in terms of the apparent discrepancy between the social and pair testing results for mounting is the fact that it was only under the pair test situation that the young males and castrates had exposure to estrogen-primed females. This fact alone, however, was not enough to stimulate sexual behavior in the young intact males but it may have been a factor in the failure of the young castrates to respond during the treatment period which accompanied the social testing. The increases in approach, contact, and mount by the young castrates are a clear demonstration of the sexual behavior potentiality which these young animals have. The occurrence of intromission and ejaculation by these young males during the period of treatment is the first report of such behaviors in rhesus of this young age and could possibly be described as precocious. An interesting sidelight in terms of the castrate's response to testosterone was the increase in frequency of the facial expression "Purselip". Chevalier-Skolnikoff (1973) has suggested that the lip smack expression known to be connected with sexual interactions of rhesus pairs (Lindburg, 1971) may be influenced by the female's hormonal state. The data from this study suggests that in addition it is also influenced by the individual male's hormonal state. During a period of testosterone treatment at the termination of the pair testing the young castrates were tested with adult estrogen primed females. The young castrates showed great interest in the females and purselipped to these partners, in addition they also exhibited the stiff-legged walk which is scored as strut. This behavior pattern has also been described for adult rhesus pair interactions (Lindburg, 1971) and the observations from this study suggest that some element of the female partner influences this particular display. Eaton _et al_. (1973) have also reported an increase in this social behavior pattern during androgen treatment of female pseudohermaphrodites.

One of the most startling observations to come from this study was the occurrence of the ejaculatory response pattern in prepubertal animals and also in older castrates not receiving androgen. These observations for the rhesus monkey are consistent with human. In the case of the human, orgasm can occur for the male far in advance of the onset of physiological puberty (cited as general knowledge by Bermant and Davidson, 1974). These observations suggest that social and hormonal variables connected with puberty operate on an already complete neural substrate, and that prepuberal sexual behavior may possibly provide positive reinforcement to the individual. Such reinforcement may be very important in species such as the rhesus in which there is a lengthy development of sexual behavior prior to the onset of puberty.

SECTION 4

SEXUAL BEHAVIOR OF ADULT LABORATORY-REARED INTACT MALE RHESUS MONKEYS: COMPARISON WITH WILD-CAUGHT ADULT INTACT MALES AND LABORATORY-REARED PREPUBERALLY CASTRATED ADULT MALES

4.1 Introduction

The rhesus monkey (Macaca mulatta) is a comparatively long-lived animal, and shares with many other primates including man a period of extended social development preceding sexual maturity. The sociality of primates and their well-organized and stable interaction networks are features which are firmly rooted in phylogeny (Gartlan, 1973). When young rhesus are prevented from interacting with peers or reared without maternal care, serious and long-term effects on individual adjustment and social behavior may be observed (Harlow and Harlow, 1969). When the social testing has been carried out in adulthood, a time when infantile gonadal state should no longer be a consideration for the behavior of either the male or his stimulus partner, the sexual behavior of these restriction reared animals was revealed to be deficient (Harlow, 1965; Harlow, Joslyn, Senko, and Dopp, 1966). It would appear from the work which has been carried out that the social and sexual behavior patterns of male primates are sensitive to early social and environmental restriction. This proposition appears valid for both catarrhine monkeys (Meier, 1965; Missakian,

1969) and apes (Rogers and Davenport, 1969; Riesen, 1971). At least in the case of the rhesus these deficits don't appear to be moderated even after lengthy periods of rehabilitative social exposure (Missakian, 1972).

Though early reports were difficult to interpret (Thorek, 1924; Zuckerman and Parkes, 1938; 1939) it is now clear that the sexual behavior of the adult male primate is adversely affected by gonadal insufficiency. Bilateral gonadectomy has been shown to significantly affect the occurrence of the ejaculatory pattern as well as the occurrence of intromission, mounting, spontaneous erection, and yawning (Michael, 1972; Michael, Wilson and Plant, 1973; Phoenix, Slob, and Goy, 1973; Michael and Wilson, 1974). Behavior can be restored to castrate male primates through exogenous androgen (Michael et al., 1973; Phoenix 1973; Phoenix et al., 1973; Michael and Wilson, 1974; Phoenix, 1974). Consistent with the effects of castration are those obtained following treatment with the anti-androgen, cyproterone acetate. Cyproterone acetate treatment lowers peripheral androgen levels and in addition causes a deterioration in sexual behavior (Michael, Plant, and Wilson, 1973).

Recently papers have attempted to assess the social and environmental factors which may have a determining influence on the development and exhibition of mature sexual behavior for primates under laboratory conditions (Goy and Goldfoot, 1974; Goy, Wallen and Goldfoot, 1974). However no attempt has yet been made to assess the extent to which social restriction and gonadal state may interact to affect male primate sexual behavior. With this in mind an attempt will be made to describe and characterize the sexual behavior of adult laboratory reared male rhesus and place this behavior in perspective through comparisons with wild-caught adult males. In addition, attention will be given to the sexual behavior displayed by adult neonatally castrated laboratory reared male rhesus. Further data will be presented for these castrates from a series of pair tests conducted while testosterone propionate therapy was being given.

4.2 Methods

Subjects. The animals selected for this paper's analysis were all adult male rhesus of at least four years of age at time of testing. It has been reported that males of this age exhibit high peripheral levels of testosterone (Resko, 1967). A total of nineteen laboratory reared males were tested. Five of these nineteen were castrated. The castrations were performed on the day of birth in the case of two animals and the remaining three were castrated at approximately three months of age. All castrations were performed under general anesthesia by way of a subumbilical incision. The operations were carried out in a fashion consistent with routine sterile surgery practice. A total of ten wild-caught adult male rhesus monkeys made up the wild-caught test group. Eight were proven breeders and had been members of the Wisconsin

Regional Primate Research Center Breeding Colony for at least a year. The females used were fully adult wild-caught rhesus which had been bilaterally ovariectomized. The females were brought into a receptive condition through estradiol benzoate injections of 10 ug/day or silastic tubing implants of crystalline estradiol. The implants were placed subcutaneously in the subscapular region of the back. The surgical placement of the implants was done under anesthesia. The implants were similar to those which have been previously described (Karsch, Dierschke, Weick, Yamaji, Hotchkiss, and Knobil, 1973). The silastic tubing had only a 3 cm crystalline estradiol exposure length packed. All animals were caged individually and maintained on commercial monkey chow supplemented with vitamins and periodic fruit and vegetables.

Rearing procedures. All of the laboratory-reared males tested received similar social experience during their first four years of life. The males were reared under what has been described as a peer-group procedure (Phoenix, Goy, and Young, 1967; Goy and Goldfoot, 1974; Goy, Wallen and Goldfoot, 1974). These groups varied in total membership from 4-6 individuals. All groups had at least two female members and varied in terms of whether the remaining members were intact males, neonatal castrates, female pseudohermaphrodites or a combination of several of these treatment classes. All infants were allowed to live with their mothers until the age of approximately 3 months, at which time they were separated from their mothers, weaned, and caged individually. Peer-groups were made up of similarly aged animals and once a peer-group was set up as such, its membership remained constant. Daily one-half hour group tests were carried out 5-days a week for a total of 100 test days during thefirst year of life. For a daily testing, all the animals of a group were removed from their home cages and released into a small testing room which contained a stainless steel ramp and platform. They were allowed to interact for one-half hour after which they were returned to their home cages. Following the 100-day test run, animals remained caged individually. The animals of a peer-group were again tested for social behavior when the mean age of the animals in a group reached 12, 24, 36 and 48 months. The groups were tested 5-days a week for 50 test days during these later social test runs. The only deviation from the previous test run was that the animals were tested in a slightly larger test room during these runs. Animal care and maintenance procedures were relatively constant and no unique manipulations were carried out on any of the peer-groups from which the animals with which this study is concerned were from. At various times and for varying periods of time peer=groups received 24 hour continuous living experience; during these periods the entire peer group was released into a large indoor-outdoor cage facility. Periodically animals of a specific peer-group were given round-robin testing during which two members of a peer-group would be released into a testing cage and allowed to interact for a ten-minute period. These exposures were systematic and occurred during the animals' second, third and fourth years of life.

Data collection. The data analyzed in this paper were collected over a period of time at both the Wisconsin Regional Primate Research Center and the Oregon Regional Primate Research Center. As a result of this not all animals saw the same female partners, but the partners were always strange to them and were always sexually experienced and fully adult. The males were tested on different occasions and saw a total of from 3 to 6 females. The data for a particular male represents the mean for all the tests which he received. All tests were of 15 minutes in duration. The testing was conducted in either a testing cage or a small testing room. At the start of a test the female was introduced by way of a guillotine door into the testing area which already contained the male. Scoring of the pair's interactions was done by experienced observers utilizing a standardized scoring taxonomy. No attempt was made to hide the observers, although no efforts were made on their part to interact with the pair.

Definitions. A total of five behaviors were scored whenever they occurred, no matter which animal exhibited them.

1. Fear grimace: A facial expression in which the lips and cheeks are retracted so that the teeth, sometimes tightly clenched, and gums are exposed and deep furrows appear on the cheeks. The ears are usually flattened back and there may be a tenseness of body musculature.

2. Yawn: A hyperextension of the mandible and retraction of the lips which exposes the teeth. This expression closely resembles that of the yawn displayed by human beings.

3. Groom: A stereotyped sorting and or brushing aside of the fur, very often accompanied by lip smacking. This behavior pattern may involve one or two hands and was only scored when directed towards another animal.

4. Aggression: A vigorous biting accompanied by head shaking as if to tear or rip.

5. Threat: Any of the following behaviors or combination of these behaviors which contain obvious and directed orientation towards another animal.

   a) Contact threat: Brief bouts of gentle or moderate biting; shaking or slapping. Distinghished from aggression by degree of intensity.

   b) Body lunge: A sudden body thrust with an intense and directed stare. This may be followed by genuine aggression or possibly cage shaking.

   c) Charge: A directed pursuit of another animal which may be accompanied by a woofing vocalization and followed by body contact.

A total of six behaviors were scored for only the male partner.

1) Contact: The male lightly touches the perineum, back, hind quarters, or hip (s) of the female with one or both hands.

2) Mount: An erect stance associated with coitus in the monkey, in which the hands are placed on partner's hips, perineum or back. One or both feet of the male clasp one or both legs of the partner. Pelvic thrusting may occur. The rhesus monkey usually exhibits a series of mounts which may or may not include intromissions preceding an ejaculation.

3) Intromission: Penile insertion into the vagina recognized by deep and regular pelvic thrusting. The rhesus monkey characteristically exhibits several intromissions preceding an ejaculation.

4) Ejaculation: Recognized during copulation by a series of deep pelvic thrusts followed immediately by full-body tenseness, immobility and slight quivering of the flanks.

5) Purselip: A facial expression in which the lips are slightly extended and rhythmically opened and closed. This expression is usually accompanied by a neck thrust and often associated with a strut like locomotion. During this strut the male walks in a stiff legged fashion with his tail crooked and curled over his back.

6) Erection: An engorgement of the penis sufficient to permit extension of the glans beyond the prepuce. This turgidity may or may not be accompanied by penis flips. Erection

was scored when obvious such as during grooming bouts, often preceding occassional mounting attempts, as well as under situations of seemingly unprovoked circumstances.

The behaviors scored for the female alone included the following:

1) Presenting: A stereotyped posture of receptivity characterized by quadrupedal immobility orientation of the perineum towards the partner, tail deflection, and modest extension of fore and hind limbs. Presenting was classified during testing as follows:

a. Presenting to contact: Presenting posture assumed as partner makes a contact.

b. Presenting spontaneously: Presenting without physical partner interaction.

2) Proximity: A behavioral measure of interindividual distance. A female was scored for proximity when she was seated within one foot and a half of her seated partner. Body orientation was not a part of the criterion for this behavior.

4.3 RESULTS

Comparisons between the two intact groups revealed marked differences for several measures of male sexual behavior. Peer-reared intact males contacted, mounted, intromitted and ejaculated at statistically significant lower levels than wild-caught males. Yawning frequency also differed between these groups with the wild-caught males exhibiting this behavior at a significantly higher frequency than the intact peer-reared males. There were no differences for the measures of purselip or spontaneous erection, although the wild-caught males did purselip more and exhibit erections less frequently than the intact peer-reared males. Grooming by the males was rare and no difference between the groups was obtained for this measure. The agonistic behavior measures of threat and aggression also failed to differ significantly between the two intact groups (Table 4.1; Table 4.2).

Behavior by the female partners was exhibited at significantly different levels for several patterns. Spontaneous presents occurred at a higher level during the tests with the intact peer-reared males. In marked contrast to the spontaneous present measure presents to contact occurred at a much higher frequency when the female was with a wild-caught male, although in this regard it should be noted that the wild-caught males were showing more contacting. Females also showed proximity more frequently to the wild-caught males. The agonistic behavior of the females appeared greatly affedted by the type of partner she was with. No female aggression was ever directed to a wild-caught male. Females also directed fewer threats to wild-caught males than they did to the intact peer-reared males (Table 4.1; Table 4.3).

Comparisons between the two peer-reared groups also revealed significant differences related to the gonadal state of the male being tested. Castrate males exhibited fewer contacts

Table 4.1 Sex behavior scores for tests of castrate peer-reared, intact peer-reared and intact wild-caught adult male rhesus monkeys.

Table 4.1

Behavioral Measures		Castrate Peer-reared	Intact Peer-reared	Intact Wild-Caught
		N = 5	N = 14	N = 10
Male	Contact	0.1 ± 0.1	1.7 ± 0.5	4.6 ± 0.6
	Mount	0.1 ± 0.1	1.6 ± 0.4	3.7 ± 0.5
	Intromission		0.6 ± 0.3	1.7 ± 0.3
	Ejaculation		0.1 ± 0.1	0.4 ± 0.1
	Erection	0.3 ± 0.3	1.5 ± 0.4	0.7 ± 0.3
	Purse Lip	0.9 ± 0.5	3.1 ± 1.2	6.5 ± 1.7
	Yawn	1.7 ± 1.4	3.1 ± 1.0	9.6 ± 2.4
	Aggression	0.6 ± 0.2	0.1 ± 0.0	0.1 ± 0.0
	Threat	2.2 ± 0.8	0.8 ± 0.1	0.5 ± 0.2
	Groom	0.3 ± 0.2	0.9 ± 0.5	0.1 ± 0.0
Female	Spontaneous Present	1.8 ± 0.3	3.0 ± 0.5	1.1 ± 0.2
	Contact Present	0.1 ± 0.1	1.3 ± 0.4	3.2 ± 0.5
	Proximity	0.2 ± 0.1	0.6 ± 0.2	3.9 ± 0.6
	Yawn	2.5 ± 0.6	0.1 ± 0.1	0.4 ± 0.1
	Aggression	0.9 ± 0.4	0.1 ± 0.0	
	Threat	1.1 ± 0.4	0.6 ± 0.2	0.1 ± 0.0

Mean ± S. E. for a 15 minute pair test.

Table 4.2 Results of the statistical analyses of male sexual behavior during pair tests for castrate peer-reared, intact peer-reared, and intact wild-caught adult male rhesus monkeys.

Table 4.2

Behavioral Measure:	F	Level of Significance
Contact:	13.57	$p < .001$
Wild-caught vs. intact peer		$p < .01$*
Intact peer vs. castrate		$p < .01$*
Mount:	10.35	$p < .005$
Wild-caught vs. intact peer		$p < .01$*
Intact peer vs. castrate		$p < .01$*
Intromission:	5.83	$p < .01$
Wild-caught vs. intact peer		$p < .01$*
Intact peer vs. castrate		$p < .05$*
Ejaculation:	6.84	$p < .005$
Wild-caught vs. intact peer		$p < .01$*
Intact peer vs. castrate		n.s.
Erection:	2.22	n.s.
Purse lip:	2.85	n.s.
Yawn:	5.73	$p < .01$
Wild-caught vs. intact peer		$p < .01$*
Intact peer vs. castrate		n.s.
Aggression:	9.78	$p < .001$
Wild-caught vs. intact peer		n.s.
Intact peer vs. castrate		$p < .01$*
Threat:	5.88	$p < .01$
Wild-caught vs. intact peer		n.s.
Intact peer vs. castrate		$p < .01$*
Male groom:	1.16	n.s.

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*Post hoc comparisons. (Newman-Kuels test)

Table 4.3 Results of the statistical analyses of female sexual behavior during pair tests with castrate peer-reared, intact peer-reared, and intact wild-caught adult male rhesus monkeys.

Table 4.3

Behavioral Measure:	F	Level of Significance
Spontaneous Present:	5.49	$p < .025$
Wild-caught vs. intact peer		$p < .01$*
Intact peer vs. castrate		$p < .01$*
Contact Present:	8.08	$p < .005$
Wild-caught vs. intact peer		$p < .01$*
Intact peer vs. castrate		$p < .01$*
Proximity:	25.93	$p < .001$
Wild-caught vs. intact peer		$p < .01$*
Intact peer vs. castrate		n.s.
Yawn:	33.47	$p < .001$
Wild-caught vs. intact peer		n.s.
Intact peer vs. castrate		$p < .01$*
Aggression:	8.57	$p < .005$
Wild-caught vs. intact peer		n.s.
Intact peer vs. castrate		$p < .01$*
Threat:	4.38	$p < .025$
Wild-caught vs. intact peer		$p < .01$*
Intact peer vs. castrate		$p < .01$*

*Post hoc comparisons. (Newman-Kuels test) and mounts than their intact counterparts. No castrate male was ever seen to exhibit an intromission or the ejaculatory response as defined for this study (Table 4.1; Table 4.2).

One of the castrates, however did masturbate to a point of exhibition of the ejaculatory response. No seminal emission was seen but the flank quivering and the general body tenseness was indistinguishable from that which has been described for the rhesus during ejaculation (Bielert and Goy, 1973). Interesting in this regard was the great similarity between the autogenital stimulation pattern and that which could normally be expected to be associated with coitus. The rhesus exhibits a series of intromissions with pelvic thrusting prior to ejaculation and only ejaculates on a single intromission. The masturbatory pattern shown by this castrate consisted of a series of autogenital stimulation bouts finally culminating in the ejaculatory response pattern. The great regularity between these stimulation bouts was similar to what is typical of normal heterosexual sexual interaction. The masturbatory behavior of the castrate in this study was similar to that of other intact males in regard to the pattern of stimulation exhibited. It is tempting to speculate that for species in which the multiple intromission pattern is typical the masturbatory behavior will follow a similar stimulation sequence, and that for species in which only one intromission precedes ejaculation a single autogenital stimulation session will frequently result in ejaculation and be the typical pattern shown during masturbation.

Castrates also exhibited fewer yawns than the intact peer reared males. The castrates failed to differ significantly from the other groups on the measures of purselip and erection, but they did exhibit the lowest mean values for both of these behavior patterns as reference to Table 4.1 clearly indicates. In terms of the measures of agonistic behavior followed in this study, the castrates exceeded all other groups. They differed significantly from the intact peer-reared males for measures of both threat and aggression (Table 4.2).

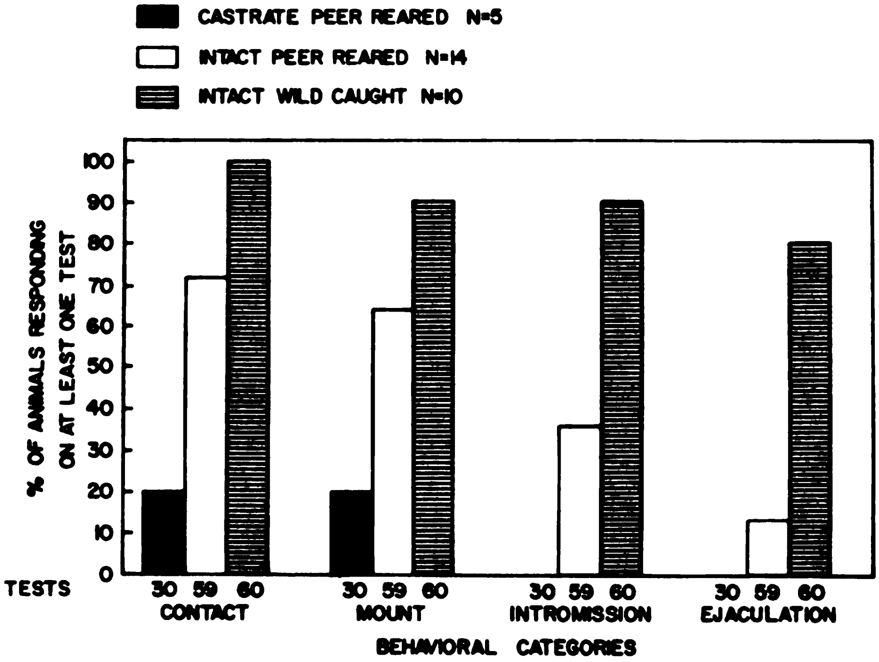
Female interactions with castrate peer-reared males set them apart from the other groups in several respects. Castrates received significantly fewer spontaneous presents than the intact peer-reared males, and their tests also had fewer presents to contact. Females yawned much more when in the presence of a castrate male, and in addition they also exhibited higher frequencies of threat and aggression to their castrate partners. In at least one regard the castrates were treated similarly to the intact peer-reared males and this was for the measure of female prozimity. Females did not move into proximity of the castrates with any great frequency (Table 4.1; Table 4.3).

Though the differences across the groups were clear cut, a check of the data revealed a high number of nonresponders. Since one of the concerns of this analysis was that of the way in which sexual behavior had been affected, further data analysis was carried out for the three groups involved. Figure

4.1 presents a graphic illustration of the way in which the gonadal state and rearing condition affected the measures of male sexual behavior examined in this study. For all measures examined the percentage of responders from the castrate group was the lowest. In addition it was only for the measures of contact and mount that the intact peer-reared males exhibited a response level of at least 50%.

As one makes comparisons between the behavioral categories presented, it is clear that the progression from contact to mount to intromission and finally ejaculation corresponds to a steady decline for all groups in terms of percentage of animals responding. This decline is the most rapid for the castrate group and least for the wild-caught male group. This progression is probably related to the mating pattern characteristic of the rhesus. This pattern is characterized by a series of mounts, some of which are accompanied by intromission and thrusting, following a series of intromissions, ejaculation is finally achieved. It was decided that for the two behavior patterns for which both the intact peer-reared males and the wild-caught males exhibited at least a level of 50% responders, comparisons would be made. Limiting analysis to responders only the intact peer-reared males differed from the wild-caught males in terms of frequency for measures of both contact and mount (contact, unpaired *t*-test = 2.67, df = 18, $p < .01$; mount unpaired *t*-test, t = 2.75, df = 16, $p < .01$ (Winer, 1962).

Figure 4.1 Percentages of castrate peer-reared, intact peer-reared, and intact wild-caught males exhibiting various measures of male sexual behavior.


CASTRATE PEER REARED N=5
INTACT PEER REARED N=14
INTACT WILD CAUGHT N=10
% OF ANIMALS RESPONDING ON AT LEAST ONE TEST
100
90
80
70
60
50
40
30
20
10
0
TESTS
30 59 60
CONTACT
30 59 60
MOUNT
30 59 60
INTROMISSION
30 59 60
EJACULATION
BEHAVIORAL CATEGORIES

The agonistic interactions between the pair were also examined across the three groups. Figure 4.2 presents a graphic representation of the data. All castrate males directed threats and aggression to their female partners. All intact peer-reared males also threatened their female partners although not all of the males aggressed the same animals. The wild-caught males had the lowest percentage of responders for these measures. Females responded agonistically to the castrate males and at a somewhat lower level to the intact peer-reared males. An examination of figure 4.2 makes it clear that no matter what the sex or gonadal status of the animal aggression as defined for this study was exhibited by a lower percentage of the animals than was the case for the measure of threat.

It was the disproportionate frequency of agonistic behavior that led to a consideration of dominance interaction between the pair and its possible affect on thebehaviors examined. Dominance criteria were set up as follows: 1) an animal was considered to be the dominant animal of a test if its partner directed a fear grimace to him or her. 2) an animal was considered to be the dominant animal of a test if its threats or aggression were totally unreciprocated. The entire group of 149 tests was examined and using the two criteria in order listed, all tests were classified as one in which the male was dominant, one in which the female was dominant,

Figure 4.2 Percentages of males and females showing agonistic behavior during their sex tests.


CLASSES OF MALES
CASTRATE PEER REARED N=5
INTACT PEER REARED N=14
INTACT WILD CAUGHT N=10
% OF ANIMALS RESPONDING ON AT LEAST ONE TEST
100
90
80
70
60
50
40
30
20
10
THREAT
AGGRESSION
TESTS
30 30 30 30
59 59 59 59
60 60 60 60
MALE
FEMALE
MALE
FEMALE
MALE
FEMALE
SEX OF ACTOR

or as one in which no decision could be made using the criteria as set up. Figure 4.3 gives a graphic representation of the data. For both intact groups, the males were more frequently given the dominant animal status. However, females were dominant more frequently than males when their partners were castrate peer-reared males. The percentage of tests for which a dominance decision could not be made was very similar for both groups of intact males. In contrast to this the percentage of undeterminable tests for the group of castrates exceeded the percentage for which a dominance decision could be reached. When all the pair tests were considered, males were dominant to females more frequently than they were subordinate to them.

The frequencies with which certain behaviors occurred seemed strongly influenced by the dominance relationship of the pair. Figure 4.4 presents data on the effect which partner dominance had with respect to the occurrence of certain behavior patterns. The data are from a total of 83 of the 149 tests for which a dominance decision was possible. Males were dominant in a total of 67 of the tests. This is equivalent to 45% of all tests given or 81% of tests for which a dominance decision with the criteria of this study could be made. Females were dominant to their partners in 16 tests. The tests occurred across all three groups. The females were the dominant pair member in 11% of all the tests and 19% of the tests for which a dominance decision could be reached. The

Figure 4.3 Dominance relationship between a pair for castrate peer-reared, intact peer-reared, and intact wild-caught male rhesus monkeys.

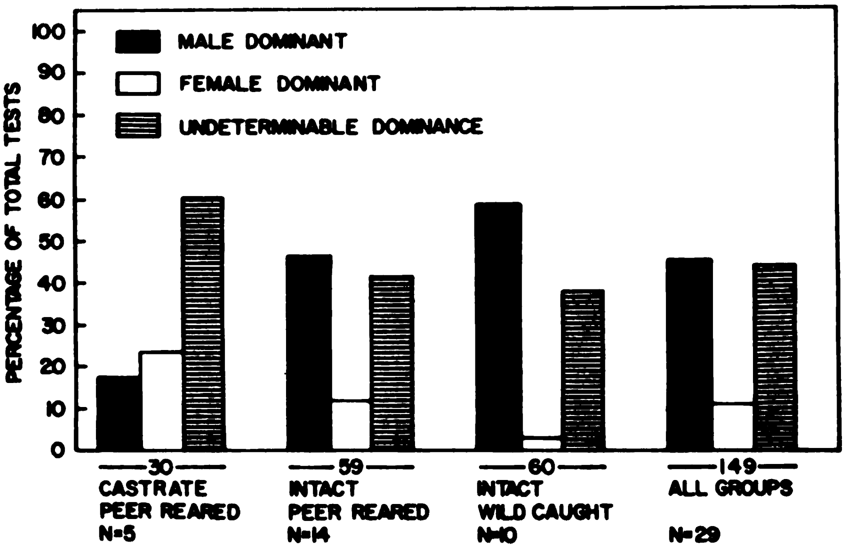
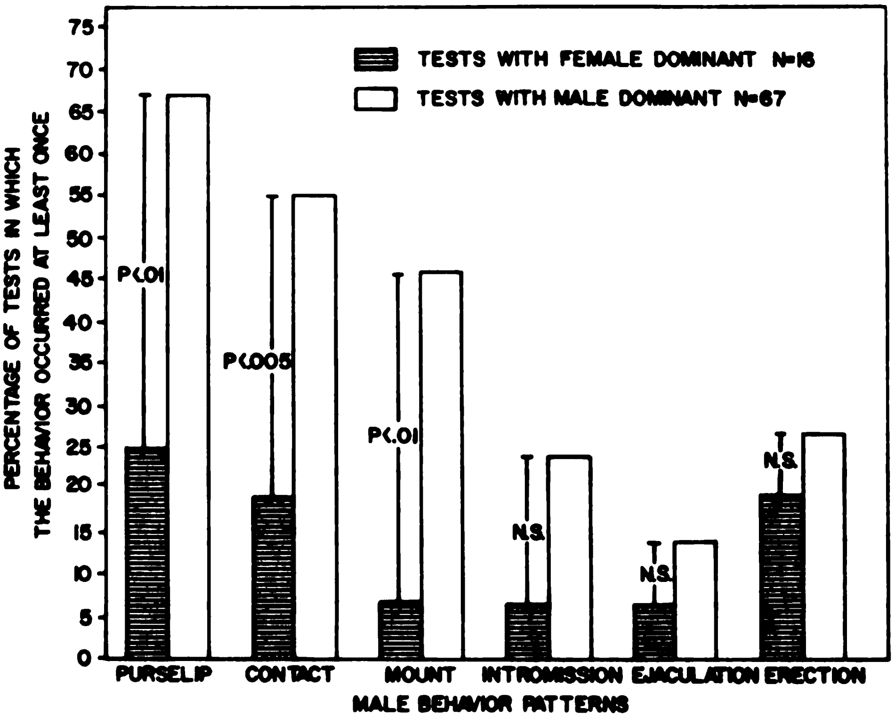

PERCENTAGE OF TOTAL TESTS
100
90
80
70
60
50
40
30
20
10
0
MALE DOMINANT
FEMALE DOMINANT
UNDETERMINABLE DOMINANCE
30
CASTRATE
PEER REARED
N=5
59
INTACT
PEER REARED
N=14
60
INTACT
WILD CAUGHT
N=10
149
ALL GROUPS
N=29

Figure 4.4 Dominance relationship between a pair and its effect on male sexual behavior measures.


TESTS WITH FEMALE DOMINANT N=16
TESTS WITH MALE DOMINANT N=67
PERCENTAGE OF TESTS IN WHICH THE BEHAVIOR OCCURRED AT LEAST ONCE
75
70
65
60
55
50
45
40
35
30
25
20
15
10
5
0
P<.01
P<.005
P<.01
N.S.
N.S.
N.S.
PURSELIP
CONTACT
MOUNT
INTROMISSION
EJACULATION
ERECTION
MALE BEHAVIOR PATTERNS

occurrence of certain male behavior patterns seemed markedly affected by the factor of dominance. Males contacted, mounted, intromitted and ejaculated no a lower percentage of tests when they were tested with a female partner who was dominant. A statistical analysis was carried out on the data using a Yates analysis (Ferguson, 1959) and statistical significance was obtained for measures of male contact ($X^2 = 5.5$, df = 1; $p < .025$) and male mount ($X^2 = 7.12$, df = 1; $p < .01$). Males also had a lower percentage of tests with occurrence of erection if their partner was dominant to them. The purselip facial expression was exhibited on a higher percentage of tests if the male was dominant and this was a statistically valid difference ($X^2 = 7.83$, df = 1; $p < .01$).

Female behavior measures were also influenced by the dominance interaction of the pair. Figure 4.5 presents a graphical display of the relation between dominance and female behavior measures. No female ever came into proximity of a male if she was the dominant partner. Females did, however, spontaneously present to males even when they were the dominant partner, but they did so at a level lower than that of the situation in which the male was dominant. Females were observed to mount males. These occurrences were rare and never occurred with a wild-caught male. Female mountings of males did occur on a higher percentage of tests if the female was the dominant member of the pair but there was no statistically significant difference.

Figure 4.5 Dominance relationship between a pair and its effects on female behavior measures.

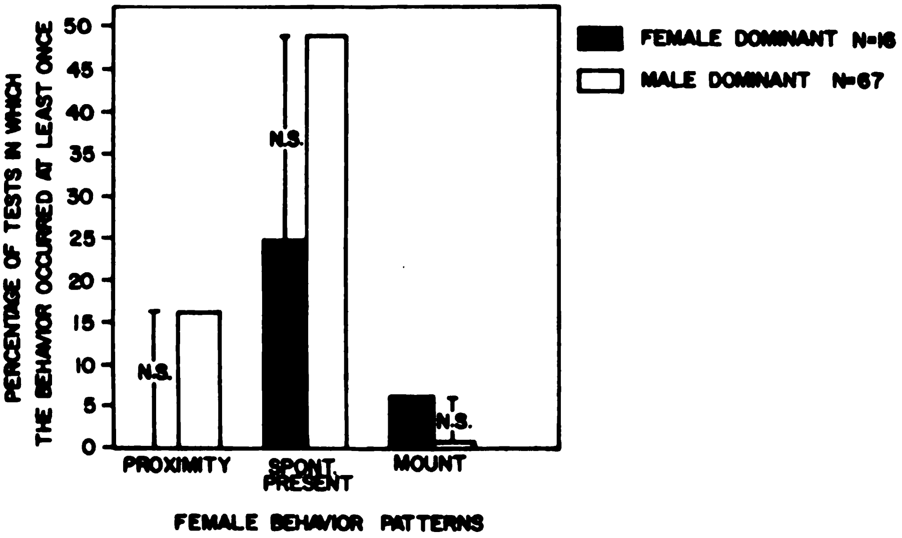

PERCENTAGE OF TESTS IN WHICH THE BEHAVIOR OCCURRED AT LEAST ONCE
50
45
40
35
30
25
20
15
10
5
0
N.S.
N.S.
N.S.
PROXIMITY
SPONT. PRESENT
MOUNT
FEMALE BEHAVIOR PATTERNS
FEMALE DOMINANT N=16
MALE DOMINANT N=67

Figure 4.6 presents the data for two specific behavioral categories; those of groom and yawn. Grooming was not a frequent behavior shown by pairs under the testing conditions of this study. Females exhibited grooming on a higher percentage of tests than the males and exhibited this behavior regardless of their dominance status. Males never exhibited grooming on tests in which the female was the dominant partner. Yawning was exhibited by both males and females but occurred in a higher percentage of the tests for males regardless of the dominance relationship they held. Female yawning occurred on a statistically significantly higher frequency when the female was the dominant member of the pair ($X^2 = 9.7$, df = 1, $p < .005$). Though yawning has been suggested to be andorgen-dependent (Goy and Resko, 1972) it appears clear from this data that for females social interactions also affect its display.

Part of the concern of this study was the role which gonadal hormones might play in influencing the interaction between rhesus pairs. In this regard the 5 castrate rhesus were injected with testosterone propionate (1 mg/per day/ per kg.) for one month and then retested with the same females with which they had already been tested. In addition to the castrates retestings were carried out with five intact peer-reared males and five wild-caught males. All males were exposed to the same six females for a second 15 minute testing using a balanced testing schedule.

Figure 4.6 Dominance relationship between a pair and its effects on yawning and grooming.

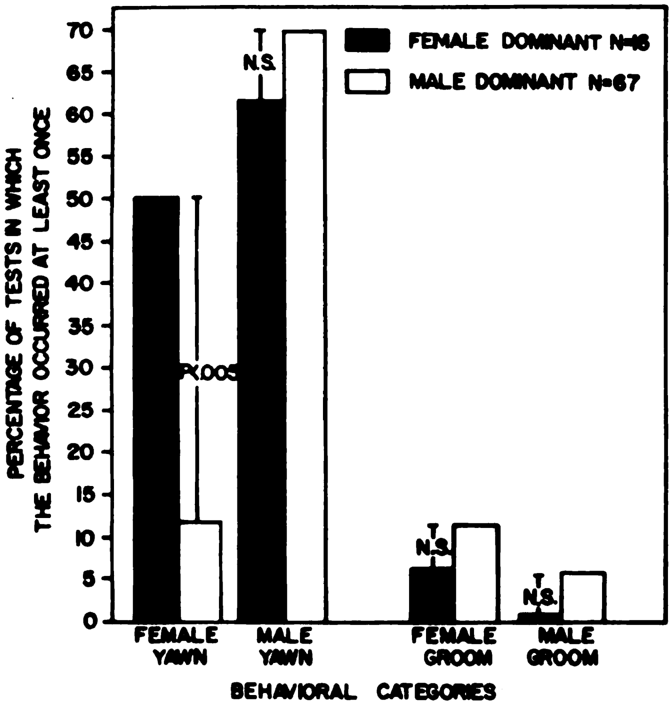

FEMALE DOMINANT N=16
MALE DOMINANT N=67
PERCENTAGE OF TESTS IN WHICH
THE BEHAVIOR OCCURRED AT LEAST ONCE
70
65
60
55
50
45
40
35
30
25
20
15
10
5
0
N.S.
P<.005
N.S.
N.S.
FEMALE YAWN
MALE YAWN
FEMALE GROOM
MALE GROOM
BEHAVIORAL CATEGORIES

Table 4.4 presents data on the trends of change for these retestings. Several of these trends are noteworthy. First, two castrates showed increases in contacts and mounts, however neither one ever achieved an intromission or exhibited an ejaculation during this series of tests. It might be added that on subsequent testing one of these castrates did go on to exhibit intromissions and ejaculate. All of the castrates exhibited increases in yawning. In this regard, a reference to Table 4.1 makes it clear that prior to androgen treatment castrates were yawning very little. Three castrates exhibited increases in erection. Two castrates also exhibited increases in purselip, this is in sharp contrast to the other groups where there was a tendency of decrease for this behavior pattern. All castrates exhibited decreases in aggression and four of the five showed decreases for threat as well. These decreases in aggression and threat were also seen in the other groups although many animals in these other groups remained relatively static because they had failed to exhibit the response on their first testing. The behavior of the female partners upon retesting was characterized by decreases in yawning, aggression, and threat across all three groups. The changes for spontaneous present occurred in both directions for the castrate peer-reared and wild-caught groups while there was a consistent decrease in this category for the group of intact peer-reared males, a reference to Table 4.1 documents the fact that this behavior pattern had occurred at its highest level on the tests for this group.

Table 4.4 Trends of change shown during a second testing with the same group of stimulus females by castrate peer-reared, intact peer-reared, and intact wild-caught adult male rhesus monkeys.

Table 4.4

Behavioral Category		Castrate Peer-Reared	Intact Peer-Reared	Intact Wild-Caught
Male	Contact	↑ ↑ - - -	↑ - - - ↓	↑ ↑ ↑ ↓ ↓
	Mount	↑ ↑ - - -	- - - - ↓	↑ ↑ ↑ ↓ ↓
	Intromission	- - - - -	- - - - -	↑ ↑ ↓ ↓ ↓
	Ejaculation	- - - - -	↑ - - - -	↑ ↑ ↑ ↓ ↓
	Yawn	↑ ↑ ↑ ↑ ↑	↑ ↑ ↑ - ↓	↑ ↓ ↓ ↓ ↓
	Erection	↑ ↑ ↑ - ↓	- - ↓ ↓ ↓	↓ ↓ ↓ ↓ ↓
	Purselip	↑ ↑ - ↓ ↓	- - ↓ ↓ ↓	↓ ↓ ↓ ↓ ↓
	Aggression	↓ ↓ ↓ ↓ ↓	- - ↓ ↓ ↓	- - - - ↓
	Threat	↑ ↓ ↓ ↓ ↓	↓ ↓ ↓ ↓ ↓	- - - ↓ ↓
Female	Spontaneous Present	↑ ↑ ↑ ↓ ↓	↓ ↓ ↓ ↓ ↓	↑ ↑ ↑ ↑ ↓
	Aggression	- ↓ ↓ ↓ ↓	- - - ↓ ↓	- - - - -
	Threat	↓ ↓ ↓ ↓ ↓	- - ↓ ↓ ↓	↓ ↓ ↓
	Yawn	↓ ↓ ↓ ↓ ↓	- - - - ↓	↓ ↓ ↓ ↓ ↓

Tests =

n = 5 for all groups

Tests were 15 minutes duration.

↑ = increase in mean

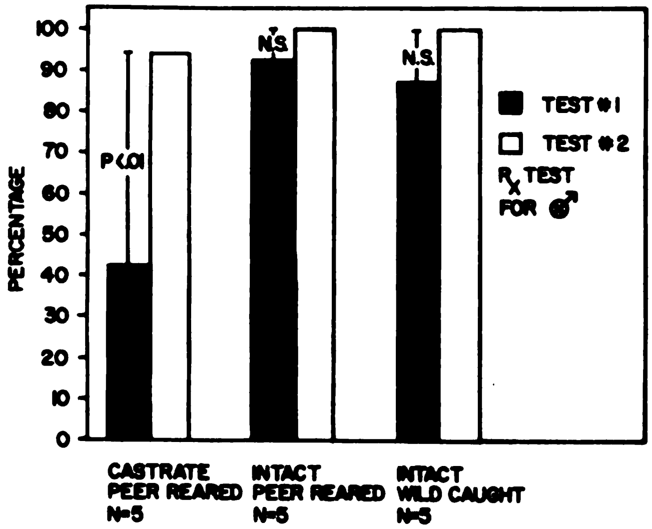
- = no change in mean

↓ = decrease in mean

A dramatic change occurred in the interaction of the pair after the castrate peer-reared males had received one month of androgen treatment. Using the same criteria for determining dominance which had been previously employed, the thirty retests were categorized as tests in which the male was dominant, the female was dominant, or a test for which the criteria could not be met. Figure 4.7 presents a graphic representation of the outcome of this dominance evaluation. It can be seen that although neither of the intact male groups changed markedly in terms of the dominance interactions with their female partners, the castrates increased in their percentage of tests dominant at a statistically significant level ($X^2 = 7.24$, df = 1, $p < .01$).

Figure 4.7 Percentage of tests dominant for castrate peer-reared, intact peer-reared, and intact wild-caught males on repeated testings with the same female partners.

PERCENTAGE TESTS DOMINANT FOR ALL TESTS IN WHICH DOMINANCE WAS DETERMINED



4.4 DISCUSSION

The data from this study are consistent with thsoe of others which have suggested that the extent of the sexual behavior deficit resultant from early social restriction is much broader than that of a mere motor pattern failure (Rosenblatt, 1965; Missakian, 1969; Goy and Goldfoot, 1974). Mason (1968) in a discussion of early social deprivation in non-human primates described a deprivation syndrome which had four distinct elements. Sexual behavior was given as an example of the poor integration of motor patterns which occurred when early developmental interactions were restricted. Monkeys which received such restricted social interaction were also said to have: 1) deficiencies in social communication; 2) motivational disburbances; 3) abnormal postures and movements. Mason felt that the elements of this syndrome were distinct and could be selectively affected. Data were given which were consistent with this hypothesis. The animals of the present study were not reared as Mason's were reared and the nature of the sexual behavior deficit of the intact peer reared males doesn't appear to be of the sort that is equitable with that of a motor pattern disturbance. The intact peer reared males of this study exhibited appropriate mounting, but their sexual behavior was still quantitatively different from that of the intact wild-caught males. To the extent that the elements of the syndrome described by Mason are distinct, they may well be differentially affected by early social restriction and in addition their status as discrete entities would allow them to interact in different fashions dependent upon the nature of the early social stimulation. The clearest effect on sexual behavior for the rearing condition under which the animals of this study were raised was that of "elimination"; over one-half the intact peer-reared males surveyed in this analysis failed to exhibit intromission or ejaculation. A second effect of the rearing procedure on the sexual behavior of the intact male rhesus followed in this analysis was that of frequency modification; even when peer-reared intact monkey responders were compared with intact wild-caught monkey responders, differences were obtained for frequencies of the measures of contact and mount. It appears that the rearing condition under which these monkeys matured affected sexual behavior qualitatively as well as quantitatively, and there is the suggestion that motivational systems and not simply motor pattern systems were those adversely affected. In this regard attention might be drawn to some recent data of Dr. Robert Rose (1974). Social manipulation of adult male rhesus monkeys were carried out in an attempt to assess the fashion in which social situations might affect peripheral testosterone titers. When introduced to an established group of adult male rhesus, the testosterone levels of all his experimental subjects fell rather sharply. A contrasting result was obtained if the subjects were then exposed to females. In this case almost all of the animals exhibited a rise in testosterone values. Rose described the exception in this manner, "a single individual male (Zorro) failed to show an increase in plasma testosterone in response to females and was found to have had a history of early deprivation. Zorro also lacked a proper mating and social repertoire." It would appear that although no social background history is offered that early social restriction may selectively alter the sensitivity of an individual animal to certain social stimuli. Although wild-caught males appear interested and aroused by stimulus females, restriction reared males may not respond to these same females in a similar fashion.

Sexual behavior is a social behavior and should be viewed as an interaction between two partners (Larsson, 1973). In this regard, it is important to consider the role that the female stimulus partner may have played in the outcome of the behavioral testing. The high frequency of spontaneous presents by females when paired with intact peer-reared males suggests that the males were at least exposed to female solicitation at a level equivalent to that of the wild-caught males. The high level of this behavior may have been related to the frequency of threat which was directed to the females by the intact peer reared males, but other interpretations may also be entertained. Data were recently presented by Dixson, Everitt, Herbert, Rugman, and Scruton (1973) which documented an increasingly active role for the female, through her initiation of mounts, in the sexual behavior of a pair as the pair went through successive ejaculatory series. It has previously been suggested (Bielert and Goy, 1973) that successive ejaculations may have a definite affect on a sexual arousal mechanism in the male primate and it would appear possible to suggest that under conditions in which a male's sexual arousal is apparently low, the female may modify her behavior in a compensatory fashion. Only a little over half of the intact peer reared males showed contacts and mounts of their female partners and when this behavior was shown it was shown at a low frequency. If these facts can be interpreted to suggest a condition of low sexual arousal for the intact peer reared males the high number of female spontaneous presents may be taken as evidence for compensatory behavior on the part of the female. The low number of spontaneous presents with the castrate peer reared males would suggest that gonadal integrity can affect the fashion in which peer reared males are treated or responded to. The high number of contact presents shown by females on tests with intact wild-caught males is most probably related to the high level of contacting by these males and appears only loosely related to the female's perception of her partner for the intact peer-reared males contacts were responded to.

Gonadal state appeared to have an affect on the interactions of the pair although there were certainly social factors interacting with this condition as well. The castrates yawned much less than the intact peer reared males and this is probably due to the fact that this behavioral endpoint appears clearly testosterone dependent (Phoenix, 1973; Phoenix et al., 1973; Eaton, Goy and Phoenix, 1973; Phoenix, 1974). They also exhibited fewer erections, but when placed on testosterone therapy this measure showed increases for some males. It has been suggested that testosterone levels affect penile integrity for both rhesus (Michael and Wilson, 1974) and human (Hamilton, 1937a) and it would appear that the data from this study are consistent with this suggestion.

The castrates showed few contacts and mounts of their female partners. The fact that two castrates responded to androgen therapy with increases for these measures makes the role of gonadal hormones evident and consistent with the reports on adult castrate rhesus (Michael, 1972; Michael et al., 1973; Phoenix et al., 1973). One of the more interesting sidelights was the level of agonistic behavior shown by the castrates. Even when compared to the intact peer reared males the castrates were clearly more aggressive. It appears clear that the threats and aggression exhibited by these animals were stimulated by social factors. Further evidence for the strong role which social factors play in the display of this behavior comes from the testing during androgen treatment. If androgen was intimately related to the display of aggressive behavior one might expect an increase in this behavior with testosterone stimulation, such was not the case, all five castrates showed a decrease in aggression and four showed decreases in threat. They appeared to follow the decline which was shown by both the other groups upon retesting. Though testosterone may be related to aggression under specified conditions (Rose, Holaday and Bernstein, 1971) it would appear that social factors may operate to override such affects in other social settings (Eaton and Resko, 1974).

The fashion in which the dominance relationship of the pair affected certain behavioral categories was clear cut when examined in the fashion which was employed in this study and as such adds depth to a consideration of sexual expression in primates. It could be said that the effects referred to in this study were mediated not by the interaction of the pair but rather through the fact that low sexual behavior was exhibited by the peer-reared males under any condition and that they tended to be more frequently dominated by their female partners, thus biasing the data. It should be remembered however that for the two measures of male sexual behavior significantly affected i.e. contact and mount, the intact peer reared males were responding at a fairly high level. In addition the data from intact wild-caught male #1548 is offered. This male was tested with a total of six strange female partners. He ejaculated with four of these partners. It is clear from this fact that he was capable of a totally adequate sexual performance. According to the dominance criterion employed in this study, Two of his six tests were tests in which he was dominant to his partner and in one test his female partner was dominant to him. Contacts and mounts occurred in both tests in which the male was the dominant pair member. In addition, intromissions and ejaculation occurred in one of these two tests. In contrast, for the test in which the female was dominant there were few male contacts and there were no mounts, intromissions, or ejaculations. It would appear that the social relationship between a pair can have definite effects on the sexual behavior shown by that pair. There is a wide variety of data supportive of such a position, and it might well be drawn into this discussion. Trimble and Herbert (1968) carried out a study in which ovariectomized female rhesus were given testosterone injections of 15 mg/day. At this dosage, the females failed to exhibit spontaneous presents at a level different from that of their anhormonal condition. In addition, the females refused many male mounting attempts. A consideration was given to the dominance interaction of the pair by the authors and it was suggested that if a female's dominance status were increased by testosterone therapy, this might _per se_ result in her refusing male interaction of sexual behavior. It was also reported that under this treatment the females threatened one of their male partners and this went unreciprocated. There is the suggestion that using the criterion of dominance employed in this study the females of Trimble and Herbert's study may have been the dominant partners for some of their tests and the low sex behavior shown by some of the pairs may have been directly related to this fact. Rosenblum and Nadler (1971) have also offered data pertinent to a consideration of the fashion in which dominance interactions between a pair affect the display of sexual behavior. In their study young intact male bonnet macaques were tested with stimulus female partners of two classes. 1) Small stimulus females 2) Large stimulus females. Prepubertal two and three year old males tended to be clearly dominated by the larger female partners. These same young males showed few mounts intromissions or ejaculations with their larger female partners though their smaller partners were mounted, intromitted, and ejaculated with.

It may be that part of the affect which early social restriction may have had on the sexual behavior of the males of this study was exerted through the dominance status which these males were able to achieve with their female partners. This idea has not been proposed before but there have been prior studies suggesting that early social restriction may indeed affect such an endpoint (Mason, 1961; Alexander and Harlow, 1965; Jensen, Bobbitt, and Gordon, 1971).

Though it appears clear that dominance interactions between a pair of individuals may affect the sexual interaction of a pair other factors may well interact to moderate this effect. Infant rhesus have been observed to mount their mothers although it is clear that the infant is submissive to his mother if the occurrence of a fear grimace is used as an index in this regard (Bielert, unpublished observations). It has, however, been suggested that juvenile males are prevented from mounting their mothers by the dominance relationship which exists between them and that a change in this status will permit mother-son mating (Sade, 1968).

There is the suggestion from this study and several others that androgen may play an important role in the maintanance of a male's dominance position within a pair position within a pair. Clark and Birch (1945) reported that testosterone injections to a castrate male chimpanzee were able to reverse his dominance relationship with a carefully matched intact male partner. In addition, data from a recent study on the effects of castration on adult male rhesus is relevant. Michael and Wilson (1974) mention that the behavior of their study's females changed after the males of the study were castrated. The females became more aggressive and displayed more bisexual behavior such as mounting during the testing period which followed castration.

The mechanism by which androgen may affect the male and through him the pair's interaction is completely unknown. The androgen treatment of the castrates in this study failed to increase either their aggression or threats. The cues which the female may receive from her partner may be extremely subtle and related to his general demeanor. Another possibility is that of some sort of physiologically based cue may be what the female is reacting to. The sex skin of male primates such as the rhesus and the talapoin responds with color change to testosterone injections (Vandenbergh, 1965; Dixson and Herbert, 1974). There is also the possibility, though completely speculative, that the female may be responding to an odor change of the male. In this regard, it has recently been suggested that pheromones may play a role in the sexual behavior of rhesus pairs (Michael and Keverne, 1968; Keverne and Michael, 1971).

The emphasis thus far has been on cues emanating from the female, but it may be that the male rhesus may be a source of such cues also. For it is well known that for a wide variety of species gonadal hormones may interact to affect the pheromonal effects which males may have on females (Bronson, 1968; Whitten and Champlin, 1973).

It would appear clear from that data presently available that female domination of a heterosexual pair has an inhibitory effect on the sexual behavior of the pair. This may be an important biological consideration; in regard to the tremendous burden which pregnancy places on the female, any mechanism through which the female could assess the genetic potential of her mate could be of selective value. An intriguing possibility is that this condition may also have validity for the human. Though little data appropriate to this consideration is available the hypothesis has at least been recently presented (Abernethy, 1974).

5. Summary and Conclusions

In this summary an attempt will be made to consider data presented in this thesis pertinent to the questions presented in the introduction as major concerns of this research effort. In addition, discussion will be presented on other aspects of the results which may be pertinent to a general consideration of the effects which hormonal and social factors may have on male primate sexual behavior.

A clear understanding of the fashion in which gonadal hormones may affect behavior requires a great deal of accurate descriptive data and in addition data obtained from experimental manipulation . The results presented in this thesis on the development of the neonatally castrated males are important in that they may be used in the consideration of such manipulation. The results of this study allow one to state that dimorphic behavior patterns displayed by prepubertal rhesus are independent of the presence of gonadal hormones. These results are also important in that they add depth to those already in the literature which suggest that testosterone exposure in utero is all that is necessary for the determination of a male psychosexual developmental path in the rhesus monkey. It should be remembered that during gestation male rhesus are exposed to higher testosterone levels than are females (Resko, Malley, Begley, and Hess, 1973) and that if a genetic female receives such exposure she will exhibit the dimorphic behavior patterns discussed in this paper at a level which doesn't differ significantly from that of a male (Goy, 1970; Goy and Phoenix, 1971).

Normally the events of puberty include both behavioral and hormonal changes. The results of this study suggest that the occurrence of these two events can be dissociated and that in addition these events can be artificially induced at a chronologic age far in advance of that normally associated with adolescence. The results of the examination of the sexual behavior of the adult peer-reared males suggest that social interactions during development may permanently dissociate sexual behavior from its hormonal substrate. Further data consistent with those from the intact males were obtained when the adult castrates were given testosterone. The fact that all of the animals were given equivalent dosage sufficient for restoration of adult castrate sexual behavior (Phoenix, Slob, and Goy, 1973) but only two of them responded is suggestive that hormones are only potentiators and not modifiers of sexual behavior in primates and that the same early development factors which dissociate sexual behavior from its hormonal substrate in intact males are active in castrates. The testosterone stimulation of the two year old castrates which resulted in increased frequencies of approach, contact and mount is a clear demonstration of the independence which may exist between these changes normally associated with puberty and the chronological age of an individual.

There were clear cut examples in this study of the fashion in which dominance interactions can affect those behavior patterns which are known to be testosterone stimulated. The dominance shift which occurred during the testosterone treatment of the young male castrates while being tested in their peer group was a fine example of how the relative dominance position within a group may affect the display of certain behavior patterns which are clearly androgen sensitive. In addition the analysis of the dominance relationship between the male and female of a pair revealed that a male's sexual behavior may be markedly inhibited by an inferior status with his partner. Further, it was clear from this analysis that females are affected by these same status factors.

An important observation offered in this thesis was that of the sexual capability of adult prepuberally castrated rhesus. It is clear that an agonadal rhesus can develop and display intromission and ejaculation patterns. This observation when considered with that from studies of adult castrate rhesus in which copulation has continued for years following gonadectomy (Michael, 1972) suggest that gonadal hormones are not a necessary substrate for at least low levels of male sexual behavior and that social factors may play an overriding role in the display of copulatory behavior.

This thesis also presented clear evidence for an activational action of testosterone for several males social and sexual behavior patterns. Chronologic age and or level of social development appeared to play an important role in determining the effects which testosterone therapy might achieve. Reduced to its simplest it would appear that individual experiential factors affect the outcome of physiological manipulations.

It is difficult to say how relevant the observations made on the rhesus monkeys of this study are for human clinical problems, but it would appear that, to the extent that humans show a social organization and development in common with other primates including the rhesus monkey, the social and hormonal variables dealt with in this thesis may have validity.

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