

## Neuroendocrinology: Animal Models and Problems of Human Sexuality<sup>1</sup>

Robert W. Goy, Ph.D.,<sup>2</sup> and David A. Goldfoot, Ph.D.<sup>3</sup>

### ANIMAL MODELS OF BISEXUALITY

The hypothesis has been advanced (Phoenix *et al.*, 1959) that hormones present during early stages of development can determine the pattern of sexual behavior displayed by an individual as an adult. The basic position is that during a very restricted period of development (fetal in some mammals such as the guinea pig and monkey, larval in others such as the mouse and rat born incompletely differentiated) secretions from the XY gonad produce changes not only in the gonaducts and external genitalia, but also in the neural tissues mediating sexual behavior. For sexual behavior, at least two distinct behavioral systems are affected: (1) there is a facilitation or an augmentation of sexual responses normally characteristic of the genetic male, and (2) there is an inhibition or suppression of sexual responses normally characteristic of the genetic female.

Data from several laboratories are difficult to reconcile with this hypothesis. First, many species display bisexuality during mating, in that females mount available partners or males accept the mounts of partners and display lordosis or presenting postures. Second, experiments have been able to augment mounting potentials without suppressing lordosis, and, to a lesser extent, they have suppressed lordosis without augmenting mounting. The hypothesis as originally stated does not cover these conditions of bisexuality which are seen throughout the mammalian species, and in fact could be interpreted as a statement of the ideal case that mounting be expressed only by males, lordosis only by females (Beach, 1968). This paper represents an attempt to reformulate the original

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<sup>2</sup> Director, Wisconsin Regional Primate Research Center, and Professor, Department of Psychology, University of Wisconsin, Madison, Wisconsin.

<sup>3</sup> Assistant Scientist, Wisconsin Regional Primate Research Center, Madison, Wisconsin 53706.

hypothesis of the origin of sexual dimorphism, taking into account the new data collected during the last decade and a half. The discussion will be limited strictly to mounting behavior and the receptive behaviors of lordosis in rodents and presenting in the bitch and the rhesus monkey.

Researchers from several laboratories have now demonstrated that the ideal condition of complete dimorphism does not exist for any species studied. Many years ago, Beach (1942) described normally behaving male rats which mounted at high frequencies and which also displayed lordosis when suitably stimulated. In our own laboratory, lordosis was shown to be a common response of newborn normal male guinea pigs (Goy *et al.*, 1967), although lordosis in adult males is very limited (Phoenix *et al.*, 1959). For at least one strain of rat, Whalen and Edwards (1967) have shown that females mounted as frequently as males when injected with testosterone propionate and also displayed lordosis when suitably treated and tested. A comparable bisexuality has been shown for female mice (Edwards and Burge, 1971b) and genetic female guinea pigs (Young, 1969; Phoenix *et al.*, 1959; Goy *et al.*, 1967). Moreover, the normal female guinea pig displays mounting at the time of both spontaneous and induced estrus (Young and Rundlett, 1939; Goy and Young, 1957), and a similar finding has been reported for the female dog (Beach *et al.*, 1972).

More recently, information has been provided on hamsters from a number of laboratories (Swanson and Crossley, 1971; Tiefer and Johnson, 1971; Eaton, 1970). In this species, a limited expression of lordosis in normal males can be regularly and easily induced. The quantitative studies of lordosis in the male hamster carried out by Noble (1973) show that the expression of the behavior is not as good in males that are allowed to complete sexual differentiation as in males that are not. Nevertheless, the expression of lordosis is more complete in normal male hamsters than in normal male guinea pigs and rats. Thus, for the male hamster, bisexuality exists and sexual dimorphism for lordosis is incomplete.

The behavior of male rhesus monkeys parallels that of male hamsters, with the interesting difference that neither mounting nor presenting (the sex response analogous to lordosis in rodents) depends on hormonal stimulation at the time of its expression. Nevertheless, male rhesus monkeys, both intact and castrated, display both mounting and presenting responses, and a marked degree of bisexuality exists in males of this species (Goy, 1968; Goy and Phoenix, 1971). It could be said, in fact, that bisexuality is more completely expressed in male rhesus monkeys than in males of any other species studied so far in the laboratory and possibly in the natural habitat as well. In his early studies of rhesus social groups, Carpenter (1942) remarked on this subject in discussions of homosexual behavior, and the degree of completeness of the feminine repertoire in adult males has been striking to many observers.

The observation of bisexuality in various mammalian species is not new, but from the information currently available a new relation is discernible. Young (1961), in a review of the information available at that time, stated the general

conclusion that for mammals bisexuality was more common among females than among males. We have no evidence indicating that this is not the case when all mammalian species are surveyed. However, from the data which have become available in the last 10 years it is also possible to conclude that bisexuality is not expressed equally by both sexes in a given species. In fact, there appears to be an inverse relation between the sexes with respect to bisexuality; thus, for a given species, the greater the bisexuality of the male, the less the bisexuality of the female, and *vice versa*.

Examples of this are not numerous because the number of species investigated in the manner required to reach such a conclusion is still small. In our own work, however, the relationship is clear. Among rhesus monkeys, males show a conspicuous bisexuality throughout early development (Goy, 1968) and to some extent even into adulthood (Carpenter, 1942). Among female rhesus, on the other hand, male behavior is rare or infrequent during the first years of life (Goy and Phoenix, 1971), and there is no evidence that it can be brought to expression in nonmounting females in adulthood even with large doses of testosterone propionate (Goy and Resko, 1972; Eaton *et al.*, 1973).

Our work with guinea pigs illustrates the opposite relationship between the sexes. Male guinea pigs show little or no bisexuality, and lordosis is difficult to discern in adulthood even after treatment with large amounts of estradiol benzoate and progesterone. Female guinea pigs, in contrast, display lordosis and mounting under a variety of endocrine conditions. The relationship for the guinea pig, in which the female displays more bisexuality and the male less, is duplicated in several other mammalian species: rat (Pfaff, 1970; Pfaff and Zigmond, 1971), dog (Beach *et al.*, 1972; Beach, 1970), mouse (Edwards and Burge, 1971a,b). Insofar as we are aware, however, the relationship between the sexes represented by the monkey has been reported in only one other species. With the exception of work reported by Ciaccio and Lisk (1971), other laboratories have consistently found a high degree of bisexuality among male hamsters and a very low degree among females (Swanson and Crossley, 1971; Paup *et al.*, 1972).

The difference between species with respect to whether the male or female displays the greater bisexuality is found as well in different genetic strains of the same species. Most of our published work on the dimorphic expression of mounting and lordosis in guinea pigs has been with those of the Topeka stock. In this stock, which is not inbred, males display little or no bisexuality and females a moderately high degree, but with considerable individual variation, as would be expected (Phoenix *et al.*, 1959; Goy *et al.*, 1964). We have shown in previous publications that female guinea pigs from strain 2 show little or no bisexuality (Goy and Young, 1957) and display mounting behavior infrequently. In addition, we have recently obtained data which are still in preliminary form but which indicate the presence of a fairly marked bisexuality of behavior in males of this strain. Thus the differences in bisexual expression which exist for guinea

pigs are identical to the differences which exist across species; namely, the greater the expression of bisexuality for one sex, the less the expression for the other, but the sex displaying the greater degree of bisexuality may vary with the strain.

### **ORIGINS OF SPECIES DIFFERENCES IN THE COMPLETENESS OF SEXUAL DIMORPHISMS FOR MOUNTING AND LORDOSIS**

Once it is recognized that an inverse relationship for bisexual potential exists between the sexes within a species, and that the ideal case of complete sexual dimorphism is not to be found except perhaps for the mythical ramstergig (Beach, 1971), then the task of reconciling these apparent discrepancies with the original organizational hypothesis can be undertaken. We propose that the inverse relationship for bisexual expression by the two sexes can be understood on the basis of the prenatal or larval hormonal conditions which contribute to bisexuality for each sex. The inverse relationship suggests that the hormonal conditions which contribute to bisexuality in the female act to prevent or limit bisexual expression in the male, and the converse is also true.

This position necessarily deviates from an older view that the female of any species represents the "anhormonal" and undifferentiated state, the condition of sexuality that develops in the complete absence of hormonal stimulation during early periods of differentiation. According to that view, if a female from a given species displays mounting, the assumption could be made that this degree of bisexuality could occur without early hormonal action. Correspondingly, one older view of bisexuality in normal males (Young, 1961) held that lordosis could be expressed, but rarely and only under conditions of unphysiological amounts of hormonal stimulation, unusual forms of environmental stimulation, or both combined. We regard the expression of bisexuality by normal males and females entirely differently and see it as relatable to the specific parameters of endocrine stimulation in early stages of development. Accordingly, the differences between species or between genetic strains in the degree of dimorphism for mounting and lordosis can have the same origins as those for bisexuality in each sex.

### **ORIGINS OF BISEXUAL BEHAVIOR IN THE FEMALE**

Most investigators interested in sexual behavior have been concerned with the problem of bisexuality. Beach (1968), in his chapter on mounting behavior of female mammals, came to the conclusion that the neural tissues essential for the display of this behavior were ubiquitously represented among females of all species, and that the causes for differences among species in degree of expression were to be found in the hormonal and stimulus conditions essential for the evo-

cation of the behavior in adults. His article did not speculate on the biological origins of mounting behavior in females, but one could assume that his position on the matter is not greatly different from that articulated by Whalen (1971). Essentially, the position adopted by Whalen states that mounting behavior is an inherent capability of the female rat (and probably other female mammals), and that no hormonal conditions during early development are essential to its later expression. In Whalen's experiments, normal female rats show high frequencies of mounting under suitable conditions, and no endocrine treatment which he has given to the developing female rat has increased the expression of mounting behavior in adulthood.

An alternative to Whalen's hypothesis regarding the origins of bisexuality in the female rat can be formulated from recent experiments. This hypothesis is that the bisexuality of females is a result of endocrine conditions prevailing during a specific stage of early development. Ward and Renz (1972) and Stewart *et al.* (1971), working on the assumption that androgens were the steroids most relevant to development of the potential for mounting, showed that treatments of female rats perinatally with an antiandrogen (cyproterone) resulted in a significant reduction of bisexuality for the female, although the effect was largely limited to a reduced sensitivity to testosterone propionate administered in adulthood. Females treated perinatally with antiandrogen required more testosterone propionate in adulthood than normal females to display mounting behavior. Ward and Renz appear to have obtained stronger effects than Stewart *et al.*, perhaps because the acetate rather than free cyproterone was used. In addition, the report by Ward and Renz demonstrated that with a specific prenatal treatment lordosis was relatively unaffected but reduction of mounting was marked.

An additional experiment compatible with the hypothesis that early endocrine conditions determine the degree of bisexuality in the female is that of Clemens and Coniglio (1971). They found that the amount of male behavior displayed by adult female rats was directly related to (1) the number of male siblings in the litter and (2) the proximity of the female to a male fetus *in utero*. The data of Clemens and Coniglio are compatible with the view that the origins of mounting in the female rat exist in part in the exposure *in utero* to the relevant steroids which determine the development of mounting in the male siblings. Such an interpretation would have to postulate transplacental transfer of the relevant steroids from the male to the female fetus. If this is in fact the case, then the origins of bisexuality in the female rat might be unique, either to the rat or to polytocous species, and the mechanism could not account for bisexuality in species which ordinarily give birth to only one offspring. The comparative data show, however, that mounting behavior is displayed by females of monotocous species such as the cow and ewe (Young, 1961). In addition, the mechanism cannot adequately account for strain differences of bisexuality of the female which exist in polytocous species such as the guinea pig. Strain 2 female guinea pigs, which show much less mounting than Topeka females, do not differ from the

Topeka stock in terms of litter size or the average number of male siblings per litter. A preliminary evaluation of the effect of male siblings on the mounting of female guinea pigs from a genetically heterogeneous stock (Topeka) indicates that no significant relationship exists (Goy and Bridson, preliminary findings). To be consistent with the new hypothesis, it is proposed that appropriate steroidal exposure must occur *in utero* for these species via ovarian, adrenal, or placental sources. The steroid moiety and/or the temporal parameters of stimulation would necessarily be such as to have little or no effect or lordotic mechanisms or genital structure, while they would serve to augment mounting.

### ORIGINS OF BISEXUALITY IN THE GENETIC MALE

Hypotheses regarding the bisexuality of males in various mammalian species have not been as diverse as those formulated regarding bisexuality of females. This may be because, as Young pointed out, bisexuality is more common among females, especially in those species usually studied in the laboratory. There has been a tendency on the part of most investigators to view the bisexuality of males as (1) inherent, (2) limited, and (3) directly controlled by the amount of steroid present in critical stages of early development. It was a surprise to us and probably to many other investigators when the first reports from Swanson's laboratory (Swanson and Crossley, 1971) and from the work of Tiefer and Johnson (1971) showed that normally differentiated male hamsters could easily be induced to display lordosis by suitable treatment with estradiol benzoate and progesterone in adulthood. No investigator has postulated directly that the display of lordosis in the male hamster results from a deficiency in early steroids during critical periods of development. The reluctance to do so may arise from the fact that there clearly has been an amount of steroid present which is sufficient for the differentiation of normal male genitals. Accordingly, the bisexual behavior of the male hamster seems puzzling. Nevertheless, the experimental data indirectly support the hypothesis of a bisexuality originating from conditions of early steroid deficiency or early insensitivity to steroids present. In three laboratories currently studying the problem, the administration of additional steroids, either testosterone or estrogens, to the newborn male hamster has been associated with a decrease in bisexuality, as indicated by inhibition or suppression of lordosis responses in adulthood (Eaton, 1970; Swanson and Crossley, 1971; Paup *et al.*, 1972). The effect is not unique to the male hamster. Even though the expression of lordosis in the male rat is much more limited than in the male hamster, it can be reduced still further by the administration of steroid during the neonatal period (Hendricks, 1972).

Not all endocrine manipulations during early development act to suppress the development of lordosis and thereby decrease bisexuality of the genetic

male. It is a well-documented principle that removal of the testes at a specific time in early development results in the development of lordosis in the genetic male without loss or diminution of mounting behavior. Thus deprivation of testicular steroids at a specific time can produce bisexual males. This effect of castration during the period of psychosexual differentiation does not produce a complete bisexuality, since such males fail to display all of the male sexual repertoire and intromission and ejaculatory responses are absent or deficient in adulthood. The effect of castration at this early developmental stage is reversible by treatment with exogenous steroids, provided that the replacement therapy is begun at once and not postponed to a later developmental stage.

Both the kind and amount of steroid hormone present in the developing male influence the degree of bisexuality that develops. When the testes are removed from the genetic male rat at birth and injections of relatively low amounts of androstenedione are given as replacement therapy, it is possible to produce an individual that displays lordosis readily in adulthood and that also displays mounting, intromission, and ejaculatory behavior (Goldfoot *et al.*, 1969). If the amount of androstenedione injected during the neonatal period is increased, then the adult animal will not display lordosis (or will do so only to a very limited extent), and it will display the complete male sexual behavior repertoire (Stern, 1969). In other words, high concentrations of this steroid result in very limited bisexuality. Quite probably the same effects on development of bisexuality can be produced by quantitative variation of the amount of other steroid hormones such as estradiol or testosterone. Usually, however, these other steroids are so potent in suppressing lordosis that it is difficult in practical terms to find a dosage which both achieves full masculine development and fails to suppress lordosis.

The fact that males behave bisexually, even though they possess completely differentiated genitals, is not today as perplexing to behavioral endocrinologists as it was 10 years ago. The reason for the lack of concordance lies in the differing hormonal requirements for behavioral and genital systems. Despite the reliance of both systems on exposure to relevant steroids at a particular time in early development, it is possible that the two systems require different steroids and possibly different amounts of steroids at differing critical periods.

The possibility is not without experimental support. Estradiol benzoate administered at early stages of development is effective in reducing the expression of lordosis in both genetic males and females in adulthood, but the same steroid cannot cause normal phallic differentiation (Levine and Mullins, 1964; Paup *et al.*, 1972). Two studies (Goldfoot *et al.*, 1969; Stern, 1969) demonstrate that androstenedione in low to moderate amounts can induce good phallic differentiation in male rats castrated at birth but fails to suppress the expression of lordosis unless it is administered in high doses. Androstenedione, according to Stern (1969), has comparable effects in the genetic female and castrated male,

the primary difference being that the phallus is not as differentiated in the female as in the male at birth.

The experimental induction of hermaphroditism is certainly germane to the issue of differing hormonal requirements for phallic and behavioral systems. Two examples from older studies provide evidence in support of this view. In the female guinea pig, Goy *et al.* (1964) showed that it was possible to separate effects on phallic differentiation and suppression of lordosis by varying the time in development when high concentrations of exogenous testosterone propionate were present. More recently, in the female rat, Whalen and Luttge (1971) and, in the guinea pig, Goldfoot and van der Werff ten Bosch (1975) showed that dihydrotestosterone propionate induced moderately good phallic differentiation without greatly impairing the expression of lordosis when the animals were mature.

#### PARAMETERS OF HORMONAL ACTION DURING EARLY STAGES OF DEVELOPMENT

An extensive literature has developed which indicates that the major parameters of hormonal influence on development of mounting and lordosis are (1) concentration of hormonal substance in peripheral blood or at neural sites of action, (2) temporal aspects of early hormonal stimulation, and (3) chemical nature of the hormone at the site of action. Most of these variables have been identified by physiological experiments modifying the behavior of genetic females by treatment with exogenous steroids, or by modifying behavior of genetic males by castration with or without replacement procedures. Early in the work with experimental modification of the sexual behavior of the female guinea pig, the crucial nature of some of these variables was suggested (Goy *et al.*, 1964). In those studies, it was found that high concentrations of exogenously administered testosterone propionate could at one stage of prenatal development inhibit the ultimate expression of lordosis without augmenting mounting behavior. At quite another stage of prenatal development, the same hormone in the same concentration augmented mounting behavior and had little or no effect on the later display of lordosis.

The empirical demonstration that mounting and lordosis behaviors are susceptible to hormonal influences at specific and different times in early development has suggested to some the existence of "critical periods." The concept of critical periods may not be relevant to hormonal effects on behavior in the sense that the necessity for the relevant hormone is limited to a very brief period in development and that the hormone is ineffective at any other time. We prefer the concept of a "period of maximal sensitivity" to hormonal influences, probably preceded and followed by periods of lesser sensitivity. During the periods of



lesser sensitivity, the behaviors of mounting and lordosis can still be influenced by the relevant steroids, provided that high dosages are used. This view is consistent with Ward's view as well as with other data (Goy *et al.*, 1964) showing a relatively prolonged period even in the rat when steroids act to partially reduce the expression of lordosis in the adult. As is well known, however, even the periods of lesser sensitivity come to an end, and during other periods of development the hormones appear to be incapable of producing the same type of effect.

The overall picture that is emerging from laboratory studies of males from lower mammalian species can be summarized succinctly as follows: the degree of bisexuality expressed by the genetic male can be accounted for either by the amount and kind of steroid hormones present during a critical stage of psychosexual differentiation which occurs early in development or by a relative insensitivity to the steroid during this period. When the biologically active concentration of relevant steroids is high (either naturally or artificially elevated by injection), the adult male will display either very limited or no bisexuality as measured by the limited expression of lordosis and the frequent expression of mounting behavior. When the concentration of relevant steroids is low or the target tissues are insensitive, then the adult will be extensively bisexual; lordosis or presenting behavior will be frequently displayed and readily elicited and mounting can under appropriate circumstances also be displayed at frequencies judged to be normal for males of that species.

The hypothesis of tissue insensitivity seems to be a better model for the genetic male rhesus than a hypothesis based on absolute levels of steroid. Males from this higher primate species are highly bisexual, but their bisexuality seems not to be greatly influenced by the characteristics of the steroid environment of fetal life. Male rhesus monkeys, for example, display high levels of presenting behavior, even after extensive *in utero* exposure to testosterone or dihydrotestosterone. It is therefore possible that developing neural tissues destined to mediate presenting are insensitive to the steroids, and that in fact this may be a heritable trait developed under evolutionary selective pressures to protect the behavior from being suppressed. Wickler (1973) has suggested, for example, that male primates benefit from the ability to display presenting postures since it is used as a social *bonding* mechanism, important to the survival of the group.

Further evidence consistent with this hypothesis comes from studies of androgenization in the rhesus female. As in other species, androgen can masculinize the genitals and the behavior of a chromosomal female; but, unlike the case in other species, it cannot repress female responses, physiological or psychological. Thus a chromosomal rhesus female who is heavily androgenized both prenatally and in adult life nevertheless continues to menstruate (through the penis), to ovulate, and to exhibit feminine presenting behavior along with masculine mounting behavior. The presence of a gene which protects the relevant female tissues from androgen effects seems to us the most plausible explanation, and future experiments in this field should be focused in that direction.

## RHESUS MONKEY AS A MODEL FOR OTHER HUMAN SEXUAL BEHAVIORS<sup>4</sup>

In addition to serving as a model for bisexuality in the human species, the rhesus monkey may also in certain respects serve as a model for studies of human homosexuality, bachelorhood, and impotence.

### Homosexuality

There can be little question that homosexuality in the behavioral sense requires a high degree of bisexuality at the neuroendocrinological level, and that this prerequisite exists in both the rhesus and the human species.

There is a process known to students of field behavior as *peripheralization of the male* which occurs in every troop that has been studied. Rhesus troops (like baboon troops) contain a group of males that form the apex of the central hierarchy – the leader males or alphas. Surrounding them are the females. All males not admitted to the central group are gradually forced to live on the edges of the troop; that is, they are “peripheralized.” In a sense, they exist in a prison without walls, and homosexual behavior occurs very frequently in these peripheralized males.

The question of peripheralization in human societies, and of the effects of peripheralization on sexual behavior and life style, is one which should receive very great attention in connection with the etiology of homosexuality. Indeed, the process of alienation from fathers and peers among some feminine-behaving boys described earlier by Dr. Green is quite reminiscent of this process of peripheralization in rhesus troops. The differences between the sexuality characteristics of peripheralized male monkeys and homosexual human males may not be great. What is different is that the former are described and identified in terms of their behavior and geographic relationship to the leader males, whereas the latter are described in terms of their attitudinal relations to and feelings of alienation from so-called normal human males.

### Bachelorhood

In addition to the males peripheralized to the edges of the rhesus troop, some males are further peripheralized to a state called *solitarization*. These monkeys become in effect hermits or bachelors.

In human societies, for some reason, bachelorhood is no longer considered a psychosexual disease (although someone once called celibacy the ultimate perversion). Bachelorhood, indeed, is no longer talked about as a problem. Very

<sup>4</sup>Dr. Goy made the following points during his oral presentation.

little concern or attention is paid to the sexual requirements or sexual role of the human bachelor. If such studies come back into style, the solitarized rhesus male should prove an excellent model for study, both in terms of the dynamics which lead to solitarization and in terms of the sexual consequences of solitarization.

As might be expected, the solitarized rhesus male is primarily autoerotic, but the frequencies and modes of autoerotic expression in these animals, as in human bachelors, have not to date been studied.

### Impotence

Studies with nonhuman primates may provide some justification for the clinicians' views on human male impotence and its psychogenic origins and susceptibility to psychotherapeutic procedures. A very extensive study that Charles Phoenix, Adrien Slob, John Czaja, Kim Wallen, and R. W. Goy conducted on the sexual behavior of adult male rhesus monkeys illustrates the point. The study dealt with effects of castration (Phoenix *et al.*, 1973), but the data from the noncastrated controls are the focus of this discussion.

Nine feral males served as subjects. Approximately once each week each male was paired for a 10-min stand with one of eight different females. The procedure was repeated until every male had been paired eight times with each of the eight females, i.e., until each male had been paired a total of 64 times. The eight female partners were not allowed to undergo ovarian cycles. Instead, they were all ovariectomized and their endocrine condition was made equal by treating each with 13 daily injections of 10  $\mu$ g estradiol benzoate before pairing with the males. A female was paired with a given male only at 2-month intervals, and all tests were not completed before 16–18 months had elapsed. This means that the overall performance shown was not based on tests given all on one day when either the male or female of the pair might be showing unusual kinds of behavior.

The numbers within the cells of Table I represent the frequency of ejaculation by each male with each female. Considered as a whole, they provide information on a characteristic of primate sexuality that Phoenix (1973) has called "compatibility" of the pair.

The development of the concept of compatibility is a judicious step in the analysis of nonhuman primate sexual behavior. The significance of these results in Table I cannot be revealed without the use of such a concept. For example, if we assume that there is no material difference between scores of 8 or 7 (since anyone can have a headache once in a while), then the differences among males cannot be accounted for by saying that different males have different maxima of sexual output. Every one of the nine males achieved seven or eight ejaculations out of his eight tests with one female or more. The differences among males, therefore, are not to be found in the maximum that can be achieved, but rather

**Table I.** Number of Occasions on Which Each Male Ejaculated When Paired Eight Different Times with Each Female<sup>a</sup>

Male No.	Female No.								Percent of total tests on which male ejaculated
	472	2220	2214	2224	2227	2229	2221	2203	
30	8	6	8	6	7	8	8	8	92.2
58	4	8	2	7	7	8	8	8	81.2
00	2	6	5	7	7	8	8	8	79.7
35	7	3	6	7	7	4	7	6	73.4
27	4	3	6	2	8	7	6	6	65.6
91	0	8	1	7	5	4	7	7	60.9
73	1	1	2	5	6	8	8	7	59.4
50	1	0	7	1	4	6	6	6	48.4
56	0	0	4	0	7	7	3	6	42.2
Percent of total tests that female received ejaculation	37.5	48.6	56.9	58.3	80.6	83.3	84.7	86.1	

<sup>a</sup>Data for these 576 tests were taken in part (564 tests) from Phoenix *et al.* (1973) and in part (12 tests) from Phoenix (1973).

in the availability of partners that permit, encourage, or stimulate the male to display his maximum expression. In short, the males do not differ in the attainable maximum, but pairs do, and the differences among pairs can be conceptualized along some dimension such as sexual compatibility.

What has been said above for the male is equally true for the female. Despite the fact that female 2224 seems to have had a headache more often than most (since no male ejaculated with her on all eight tests), none of the females showed consistent rejection and frigidity.

The conclusion is compelling, for nonhuman primates such as the rhesus anyway, that profound, consistent, and universal sexual apathy is not a frequently encountered condition. Moreover, a reasonable parallel exists between the performances of some of these rhesus pairs and the performances that clinical workers encounter among human beings. For example, male 50 and female 472 would neither be judged nor judge themselves as having a highly satisfactory sexual relationship. At least it would seem that only very lax standards would allow an incidence of one ejaculation out of every eight opportunities to be regarded as highly satisfactory. If male 50 were to "divorce" or separate from female 472 and establish a "legal consort bond" with female 2220, the sexual relationship might not improve and in fact might be considered worse. Our test results show that when this arrangement was made for him, he never achieved

ejaculation with 2220. Interestingly, male 56 has a nearly exact replication of this history with these two female partners. My guess is that any clinician who heard a history from a human male that was limited to the experiences of these rhesus males with these rhesus females would begin to suspect the patient had serious libidinal problems. It would not be unreasonable under such circumstances to label the case file "male impotence" or "female impotence" depending on the sex of the patient. The correctness of this diagnosis depends on the implications the label carries as well as on what it connotes for causation of the condition. If the label of "impotence" carries only the connotation of partner incompatibility, then in the rhesus cases being discussed it would be correct since males 50 and 56 ejaculated on seven out of eight possible occasions when paired, respectively, with female 2214 or females 2227 and 2229.

The matrix presented in Table I could be thought of as a "couples test," and the percentages given in the right-hand column show that the males achieve different performance levels on this test. Similarly, percentages in the bottom row of Table I show that females achieve different performance levels. These individual differences among males and among females are influenced not only by occasional "impotence" but by another factor as well. In the case of either the male or the female, the marginal percentages are not the result of a failure to achieve the maximum but they are influenced greatly by how consistent the scores for a given individual are. This may be the best operational definition that an experimentalist can give for level of libido or sexual drive, but the differences can be conceptualized alternatively as differences in "sexual finickiness." Pairs may differ in compatibility, but individuals differ in the finickiness of their sexuality. If compatibility is defined, as Phoenix has suggested, as directly related to the proportion of tests with a given partner on which ejaculation occurs, then "finickiness" might be measured by some variable such as the dispersion or variance of scores with different partners. Thus it is possible to redefine impotence of one sort in terms of pair compatibility, and libido can be redefined as sexual finickiness. We do not know or understand the factors that establish or maintain either pair compatibility or finickiness, but both are certainly important variables in primate sexuality. Some workers with nonhuman primates in the field have pointed to factors such as social status that may be related to compatibility, but it is doubtful that this variable influences outcomes in the testing situation used in this study. The whole question needs to be held in abeyance for the moment.

A final word of caution must be injected into this discussion. The concepts of sexual compatibility and sexual finickiness are neither adequate nor very useful at extremes. For example, if a male were to be tested eight times with each of eight females and failed to ejaculate on any test, then no decision could be reached regarding whether finickiness or compatibility was the factor responsible for the overall poor performance. In such a case a concept of "profound impotence" might as well be resorted to as a diagnostic category. This is a different

sort of impotence from the sort described above for two male rhesus and from the sort most commonly encountered in clinical practice. As with all diagnostic terms in this field, the label means nothing with respect to etiology, and in its best usage merely connotes a kind of performance under reasonably standard conditions.

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### *Group Discussion*

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Dr. Fordney-Settlage asked about finickiness in the female monkey. Dr. Goy replied that he knew of no studies in the natural habitat. In the laboratory, the female rhesus seems to be very finicky during the luteal phase of her cycle and early in the follicular phase; thereafter, she defies all of the evolutionary guidelines governing genetic selection and copulates with any willing male.

Dr. Goy was asked whether the zero scores in the table might represent female rejection rather than male failure of potency. He replied that there was no way to tell.

Dr. Lipman-Blumen asked Dr. Goy about the interval between exposures for the female. He replied that the female was usually tested with five males on one day, then not tested further for 3 weeks or so. Five males per day, however, is far below the rhesus female's capacity; in nontest situations she may copulate with 20 males a day with no trouble at all.

Dr. Rose reported that his monkey observations were performed on large monkey troops in large compounds rather than on pairs or trios, and that perhaps for this reason his interpretations are quite different. The difference might be illustrated by supposing that the human handshake, if brief, remains a form of greeting behavior, but when prolonged leads to orgasm. This would not convert greeting behavior into sexual behavior. Similarly in his monkey troops, much of what Dr. Goy scores as sexual behavior can be scored as dominant or submissive behavior. Presentation behavior, for example, occurs very often in both males and females as part of a chain of behavior in which a dominant animal approaches a submissive animal who responds by averting his gaze and then presenting. The dominant animal may then mount. If intromission and coitus do not follow, however, it is very difficult to say that this is sexual rather than dominant-submissive behavior. Other observations confirm the importance of distinguishing dominant-submissive presenting or mounting from sexual presenting or mounting. If this distinction is made, there may be less bisexuality observed among monkeys.

Dr. Goy replied that he agreed with Dr. Rose's observations, but thought the distinction between sexual and dominance behavior too sharp. Perhaps in human sexuality, too, there is a substantial dominance factor. Accepting the dominance function of presenting and mounting does not detract from their sexual nature. They are both dominance-related and sexual. Sexuality, in the rhesus as

in the human, can be exhibited in a context of dominant behavior, submissive behavior, greeting behavior, and so on, as well as in the context of sexual gratification. Moreover, at least some homosexual behavior between male rhesus monkeys is unquestionably sexual in the strictest sense. Thus a 45-sec film sequence of two peripheralized rhesus males shows not only mounting but also anal intromission and thrusting to ejaculation on the part of the mounting monkey while the presenting monkey is simultaneously masturbating to orgasm. This sequence can hardly be confused with dominance or greeting behavior.

Dr. Rose raised the question of whether homosexual behavior in the male rhesus might not be wholly facultative — that is, engaged in *faute de mieux*. He knew of no data showing that a rhesus male with free access to a female in estrus would by preference mount and engage in anal coitus with another male.

Dr. Goy pointed out that the position he tried to develop was that all homosexual behavior, in monkeys and men, is “facultative.” The difference between monkeys and men on the one hand and lower mammals on the other is that the neuroendocrine basis for bisexuality exists to a lesser degree in lower mammals and hence in those forms there is less likelihood of “facultative” facilitation of a homosexual pattern. In any case, as Dr. Rose pointed out, it is all for the best.

Dr. Rose called attention to recent studies indicating that social experience can alter androgen levels. Thus following a fight which he loses the androgen level of a male may fall and remain low until he engages in another fight which he wins. Dr. Goy noted that in some of his experiments males displayed presenting behavior at times when their testosterone level was high, as determined by assay.

Dr. Rose commented that, in his opinion, monkeys should be studied in a natural setting; caged monkeys are crazy. Dr. Goy replied that “crazy” is perhaps an exaggeration, and the term “legally insane” is more accurate.

Dr. Cole asked about the sexual activity of physically handicapped monkeys. Dr. Goy cited the example of a monkey female, a member of a macaque troop in a natural setting, with a neurological disease which paralyzed her hindquarters. While not a highly prized sexual object, she had twice delivered infants since her paralysis. This was true despite the fact that males were unable to copulate with her in the usual way. Instead, it was necessary for the male to grasp her hindquarters, raise them up, and then move them forward and backward on the intromitted penis.

Dr. Rubinstein speculated that infrahuman species might be arranged in a hierarchy from lower to higher, with an increasingly variegated range of behavior available at the higher levels. This might be true in particular of capacity for varied forms of sexual behavior. When one reaches the human species, however, another factor enters — social constraints on variations in sexual behavior. Thus the paradox would emerge that the species inherently capable of the most varied sexual behavior might in fact exhibit the fewest variations. Further, a compari-

son of the human species with other species high on the scale might throw light on the extent of this repression by social constraints.

Attention was called to recent studies in which pregnant rats were subjected to restraints and other stresses during pregnancy. Male offspring of these rats showed deficiencies in male behavior. Whether or not these deficiencies are traceable to prenatal hormone levels, it was suggested, the finding that pregnancy conditions can affect the masculinity of offspring is a clue which should be followed up.

Dr. Green asked about mother-son incest in rhesus troops in natural settings. Dr. Goy replied that it occurs, but only rarely. Since 80% of a troop's males leave their native troop at adolescence, only 20% have an opportunity for mother-son incest. In rhesus as in human societies, Dr. Goy added, the mother is socially dominant in relation to her sons, and sexual behavior rarely occurs where the female is the dominant member of a pair. Thus no magical or biological incest taboo is needed to explain the observed rarity of mother-son incest.