EXPERIENTIAL, HORMONAL AND GENETIC FACTORS IN THE ORGANIZATION OF SEXUAL BEHAVIOR IN THE MALE GUINEA PIG

by

Elliot S. Valenstein
B.S., College of the City of New York, 1949
M.A., University of Kansas, 1953

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Co-Chairman

Co-Chairman

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I. INTRODUCTION AND FORMULATION OF THE PROBLEM

The research to be reported consists of a number of experiments which were conducted during an investigation of hormonal, experiential and genetic factors involved in the sexual behavior of the male guinea pig. These experiments have been performed during the past three years. Some of the work has been published in abstract form (29, 30, 32), all is being prepared for definitive publication. Experimental work that has been in progress for a number of years frequently is difficult to describe in the usual fashion which dictates a listing of all hypotheses in advance. Many of the problems investigated were not anticipated, but rather emerged from the data as the work progressed. The procedure to be employed here will be to define the problem-area studied and to describe each experiment or sub-experiment in chronological order reflecting the sequence in which the problems arose and were studied.

Grunt and Young (10, 12) demonstrated: 1) There are consistent individual differences in sexual behavior between male guinea pigs. 2) After the animals had dropped to a base line of sexual activity following castration and were given the same amount of testosterone propionate, the sexual performance of each animal tended to return to that of the precastrational period.

With respect to sexual behavior the authors conclude:

". . .much of the difference between individuals is attributable to the reactivity of the tissues rather than to differences in the amount of hormone" (10, p. 247).

This experiment suggested an interesting area of investigation. If differences in androgen level are not sufficient to explain the differences in sexual performance that exist between male guinea pigs, what factors are responsible? At least two possible explanations exist. The first would assume that individual differences in reaction to testosterone propionate are governed by hereditary (genetic) factors. There are numerous studies that have demonstrated that, within a species, specific behavioral characteristics are peculiar to certain strains. A number of such cases have been described in recent reviews (9, 13). It is important to bear in mind that it is never the behavior that is inherited directly, but rather some feature of the somatic sub strate that influences the direction of the developing behavior patterns. In the case on hand, inherited differences in the tissues mediating sexual behavior may account for differences in reactivity to gonadal hormones. Or, to look at the problem somewhat differently, the genetic character of the soma may be responsible for individual differences in vigor and these may require gonadal hormones in order to be fully expressed.

Another explanation for the individual differences in reactivity to androgen could involve the experiential background of the male. If one could demonstrate that experiences during the life of an animal heighten or suppress sexual behavior, or, that certain types of experience are necessary for the acquisition of the sexual pattern, then the possibility that experiential factors influence the reaction to the androgen would exist. It should be emphasized, and the point will be treated more fully in subsequent sections of this study, that the two explanations are not

mutually exclusive and may in fact be complementary. The writer was particularly interested in the role of experience in determining the effectiveness of androgen treatment, but some of the first results revealed that the genetic background is also important and had to be considered.

A review of the literature is not encouraging to anyone intending to use rodents to test the necessity of experience for the organization of patterns of sexual behavior. Experiments by Stone (28) and Beach (3) suggest strongly that the male rat does not require contact with other animals in order to exhibit the complete sexual act at maturity. The literature is replete with such statements as:

"Given an inexperienced male rat which has reached the state of physiological development denoting copulatory ability, one needs only to supply the adequate stimulus to evoke the copulatory act." (28, p. 131)

And again

"The results of this investigation substantiate the generally accepted view that the copulatory response is the action of an hereditary mechanism." (28, Pp. 146-147)

Or

"The instinctive character of the copulatory pattern of the male rat seems to be firmly established." (2, p. 163)

And the following:

"The mating behavior of male rats appears in well-organized, biologically effective form at a predictable stage of ontogenetic development; and the initial susceptibility to sexual arousal as well as the accuracy of overt copulatory performance appear to be independent of previous sexual experience on the part of the individual." (7, p. 91).

However, the literature also contains such statements as:

"Although practice or learning is not necessary for biologically adequate coital responses there is evidence indicating that the sexual behavior of adult males of this species (the albino rat) may be altered by the conditions under which the animals are reared." (14, p. 204)

And,

"Practice is not essential for effective coitus in many animals, but susceptibility to sexual arousal and the kinds of behavior shown by the sexually excited individual can be altered by experience." (6, p. 408)

Also

". . .even those lower mammalian species which are capable of mating without previous experience exhibit various modifications of sexual activity on the basis of individual learning." (5, p. 277)

To summarize, the relevant literature indicates that at the rodent level previous experience with other animals is not a prerequisite for the appearance of sexual behavior in mature animals, but experience may be instrumental in both determining the range of stimuli which can arouse an animal sexually and the level of excitement or arousal produced. It should be noted, however, that at the rodent level the role of experience in the acquisition of sexual behavior has been investigated primarily with rats although conclusions have frequently been extended to all rodents, and occasionally to animals of higher phylogenetic levels, e.g., ". . .rodents and carnivores are capable of effective copulatory behavior without specific practice. . ." (5, p. 276)*

To be sure, other investigators (1, 18, 19, 26, 27, 36) have studied the sexual behavior of the male guinea pig, however, there have been no studies which were designed specifically to examine the question of the role of experience. The experiments to be reported were designed for the

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* Although this specific problem has been investigated exclusively with the rat, observations on other rodents and lagomorphs made for different purposes have a bearing on the question. In this context one should include Macirone and Walton (20) on the rabbit and Bond (8) on the golden hamster, for example.

purpose of 1) determining the extent to which the appearance of the mature sexual pattern of the male guinea pig depends upon previous experience and 2) the influence, if any, this experience has in determining the reaction to injections of androgen.

II. THE ANIMALS, METHODS OF OBSERVATION AND SCORING PROCEDURES

The procedures which were common to all the experiments will be described first, those specific for each experiment will be discussed in the appropriate sections.

Male guinea pigs from three strains were used. Strains 2 and 13 are highly inbred animals that have been maintained by brother-sister matings since 1906. Sufficient males were obtained from the two inbred families by back crosses and matings of cousins as well as brother-sister matings. Crosses other than brother-sister have the effect of reducing homozygosity. However, these crosses were made after at least 80 generations of inbreeding and, when one considers that approximate homozygosity is achieved in about 30 generations (13, 25), the genetic homogeneity of these animals can be appreciated. The third strain of animals was obtained from a local dealer and has been maintained with no attempt to inbreed them. These animals are referred to as the heterogeneous group. It was noted in an earlier study (31) that the Strain 2 males are characteristically the smallest animals in the colony, but they are moderately vigorous. The Strain 13 males are quite large, but extremely sluggish behaviorally. The heterogeneous males are also quite large, however, they are the most vigorous animals in the colony.

When the intensity of sexual behavior and its qualitative aspects were to be tested, a female exhibiting a good lordosis in response to fingering (36) was placed in the cage with the isolated male. The male's

behavior was then observed and recorded during a 10 minute period. Inasmuch as a male often does not show any further interest in the same female immediately after ejaculating (11), the test was terminated before the end of 10 minutes in those instances in which ejaculation occurred. Each male was given seven tests (except in experiment I, where 10 tests were given) and the average score constituted the sexual behavior score for that animal. The seven tests also provided a representative sample of the qualitative features of the sexual behavior exhibited by the male. In all, 927 sexual behavior tests were made during the work reported in this paper.

The sexual behavior of the male guinea pig and the method for estimating it quantitatively and qualitatively have been described more fully elsewhere (31, 37), however, a brief explanation of the terms employed may be helpful. Six components of sexual behavior were recorded. These are: sniffing, muzzling, abortive mounting, mounting, intromission and ejaculation.

Sniffing refers to sniffing and licking of the ano-genital region of the female. Usually (37), this category included sniffing and licking of the female regardless of the area of contact, but in this study the use of the term was restricted in an attempt to eliminate some of the general exploratory behavior which might not be sexual in nature. The effect of this change in scoring procedure is to lower the scores achieved by the animals approximately one point below that previously reported for similarly treated animals. Nuzzling is also licking and sniffing of the ano-genital region of the female, but is distinguished from sniffing by

its intensity and by a characteristic twisting and turning of the male's head as he licks the female's genitalia. Abortive mounting is recorded when the male places one or two of his front paws on the female, but does not bring his body into contact with hers. Mounting is scored when the male mounts the female and brings his body into contact with hers. The male generally, but not always, executes a series of pelvic thrusts. Mounting is usually oriented to the female's posterior end, but he may also mount elsewhere. Intromission with or without subsequent pelvic thrusts may accompany mounting, and when ejaculation occurs the male's activity is brought to an end with a grasping of the female's sides and a convulsive drawing in of the flanks.

The score for a test was determined by weighting the above behavior as follows: 0.1 for sniffing, 0.2 for nuzzling and abortive mounting, 0.3 for mounting, 0.4 for intromissions and 0.5 for ejaculation. Only the highest measure of behavior displayed in each 15 second period was scored. Therefore, if the test lasted 10 minutes, the maximum number of scoreable units was 40. If the test was shortened by the occurrence of an ejaculation, the score was multiplied by a factor which took into consideration the shorter test period. This factor was the quotient of 40 divided by the actual number of 15 second periods up to and including that during which the ejaculation occurred. With this procedure an animal that mated in the first 15 second period received the maximum score of 20, while an animal that did not come in contact with the female during the 10 minute test period was scored 0. The sexual behavior score therefore, takes into account the quantity and maturity of sexual behavio displayed.

During the months in which observations were being made, the males were isolated in cages, 2' x 2' x 1'. The laboratory temperature was maintained between 68° and 76° F. The diet included Purina rabbit chow, oats, green vegetables, alfalfa hay and water. With the exception of one animal, which will be mentioned in context below, all animals appeared healthy throughout the period of study.

III. EXPERIMENTS

Experiment I. Resistance of strain differences in male sexual behavior to maternal influence.

A previous study (31) had shown that males of the highly inbred Strain 2 were significantly lower in sexual behavior than the heterogeneous males. In line with the question of the importance of experiential factors for the sexual behavior of male guinea pigs, an investigation was undertaken to determine the role of maternal influence from birth to time of weaning which was on day 30. It was reasoned that some or all of the differences between the Strain 2 and heterogeneous males might be attributable to some aspect associated with maternal care. This could be some feature of the maternal or general behavior of the sow or some nutritional factor associated with her ability to provide nourishment for the developing male.

Procedure. Seventeen pairs of guinea pigs were interchanged at birth so that one sibling remained with its mother while the other was placed with a foster mother from the other strain. Seven pairs were composed of Strain 2 males and 5 pairs were composed of heterogeneous males. In addition there were 1 pair of Strain 2 females and 4 pairs of heterogeneous females involved in these interchanges that contributed data on the rate of growth. The animals were raised two to a sow and were weaned and isolated at 30 days. When the males were 70 days old, 10 weekly tests (instead of the usual 7) of sexual behavior were begun.

Results. The Strain 2 males were significantly ($P < .01$) lower in sexual behavior score regardless of the sow. The average score was 5.7 for the inbred males with their mothers and 5.8 for those reared with heterogeneous sows. For the heterogeneous males with their mothers the average score was 8.5 and 10.6 for those raised with inbred sows. The only significant differences between scores were those between the scores of the inbred and heterogeneous males.

The growth rate of these animals provided an interesting sidelight. Considering males and females together, Strain 2 animals with their mothers gained an average of 153 grams during the 30 days up to weaning age, while those with heterogeneous sows gained 171 grams. Heterogeneous young gained 239 grams with their mothers in contrast to 210 grams with Strain 2 sows. The greater weight gain of the animals raised with the heterogeneous sows approaches significance for both Strain 2 and the heterogeneous animals. The probability that such weight differences would occur by chance lies between 0.1 and 0.05 for both groups.

Discussion. This experiment was regarded as a pilot study designed to investigate the possibility of maternal influence during the nursing period on sexual behavior. From the results it is clear that the differences in sexual behavior between Strain 2 and the heterogeneous males could not be attributed to any maternal influence between birth and weaning age. Rather it seemed to be related to some difference existing at birth. Only the growth rates of the animals were modified by the sows. However, it was also clear from the results that growth in these animals depended primarily on genetic factors and only secondarily on the "maternal"

factors to which the animals were subjected. This is evident from the significantly faster growth of the heterogeneous animals with either sow.

Experiment II. The role of contact with other animals on the organization and display of sexual behavior.

Observations of animals raised under different caging conditions had suggested to Dr. Riss of this laboratory and the author that males with a minimum of contact with other animals frequently do not mate. It was decided, therefore, to investigate this possibility in a study designed specifically for this purpose.

Procedure. Fourteen heterogeneous, 14 Strain 13 and 36 Strain 2 males were used. The animals of each group were divided so that one-half were raised in an isolated situation and the other half in a social situation. Thus, for both the heterogeneous and Strain 13 animals, there were 7 males in the social group and 7 that were isolated. The Strain 2 animals were not divided exactly in half, there being 19 males in the social group and 17 that formed the group of isolates. All isolated males were raised alone with their mothers until day 25 when they were weaned and isolated. The social males were left with their litter mates until day 25, then weaned and placed with three to five females of approximately the same age and weight. On day 73 the "social" males were isolated. On day 77 the first of 7 weekly tests of sexual behavior was given to each of the isolated and socially reared males. The average of these tests constituted each animal's sexual behavior score. The qualitative information to be reported below was likewise based on these 7 tests of each male. Hereafter, in the terminology to be used the animals will be referred to as isolate and social males, but it should be kept in mind that these terms refer to the conditions of rearing during the first 73 days of the animals' lives. After day 73 all animals were isolated in individual cages.

Results. The results from each group of animals are summarized in Table 1. The data reflect the unique characteristics of each strain of animals and consequently are presented separately.

Strain 2 Males. The striking differences between the isolate and social groups of Strain 2 males are revealed even by a superficial examination of the data in Table 1. The difference in average sexual behavior scores (3.9 for the isolate and 6.8 for the social group) is highly significant ($P < .01$). Similarly, the differences in the higher measures of sexual behavior (mountings, intromissions and ejaculations) are also highly significant ($P < .01$) whether one considers the average frequency per animal or the percent of animals displaying the behavior. Only one isolated Strain 2 male (6% of 17) achieved intromission and ejaculation and the latter occurred just once. It is also important to point out in connection with this male, that there was a concentration of these higher units of sexual behavior in the last three tests, suggesting that some learning may have been taking place during the earlier tests. In general, however, the seven 10-minute exposures to the female were not sufficient to effectuate any change in the males' behavior.

When comparing the Strain 2 males with respect to their exhibition of the lower measures of sexual behavior (sniffing, nuzzling and abortive mounts) a different picture is seen. At this level the isolate males surpassed the social males. The former were exceedingly active, displaying a persistent and vigorous interest in the females. The isolate animals showed no sign of "freezing" but despite this lively interest in the females were unable, with the one exception mentioned, to mount them in such a way that intromissions and ejaculations could be accomplished.

TABLE 1

Comparison of sexual behavior of male guinea pigs weaned on day 25 and raised in isolation with that of males raised with females.

(Data obtained from 7 tests of each male after isolation, day 77-120)

Animals		N	Lower measures		Mountings		Intromissions		Ejaculations		Average scores
			Average per animal	percent displaying	Average per animal	percent displaying	Average per animal	percent displaying	Average per animal	percent displaying	
Strain 2	isolated	17	149.0	100	1.2	35	0.5	6	0.06	6	3.9
	social situation	19	97.3	100	18.0	100	18.0	90	3.7	84	6.8
Strain 13	isolated	7	129.4	100	2.0	71	0.0	0	0.0	0	3.6
	social situation	7	96.4	100	6.4	86	7.6	57	0.6	57	3.0
Genetically heterogeneous	isolated	7	70.2	100	17.4	71	12.6	71	4.4	71	7.5
	social situation	7	36.4	100	19.6	100	20.6	100	6.7	100	9.9

Strain 13 Males. The behavior of the Strain 13 males was considerably different. A comparison of the average sexual behavior scores reveals that the isolate group is slightly higher than the social group (3.6 for the isolated compared with 3.0 for the social animals). However, the difference is not significant. A breakdown of the score presents another story. Fifty-seven percent of the social animals had intromissions and ejaculations while none of the isolate animals exhibited any of these higher measures of behavior. This difference, when analyzed by chi-square yields a X^2 of 3.15* which lies between the 5% and 10% levels of confidence. However, inasmuch as the difference is definitely in the predicted direction there are good grounds for using a one-tail test which would place the probability below the 0.05 level of confidence. In either case the trend is clear, none of the isolate animals was able to achieve intromission and ejaculation while 4 of the 7 males in the social group exhibited these higher measures of behavior.

What seems to be a paradox between the lack of difference in average sexual behavior scores on the one hand, and the difference in the display of the higher measures of behavior on the other, is easily resolved. First, the socially raised males did not exhibit a sufficiently large number of the higher measures of behavior so that the greater activity of the isolate males in the lower measures of sexual behavior was counterbalanced. Secondly, the social Strain 13 males frequently either became disinterested in the female following an intromission or were fatigued,

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*Corrected for discontinuity.

for it was noted that the periods of inactivity following intromissions were exceedingly long. In general, it may be stated that the extreme sluggishness of the animals from this strain contributed to their low scores.

Several attempts have been or are being made to make the Strain 13 males more vigorous. In one experiment Riss (22) administered thyroxin to animals from this strain. The sexual performance of the thyroxin treated males was not elevated significantly, although there was a trend in that direction. In another experiment the author has a group of isolated and social animals from this strain receiving supra-maintenance quantities of androgen (500 µg testosterone propionate/100 gm body weight/daily) but the data are not yet complete.

Heterogeneous Males. Still another picture is presented by the heterogeneous males. The qualitative differences as well as the differences in average sexual behavior scores between the isolate and social groups of the heterogeneous stock is not very striking (Table 1). Again the differences are in favor of the social males, but they are not significant and are due solely to the presence of two isolated animals who did not mount, achieve intromission or ejaculate. However, the fact that these two males were less than the average in weight suggested an explanation of these results. Previous work (31) had revealed that the heterogeneous animals are extremely vigorous and have a very rapid growth rate. In another study, Riss, Valenstein and Young (24) have shown that the development of sexual behavior in the heterogeneous males proceeds at a much faster rate than that of Strain 2. Considering these facts it

was reasoned that the isolate animals might have had sufficient opportunity for the organization of their sexual behavior during the 25 days prior to weaning when they were with the sows. Males have been observed to attempt and sometimes succeed in mounting their sows. The two lighter males might not have been able to benefit as much from their contact with the sow. With this in mind, a supplementary experiment was designed.

Experiment IIA. Comparison of the sexual behavior of isolated and socially raised heterogeneous males weaned at 10 days.

In order to check the hypothesis suggested above heterogeneous males were weaned and isolated at an earlier age than 25 days.

Procedure. Twenty heterogeneous males were used. They were divided into two groups of 10 each. The isolate group was raised one to a sow, but they were weaned and isolated on day 10 rather than day 25. The socially reared males were raised two to a sow (2 males or 1 male and 1 female) and also weaned on day 10, but each male was then placed with three females. As in experiment II, the social animals were isolated on day 73. Seven weekly tests of the animals in both groups were begun on day 77.

Results. The results are summarized in Table 2. The significant differences between the isolate and social males are clearly apparent. The differences in average scores and in the percent of animals displaying behavior in the higher categories are significant beyond the 1% level of confidence. Again, the isolate animals exhibited a great deal of interest in the females and this is reflected in the greater amount of lower measure behavior. The sexual behavior score of the social animals is somewhat lower than that of the social animals weaned at 25 days, but this is explained by the "freezing" of one animal weaned at 10 days. This male appeared to be afraid of the female during the first four tests and as a result its score was considerably depressed. However, once the animal started to approach the female it had intromissions and ejaculated almost immediately. This was the only case of prolonged "freezing" observed in this or any other of the experiments.

TABLE 2

Comparison of sexual behavior of genetically heterogeneous male guinea pigs weaned on day 10 and raised in isolation with that of males raised with females.

(Data obtained from 7 tests of each male after isolation, day 77-120)

	N	Lower measures		Mountings		Intromissions		Ejaculations		Average scores
		Average per animal	percent displaying	Average per animal	percent displaying	Average per animal	percent displaying	Average per animal	percent displyaing	
isolated	10	120.8	100	10.6	30	6.5	30	1.5	30	4.9
social situation	10	52.9	100	14.3	100	19.6	100	5.3	100	8.1

It is important to point out that weaning the animals on day 10 seemed to have no ill effect on their health. The animals appeared to be very vigorous and their weight on day 73 which was just prior to testing compared favorably with the weight of those weaned on day 25 (558 grams for the animals weaned at 10 days, 550 grams for those weaned at 25 days). The 68-day gestation period of the guinea pig is unusually long for a rodent and the animals are born surprisingly mature (their eyes are open and they run around eating solid food shortly after birth). This condition of relative maturity at birth makes it possible to wean the animals at earlier ages than might be possible for other rodents. However, removing the sow at birth is frequently followed by a high rate of mortality among the young (34).

Discussion of Experiments II and IIA.

The data show clearly that males who have a minimum of contact with other animals have difficulty in mating. Although each of the isolated Strain 2 males was given 7 tests with females, only 1 of 17 achieved intromission or ejaculation. In contrast 16 of the 19 socially reared Strain 2 males ejaculated and 17 of 19 had intromissions. Among 7 isolate Strain 13 males, none achieved intromission or ejaculation, whereas 4 of the 7 in the social group displayed intromission and ejaculation. Of the heterogeneous males weaned at 10 days, only 3 of 10 isolate animals had intromissions or ejaculations, but all of the 10 social males displayed the full pattern of sexual behavior. The isolated animals gave evidence of being as much aroused by the presence of the

female as were those from the social group and there was no evidence of any emotional disturbance that could have interfered with their display of sexual behavior. The figures in Tables 1 and 2 giving the amount of the lower measures of sexual behavior indicate clearly the vigor with which the isolated males pursued the females. The best explanation of these results appears to be that the sexual behavior of the isolated animals had not been organized into an effective pattern.

The isolate animal exhibited many of the necessary components of sexual behavior, but they were not organized and oriented in such a way that the male was able to copulate. It is now appropriate to examine more closely the problems subsumed under the rubric "organized behavior" and to raise the question of what actually is learned. This can best be answered by describing in detail the essential difference between the sexual behavior of the social and that of the typical isolate male.

The male guinea pig that is capable of mating is oriented rather specifically to the posterior end of the female. If the female's posterior end is inaccessible the male will attempt to force her into a more favorable position. This does not mean to imply that the male will not lick and nibble at all parts of the female's body, but rather that the primary orientation is to the female's genitalia. When mounting the female, the experienced male approaches the female from the rear placing his chest over her back while simultaneously clasping her sides with his forepaws. The female is held by this clasping grip of the male and as his genitalia are brought into contact with the back of the female,

vigorous pelvic thrusts ensue. These pelvic thrusts usually result in an intromission and sometimes culminate in an ejaculation.

The inexperienced male pursues the female but when he catches up with her he frequently circles around attempting to mount her head or sides. The licking and nuzzling is generally, but by no means always, oriented to the female's genitalia, whereas the attempted mounts (abortive mounts in the scoring) may occur any place. In this connection Stone writes of the rats he observed:

"In two instances young males performed the first sexual act while mounted at the head end of the female and with the forelimbs clasping the head and shoulder rather than the sides. The pelvic movements were directed toward the face in these cases." (28, p. 126).

In addition, the mounts of the inexperienced male are attempted by placing one or both forepaws directly on the back of the female. This generally results in the female jumping away when the male places his weight against her. This is in sharp contrast with the experienced male, who places his chest over the female's back while clasping her sides.

The isolate male's mounting attempts are not oriented to the female's posterior end in spite of the fact that the female's behavior assists in orienting the male. She characteristically runs a few steps from the male and then stops and assumes the lordosis stance. When this happens the pursuing male is naturally oriented to the rear of the female, but the inexperienced male usually runs right by the female's rear in his effort to catch up with her. If the male should mount the female from the side, he is unable to clasp and hold her. As the female pulls away, she brings her posterior region past the male and, as he attempts to hold her, he

is sometimes successful in bringing his forepaws into such a position that she is clasped on both sides from the rear.

This inability of the inexperienced male to properly mount and clasp the female and his lack of posterior orientation are his greatest handicaps in achieving intromission and ejaculation. Once a male has correctly mounted a female a series of pelvic thrusts (coital reflex) ensue and these generally result in penis insertion which may "trigger" the ejaculatory reflex. In spite of Stone's general conclusion about the hereditary nature of the sexual behavior of rats, he describes the behavioral differences between young and sexually mature animals as follows:

> "Another kind of difference centers about the appearance of the elements of the copulatory act in a stage of slight disorganization. Illustrations of this are common in the copulatory attempts of the inexperienced male just prior to the first successful copulatory act. These elements may consist of mounting with or without definite clasp, mounting and palpation of her sides with feeble pelvic movements that do not effect vaginal entrance." (28, p. 125, emphasis added).

These differences between young and mature rats are very similar to the differences between guinea pigs of the same age with and without experience with other animals.

If these results are so clear cut, how can the claims that rodents require no learning to exhibit the complete sexual act be explained? The reason seems to be that there were only two experiments (3, 28) designed to attack this problem and both have been performed on the rat.

Stone (28) and Beach (3) compared the sexual behavior of mature rats which had been raised in an "isolated" situation with those raised in group situations and concluded that sexual behavior is innately

organized in this species. One possible resolution of the dilemma is that rats require no learning in order to exhibit the complete sexual act, but guinea pigs do. If so, the generalization based on experience with the rat was too broad. However, if the correct conclusion has been drawn from the present data, there is another possible interpretation. In both the Stone and Beach experiments the rats were weaned at 21 days of age and isolation was begun at this time. While in neither case is it stated specifically, the implication is given that the animals remained with their siblings and sow up to weaning age. The average rat litter size of 8 or 9 suggests that there was considerable contact with siblings prior to isolation. Indeed, rats have been observed according to Beach:

> "to pursue, mount and clasp other individuals as early as 21 days after birth. Pelvic thrusts sometimes occur and the only element lacking is the ejaculatory reflex." (6, p. 406)

With this in mind, it would appear that in both Stone's and Beach's experiments a better procedure would have been either to isolate the animals at an earlier age* or to have removed litter mates from those animals which were to be eventually isolated. In the present experiment, if the isolate and social animals had been selected exclusively from the heterogeneous animals weaned at 25 days, the conclusion drawn might have been similar to that of Stone and Beach.

In the above context, it should be noted that even when heterogeneous males were weaned at 10 days, 3 of the 10 in the isolated group attained intromission and ejaculation in subsequent tests. The heterogeneous

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* Because of their relative immaturity at birth it is unlikely that rats could be weaned as early as guinea pigs.

animals have a rapid growth rate and a great amount of general vigor. It would appear therefore, that even 10 days with the sow may prove to be sufficient time for the organization of sexual behavior in some of the more vigorous individuals. This is not surprising in view of the relative maturity of the guinea pig at birth and the fact that male guinea pigs from the heterogeneous stock have been observed to mount females as early as the tenth day of age. (24)

Each of the three groups of animals (Strains 2 and 13 and the heterogeneous stock) presents a characteristic picture. The heterogeneous animals are ideally suited for a rapid organization of their sexual behavior as they possess both large size and vigor. The Strain 2 males are also vigorous, but their smaller stature may perhaps handicap them in mounting and clasping the female. Stone recognized the importance of this point and in reference to the young rat writes:

"Limitation in the size of the male and the girth of his forelimbs cause a slight difference in the placement of the forepaws on the body of the female as he stands in the copulatory position." (28, p. 123)

The inexperienced Strain 2 males in particular tend to place their forepaws directly on the back of the female rather than around her sides. It seems possible that the relatively small "girth of the forelimbs" necessitates a greater amount of contact with other animals to master the technique of mounting and clasping. On the other hand, the sluggishness of the Strain 13 males probably retarded both learning and the display of what was learned.

At present several related experiments are being conducted. Young males are being raised with other males in a situation which is otherwise

comparable to that of the males raised with females in the present experiment. Also, much of the procedure of the present experiment is being repeated with animals 6 to 8 months of age whose sexual behavior has not shown any evidence of having become organized into an effective pattern. Some of these animals were obtained from the isolated groups of the present experiment. The fact that these animals still do not exhibit the complete sexual act even at this more advanced age is additional proof that physical maturity alone, in the absence of an opportunity to organize the sexual behavior pattern, is not sufficient. These experiments should add valuable information 1) relevant to the importance of intromission, ejaculation and drive reduction for the organization of sexual behavior, and 2) the learning capacity of animals at different ages. The results of these experiments will be reported elsewhere.

Experiment III. The role of experience in influencing the effectiveness of testosterone propionate.

In experiments II and IIA it was shown that contact with other animals plays an essential role in the organization of sexual behavior into an effective pattern. It was then possible to turn to one of the main problems posed at the beginning of the investigation. An experiment was designed to determine the role experiential factors have in influencing the effectiveness of testosterone propionate on the stimulation of sexual behavior.

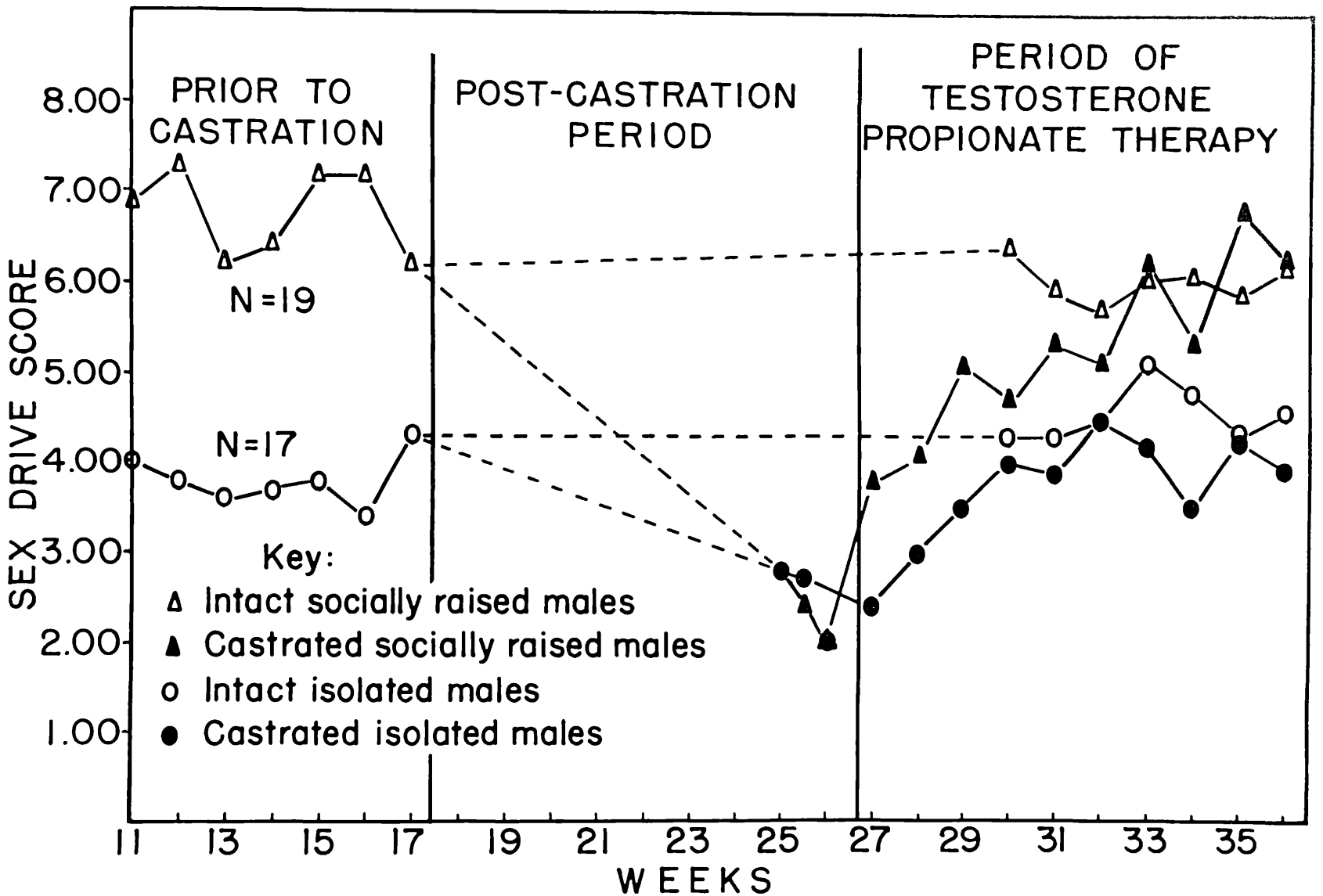
Procedure. Fifteen of the 17 isolated and all of the 19 socially raised Strain 2 males used in experiment II were selected for this part of the investigation. At the completion of the 7 tests reported in experiment II the animals were 120 days of age. At this age, 10 of the isolated males and 13 of the socially reared males were castrated. Five isolated males and 6 social males served as intact controls. The castrated males were left isolated and untested for 8 weeks. Between the eighth and tenth week three tests were made with females. These tests were used to ascertain if the sexual behavior of the males had dropped to the base line of activity characteristic of castrates (10, 12). Beginning the 10th week after castration the males received daily injections of testosterone propionate for 10 weeks. Two quantities were used. Five of the isolate and 7 of the social animals received 25 μg/100 gm body wt/daily while 5 of the isolate and 6 of the social males received 100 μg/100 gm body wt/daily. These particular quantities were selected because the lower quantity is just above the level necessary

to restore the precastrational performance of adult males of the heterogeneous stock (10, 12). The larger amount was given because it was thought desirable to determine the effect of a quantity further above the threshold, known to be between 12.5 μg and 25 μg/100 gm body wt/daily. During the period of hormonal therapy the animals were given 10 weekly tests. After the third week of this testing period the isolate and social intact controls were given 7 weekly tests. These served as a basis for evaluating the effect of androgen on the castrates.

Results. The main results are summarized graphically (Figure 1). The large differences in sexual behavior scores which existed between the social and isolate males prior to castration are clearly apparent. These are the differences reported in tabular form (Table 1) in experiment II. One can see from figure 1, however, that by the eighth to tenth week after castration the behavior of the males in the isolate and social groups had descended to the same base line. By this time none of the males was having either intromissions or ejaculations, but a few of the social animals occasionally mounted a female. In general, however, as the sexual behavior scores indicate, males of both groups exhibited relatively little interest in the female.

With replacement therapy the two groups again separated and reached the level of their respective intact controls. To be sure, the sexual behavior score of the isolate as well as the social groups increased, but only the social animals exhibited intromissions and ejaculations. This qualitative difference in the behavior of the two groups accounts for the separation in sexual behavior scores during the period of replacement

Figure 1. Sexual behavior scores of isolate and social males prior to castration, in the post-castration period and during the period of testosterone propionate therapy.


PRIOR TO CASTRATION
POST-CASTRATION PERIOD
PERIOD OF TESTOSTERONE PROPIONATE THERAPY
SEX DRIVE SCORE
8.00
7.00
6.00
5.00
4.00
3.00
2.00
1.00
N=19
N=17
Key:
Intact socially raised males
Castrated socially raised males
Intact isolated males
Castrated isolated males
11
13
15
17
19
21
23
25
27
29
31
33
35
WEEKS

therapy. A breakdown analysis of the percent of males exhibiting the higher measures of sexual behavior is summarized in Table III. A relatively large percent of the socially raised animals exhibited the higher measures of behavior prior to castration. With replacement therapy after castration, the behavior was restored to approximately the same level. On the other hand, only 1 of the 10 isolated males intromitted or ejaculated during the precastrational testing period and on the retests during replacement therapy this same male was the only animal of the group to achieve intromission. The 5 animals serving as intact isolated controls had no intromissions or ejaculations in the preliminary tests or on the retests begun 13 weeks later. This latter circumstance further supports the conclusion drawn from experiments II and IIA that, in the absence of contact with other animals, physical maturity alone is not sufficient to organize the sexual behavior pattern. It will be seen too, that the intact controls for the socially reared animals tested after 13 to 20 weeks of isolation performed at a relatively high level. This demonstrates that the inability of the isolate animals to display the higher measures of behavior is not due to any emotional factor associated with prolonged isolation. Rather it appears to be accounted for by the fact that their sexual behavior had not been organized into an effective pattern.

It will be recalled that some animals received 25 μg testosterone propionate/ 100 gm body weight/ daily and others 100 μg. The results of the social and isolate castrates have been analyzed separately. The social castrates receiving 100 μg of testosterone propionate did slightly

TABLE III. Comparison of Percentages of Isolate and Social Males Exhibiting Higher measures of Sexual Behavior Prior to Castration and 10-20 Weeks after Castration when Replacement Therapy was given.

			Percent Mounting	Percent Intromitting	Percent Ejaculating
Isolates	Castrates (N=10)	Preliminary Tests (Precastrational)	30	10	10
		With Replacement Therapy	30	10	0
	Intact Controls (N=5)	Preliminary tests	60	0	0
		Retests	40	0	0
Social	Castrates (N=13)	Preliminary tests (Precastrational)	100	85	85
		With Replacement Therapy*	92	83	75
	Intact Controls (N=6)	Preliminary tests	100	100	83
		Retests	100	83	67

* During the period with replacement therapy one male suffered from an infection in the genital region which made it impossible for him to have intromissions. This animal was not included in calculating the percentages in this row.

better than those receiving 25 μg, but the difference is not statistically significant. However, the isolate castrates receiving 100 μg did significantly better than the isolate males receiving 25 μg. The fact that there was a significant difference in the isolate group and not in the social group is not surprising in light of the greater variability in the scores of animals that have intromissions and ejaculations. The difference in the scores of the males given 25 μg and 100 μg was tested statistically by the method of paired replicates suggested by Wilcoxon (33).

On the surface the results appear to contradict those obtained by Grunt and Young (10, 12). These investigators reported that differences in sexual performance were not related to amount of androgen, provided a threshold quantity was surpassed. In selecting the quantities of hormone used in this study the figures reported by Grunt and Young were used as a guide. In the earlier studies it was found that 25 μg testosterone propionate/ 100 gm body weight/ daily was above the threshold and quantities greater than this amount were not correlated with improved sexual behavior scores. However, these figures were obtained from work with the genetically heterogeneous stock. It is possible that the threshold for Strain 2 males is above 25 μg. If so, the difference between the 25 and 100 μg groups would be understandable and consistent with the interpretation given previously. There are other possibilities, however, and at present data are being collected to reevaluate the results in the light of such variables as: age at which castration takes place, length of time animals are left without replacement therapy, etc. The solution of this problem falls beyond the scope of the present investigation and will not be discussed further at this time.

Discussion. The results show clearly that the effectiveness of testosterone propionate as a stimulant of sexual behavior depends to a significant extent on the experiential background of the male. After castration both the isolate and social animals dropped to the same base line, but with replacement therapy only the animals that had previously given evidence of possessing organized patterns of sexual behavior were capable of achieving intromissions and ejaculations. We would note, however, that with replacement therapy, all animals were activated or made more excitable.

The demonstration of this effect of experience raises an important theoretical problem with respect to the physiological action of testosterone propionate. Androgen apparently plays several roles in eliciting sexual behavior and some of its effects may be direct while others may be indirect. Obviously, in the guinea pig, and this is undoubtedly true in other lower mammals as well, there is some effect on the genitalia because in the absence of androgen the genitalia are either underdeveloped or become atrophic. But there is more to the story than this. Male guinea pigs castrated at birth and raised with other animals will exhibit sexual behavior including mounting with pelvic thrusts even in the absence of replacement therapy (24). Later, provided they have had sufficient contact with other animals and have received androgenic stimulation, intromission and ejaculation are displayed (24). But in the absence of contact with other animals, intromission and ejaculation do not occur, although the level of excitement is raised and genital development has been attained. To state the findings in another way, androgenic substance

is, on the one hand, excitatory and, on the other, necessary for the development of the equipment required for intromission and ejaculation, but it has no direct organizing action which enables the excited animal to use this equipment. It would appear then that with respect to sexual behavior androgen acts as an energizer rather than as an organizer.

There is a long history of speculation bearing on the point. In 1937, Lashley (16, p. 10) without referring specifically to sexual behavior wrote:

"There are indications that many isolated masses of cells in the central nervous system are concerned with regulation of the general level of excitation and that they contribute little, if anything, to the specific patterning or reaction."

Kinsey, Pomeroy, Martin and Gebhard (15, p 761) in their discussion of the physiological action of hormones write:

"While hormonal levels may affect the levels of sexual response—the intensity of response, the frequency of response, the frequency of overt sexual activity—there is no demonstrated relationship between any of the hormones and the individual's response to particular sorts of psychologic stimuli, an individual's interest in partners of a particular sex, or an individual's utilization of particular techniques in his or her sexual activity. Within limits, the levels of sexual response may be modified by reducing or increasing the amount of available hormone, but there seems to be no reason for believing that the patterns of sexual behavior may be modified by hormonal therapy."

Young (35), in a review, has written:

"Data bearing on the subject are scattered, but when they are brought together the case seems clearest for the conclusion that at all ages, the action of gonadal hormones is in the nature of an activation rather than an organization of patterns of behavior."

There appear to be at least three general ways that testosterone propionate could influence the excitatory level of an animal. However the present research can not be said to support one more than another.

Further, it should be pointed out in advance that these theories are not mutually exclusive, but they are offered for whatever value they may have in guiding future research.

One of the ways the androgen may influence the excitation-level of a male is through a direct effect on nervous tissue; this may occur without influencing the pattern of behavior expressed. The suggestion is consistent with the hypothesis advanced by Lashley which has already been cited.

A second way that testosterone propionate may activate a male sexually has been suggested by Kinsey, Pomeroy, Martin and Gebhard (15). These authors have suggested that androgens increase the general level of metabolic activity in the body including nervous activity. These metabolic changes account for the increased sexual responsiveness following injections of the hormone. It should be pointed out, however, that the experimental evidence in this area is deficient and that much more than these writers envisaged is involved. (21)

Still another type of relationship of hormonal action to level of excitation may occur as a result of the anatomical changes induced by androgen action. It is well known that hormonal substances are responsible for the growth and maintenance of the reproductive tract and its appendages. It is possible that the activity level of an animal may be raised by the stimulation of afferent nerve endings embedded in these structures as they respond to hormonal influence. In this case there would be an effect on nervous tissue as a result of hormonal action, but the effect would be indirect. The target organ of the hormone would not

be nervous tissue, but rather the reproductive tract and its accessory structures.

The statement will be recalled that androgenic substances have no direct organizing action which enables the animal to achieve complete copulation if it has not learned how (p. 34). We suggest, however that the hormone may act indirectly to affect the organization of the sensory-motor patterns involved in sexual behavior. The excitation-level of a male, for example, may have an indirect effect on the time necessary for organization of the motor patterns involved in sexual behavior. Perhaps the more active and vigorously a male approaches a female the greater will be his persistence in attempting to mount her and the more likely it is that his behavior would be organized relatively quickly. It will be recalled from experiments II and IIA that the heterogeneous animals, which are the most vigorous, also organized their sexual behavior at the earliest age.

There is a further possibility of indirect action on the sensory-motor patterns. If the hormone stimulates certain peripheral organs in such a way that areas of tension or erogeneous zones are created, this may exert a directing influence on the developing behavior patterns. Hypothetically, one may consider the cutaneous area around the genitalia as an erogenous zone that is under hormonal influence. This sensitive zone may act as a drive stimulus which 1) raises the excitatory level of the animal and, 2) tends to direct behavior into avenues that result in tension reduction. The latter factor may involve the repetition of behavior such as mounting, that would bring the erogenous zone into contact with another animal.

Lehrman (17) working on the relationship between prolactin and the parental feeding behavior of ring doves has come to conclusions similar to those suggested above. The ring dove feeds the squab by regurgitating a type of "milk" formed in the crop. He has shown that the ring doves "feed young for the first time, when they are breeding initially, in response to tactual stimulation of the engorged crop and of the throat." Through a learning process which takes place while feeding squabs, the ring dove will feed the young in response to non-tactual stimuli, e.g., sight and sound. Prolactin injections will engorge the crop, but will elicit feeding behavior to the sight and sound of the squab only in doves which have fed young before. If the crop is anaesthesized, prolactin will not elicit the feeding response even in experienced doves. The author concludes:

> "Prolactin acts to elicit regurgitation-feeding because it causes engorgement of the crop and supression of sexual behavior, rather than through any effect on central nervous mechanisms specific for parental behavior. The engorgement of the crop acts as a drive stimulus through which the dove learns to respond to the sight and/or sound of the squab. The effect of this drive stimulus can be reinstated in doves with breeding experience by prolactin injections."

The theoretical discussion presented above should not be interpreted to apply to all hormonal action to all kinds of behavior or to all species. What has been suggested, in a speculative vein, is that the action of testosterone propionate in stimulating sexual behavior of male guinea pigs appears to modify activity level rather than having any direct effect on the pattern of behavior. The activity level may be modified by androgenic influence on accessory sexual structures, by a direct effect on nervous tissue or by contributing to general metabolic changes. It has

also been suggested that the effect of testosterone propionate on the reproductive tract and accessory structures might indirectly influence the developing behavior patterns.

IV. SUMMARY AND CONCLUSIONS

A series of experiments were undertaken to investigate the role of experiential, hormonal and hereditary factors involved in the sexual behavior of the male guinea pig.

1. At birth 17 pairs of guinea pigs were interchanged in an attempt to determine the extent maternal influence between birth and weaning was responsible for differences in sexual behavior known to exist between two genetic stocks (a heterogeneous stock and an inbred strain) of animals (experiment I). The animals were interchanged in such a way that one male remained with its own mother while the other member of the pair was placed with a foster mother from the other genetic stock. At maturity, the males were tested with females in order to determine their level of sexual performance.

The results reflected no influence by the sow on later sexual performance. Apparently, therefore, strain differences in level of sexual behavior are not attributable to maternal influence between birth and weaning.

A maternal influence on rate of body growth was discovered. When placed with the heterogeneous sows both the inbred and heterogeneous animals grew faster than with the inbred sows. Yet the heterogeneous males gained weight significantly faster than the inbred males regardless of the placement. It would appear then that the genetic endowment plays the major role in determining growth rate and that this can be modified only within limits by maternal influence.

2. An attempt was made to determine whether sexual behavior was innately organized in the male guinea pig or whether contact with other animals played an important role in the organization of sexual behavior into an effective pattern (experiments II and IIA).

Fourteen genetically heterogeneous, 14 inbred Strain 13 and 36 inbred Strain 2 males were raised in social or isolated conditions. Significant differences were found between the sexual behavior of social and isolate Strain 2 animals. Only 1 of 17 isolate males intromitted and ejaculated, whereas 16 of 19 of the socially raised males did so consistently. Less marked but still significant differences were obtained with Strain 13 males. There were no significant differences between the social and isolate heterogeneous animals weaned at 25 days. However, when 20 additional social and isolate heterogeneous males were weaned at 10 days highly significant differences were obtained.

It is concluded for the male guinea pig: 1) Contact with other animals plays an important role in the organization of sexual behavior. 2) The influence of contact may be exerted very early. 3) Genetic differences between strains of guinea pigs are responsible for differences in the age at which organization of sexual behavior is possible and for the quantity of sexual behavior exhibited during tests.

3. An experiment was undertaken to determine the importance of the experiential background to influence the effectiveness of testosterone propionate to elicit sexual behavior. (experiment III)

Twenty-three social and isolate males of the inbred Strain 2 were castrated after their level of sexual performance had been ascertained by standard tests with females. After 10 weeks, when the animals had reached a base line of sexual activity, testosterone propionate was administered. Although large quantities were given only the social animals, who had previously given evidence of possessing an organized pattern of sexual behavior exhibited intromissions and ejaculations in subsequent tests. It is concluded that the experiential background of an animal can markedly influence the effectiveness of testosterone propionate to elicit sexual behavior. Implications for a theory of the relationship of androgen to sexual behavior were discussed.

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