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MINIREVIEW

Aging and Primate Male Sexual Behavior (42399)

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The scientific study of aging is a relatively new field of research, but with a population that is growing rapidly older, interest in the field has increased (1). Efforts have been directed primarily to the study of diseases of old age, and successful research will eventually result in an even older population.

Relatively little attention, however, has been directed toward an understanding of how aging affects sexual activity. This should surprise no one since the popular attitude is that problems related to sexual behavior, like sexual behavior itself, is the province of the young. In a landmark study on sexual behavior of the human male, Kinsey *et al.* (2) reported a decline in the sexual activity of old men. The work, however scientific in its sampling techniques and interview methods, was not experimental, and the causes of the decline in sexual activity of old men could only be surmised. In his review of aging and reproduction in the male, Bishop (3) agreed with Kinsey that psychological factors may be significant in the decline of sexual activity of aging men, but he noted the importance of age-dependent physiological factors as well. Bishop concluded that the nature of the decline is not well understood.

It is often assumed that the decline in sexual activity of old men is related to a decline in serum testosterone (T) levels and hence to reduced testicular activity. Some investigators have reported a decrease in mean serum T with age (4–6), some have found no change (7, 8), and some have found an increase (9). Some researchers have suggested that the reported decreases in T levels may have been due to sampling bias because institutionalized old men, not always in the best of health, often served as subjects (9). The circadian excursion of serum T levels is significantly lower in old men, even when healthy, than that in young men, and variations in the time of day when blood is sampled may account for the failure to find decreases in T levels (10).

If, in fact, serum T levels are not lower in old men, the decline in sexual activity may be due to a decrease in serum levels of free T (FTI). Here again there is disagreement as to whether FTI levels decline in old men. Harman and Tsitouras (9) found no change in FTI levels in healthy old men, but others found a decrease (6, 11, 12). The decline is said to precede the decline in total serum T levels. By implication, the decline in sexual activity could be attributed to a decline in the amount of FTI available to the relevant tissues.

Recently it was reported that even though serum T levels do not decline in healthy old men, sexual activity decreases (13). Unless a causal relationship between serum T levels and the decline in sexual activity of old men can be established, the fate of T levels in old men purely becomes a question of scientific interest, at least with respect to sexual behavior. To date, no causal relationship has been demonstrated (13). The broad question remains, what accounts for the decline in sexual activity of old men? Experimental study of the problem in an appropriate animal model could provide some important insights.

Until recently, with a few notable exceptions, there has been no experimental research on the sexual behavior of aging males of most species. The exceptions include a study by Minnick *et al.* (14), who reported an increase in mating activity of senile white rats treated with T, and a study by Larsson (15), who found that in 1-hr pairings, 2-year old male rats had fewer intromissions and ejaculations than 1-year-old rats. However, in a later study, when test duration was extended the 2-year-old males achieved a greater number of ejaculations than the younger males before reaching sexual exhaustion (16). Jakubczak (17) reported that the rates of intromission and ejaculation in 30-month-old male guinea pigs were significantly lower than those in 6-month-old animals. Several other studies were

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carried out on aging farm animals. Although the purpose was primarily to determine the effects of age on fertility, these studies did provide evidence of a decline in sexual interest and activity with increasing age (3).

In the past five years a number of reports dealing with sexual behavior and its hormonal control in aging male rats (18–21), mice (22–25), and hamsters (26) have been published. At least two studies have been carried out on reproductive function in old female macaques. The appropriateness of old female rhesus macaques as a model for the study of menopause in women has been extolled (27), and use of pigtail macaques as a model for the study of female reproductive senescence has received enthusiastic support (28). Female macaques may prove to be better models than chimpanzees for the study of certain aspects of human female menopause even though chimpanzees are considered to be phylogenetically closer to human beings. These studies have not addressed the question of sexual behavior in old females, postmenopausal or not. A few reports on the capacity of aging female macaques to respond behaviorally to hormonal stimulation in the peri- or postmenopausal period have been published recently (29–31).

For the past 10 years, we have intensively studied the sexual behavior of aging rhesus macaques. Since most of our males were wild-born, and ages were estimated upon arrival at the Oregon Regional Primate Research Center (ORPRC) on the basis of comparisons of general appearance, sexual maturity, dental state, and body weights between incoming monkeys and 120 rhesus males of known age born at the ORPRC, there are no definitive data on the maximum life span or mean life expectancy of male rhesus macaques born in the wild and later housed individually in laboratories (the conditions that apply to all of our male subjects). Maximum longevity records for rhesus macaques (sex not specified) vary from 19 years 6 months (32) and 21 years 6 months (33) to 25 to 27 years (34). At the ORPRC, the mean life expectancy of males born and reared on site is between 15 and 18 years. All males we designated as "old" were between 18 and 26 years of age and had been at the ORPRC for at least 11 years. The ages of the young to middle-aged males were estimated to be between 8 and 15 years and they had been at the ORPRC for at least 2 years.

In two longitudinal studies we followed the sexual behavior of eight males over a 10-year period. The average age was 10 years at the onset of the studies. The first study revealed a statistically significant decline over a 5-year period in the mean rate at which males contacted the female (a behavior that constitutes an invitation to copulate), mounted, and intromitted, and in the percentage of tests in which they ejaculated. The time from the beginning of the test until the male ejaculated (ejaculation latency) increased significantly (35). These results indicated that by 15 years of age, males tested under standardized conditions experience a loss of sexual vigor. Before completion of the second study, two males died. The behaviors of the remaining six males at the ages of 10 and 20 years were compared (Fig. 1). In addition to the differences found in the first study, the males showed a decline over a 10-year period in the percentage of tests in which they intromitted and a longer latency to intromission (36).

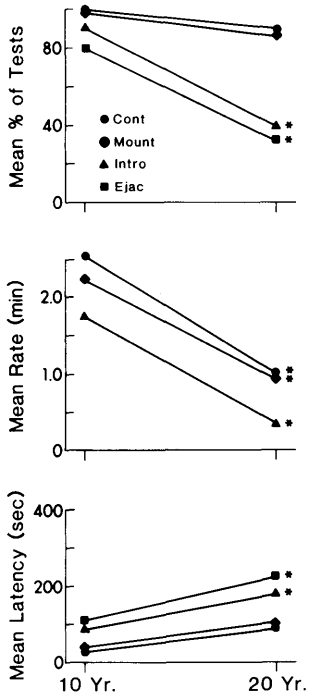

FIG. 1. Mean values for several measures of sexual behavior in intact rhesus males at 10 and 20 years of age. Abbreviations: cont, contact; intro, intromission; ejac, ejaculation. *Significant change, $P < 0.05$. Adapted from Chambers and Phoenix (36).

In subsequent prospective, cross-sectional studies, we compared the behaviors of young, middle-aged, and old males under the same standardized test conditions and found with few exceptions the same differences with increasing age (36–39). Robinson *et al.* (40) compared the ejaculation frequencies in three groups of four rhesus macaques. The old males (20 years old and older) ejaculated less frequently than the middle-aged males (10–15 years) or young males (5–8 years). Thus the decline in sexual behavior with age in the rhesus macaque is well documented. As rhesus males grow older they invite copulation, mount, intromit, and ejaculate less frequently, and when they engage in copulatory behavior it takes them longer to attain intromission and ejaculate.

Although sexual performance of old males with female partners decreases, we have no evidence of a decrease in the frequency of masturbation. Males frequently masturbate to ejaculation in their home cages whether or not they are paired daily with a female. Over a 2-week period, the number of days on which ejaculatory plugs were observed was not different in old (mean = 1.6 days, range = 0–6) and young (mean = 3.7 days, range = 1–11) males.

In accounting for the decline of sexual behavior, a major difficulty one faces is how to separate changes caused by physical inability from those caused by a loss of interest, i.e., changes with a psychological basis. Attempts to copulate persist in old males with disabilities such as paralysis of the legs, extensive kyphosis, and impaired vision. One male with mature cataracts in both eyes was functionally blind and made no attempt to locate the female in the test cage. The cataract in one eye was removed and with vision in one eye restored, he resumed mating in pair tests. Another male was castrated at 10 years of age, and he responded well to testosterone propionate (TP) therapy. When he was 15 years old, he showed signs of intestinal problems and most of his large intestine was resected. He recovered completely and was sexually active while under TP therapy for another 10 years.

When old males with no clinical signs of poor health were compared to young males in a 3-hr test with a preferred female, they showed similar performance with respect to number of ejaculatory series completed and behavior displayed within each series (Table 1). Also, when old males were repeatedly tested with a highly preferred female and young males were tested with a different randomly selected, but receptive, female in each test, their performance levels were comparable. Thus the reduced level of sexual activity in healthy rhesus males is not due to a loss of capacity to perform sexually or to physical debilitation per se. The specific nature of the decline in sexual behavior of old males appears to be a decrease in the number of females with which they will copulate.

Assessment of sexual vigor as measured here would not be possible in a free-living troop of rhesus males and females. In addition, one could expect competition for receptive females that would introduce other variables, such as dominance and aggression, also requiring assessment. Dominance and aggression may be important considerations. Their influence on sexual performance of old males require special attention. The problem has not been investigated in rhesus macaques, but some information is available on a naturally occurring troop of Japanese macaques (*Macaca fuscata*)

TABLE I. MEAN MEASURES OF PERFORMANCE OF OLD AND YOUNG MALES IN 3-hr TESTS OF SEXUAL BEHAVIOR WITH FEMALE 1339[a]

Measure	Old males	Young males	t^b	*df*
No. ejac series	2.7	2.3	0.48	10
Mounts to ejac				
ES1	4.7	2.6	1.57	9
ES2	7.0	22.4	1.62	8
ES3	15.5	12.3	0.51	5
Intros to ejac				
ES1	2.3	2.2	0.18	9
ES2	3.8	14.2	1.23	8
ES3	9.5	6.7	0.64	5
Ejac latency				
ES1	793.0	285.0	1.01	9
ES2	2785.0	2946.3	0.15	8
ES3	4712.2	3605.0	0.77	5
PEI				
ES1	30.7	16.5	1.4	8
ES2	56.5	39.1	0.8	5

[a] Time measures are reported in seconds. Abbreviations: Ejac, ejaculation; ES, ejaculatory series; intros, intromissions; PEI, postejaculatory interval.

[b] Differences were not statistically significant.

living in a seminatural environment. The frequencies of mounting and ejaculation decline in old Japanese macaque males (41). The causes are not known, but loss of dominance has been excluded as an explanation. Whether the same is true in established troops of rhesus macaques remains to be determined, and the influence of social forces needs to be investigated.

There may still be some question as to whether serum T levels decline in old healthy men, but there is little doubt that they do not decline in old rhesus macaques. Robinson *et al.* (40) found no significant differences in serum T levels among young, middle-aged, and old males (20 years or older). In five studies between 1981 and 1984, we never found statistically significant differences between serum T levels in young, middle-aged, and old males either in the morning (0900 hr) or in the evening (2100 hr) (37–39, 42, 43). The diurnal patterns of serum T were the same for young and old males; levels were lowest at 0900 hr and highest at 2100 hr (Fig. 2). Some of the serum T determinations (radioimmunoassay) were based on a single blood sample from each male, but others were based on two to five samples taken on consecutive days from each of five or more males in each group. Our most recently published results were based on samples taken from eight males ranging in age from 19 to 25 years (mean about 22 years) and from middle-aged males ranging from 9 to 15 years (mean about 12 years); blood samples were taken at 0900 hr on 2 consecutive days (39).

Accepting of the no-difference hypothesis warrants caution. Most of the old males studied were wild-born and their exact ages were not known. However, the males had been at the ORPRC for at least 15 years at the time of testing, and we are confident of the age estimates. The consistency of observations with respect to behavior and hormone levels argues for the validity of the findings.

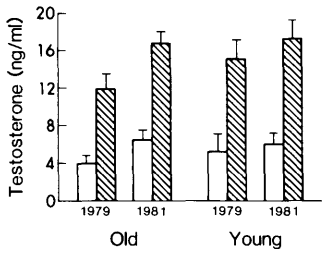

FIG. 2. Mean (+SE) levels of testosterone in old and young male rhesus macaques at 0900 hr (clear bars) and 2100 hr (hatched bars) in 1979 and 1981. All 0900-hr values differed significantly from 2100-hr values ($P < 0.05$) for both old and young males. Adapted from Chambers and Phoenix (43) and Chambers *et al.* (37).

Because of the reports of a significant decline in FTI in old men (12, 6, 11), the possibility of such a decline in old rhesus males needed to be explored. Blood was drawn from nine 20-year-old and nine 10-year-old males for 5 consecutive days and was assayed for FTI by the method of Harman and Danner (44) to obtain an index. The FTI values did not differ significantly between young and old males and did not differ across the 5 days. There were no significant correlations of FTI with any measure of sexual performance (42). Mean fractional binding of T was significantly greater in the 20-year-old males than in the 10-year-old animals. What causes the higher fractional binding of T to T-binding globulin (TeBG) in old age is unclear. It has been suggested that the increased binding capacity in old men is related to an increase in circulating estradiol (E) and that the increase in this hormone is the result of increased peripheral aromatization of androgen to estrogen (12). Not only do researchers disagree as to whether estrogen or other metabolites of androgen change with age, but when they have found changes they have not agreed on the causes (9).

Differences between young and old rhesus males in serum levels of T metabolites or other gonadal or related hormones, as well as differences in diurnal variations in these hormones, might account for differences in sexual performance. However, young and old males did not differ in overall mean levels of dihydrotestosterone (DHT), E, luteinizing hormone (LH), or cortisol (37, 42). There were no significant differences between old and young males in serum levels of these hormones at 0900 and 2100 hr. The DHT and LH levels were higher at 2100 than at 0900 hr and E and cortisol levels were higher at 0900 than at 2100 hr for both old and young males (37; Fig. 3). Serum levels of E were higher at 0900 than at 2100 hr for old and young males combined, as indicated by an analysis of variance, and the age × time interaction effect was not significant. Separate statistical tests (paired *t*) for

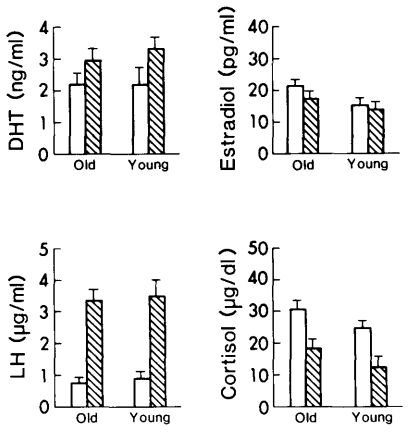

FIG. 3. Mean (+SE) levels of dihydrotestosterone (DHT), estradiol, luteinizing hormone (LH), and cortisol. All 0900-hr values differed significantly from 2100-hr values ($P < 0.05$) for both old and young males for each hormone. Data from Chambers and Phoenix (43) and Chambers *et al.* (37).

day–night differences within each group indicated that only among old males was the 0900-hr serum level of E significantly higher than the 2100-hr level. In an earlier study (43), we used different males and took more blood samples per day but for fewer days. We found that serum E levels of young and old did not differ between 0900 and 2100 hr. In the same study cortisol levels were lower in old than young males at 2100 hr. We are uncertain if and how the difference in sampling could account for the disparate findings, and await additional information.

Institutionalized old men that served as subjects in studies on serum T levels were probably not sexually active for a considerable period of time before blood samples were taken. At least in young men, mean levels of urinary T were higher in weeks of sexual activity with a woman than during periods of no sexual activity (45). If T levels are related to sexual activity, some of the differences obtained in studies of T levels in old men might be clarified. Here interest was focused on the effects of sexual activity and ejaculation that lasted for several hours or days rather than on immediate effects (46). It also seemed useful to learn whether an initial high level of performance would follow the end of sexual deprivation and whether this level would soon fall during repeated daily pairings with receptive females. After about 6 months without access to a female, eight old males (19 to 25 years) and eight middle-aged males (9 to 15 years) were given daily 10-min pair tests for 9 consecutive days with a receptive female. There were no significant differences between serum T levels after 6 months of sexual deprivation and after nine daily tests of sexual behavior. Serum T levels did not differ between middle-aged and old males, and were higher at 2100 than at 0900 hr for both groups (Fig. 4). Repeated testing had little effect on the major components of male sexual behavior. Middle-aged males again outperformed old males (Fig. 5).

Repeated attempts to find meaningful and reliable patterns of rank-order correlations between serum hormone levels and sexual performance in old males have proved futile (37, 38, 42, 43). In only one of four studies was T found to be significantly correlated with different measures of sexual performance. Significant correlations between rates of contacting and mounting and frequency of erection and cortisol levels were found in one study but not in another. No significant correlations have been found between sexual performance and serum levels of DHT and E. The results of these studies have led us to conclude that any correlation, even with the highest level of

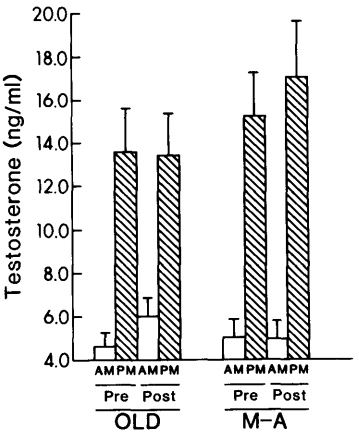

FIG. 4. Mean (+SE) levels of serum testosterone in old and middle-aged (M-A) rhesus macaques at 0900 (AM) and 2100 (PM) hr after 6 months without a female partner and after 9 consecutive days of testing with receptive females. The AM levels were significantly lower than the PM levels in each instance ($P < 0.01$). Differences between old and M-A macaques and between before and after tests were not statistically significant ($P > 0.05$). Adapted from Phoenix and Chambers (39).

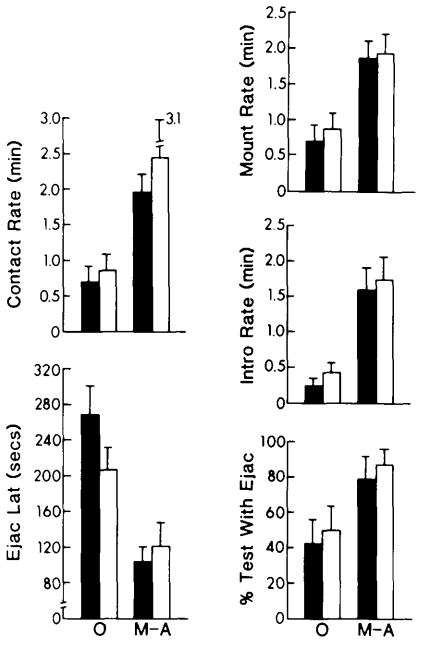

FIG. 5. Sexual performance (mean + SEM) of old (O) and middle-aged (M-A) rhesus males in deprived states (black bars) and nondeprived states (white bars). Performance of the old males differed significantly from that of the M-A males in each measure ($P < 0.05$), but values did not differ for either group between the deprived and nondeprived state ($P > 0.05$). Abbreviations: Ejac, ejaculation; Intro, intromission; Lat, latency. Adapted from Phoenix and Chambers (38).

statistical significance, must be regarded as tentative unless repeated in successive independent studies. The difficulty is probably related to the small number of animals used in each study. Current information has led us to propose that hormones in peripheral vein blood, specifically T, DHT, E, and cortisol, have varying suprathreshold amounts with respect to behavior. Therefore, specific serum levels of a hormone such as T need not be correlated with levels of sexual performance, even though depletion of this hormone has significant effects on the level of sexual performance (37).

The only behavior found to have repeated significant correlations with T levels is yawning (38, 43). Yawning is most commonly displayed by the male when he is paired with a female. Although yawning has been labeled a "dominance display" (47), its significance is unknown. The facial expression resembles that displayed by human beings but to our knowledge it is not readily analogous to any aspect of sex-related behavior in man. In the rhesus macaque, given the appropriate environmental conditions, display of the response depends upon T stimulation. Daily injection of as little as 0.004 mg/kg of TP/kg of body weight increases the frequency of yawning in old long-term castrated males to that observed in equally old intact males (48). Normal levels of serum T in males (old or young) does not ensure that males will yawn during pair tests with females, but with low levels of T such as those found in untreated castrated males, yawning rarely if ever occurs. Although we have not found any differences between old and young males in the frequency of yawning, others have found that yawn rate is significantly less in old and middle-aged males than in young males (40).

If sexual function declines or is lost in old men as a result of reduced serum T levels then treating such men with T would presumably restore sexual function. Masters and Johnson (49) have reported such a case, but Tsitouras *et al.* (13) point out that there are no published data showing a causal relationship between sexual behavior and serum T levels in old men.

We attempted to increase the sexual performance of the four poorest performing intact rhesus males in a group of seven 15-year-old males by injecting them daily with 1 mg of TP/kg of body weight. Overall the treatment was ineffective. The TP-treated males continued to differ significantly from the untreated males in rate of contacting, rate of mounting, percentage of tests with ejaculation, and ejaculation latency (35). We propose that T treatment is effective only when there is a measurable deficiency in the hormone. Such instances are probably rare in men and rhesus males.

The effect of T treatment on sexual behavior of old males was examined further in a group of sexually experienced castrated males (36). These males had been castrated when they were about 10 years old. One year after castration, daily injection of 10 mg of TP (mean weight was about 10 kg; $N = 10$) completely restored behavior to precastration levels and to the level in an intact group of the same age (50). However, when the castrated monkeys were 20 years of age, this dose of TP no longer restored behavior to precastration levels or to levels found in young intact males despite the fact that serum levels of T were five times

higher in the castrated monkeys (mean = 43.9 ng/ml) than in the young monkeys (8.9 ng/ml). Testosterone treatment did increase the sexual performance of castrated males to that of 20-year-old intact males. Further daily injections of 50 mg (mean serum T levels = 187.7 ng/ml) did not increase any measure of sexual performance above the level displayed when 10 mg was given. These experiments indicate that old males given appropriate TP treatment will perform to the mean level of their age group and that even supraphysiological amounts of serum T will not produce superior performance. Similar results have been found in a study of old male rats (19).

Sexual behavior in aging males may be directly affected by degenerative changes in pathways mediating the behavior or it may be indirectly affected by degenerative changes in other systems, e.g., general arousal. Larsson increased the sexual activity of old male rats by handling them (51). Handling was conceptualized as a source of nonsexual sensory stimulation that would have a general arousal function. Novelty, which could be considered an aspect of the same principle, was shown to increase sexual responsiveness in adult dairy bulls (52, 53) but the effect has not been investigated in old bulls. Kinsey *et al.* (2) proposed that sexual activity increases in old men in new situations. A decline in the capacity for general arousal in old age could account for part of the decline in sexual behavior in old males. In a series of studies, we tested the hypothesis that increases in general arousal lead to increased sexual performance in old males.

We attempted to increase sexual performance in old males by introducing a source of nonspecific stimulation during tests of sexual behavior. An active young adult male "stranger" was used as a nonspecific stimulus. He was placed in the test room in view of the experimental animals but not in the test cage. Only one significant difference was observed when the "stranger" was present: mean latency to the first mount increased from 58.2 to 114.5 sec. It was apparent that the old males were not sufficiently distracted or excited to alter their typical level of sexual performance.

In another attempt to increase general arousal, we moved old and middle-aged rhesus males that had been housed in the same cage and room for several years to a new location in an adjacent building. The new room contained other unfamiliar rhesus males and females and the sounds of different nonhuman primate species housed in adjoining rooms could be heard. The personnel caring for the animals also were different. Their sexual behavior and hormone levels in the weeks preceding the move were compared to those after the move. The hypothesis that the nonspecific sensory stimulation provided by the move would increase levels of sexual behavior was not supported by the data. To the contrary, the percentages of tests with contacts, mounts, and penile erections, and the rate of contacting the female, declined (Table II). As in previous studies, middle-aged males displayed significantly higher levels of sexual activity than did old males. Serum T levels did not differ between middle-aged and old males, and the new environment did not produce significant changes in serum T levels. Serum cortisol levels were significantly higher about 1 hr after the move but returned to premove levels the following day (38).

Masters and Johnson (54) described a slower arousal and general delay in the sexual response as characteristic of coitus in aging men; they also take longer to develop penile erections in response to erotic stimuli than do young men (55). The standard test used in experiments reported here lasted 10 min or until the males ejaculated. If old males failed to ejaculate it may have been that with a heightened arousal threshold they required more time with the female. The hypothesis was tested in rhesus males in an experiment in which the sexual behavior displayed by nine old (20 years old and older) rhesus males in 10-min tests was compared to that displayed by the same monkeys in 1-hr tests. Each male was paired with each of 10 receptive females under each condition. The percentages of males that achieved intromission and ejaculated under the two test conditions were the same. Although the percentage of tests in which males displayed these behaviors was higher in the longer tests, there was a significant positive correlation of performance in 10-min tests with performance in 1-hr tests. The mean percentages of contacts, mounts, intromissions, and ejaculations in 1-hr tests were significantly lower than those in 10-min tests conducted with the same males 11 years earlier

TABLE II. SEVERAL MEASURES OF SEXUAL BEHAVIOR IN OLD AND MIDDLE-AGED RHESUS MACAQUES BEFORE AND AFTER BEING MOVED TO A NEW LOCATION[a]

	Old		Young	
	Before	After	Before	After
Rate (min)				
Cont[b,c]	0.52 (0.10)	0.34 (0.08)	1.41 (0.29)	1.14 (0.21)
Mount[b]	0.47 (0.11)	0.30 (0.09)	1.11 (0.16)	0.96 (0.19)
Intro[b]	0.18 (0.07)	0.14 (0.07)	0.80 (0.19)	0.69 (0.22)
Percentage of tests				
Cont[c]	81 (7)	69 (6)	89 (4)	83 (4)
Mount[c]	64 (10)	56 (10)	92 (4)	75 (4)
Intro[b,d]	28 (10)	33 (10)	83 (7)	61 (8)
Ejac[b]	19 (7)	19 (12)	61 (10)	58 (10)
Erection[b,c]	75 (8)	61 (8)	92 (6)	83 (6)
Latency (min)				
First mount	1.8 (0.39)	2.2 (0.44)	1.4 (0.25)	1.3 (0.28)
First intro[d]	2.2 (0.42)	3.9 (0.75)	2.4 (0.46)	2.0 (0.49)
Ejac	3.3 (0.23)	4.6 (1.80)	3.7 (0.56)	2.8 (0.48)

[a] Mean and SEM in parentheses. Abbreviations: Cont, contact; Ejac, ejaculation; Intro, intromission. Adapted from Phoenix and Chambers (38).
[b] Analysis of variance, significant age effects ($P < 0.04$).
[c] Analysis of variance, significant treatment effects ($P < 0.04$).
[d] Analysis of variance, significant age × treatment interaction ($P < 0.01$).

(Table III). Hence, the decline in sexual performance was not an artifact of limited test duration (56).

Kinsey *et al.* (2) suggested that the loss of interest that accompanies the repetition of the same kind of experience with the same sexual partner might account for the declining sexual performance of old men. Whether this be true and if so, how long new partners are effective in increasing sexual activity remain scientifically untested. We tested a parallel hypothesis in old rhesus males that had been paired with the same ten ovariectomized estrogen-treated females periodically for 10 years or more. Ten ovariectomized females of the same age (14 to 23 years), 11 old intact cycling females (14–18 years), and 10 young intact females (4 years) that were totally unknown to the males were selected as new partners. The ovariectomized females were treated with estradiol benzoate as other females had been, and the intact females served as partners during the periovulatory period. The new partners failed to increase the performance levels of the old males (57). Although the experiments are not directly comparable, young males, housed in the same room and repeatedly tested with the same 4 females displayed increased potency when paired with new female partners (58). Whether the same would be true for old males remains untested, but in view of present evidence, it appears unlikely.

TABLE III. MEAN PERCENTAGES OF 10-min TESTS IN 1969 AND 1-hr TESTS IN 1981 IN WHICH SIX RHESUS MALES CONTACTED, MOUNTED, INTROMITTED, AND EJACULATED[a]

	% Tests in which behavior occurred		
Behavior	1969	1981	t^b
Contacting	98.3	79.2	3.14
Mounting	98.3	73.8	4.56
Intromission	91.7	43.8	4.56
Ejaculation	80.0	37.2	3.72

[a] Adapted from Phoenix and Chambers (56).
[b] $df = 5$, $P < 0.05$ in each case.

Although the sexual behavior of old males did not increase when they are paired with unfamiliar or young females, we have demonstrated the critical role played by females in studies pairing old males with preferred females. Preferred females are more sexually receptive and they invite old males to copulate more often than do females chosen at random. Most females are more receptive and solicit

copulation more often from young males than from old (59).

For centuries men have searched for effective aphrodisiacs. Despite tremendous progress in the development of drugs that control behavior and disease, no drugs are known to enhance sexual interest or performance other than indirectly through control of disease. As we learn more about the changes in the nervous system that accompany aging, drugs effective against the declining sexual performance that accompanies aging may be developed. Because we know so little about brain systems that control sexual appetite (drive, libido, and desire) attepts to enhance sexual behavior pharmacologically are still somewhat haphazard.

One popular hypothesis generated on the basis of pharmacological studies in male rats is that dopaminergic transmission is facilitatory (60–63), and serotonergic transmission is inhibitory (64–67). More recent reports suggest the noradrenergic system plays an inhibitory role as well (68).

Apomorphine, a dopaminergic agonist, para-chlorophenylalanine, a serotonergic antagonist, and yohimbine, a noradrenergic antagonist, have been shown to increase sexual behavior in adult male rats (62, 64, 68). Further, (−)deprenyl, a dopaminergic agonist, has been shown to increase sexual behavior in old male rats (69).

On the basis of these reports, we initiated a series of experiments designed to determine the effects of dopaminergic agonists and serotonergic and norandronergic antagonists on sexual behavior of old rhesus males. We tested 10 old intact males after injection of vehicle and after 0.15- and 0.20-mg/kg injections of apomorphine. Apomorphine did not alter the percentages of tests in which males mounted, intromitted, or ejaculated, or the number of males exhibiting these behaviors (Table IV).

Two old males were tested after injections of vehicle and after injections of yohimbine at three dose levels (1.0, 1.5, and 2.0 mg/kg). Yohimbine did not increase the number of mounts, intromissions, or ejaculations in the two males. The results of preliminary tests in which we treated six old rhesus males with (−)deprenyl (0.25 and 0.40 mg/kg) do not appear promising (Chambers and Phoenix, unpublished data). Thus far the very limited use of drugs to increase sexual behavior in old rhesus males has not been successful. Whether these failures reflect a general difference in the systems mediating sexual behavior in the rat and rhesus macaque or are indicators of differential age-related changes in the systems on which these drugs act has yet to be determined.

Summary. Old male rhesus macaques display less sexual behavior than young and middle-aged males. The decrease in sexual activity occurs without a statistically significant decline in gonadal hormones or change in diurnal patterns of serum T, DHT, or LH. Levels of sexual activity are not increased by administering T to old intact males. However, the hormone is effective in increasing sexual behavior in old long-term-castrated males. Performance can be increased to levels observed in equally old untreated intact males. Readily

TABLE IV. PERCENTAGES OF OLD MALES EXHIBITING A MOUNT, INTROMISSION, AND EJACULATION, AND PERCENTAGES OF TESTS IN WHICH OLD MALES EXHIBITED THESE BEHAVIORS WITHOUT AND WITH APOMORPHINE[a]

	Saline	APO (0.15 mg)	Saline	APO (0.20 mg)
% Males exhibiting				
Mount	100	90	100	60
Intromission	60	60	40	30
Ejaculation	40	20	30	10
% Tests with				
Mount	80 ± 5	65 ± 9	80 ± 8	50 ± 15
Intromission	37 ± 12	35 ± 12	30 ± 13	30 ± 15
Ejaculation	22 ± 11	10 ± 7	25 ± 13	5 ± 5

[a] None of the differences were significant ($P > 0.05$).

detectable physical disabilities of old age have been observed to impair sexual performance, but the observed general decline in sexual activity cannot be accounted for by known physical disabilities. Novelty, as represented by a change in female partner or by a change in environment, has not increased sexual performance in old rhesus males. Only when old males were paired with empirically selected preferred females is their sexual behavior increased to levels displayed by young males. Drugs reported to increase levels of sexual behavior in rats have thus far been less effective in old rhesus males than powdered rhinoceros horn has been in man. The probable absence of a placebo effect in rhesus males should increase their usefulness as an animal model for the study of sexual behavior in aging men.

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