Effects of prolonged interintromission delays on the copulatory behavior of the male golden hamster

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When male hamsters were forced to delay copulation for 60 sec after the first intromission, the total number of intromissions required to produce ejaculation was significantly decreased. However, if a 60-sec delay was imposed after each intromission, the frequency of intromissions to ejaculation was significantly increased. Both delay conditions significantly reduced the postejaculatory interval following the first ejaculation. These results were compared to the effects of enforcing interintromission delays on the male rat, as reported in previous studies, and the similarities and differences between the two species were noted. An attempt was made to account for the present results in terms of an interaction between a central excitatory mechanism and a peripheral excitatory mechanism.

The copulatory patterns of the male golden hamster and the male rat are similar in certain respects. Males of both species achieve several ejaculations within a single mating session with each ejaculation preceded by a number of vaginal intromissions. Successive intromissions are separated in time by a sexually inactive period termed the interintromission interval.

Several studies have shown that the intromission frequency preceding the first ejaculation of the male rat can be altered by artificially prolonging the interintromission interval. The effect of the enforced delay is dependent upon the duration of the interval imposed. Relatively short delays result in a significant reduction in the frequency of intromission (Beach & Whalen, 1959; Carlsson & Larsson, 1962; Larsson, 1959, 1960). This effect was observed initially by Rasmussen and reported in a monograph by Larsson (1956). Gerall (1958) reported a similar effect for the male guinea pig. Bermant (1964) found that a single enforced delay imposed after the first intromission or after the fourth intromission of the male rat significantly reduced the number of intromissions prior to ejaculation but the reduction effect was maximized if a delay was imposed after every intromission. When relatively long delays are imposed between successive intromissions, the frequency of intromission increases and the occurrence of the ejaculatory reflex may be prevented. Larsson (1960) stated that the ejaculatory reflex is not likely to appear when the interintromission interval is prolonged to 10 min or more, even after numerous intromissions. In the same study, Larsson found that a 20-min

delay between intromissions of the male rat greatly reduced the probability of ejaculation.

The interpretation of the "enforced interval effect" is that the excitation produced by an intromission does not reach a maximum until some point in time that exceeds the male's ad lib interintromission interval. As a result, relatively short delays allow the maximum excitatory effects of an intromission to be realized and fewer intromissions are required to produce ejaculation. Beyond that point, the excitatory effects of an intromission begin to decay and an increasingly greater number of intromissions are necessary for ejaculation. According to the model developed by Bermant (1967), the excitatory effects are at a peak 3-4 min following intromission and gradually decay thereafter until, at 7-8 min, no excitatory effects of the previous intromission remain.

Sessions & Miller (1970) found that a 60-sec interintromission delay imposed after each intromission significantly increased the frequency of intromissions preceding the initial ejaculation of the male hamster. A 30-sec interval imposed after each intromission had a similar effect, but the increase was not statistically significant. The present study was intended to confirm the results of Sessions and Miller and to extend the investigation to the effects of a single delay enforced after the first intromission only.

SUBJECTS

Fourteen male golden hamsters, each approximately 150 days old, served as Ss. The males were experienced in that each had copulated to a satiety criterion of 15 min without intromission on seven

different occasions prior to the present experiment. Females of the same age and strain served as mating partners. The females had been ovariectomized and were brought into estrus by an intramuscular injection of 0.1 mg of estradiol benzoate 75 h prior to testing and an intramuscular injection of 1.0 mg of progesterone 3 h prior to testing.

All animals were individually housed with constant access to food and water. The colony was maintained under an altered light-dark cycle, in which the lights came on at 12:00 midnight and went off at 12:00 noon. Testing was conducted in the early portion of the dark cycle, between 1:00 p.m. and 4:00 p.m.

APPARATUS AND PROCEDURE

The observation arena was a circular Plexiglas enclosure 45 cm in diam. The arena had a clear glass floor and was mounted in a frame so that a mirror could be positioned beneath the floor to afford the E a ventral view of the animals. This allowed the E to easily distinguish mounts (abortive copulatory attempts), intromissions, and ejaculations. An Esterline-Angus event recorder was used to record intromissions, ejaculations, and interresponse intervals.

Preceding each test, the male was allowed a 5-min period to adapt to the apparatus. Each S was tested on four different occasions with each test separated by a period of 7 days. In the first test, or pretest, each male was allowed to copulate without E intervention until five ejaculations had been recorded. At that point, the test was terminated. For the second test, the males were divided randomly into two groups of seven animals each. One group was tested under the single delay condition and the other was tested under the multiple delay condition. In the single delay test, the female was removed, by hand, from the arena for a 60-sec period immediately after the male achieved the initial intromission. At the end of the 60-sec interval, the female was returned and the male was allowed to continue without interruption until two ejaculations were achieved, at which point the test was stopped. The multiple delay tests were procedurally identical to the single delay tests, except that the female was removed for 60 sec after each intromission until the first ejaculation occurred. For the third test, the testing conditions for the two groups were reversed from those of the second test. Otherwise, there were no procedural differences between the second and the third tests. Finally, each male was given a postexperimental test under conditions identical to that used in the pretest. Since the previous study by

Table 1
Mean Intromission Frequency Preceding the First Ejaculation (IF₁), Mean Postejaculatory Interval (PEI), and Mean Intromission Frequency Preceding the Second Ejaculation (IF₂) in Each Test

Test	Measure		
	IF ₁	PEI	IF ₂
Pretest	16.5	62.4	3.7
Single Delay	7.7	36.3	3.5
Multiple Delay	28.9	34.3	2.8
Posttest	14.4	61.6	3.2

Sessions & Miller (1970) included controls for the effects of handling, such procedures were not included in the present study.

A record was made of the intromission frequency preceding the first ejaculation, the interval between the first ejaculation and the next intromission, termed the postejaculatory interval, and the number of intromissions required for the second ejaculation. Between-test comparisons of the frequency data were made by means of the Wilcoxon T test (Siegel, 1956), and the interval data were analyzed by means of the t ratio for matched observations.

RESULTS

During the multiple delay tests, 2 males achieved successive intromissions so quickly that it was not possible to remove the female before the next intromission occurred. The data from these two males were excluded from the study. For the remaining 12 males, there were no significant differences between the pre- and posttests on any measure employed. Consequently, the remaining between-tests comparisons used the pretest only as the basis for the comparison of the enforced delay effects.

When interintromission delays were imposed, there were statistically significant changes in the intromission frequency preceding the first ejaculation and in the postejaculatory interval. The intromission frequency of the second copulatory series was not significantly altered under any testing condition. When a 60-sec delay was imposed after the first intromission only, the intromission frequency preceding the first ejaculation was significantly reduced in comparison to that observed during the pretest ($T = 0$, $p < .01$). In contrast, when a 60-sec delay was imposed after each intromission, the frequency of intromission preceding the first ejaculation was significantly increased ($T = 9$, $p = .02$). One male required 105 intromissions before ejaculation was achieved with multiple enforced delays. An inspection of the data from this male's last test to satiety, which took place 21 days prior

to the beginning of the present study, showed that the animal had achieved 12 ejaculations prior to satiety, all of which had required only 34 intromissions.

The postejaculatory interval was significantly reduced from that recorded in the pretest in both the single delay condition ($t = 3.30$, $df = 11$, $p < .01$) and the multiple delay condition ($t = 3.54$, $df = 11$, $p < .01$). The mean value for each measure in each testing condition is presented in Table 1.

Throughout the study, no male required longer than 15 sec to renew copulatory activities when the female was returned at the end of the delay period. During the multiple delay tests, it was obvious that some males were maintaining intromission for an extended period of time. Some even began rhythmic pelvic thrusting without terminating vaginal penetration, a form of intromission also observed late in a mating test to satiety. Furthermore, when multiple delays were imposed, several males greatly abbreviated or eliminated altogether the autogenital grooming period typically observed between intromissions and, instead, attempted to remount the female immediately. To prevent the male from achieving two closely spaced intromissions, the E had to remove the female very quickly.

DISCUSSION

The results of the present study confirm the findings of Sessions & Miller (1970) that multiple 60-sec interintromission delays significantly increase the number of intromissions required by the male hamster to achieve ejaculation. However, a single delay of the same duration imposed only after the first intromission significantly reduced the number of intromissions required for ejaculation. This is in contrast to the results reported by Bermant (1964) on the effects of single and multiple enforced delays imposed on the male rat. In the Bermant study, multiple delays enhanced the frequency reduction effect produced by single delays imposed after the first or fourth intromission. In the present study, both delay conditions significantly reduced the postejaculatory interval, and a similar effect was observed in the male rat by Bermant.

As Bermant noted, a reduction in intromission frequency and a decrease in the postejaculatory interval suggest an increase in sexual efficiency. It also suggests a heightened state of sexual excitation in that less genital stimulation is required to produce ejaculation and the pacing of the male's responses is accelerated. For the hamster, the assumption of heightened

sexual excitation is further supported by the immediacy of the male's response when the female is returned, the quickening of successive intromissions, and the change in the pattern and duration of the intromission response. Carlsson & Larsson (1962) recorded significant increases in the duration of intromission following artificially prolonged interintromission intervals in the male rat and suggested that the increase in duration compensated in time for a decrease in intromission frequency.

Under the multiple delay conditions, the male hamster gave every indication of being in a high state of sexual excitement. This is particularly true in terms of the male's immediate response when the female was returned. Hard & Larsson (1970) found that the mount attempt latency of the male rat following interintromission delay decreased as the enforced interval increased up to approximately 2 min and thereafter increased as the duration of the delay increased. This was interpreted as indicating that the excitatory effects of the preceding intromission begin to extinguish beyond a 2-min delay, and, since intromission frequency did not show a corresponding increase as mount latency increased, it was concluded that the latency measure was a more sensitive index of changes in the excitatory effects of intromission. If this is true of the hamster as well, it may be concluded that the male hamster is in a highly excited state when multiple delays are imposed, since the latency of the male's response was quite brief. Nevertheless, significantly more intromissions were required for ejaculation than under ad lib copulatory conditions. While observing these males copulate, the impression given was that the animal was highly excited but lacked the necessary repetitive genital stimulation to achieve ejaculation. This suggests that the male's behavior is jointly determined by an interaction between a central mechanism and a peripheral mechanism. The primary source of stimulation for the peripheral mechanism seems to be genital stimulation, whereas the central mechanism is probably activated by several factors such as general arousal, stimuli from the receptive female, feedback from genital stimulation, as well as other factors. Whatever the nature of the effect of enforced delays, it appears to act on the central mechanism and can be offset by multiple interintromission delays, at least in the hamster. On the other hand, the central effects of a single delay appear to override the

momentary postponement of genital stimulation resulting from a single delay.

The present study represents an initial investigation of the effect of delayed copulation on the mating pattern of the male hamster. More complete and parametric studies are needed for a better understanding of these effects.

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