Interaction Between Penile Reflexes and Copulation in Male Rats

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Intact, unanesthetized male rats were placed in a supine position, with the penile sheath continuously retracted. Three forms of penile reflex were displayed: erections, cups, and flips. The reciprocal relation between copulation and the penile reflexes occurring in supine tests was explored in four experiments. In Experiment 1, sexual exhaustion depressed all penile reflexes, but the reflexes returned to baseline levels within 8 hr, long before copulatory potential. In Experiment 2, reflexes were depressed to exhaustion levels after fewer ejaculations than were required for sexual exhaustion, an indication that reflexes are more readily evoked during copulation than in supine tests. Experiment 3 determined that a rat's penile-reflex potential may be enhanced by placing the rat in a copulation-test cage, by allowing the male a few antecedent intromissions, or by allowing an antecedent ejaculation. The display of penile reflexes within 1 min after ejaculation suggests that the period of reduced sexual arousability following ejaculation is not due to reduced excitability in the spinal mechanisms controlling penile reflexes. In Experiment 4, 1 hr of penile-reflex elicitation had no effect on subsequent copulatory behavior. Thus, sexual stimulation may increase or decrease penile-reflex potential, but a reciprocal influence was not detectable.

Copulation, like most other vertebrate activities, requires the integration of spinally mediated reflexes into an ordered sequence of movements of the whole animal. Therefore, an understanding of copulatory behavior requires analysis of the relation between the reflexes and the integrated behavior pattern. That relation is the topic of this article.

Penile reflexes may be elicited from spinaly transected humans (Zeitlin, Cottrell, & Lloyd, 1957), cats (Dusser de Barenne & Koskoff, 1932), dogs (Hart, 1967; Hart & Kitchell, 1966; Sherrington, 1900), guinea pigs (Bacq, 1931), and laboratory rats (Hart, 1968), which indicates that penile reflexes are organized substantially at the spinal level. However, the reflexes are also subject to considerable supraspinal control (for a review, see Beach, 1967).

Much of the recent work has been done with rats. The male is held in a supine position, and the penile sheath is continuously retracted by maintaining light pressure at the base of the penis. No further stimulation is applied. Three forms of penile response may occur: erection, which is penile extension and distension; cup, in which the distal end of the erect penis flares out; and flip, which is a rapid dorsal flexion of the penis. Clusters of erections, cups, and flips continue at 1–3-min intervals for an hour or more without apparent phasic stimulation. These penile actions are observable in neurally intact males and they are potentiated by spinal transection (Hart, 1968). The reflexes occurring in supine tests are presumably related to penile actions occurring during copulation. At least there is a morphological similarity of the actions under the two conditions (Hart, 1968; Pollak & Sachs, 1976; Sachs & Garinello, Note 1). However, the temporal patterning of penile actions during reflex tests is not similar to those occurring during copulation (Hart, 1968; Sachs & Garinello, Note 1).

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This research was supported by U.S. Public Health Service Grant HD-08933 and by a grant from the University of Connecticut Research Foundation to Benjamin D. Sachs. Experiments 1 and 2 are similar to studies reported by Sachs and Garinello (Note 1), but different animals and procedures were used.
The copulatory behavior of rats consists of bouts of mounting interrupted by intervals without overt sexual activity. During each bout the male may mount the female one or more times, but rarely does the male achieve more than one intromission during a mount bout. Mounts involve one to five or more thrusts of the penis against the female's perineum while the penis is within or slightly extended from its sheath. The interthrust interval is 20–50 msec. When intromission does not occur, mounts may be repeated at intervals of 3–10 sec within a mount bout. Intromission is marked by a deep pelvic thrust synchronous with full penile extension, followed by synchronous pelvic and penile retraction. The duration of intromission is 200–300 msec. The interval between successive mount bouts averages about 1 min, and it is not affected by the number of mounts in the bout or by whether intromission occurs in a bout. The ejaculatory thrust is maintained 1–2 sec and is accompanied by full penile extension during which the tip flares into the cup-shaped structure. The coagulated semen is ejaculated into this cup and deposited in the vagina when the penis is partially retracted coincidentally with pelvic retraction. Soon after withdrawal, repeated penile flips are evident in males prevented from engaging in normal postwithdrawal oral–genital grooming (Hart & Haugen, 1971). Following the first ejaculation a male rat generally shows no further sexual activity for about 5 min. (For a more complete description, see Sachs and Barfield, 1976, and references cited therein.)

The male rat's penile responses during copulation differ in several respects from the penile actions in supine tests, as described by Hart (1968, 1978). In supine tests, the actions occur in clusters spaced 1–3 min apart. Full erection may occur several times within a reflex cluster, rather than only once as during a bout of mounting. Also, flips may be interspersed with erections during a reflex cluster, whereas flips are rarely seen during copulation (even with ventral viewing) except immediately after ejaculation. Furthermore, penile cups may be displayed several times during a response cluster (Sachs & Garinello, Note 1), whereas this cup occurs only during the terminal (ejaculatory) intromission during copulation (Pollak & Sachs, 1976). Finally, erections may last as long as 5 sec in reflex tests, compared with the 200–300 msec during copulation.

Thus, the penile actions in reflex tests have a very different duration and sequence from those that occur during copulation. Only the morphology of the actions is similar in the two conditions.

Beach (1967) cautioned that morphological resemblances among reflexes should not lead to premature conclusions about function; for example, sexuality need not be ascribed to newborn mammals simply because they may display erection or lordosis. The relation of the adult rat's penile reflexes to its copulatory behavior has not been established. Hart (1968) speculated cautiously about the functional role of the various penile reflexes. However, with rare exceptions (i.e., Davidson, Stefanick, Sachs, & Smith, in press; some animals in Hart, 1968; Sachs & Garinello, Note 1) studies of penile reflexes in rats have used males that were spinally transected or lightly anesthetized. These conditions have restricted the inferences that can be made about the functional significance of the reflexes.

In the following experiments we asked what the relation is between the rat's copulatory behavior and its penile responses emitted during supine tests. Specifically, we tested intact, unanesthetized, male rats to learn whether copulatory behavior and the penile reflexes of supine rats have reciprocal influences.

**General Method**

**Subjects**

Sexually experienced male rats (Long-Evans from Blue Spruce Farms, Altamont, New York), 120–150 days old, were chosen on the basis of their displaying penile reflexes during screening tests.

**Evaluation of Penile Reflexes**

Penile reflexes were elicited in a manner similar to the method described by Hart (1968). The animal was restrained on its back with the anterior portion of its body loosely enclosed in a glass cylinder, 6 cm in diam-
eter and 14 cm long. The legs were held manually, and a belt placed between the hip and ribs helped restrain the animal. The penis sheath was pushed behind the glans and held in position with a glass rod throughout the test. Tests were terminated 15 min after the first penile response or after 30 min if no responses occurred before then. Toe-activated buttons recorded penile responses on a Rustrak event recorder.

Reflex Classification and Description

The criteria for recording erection were distention and extension of the penis associated with increased reddening. Cups were defined as erections with a flaring of the tip sufficient to cause the distal end of the penis to be wider than the proximal portion. Sometimes an erection is held momentarily before the cup develops. At other times, an erection with cup forms directly from the resting state. In either case, erection was scored as well as cup. Thus, the erection totals include non-cup and cup erections. (It is unclear whether cups are simply intense erections or distinct responses having different underlying mechanisms.) Flips are quick dorsal flexions of the penis, which may or may not be erect. During some flips the os penis protrudes past the tip of the penis. The long flips described by Hart (1968) were not observed in our animals, and Hart saw them only rarely in his intact males.

Copulation Tests

Copulation occurred in a glass aquarium, 50 X 27 X 30 cm, with wood shavings on the floor. Stimulus females were made receptive by sc injection of 50 µg of estradiol benzoate 48 hr prior to testing and 500 µg of progesterone 4 hr prior to testing.

Data Analysis

Data in Experiments 2, 3, and 4 were initially analyzed by appropriate analyses of variance, with the Newman-Keuls test used for pair-wise comparisons. In Experiment 1, many zero scores and heterogeneity of variance required analysis by the nonparametric Friedman analysis of variance, with the Mann-Whitney U test used for paired comparisons.

Experiment 1: Penile Reflexes Following Sexual Exhaustion

When a male rat ejaculates for the first time after a long sexual rest, 5–7 min elapse before it resumes sexual activity. After five to eight ejaculations, most males are sexually exhausted (the criterion is 30–45 min without an attempted mount), and they may not attempt copulation again for 2 or 3 days. Full recovery of copulatory potential may take 7 days (Beach & Jordan, 1956; Jackson & Dewsbury, in press; Karen & Barfield, 1975). Does the prolonged sexual refractoriness that follows sexual satiation derive in part from refractoriness of the penile reflexes?

Hart (1968) noted a reduction in the number and frequency of penile reflexes in spinal male rats tested for 2 hr. When the males were retested 24 hr later, full recovery of the reflexes had occurred. Hart concluded that exhaustion and recovery of spinally controlled sexual reflexes do not play an important role in the recovery from sexual exhaustion, which was presumed to be controlled by supraspinal systems.

Hart did not test the effects of copulatory behavior on penile reflexes, and it seemed conceivable that such tests might reveal greater correspondence between sexual exhaustion and reflex probability. In this experiment we examined the relative rates of recovery of penile reflexes and copulatory behavior following sexual exhaustion.

Method

Subjects. Eight sexually experienced, 140-day-old male rats met a selection criterion by displaying the three classes of penile reflexes in at least two of three reflex tests.

Copulatory tests. Males copulated with two receptive females until 15 min elapsed without a mount. The females were then replaced by two fresh receptive females. When an additional 30 min elapsed without a mount, the males met the criterion of sexual exhaustion (M = 7.8 ejaculations before exhaustion). Immediately after each postexhaustion reflex test, experimental males were again placed with two receptive females for 15 min to test for recovery from sexual exhaustion.

Reflex test schedule. Experimental males (n = 5) were tested to sexual exhaustion. Test 1 for penile reflexes was given immediately after the exhaustion criterion was met, 45 min after the last ejaculation. Tests 2, 3, and 4 followed Test 1 by 4, 8, and 16 hr, respectively. Control males (n = 3) were tested for penile reflexes at the same intervals as the experimental males, but they received no tests for copulatory behavior.

Results

Of the experimental males, one copulated after Reflex Tests 3 and 4, but none of the other males copulated after any of the tests. Hence, four of the five experimental males were clearly sexually exhausted during all reflex tests.

Control males tested for reflexes at the same intervals as experimental males.
showed little change in the number of erections, cups, and flips over the five tests (Table 1). In experimental males tested immediately after sexual exhaustion, the median number of occurrences of each type of reflex was zero. Four hours later, erections had recovered to half the baseline rate, but the median number of cups and flips was still zero. By 8 hr after sexual satiation, all three reflexes of the experimental males had returned to levels comparable with their baseline and with those of control males.

Discussion

This experiment establishes for the first time that penile reflexes evoked in supine tests are functionally related to copulation. The reflexes are depressed to zero or near-zero levels following sexual satiation. Within 8 hr following satiation, reflex evocability has returned to baseline, but males do not normally attempt copulation within 24 hr of satiation. Hart’s (1968) conclusion that recovery from sexual exhaustion does not depend upon recovery of penile reflexes is supported by this direct test of the hypothesis.

Copulation in rats is most probable during the dark (active) phase of the photoperiod (Beach & Levinson, 1949; Dewsbury, 1968a; Richter, 1970) and shows considerable temporal variation over the course of the dark period. The control males in this experiment were tested at four times spanning 16 hr, and the variation in number of reflexes for each type of reflex was small and statistically insignificant. Hence, there does not appear to be a 24-hr rhythm in the penile reflexes, and such a penile reflex rhythm is presumably not the source of the 24-hr rhythm in copulatory potential.

Experiment 2: Penile Reflexes as Sexual Exhaustion Is Approached

In this experiment we explored the effects of preexhaustion levels of copulation upon the elicitation of penile reflexes. This experiment was also a test of our working assumption in Experiment 1, namely, that prior to sexual exhaustion the penile reflexes must be relatively intact, since the male continues to employ penile reflexes in copulation up to the terminal (exhaustion) ejaculation.

Method

Subjects. Seven sexually experienced, 120-day-old rats were selected as in Experiment 1.

Procedure. At 2-wk intervals, penile reflexes were tested after two ejaculations, after four ejaculations, after sexual exhaustion (M = 7.4 ejaculations), and prior to any copulation. The order of conditions was balanced among males. The control condition, males were allowed to copulate ad lib with a receptive female.

<table>
<thead>
<tr>
<th>Reflex/group</th>
<th>Median (Range)</th>
<th>Median (Range)</th>
<th>Median (Range)</th>
<th>Median (Range)</th>
<th>Median (Range)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Erection</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Experimental</td>
<td>19 (12-22)</td>
<td>0* (1-6)</td>
<td>10** (3-17)</td>
<td>19 (14-26)</td>
<td>20* (15-21)</td>
</tr>
<tr>
<td>Control</td>
<td>18 (15-25)</td>
<td>19 (17-22)</td>
<td>19 (16-20)</td>
<td>20 (13-21)</td>
<td>18 (17-23)</td>
</tr>
<tr>
<td>Cup</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Experimental</td>
<td>3 (1-4)</td>
<td>0* (0)</td>
<td>0** (0)</td>
<td>2 (0-8)</td>
<td>2* (1-4)</td>
</tr>
<tr>
<td>Control</td>
<td>4 (2-6)</td>
<td>3 (2-5)</td>
<td>2 (2-3)</td>
<td>3 (0-4)</td>
<td>3 (1-6)</td>
</tr>
<tr>
<td>Flip</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Experimental</td>
<td>3 (2-5)</td>
<td>0* (0)</td>
<td>0* (0-2)</td>
<td>2 (1-8)</td>
<td>3* (1-6)</td>
</tr>
<tr>
<td>Control</td>
<td>4 (3-9)</td>
<td>4 (3-4)</td>
<td>3 (3-5)</td>
<td>5 (2-5)</td>
<td>4 (2-7)</td>
</tr>
</tbody>
</table>

Note. After each test number is the number of hours prior to the test that the experimental males met the criterion of sexual exhaustion. The control males were tested at the same intervals without prior copulation. R = sexually rested. The n = 5 in experimental group; n = 3 in control group.

* significantly different from control group by Mann-Whitney U, p < .04.
** significantly different from control group by Mann-Whitney U, p < .02.
† p < .01, for differences among tests by Friedman analysis of variance.
until 15 min elapsed without a mount. The female was then replaced with a new receptive female until 30 min elapsed without a mount. At that time, the male was considered sexually exhausted and was removed for penile reflex testing. Thus, most postexhaustion reflex tests started 45 min after the last ejaculation. For facilitation of comparison among conditions, penile reflex tests after two and four ejaculations also began 45 min after the preceding ejaculation.

Results

As reflected in Table 2, at baseline (no ejaculations) the reflexes were at their highest level and comparable with the number displayed at baseline in Experiment 1. Following sexual exhaustion, cups and flips were eliminated and erections were substantially reduced. Two ejaculations reduced erections \( p < .05 \) but not cups or flips. Four ejaculations reduced the number of erections \( p < .01 \), cups \( p < .05 \), and flips \( p < .01 \) to levels below those displayed after two ejaculations, and statistically indistinguishable from the levels reached after exhaustion.

Discussion

This experiment extends the evidence that copulation influences the display of penile reflexes. However, the combined data of Experiments 1 and 2 yield an apparent paradox. Penile reflexes become refractory to elicitation before sexual exhaustion sets in, but after sexual exhaustion the reflexes recover more rapidly than copulatory potential itself does. One resolution of this apparent paradox is to assume that supine reflex tests are less effective in eliciting penile reflexes than are copulatory attempts (as evident in the preexhaustion tests), but in the absence of copulatory attempts, reflexes may only be elicitable in supine tests. One inference from this assumption is that if a male rat were induced to attempt copulation within 8 hr of sexual exhaustion, the penile reflexes would have recovered sufficiently to permit consummation.

As sexual exhaustion is approached, there is an increase in the number of intromissions required for ejaculation and in the interval between intromissions (Dewsbury, 1968b; Karen & Barfield, 1975). The physiological processes that give rise to these changes in the parameters of copulation may also be reflected in the increased refractoriness of the penile reflexes after two and four ejaculations.

Experiment 3: Effects of Sexual Stimulation on Reflexes

In Experiments 1 and 2, we analyzed the effects of multiple ejaculations on penile reflexes. In this experiment we asked whether copulatory stimulation without ejaculation could potentiate these reflexes. We also tested reflexes immediately after the first ejaculation.

Method

Subjects. Eight sexually experienced, 150-day-old male rats were selected as in Experiment 1. Procedure. Males received five weekly reflex tests, one under each of five conditions, in counterbalanced order. In one condition, the animals were carried to the copulation-test room in their home cage where they remained for 10 min prior to the reflex testing. In an

<table>
<thead>
<tr>
<th>Reflex</th>
<th>Amount of copulation prior to penile reflex test</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>None</td>
</tr>
<tr>
<td></td>
<td>M</td>
</tr>
<tr>
<td>Erection</td>
<td>22.4</td>
</tr>
<tr>
<td>Cup</td>
<td>4.1</td>
</tr>
<tr>
<td>Flip</td>
<td>4.4</td>
</tr>
</tbody>
</table>

* \( p < .01 \), for differences among conditions, by analysis of variance.
** \( p < .001 \), for differences among conditions, by analysis of variance.
other condition, the animals were tested after being alone for 10 min in an aquarium previously used for copulation testing. In the other conditions, reflexes were tested immediately after the males achieved three intromissions, six intromissions, or one ejaculation.

An additional response measure taken in this study was reflex latency, the time from sheath retraction to the first reflex, which was usually an erection.

**Results**

As Table 3 indicates, copulatory stimulation reduced reflex latencies and increased the number of reflexes per test. The most dramatic effect of sexual stimulation was on reflex latency. Even placing the rat in the copulation-test arena for 10 min reduced the latency by 40% ($p < .01$). Three or six intromissions reduced reflex latency by more than 85% ($p < .01$). The shortest latencies occurred in the postejaculatory tests, but these were not statistically different from the latencies after three or six intromissions ($p > .05$).

More erections occurred after three intromissions, six intromissions, and ejaculation than after zero intromissions ($p < .01$ for each comparison), and there were more erections after three intromissions ($p < .01$) and six intromissions ($p < .05$) than after test-cage exposure. Other paired comparisons were not reliable.

Cups occurred with greater frequency after three intromissions ($p < .05$) and six intromissions ($p < .05$) than after zero intromissions, with other comparisons not statistically reliable.

Compared with flips after zero intromissions, there were more flips after three intromissions ($p < .01$), six intromissions ($p < .01$), and one ejaculation ($p < .01$), and one ejaculation ($p < .01$), and relative to flips after test-cage exposure, more flips occurred after three intromissions ($p < .05$), six intromissions ($p < .01$), and one ejaculation ($p < .05$).

**Discussion**

Noncopulatory sexual stimulation potentiated penile reflexes elicited in supine tests. Three or six intromissions before the reflex test further reduced the latency and increased the number of erections, cups, and flips. It was surprising that males had short-latency reflexes, and a high number of erections and flips, in postejaculatory tests. The reduced sexual arousability characteristic of the postejaculatory refractory period, which lasts five or more minutes, apparently did not extend to the evocation of these reflexes. However, postejaculatory tests were characterized by a low number of cups, the penile form uniquely associated with the ejaculatory pattern during copulation.

This is the first experiment in which erections and cups have been differentially affected by an experimental treatment. Such a difference does not necessarily mean that erections and cups are different reflexes—cups could be a more intense form of erection. However, these data, together with the intuitive impression of a qualitative difference between cups and erections, point to the value of scoring the responses separately.

Even 10 min alone in a copulation-test cage was sufficient to reduce the latency of the first penile reflex. It remains to be de-

### Table 3

*Mean Latency and Number of Penile Reflexes After Varying Amounts of Antecedent Sexual Stimulation*

<table>
<thead>
<tr>
<th>Reflex</th>
<th>Experience immediately preceding reflex tests</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Home cage</td>
<td>Test cage</td>
<td>Three intromissions</td>
<td>Six intromissions</td>
<td>One ejaculation</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>$M$</td>
<td>$SE$</td>
<td>$M$</td>
<td>$SE$</td>
<td>$M$</td>
<td>$SE$</td>
<td>$M$</td>
</tr>
<tr>
<td>Latency (in sec)</td>
<td>316.9</td>
<td>47.9</td>
<td>188.6</td>
<td>47.5</td>
<td>47.0</td>
<td>8.96</td>
<td>43.4</td>
</tr>
<tr>
<td>Erection</td>
<td>17.5</td>
<td>2.95</td>
<td>23.8</td>
<td>2.78</td>
<td>33.4</td>
<td>1.59</td>
<td>32.1</td>
</tr>
<tr>
<td>Cup</td>
<td>5.6</td>
<td>1.48</td>
<td>9.0</td>
<td>1.58</td>
<td>12.4</td>
<td>2.04</td>
<td>11.8</td>
</tr>
<tr>
<td>Flip</td>
<td>5.5</td>
<td>1.25</td>
<td>8.6</td>
<td>1.77</td>
<td>14.4</td>
<td>1.80</td>
<td>15.4</td>
</tr>
</tbody>
</table>

* $p < .05$, for differences among conditions, by analysis of variance.

** $p < .01$, for differences among conditions, by analysis of variance.
terminated whether this potentiation was due to unconditional cues (i.e., olfactory stimuli in the shavings), to conditional cues dependent upon copulatory experience in the cage, or to a combination of these factors.

Experiment 4: Effects of Reflex Elicitation on Copulation

In the previous experiments we determined that the evocability of penile reflexes may be reduced or increased by antecedent copulation. We next asked whether the effects were reciprocal, i.e., whether elicitation of penile reflexes in supine tests would alter the parameters of subsequent copulatory behavior.

Method

Subjects. Six sexually experienced male rats, 120 days of age, were selected as in Experiment 1.

Procedure. Each male copulated to sexual exhaustion under two conditions: (a) an experimental condition in which penile reflexes were elicited for 1 hr immediately prior to copulation and (b) a control condition in which the subjects were simply held in supine position in the glass cylinder for 1 hr prior to copulation. Copulation conditions were counterbalanced and occurred at 2-wk intervals. The method of copulatory testing and the criteria for sexual exhaustion were the same as in Experiment 2.

Results and Discussion

The parameters of copulation were not significantly altered by the antecedent evocation of reflexes. As Table 4 indicates, for the seven variables deemed most likely to be affected by evocation of reflexes, males obtained similar values in the experimental and control conditions. These data, in conjunction with those of the first three experiments, suggest that the relation between sexual behavior and penile reflexes evoked in supine tests is a "one-way street" in terms of potential influence. This relation presumably reflects the neural organization underlying copulation and penile reflexes. Beach, Westbrook, and Clemens (1966) found that seminal emission induced by electrically stimulating the brain of male rats did not lead to the normal sequelae seen after copulatory ejaculation. Similarly, in this study, repetitively evoking cup, the penile morphological component of the ejaculatory pattern, did not alter subsequent copulation. Hence, we still do not know what aspect of the ejaculatory pattern and its associated physiological activity induces normal postejaculatory behavior and its associated state (Barfield & Geyer, 1975; Kurtz & Adler, 1973).

Table 4

<table>
<thead>
<tr>
<th>Measure</th>
<th>Experimental condition</th>
<th>Control condition</th>
<th>(5 df)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>M</td>
<td>SE</td>
<td>M</td>
</tr>
<tr>
<td>Mount latency (in sec)</td>
<td>199</td>
<td>105.9</td>
<td>360</td>
</tr>
<tr>
<td>Intromission latency (in sec)</td>
<td>1,288</td>
<td>729.4</td>
<td>505</td>
</tr>
<tr>
<td>Mounts preceding first intromission</td>
<td>5.3</td>
<td>2.02</td>
<td>2.0</td>
</tr>
<tr>
<td>Mounts preceding first ejaculation</td>
<td>10.5</td>
<td>1.29</td>
<td>10.0</td>
</tr>
<tr>
<td>Intromissions preceding first ejaculation</td>
<td>6.4</td>
<td>.73</td>
<td>6.9</td>
</tr>
<tr>
<td>First ejaculation latency (in sec) from first intromission</td>
<td>824</td>
<td>238.6</td>
<td>862</td>
</tr>
<tr>
<td>Ejaculations preceding sexual exhaustion</td>
<td>5.5</td>
<td>.43</td>
<td>5.3</td>
</tr>
</tbody>
</table>

Note. Six males were tested once in each of two conditions: experimental (1 hr of actual reflex testing before copulation) and control (1 hr in reflex testing apparatus before copulation). Order of testing was balanced.

* p > .10 in all cases.
crease the number of erections, flips, and cups. A single ejaculation during copulation has a similar influence except that the incidence of cups is decreased to baseline levels. More copulatory ejaculations reduce the number of all penile reflexes, but after sexual exhaustion, reflex potential returns to normal long before copulatory potential does. The effects are not reciprocal. Even 1 hr of reflex elicitation is without significant effect on subsequent copulatory behavior.

This evidence for a functional relation between penile actions occurring during copulation and in supine reflex tests, together with the morphological similarity between the reflexes in the two conditions, supports the description of these reflexes as “sexual” (Hart, 1968, 1978). Differences in the temporal patterning of the penile reflexes in the two conditions are considerable, and the absence of ejaculation during reflex testing is particularly noteworthy. In these experiments expulsion of coagulated seminal fluid (the ejaculatory “plug”) occurred only four times during reflex tests, and three of those occasions were in Experiment 3 in males that had intromissions before testing. In every case, ejaculation occurred during the first cluster of penile reflexes. Possibly ejaculation occurs in supine tests only when the plug has already entered the urethra prior to the start of testing. In another experiment on intact male rats, ejaculation was observed during only 3 of 129 tests (Davidson et al., in press). Hart (1968) ascribed the rarity of ejaculation during reflex tests of spinal male rats to the absence of some supraspinal neural input, but intact males are clearly not more likely to ejaculate. Presumably ejaculation requires stimulation that is not given in reflex tests. The penile cup is reliably associated with ejaculation during copulation in laboratory rats (Pollak & Sachs, 1976) and mice (McGill & Coughlin, 1970). Its dissociation from ejaculation in reflex tests indicates that the penile and seminal components of ejaculation are separate, but normally synchronized, actions.

Beach (1967, p. 301) suggested “that the sequential pattern of successive preejaculatory intromissions and their (presumed) additive effects may be ‘programmed’ at a spinal level; and furthermore that the temporary postejaculatory refractory period is a reflection of transitory reduction of excitability in spinal mechanisms.” Similar hypotheses have been proposed by others (e.g., Barfield & Geyer, 1975; Hart, 1968, 1978; Sachs & Barfield, 1976). Direct tests of these hypotheses will prove difficult because spinal males can not be tested for copulation and supraspinal influences can not be ruled out in intact males. However, data from Experiment 3 constitute an indirect test of the hypothesis that spinal mechanisms mediate postejaculatory refractoriness. We found that all three types of penile reflex could be elicited within 1 min of ejaculation, at a time that the males could not have been induced to resume copulation. Therefore, we conclude that at least the spinal mechanisms controlling sexual reflexes are readily excitable after ejaculation and that a supraspinal neural system mediates postejaculatory refractoriness. Some components of this system may have been identified (Barfield, Wilson, & McDonald, 1975; Clark, Caggiula, McConnell, & Antelman, 1975; Heimer & Larsson, 1964).

Reference Note


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