Intracavernous pressure during erection in rats: an integrative approach based on telemetric recording

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1Laboratoire de Neurobiologie des Fonctions Végétatives, Institut National de la Recherche Agronomique, F-78352 Jouy-en-Josas Cedex; 2Groupe de Recherche en Urologie, Faculté de Médecine Paris-Sud, F-94270 Le Kremlin Bicêtre Cedex, France; and 3Department of Psychology, University of Connecticut, Storrs, Connecticut 06269-1020

Bernabé, Jacques, Olivier Rampin, Benjamin D. Sachs, and François Giuliano. Intracavernous pressure during erection in rats: an integrative approach based on telemetric recording. Am. J. Physiol. 276 (Regulatory Integrative Comp. Physiol. 45): R441–R449, 1999.—To better understand the similarities and differences in the neural control of penile erection occurring in different contexts, we recorded intracavernous pressure (ICP) in conscious rats using a miniaturized telemetric device. ICP changes during reflexive, noncontact, and apomorphine-induced erections were characterized by a plateau increase surmounted by peaks. Plateaus were also elicited by cavernous nerve stimulation in anesthetized rats, suggesting that the cavernous nerve represents the final common proerectile autonomic pathway in these contexts and that it responds similarly to information originating in the periphery or in supraspinal nuclei. During reflexive, noncontact, and apomorphine-induced erections, activation of spinal autonomic nuclei, considered the spinal generators of erection, would take place first, representing a prerequisite for the occurrence of peaks. Suprasystolic peaks would result from the addition of pudendal motoneuron activity. In contrast, only peaks were recorded during copulation. In this context, the convergence of peripheral and supraspinal information apparently elicits the best temporal arrangement of autonomic and somatic outflows, reflecting a highly organized and integrated spinal activity.

penis; sexual behavior; sexual reflexes; apomorphine; noncontact erections

ENGORGEMENT OF THE PENIS with blood, leading to erection, is caused by active arterial dilatation and relaxation of the smooth muscle fibers of the erectile tissue present in the corpora cavernosa and corpus spongiosum (1). These autonomic responses depend on the activity of sacral parasympathetic and thoracolumbar sympathetic outflows (9). Additional contraction of the ischiocavernosus and bulbospongiosus muscles, innervated by pudendal motoneurons, augments penile rigidity (20, 30). Accordingly, both autonomic and somatic outflows from the spinal cord participate in penile erection. The pharmacology and physiology of the peripheral autonomic control of penile erection have been the subject of considerable recent investigations (1). In contrast, the more complex spinal and supraspinal regulations of penile erection have been less extensively explored and therefore remain less well understood (2, 23). Erection occurs in response to a variety of stimuli originating in the periphery or in supraspinal nuclei, suggesting that different neural networks may play a role in the control of erection occurring in different contexts (25). The understanding of the central neural control of erection has been enriched by behavioral observation in a variety of sexual contexts, e.g., copulation, reflexive erections, noncontact exposure to estrous females (an animal model of psychogenic erection; see Ref. 26), and solitary males receiving drugs systemically or centrally (2, 20). Missing from most of these behavioral studies, however, has been any direct measure of penile erection. Through measurement of intracavernous pressure (ICP) in conscious rats in different erectile contexts, we report on the similarities and differences of ICP changes. From this comparison, we infer that the contribution of peripheral and supraspinal information to the activation of pro- and antierectile autonomic and somatic efferent pathways varies according to the erectile context.

MATERIALS AND METHODS

Animals

Adult male Long-Evans rats (Centre d’Elevage René J anvier, Le Genest-St-Isle, France) weighing 300–450 g were used. Rats were housed singly in plastic cages containing wood chip bedding, commercial pelleted rodent chow, and water ad libitum. Cages were placed in an animal facility maintained at 20°C and kept in a 12:12-h light-dark cycle, with lights on at 10 PM. ICP monitoring was performed in different rats during copulation (n = 10 rats), reflexive erection tests (n = 5 rats), noncontact erection tests (n = 4 rats), and apomorphine-induced erections (n = 5 rats). In three other rats, blood pressure (BP) and heart rate (HR) were recorded during copulation. All experiments were conducted between 2 and 7 PM. Where appropriate, adult females were made receptive with 20 µg estradiol benzoate and 0.5 mg progesterone, both diluted in sesame oil and subcutaneously injected in a volume of 0.3 ml 48 and 6 h, respectively, before the test. Before the test, the female’s receptivity was verified with nonexperimental males that were allowed to achieve one intromission.

All animal experiments were carried out in accordance with the European Communities Council Directive of 24 November 1986 (86/609/EEC) on the use of laboratory animals. All efforts were made to minimize animal suffering and to reduce the number of animals used.

Telemetric Device Implantation

ICP and BP were measured using a surgically implanted telemetric device. This device (model C40; Data Sciences, St.
Paul, MN) comprises an open-tip fluid-filled catheter, 0.7-mm outer diameter, connected to a miniature pressure transducer. The telemetric device, calibrated with a mercury column before and after each implantation, recorded pressures in the range of 0–1,500 mmHg for ICP and 0–300 mmHg for BP. The telemetric device was sterilized in benzalkonium chloride before surgical implantation. Rats were anesthetized with an intraperitoneal injection of pentobarbital sodium (60 mg/kg) and placed on a homeothermic blanket. To record ICP, we inserted the tip of the catheter into the proximal shaft of the right corpus cavernosum, exposed through a midscrotal incision, and the pressure transducer was placed subcutaneously at the lateral aspect of the abdominal wall (Fig. 1A). To record BP, we inserted the tip of the catheter in the aorta 10 mm rostral to the aortic bifurcation and oriented toward the heart. The pressure transducer was intraperitoneally located and secured to the abdominal wall. Surgical wounds were stitched in separate layers. Then males were kept one per cage in the animal facility for 7 days before tests. After completion of the tests, the rats were killed by an overdose of intraperitoneally injected pentobarbital sodium. The tip of the catheter was removed from the corpus cavernosum or the aorta, and the site of the catheter implantation was checked. Rats displaying a fibrotic reaction in the corpus cavernosum or the aorta were discarded from the study.

Data Recordings

ICP and BP signals were translated into potentials, amplified by the telemetric device, and then telemetrically transmitted in the form of a radio signal to an external receiver (model RA 1000, Data Sciences) placed under the observation chamber during all tests except the reflexive erection test, during which the receiver was placed under the plastic cylinder used for restraint. The receiver converted the radio signal into an analog voltage (V), which was further digitized (LabMaster DMA 100, Scientific Solutions, Solon, OH) and recorded at a sampling rate of 100 Hz (Axotape Software, Axon Instruments, Foster City, CA) on a personal computer (Advanced France Composants, Paris, France). During all tests, penile erection or related sexual events were visually identified and manually scored by an observer on a separate channel of the computer. Scores were recorded as square pulses of 80-ms duration whose amplitude (1–5 V) depended on the event.

Behavioral Observation

Mating tests. Males were selected for implantation on the basis of their achievement of ejaculation in at least two of three screening mating tests. During mating tests, a male was placed for a 5-min adaptation period in an observation chamber made of glass (50 × 40 × 30 cm) whose floor was covered with wood chip bedding. ICP or BP was continuously recorded from this moment. Then a receptive female was placed in the chamber. Copulatory events including mounts, intromissions, and ejaculations were visually scored according to previous reports (15). If an intromission pattern occurred, ICP recordings and behavioral observations continued for 30 min or until the first intromission after an ejaculation appeared. Without an intromission pattern, the test was stopped after 15 min. Each ejaculation was confirmed a posteriori by the presence of a seminal plug in the female's vagina. Comparison of the recordings of ICP peaks during mounts and intromissions and the behavioral scores allowed an estimation of the reaction time of the observer. This time had a maximal value of 1.25 s.

Noncontact erection tests. Four males were selected for implantation on the basis of achievement of ejaculation in at least two of three mating tests and display of noncontact erections in at least two of three noncontact erection tests performed before implantation. During noncontact erection tests, males were placed alone for a 5-min adaptation period in one side of the observation chamber. The chamber was divided in half by a barrier made of two sheets of wire mesh 3 mm wide and 2.5 cm apart. The barrier prevented direct contact between animals on either side but was permeable to auditory, visual, and olfactory stimuli. Then a receptive female was placed in the chamber, and ICP recordings and behavioral observations were performed for 30 min. After each test, the observation chamber and barrier were washed with detergent, rinsed, and dried. Noncontact erections were visually scored when the male stood up on the extremity of its hindlimbs, bent its head toward the genital region, and displayed hip movements. These criteria met the description of penile erection evoked in the male in the presence of estrous females observed through lateral and ventral viewing (26).

Apomorphine-induced erection tests. Five sexually experienced males were implanted with the telemetric device. Males were placed alone in the observation chamber for a 5-min adaptation period. Males received a subcutaneous injection of a single dose of apomorphine (60 µg/kg). Observation was carried out for 30 min after injection. Penile erection was scored when the rats displayed the same motor pattern as during noncontact erections.
Reflexive erection tests. Five selected rats displayed sequences of reflex responses in at least two of three reflexive erection tests. To perform the test, the males were restrained on their back in a plastic cylinder (8-cm diameter × 20-cm length) for a 5-min adaptation period. Then the preputial sheath was tonically retracted with a loose metal loop. Reflex responses were visually scored as lengthening of the penile body, glans engorgement involving some dilation of the glans, cups (intense glans erection with flaring of glans extremity), and flips (dorsiflexions of penile body) (15). Tests lasted 15 min, starting from the first response.

Data Analysis

ICP tracings were analyzed retrospectively using software designed in our laboratory and based on previous ICP recordings with the same device during copulation and penile reflex tests (5, 12). In each test, ICP recorded during the 5-min adaptation period was averaged and termed flaccid ICP. In each test, flaccid ICP + 2 SE was the calculated threshold for automated detection to be considered a significant ICP change. ICP recordings evidenced pressure increases occurring as peaks superimposed on plateaus that were closely associated with sexual events during reflexive, noncontact, and apomorphine-induced erections. A first automated analysis of each ICP recording identified intervals, aiming at rapidly identifying the parts of recordings containing significant ICP increases. Intervals started when ICP exceeded the threshold (ICP + 2 SE) and lasted 30 s (Fig. 2). Intervals during which a sexual event had been visually detected and behaviorally scored were numbered and stored according to their detection time. The very few intervals not associated with sexual events were rejected from further analysis. A second, more accurate analysis was performed using two manual cursors aimed at delimiting the beginning and the end of ICP changes above the threshold. The time period between the two cursors was called an episode (Fig. 2A). Within each episode, the software searched for valleys, i.e., points whose ICP value was lower than the previous and the next values (Fig. 2B). Between two valleys, a curve segment was delimited, referred to as a peak. Peak amplitude was then measured, relative to 0 mmHg, and the duration and positive and negative slopes of each peak were also calculated. Measurement of peak area only considered the area over the plateau (Fig. 2C). Because during mating tests only peaks were recorded, peak area in this context was measured relative to 0 mmHg. The software also calculated the duration and total area (i.e., area under the curve) of each episode. Subtraction of the total area of the peaks from the total area of the episode provided the value of the plateau area (Fig. 2D). Duration, positive and negative slopes, and amplitude of the plateau were calculated relative to the threshold value.

BP and HR

BP and HR were measured over a 5-s period sample during the minute before and the minute after introduction of the female in the observation cage. The maximal systolic and adjacent diastolic values were measured during the 1.25 s before each recorded copulatory event. HR was calculated over a 5-s period accompanying each copulatory event and was expressed as beats per minute.

Comparison of ICP Changes Elicited by Cavernous Nerve Stimulation Recorded With Telemetric Device and With an Acutely Implanted Catheter in Anesthetized Rats

To test the reliability of the measure of ICP with the telemetric device, we compared ICP measures with this device and with an acutely implanted catheter. The latter technique represents a reliable method of recording ICP in anesthetized rats. Two rats implanted with a telemetric device in the right corpus cavernosum that displayed ICP increases during previously performed mating tests were anesthetized by an intraperitoneal injection of pentobarbital sodium (60 mg/kg). ICP and BP were recorded as described previously (11). The erectile response elicited by cavernous nerve stimulation was recorded through the two catheters, one inserted in the right corpus cavernosum and connected to the telemetric device and the other acutely inserted in the left corpus cavernosum.

Statistical Analysis

Parameters characterizing the ICP increases accompanying the same type of erectile response were averaged for each rat, then for each group, and are presented as means ± SE. A
one-way ANOVA was used to compare parameters of ICP plateaus between penile reflex tests, noncontact erections, and apomorphine-induced erections. A one-way ANOVA with repeated measures was used to compare characteristics of ICP peaks 1 among glans erections, cups, and flips in penile reflex tests; 2) among mounts, intromissions, and ejaculations during copulation; and 3) between the different peak profiles recognized during apomorphine-induced and noncontact erections. Post hoc analysis using a Student-Newman-Keuls test was then performed, and differences were considered significant at P < 0.05.

Drugs

Pentobarbital sodium was purchased from Sanofi (Lilouerne, France). Estradiol benzoate and progesterone were purchased from Sigma (Saint-Quentin-Fallavier, France) and dissolved to the required concentration in sesame oil. Apomorphine hydrochloride, purchased from Sigma, was dissolved in 0.1% ascorbic acid in saline to the required concentration.

RESULTS

Checking the implantation site at the end of the experiment revealed that the catheter was correctly implanted in the corpus cavernosum in 21 of 24 rats and in the abdominal aorta in 3 of 3 rats. In 3 of 10 rats selected for mating tests, the catheter was displaced from the corpus cavernosum, and these rats were eliminated from further analysis. Data from ICP recordings in 21 rats and BP and HR recordings in 3 rats are therefore considered in the study. Each implanted rat displayed behaviorally identified erections and, apart from those rats implanted in the aorta, ICP increases during the recording sessions. Rats displayed a mean of 8.8 ± 4.0 episodes of ICP increase during the reflexive erection test, 4.5 ± 0.3 episodes during the noncontact erection test, and 2.6 ± 0.9 episodes during the apomorphine-induced erection test. During the mating test, rats displayed an average of 9 ± 3 mounts and 19 ± 5 intromissions before ejaculation.

ICP Changes Elicited by Cavernous Nerve Stimulation Recorded With Telemetric Device and With an Acutely Implanted Catheter in Anesthetized Rats

In two anesthetized rats, electrical stimulation of the cavernous nerve elicited an ICP increase recorded through the two devices. The ICP increase reached 73.45 ± 29.67 mmHg when recorded with the catheter and 54.71 ± 17.29 mmHg when recorded through the telemetric device. The latency of the ICP increase was 4.64 ± 2.27 s when recorded with the catheter and 4.23 ± 1.11 s when recorded with the telemetric device. Finally, the slope of the ICP increase was 23.17 ± 10.83 mmHg/s when recorded with the catheter and 16.90 ± 6.08 mmHg/s with the telemetric device. Therefore, the two devices provided measures within the same range.

Description of ICP Changes Associated With Erectile Events in Various Contexts in Conscious Rats

ICP changes recorded in the different contexts occurred as peaks superimposed on plateaus, with the exception of mating tests, during which only peaks were recorded (Fig. 3D). The area of an episode of ICP increase varied significantly according to the context during which erection occurred [F(2,11) = 6.67, P < 0.05]. During noncontact erections, the area of ICP increase (3,220 ± 265 mmHg·s) was greater than during apomorphine-induced (1,655 ± 226 mmHg·s, P < 0.05) and reflexive erections (1,554 ± 464 mmHg·s, P < 0.05).

During noncontact and apomorphine-induced erections, ICP increases occurred as plateaus with many superimposed peaks (Fig. 3, B and C). The plateau increase often occurred before any behavioral event could be visually detected. In view of further evidence of similarities and differences among erectile events in the ICP recordings within and between contexts, separate analyses of peaks and plateaus were performed.

Plateaus

The average duration, amplitude, positive and negative slopes of ICP rises, and area of the plateaus recorded in the three erectile contexts are displayed in Table 1. A one-way ANOVA revealed a statistical difference in the duration of the plateaus [F(2,11) = 11.3, P < 0.01]. Plateau duration was longer during noncontact erections than during apomorphine-induced and reflexive erections (P < 0.05 for each). In contrast, no significant differences among contexts were found for amplitude and area.

Peaks

During copulation and reflexive erections, brief, sharp ICP increases called “peaks” accompanied each behaviorally scored erection or sexual event. Because each ICP rise could clearly be associated with one or the other erectile response, the characteristics of the ICP peaks occurring in the two contexts are presented in Table 2 and examples of ICP peaks during reflexive erections are displayed in Fig. 4. ICP peaks occurring during glans erections had a significantly longer duration than those recorded during cups and flips [F(4,14) = 12.2, P < 0.004]. A one-way ANOVA also revealed differences in ICP peak amplitude [F(4,14) = 9.18, P = 0.008] and area [F(4,14) = 5.42, P = 0.03] among glans erections, cups, and flips. The amplitude and area of ICP peaks accompanying flips were significantly greater than those recorded during glans erection and cups (P < 0.05 for each). Conversely, the amplitude of ICP peaks was similar for glans erections and cups. During mating tests, ICP peak duration was similar for mounts, intromissions, and ejaculations [F(6,18) = 0.787, P = 0.48]. In contrast, a one-way ANOVA revealed a statistically significant difference of ICP peak amplitude among mounts, intromissions, and ejaculations [F(6,18) = 4.75, P = 0.035], with peak amplitude during mounts significantly lower than during intromissions and ejaculations (P < 0.05 for each). No reliable difference occurred in the amplitude of ICP peaks measured during intromissions and ejaculations [F(6,18) = 2.6, P = 0.123]. The characteristics of peaks recorded during noncontact and apomorphine-induced erections are presented.
in Table 3, and examples are displayed in Fig. 4. In an attempt to compare the different ICP peaks recorded during noncontact and apomorphine-induced erections, we assigned the ICP peaks in these two contexts to one of four types on the basis of the shape of the ICP rise. The typology was based on our previous analysis of ICP rises during reflexive erection tests (see Ref. 5). ICP peaks during noncontact and apomorphine-induced erections were therefore named erection-, cup-, or flip-like peaks or “other.” This last class, an example of which is displayed in Fig. 4D, included those ICP peaks whose profile was not comparable to any ICP rise already recorded during reflexive erection tests. Because we usually could not see the penis clearly during the motor patterns associated with erection during tests for noncontact and apomorphine-induced erections, we could not associate these other peaks with any particular event.

A one-way ANOVA revealed a statistically significant difference of ICP peak amplitude \( F(3,13) = 119.9, P = 2 \times 10^{-5} \), duration \( F(3,13) = 6.99, P = 0.016 \), and area \( F(3,13) = 18.9, P = 9.79 \times 10^{-4} \) among glans erection-, cup-, and flip-like erections recorded during noncontact erections. There was also a statistically significant difference of ICP peak amplitude \( F(3,13) = 25.4, P = 3.9 \times 10^{-4} \), duration \( F(3,13) = 4.69, P = 0.042 \), and area \( F(3,13) = 4.61, P = 0.044 \) among glans erection-, cup-, and flip-like erections recorded during apomorphine-induced erections. In both contexts, the fourth group (other) of ICP peaks had the highest amplitude and area relative to the other ICP increases. Comparing noncontact and apomorphine-induced erections, we found a significant difference in the maximal amplitude reached by the highest peak of one episode, the former being the higher \( 433.8 \pm 19.9 \text{ mmHg} \) vs. \( 275.0 \pm 34.9 \text{ mmHg} \), \( t(8) = 30, P = 0.016 \).

BP and HR Changes During Mating Tests

Systolic and diastolic BP and HR during the adaptation period, after presentation of the female to the male, and during copulatory events, are displayed in Table 4. Copulation did not elicit changes in either BP or HR.

DISCUSSION

The present results describe ICP increases closely associated with penile responses identified either under direct observation (e.g., reflexive erection) or inferred from behavioral activity (e.g., during copulation). To our knowledge, this is the first report of ICP increases during erectile responses in different contexts in conscious rats. We will briefly discuss some technical aspects of this study and then consider implications of the plateaus and peaks in ICP occurring in the several erectile contexts that we studied.

Technical Considerations

There was no apparent difference in the ICP increase elicited by cavernous nerve stimulation under anesthesia and recorded either through the telemetric device...
Table 1. Characteristics of ICP plateaus recorded during reflexive erection tests, noncontact erections, and apomorphine-induced erections

<table>
<thead>
<tr>
<th>Context (Observation Period)</th>
<th>n</th>
<th>n/Rat</th>
<th>Duration, s</th>
<th>ICP Increase, mmHg</th>
<th>Amplitude, mmHg</th>
<th>Area, mmHg·s</th>
<th>ICP Decrease, mmHg</th>
</tr>
</thead>
<tbody>
<tr>
<td>Reflexive erection (15 min)</td>
<td>5</td>
<td>8.8 ± 2.7</td>
<td>22 ± 3</td>
<td>5 ± 1</td>
<td>35 ± 11</td>
<td>1,192 ± 393</td>
<td>2 ± 1</td>
</tr>
<tr>
<td>Noncontact erection (30 min)</td>
<td>4</td>
<td>4.5 ± 0.3</td>
<td>43 ± 2*</td>
<td>3 ± 1</td>
<td>51 ± 8</td>
<td>2,242 ± 386</td>
<td>4 ± 0.5</td>
</tr>
<tr>
<td>Apomorphine-induced erection (30 min)</td>
<td>5</td>
<td>2.6 ± 0.9</td>
<td>31 ± 4</td>
<td>5 ± 2</td>
<td>47 ± 8</td>
<td>1,321 ± 210</td>
<td>5 ± 1</td>
</tr>
</tbody>
</table>

Values are means ± SE; n = no. of rats, n/Rat, no. of erections per rat; ICP, intracavernous pressure. *Statistically different from other groups (P < 0.05).

7–10 days after implantation or through an acutely implanted needle connected to a pressure transducer. Accordingly, chronic implantation in the corpus cavernosum did not cause detectable perturbation of the local mechanisms of penile erection. Moreover, from this and previous reports, chronic implantation does not impair the behavior related to penile erection in any of the contexts examined so far (5, 12). In a previous study using the same telemetric device, ICP peak amplitude during mounts, intromissions, and ejaculation were lower than in this study (12). This difference is very likely due to the previous use of polygraph recording, because the inertia of the polygraph pens did not allow the recording of high-frequency events.

The present study emphasizes the advantages of the telemetric recording of ICP increases in conscious rats in providing an analytic approach to the penile mechanisms during erection. For example, in anesthetized rats, ICP increases elicited by electrical stimulation applied for 30–60 s to peripheral nerves occur with a latency of several seconds (8, 11, 33). In contrast, copulating rats display sexual contacts, during which penile erection occurs, lasting 0.3–4 s (21). Obviously ICP measures in conscious rats evidence increases very similar to the above-cited behavioral events.

ICP Plateaus

A close positive correlation between ICP increase elicited by cavernous nerve stimulation and BP has been demonstrated in anesthetized rats (11). We did not record changes in either BP or HR during copulation, thereby demonstrating that the dramatic ICP rises that occurred during copulation and related to mounts, intromissions, and ejaculations were not due to general hemodynamic changes.

In anesthetized rats, electrical stimulation of the sacral parasympathetic outflow, conveyed by the pelvic and cavernous nerves to the penis, elicits an ICP increase in the form of a plateau (8, 11, 13, 33). In the present study, we confirmed this finding by recording an ICP increase to a plateau in response to cavernous nerve stimulation in two anesthetized rats. In conscious rats, ICP increases in the form of plateaus occurred during reflexive, noncontact, and apomorphine-induced erections. ICP amplitude remained inferior to BP in all contexts. Therefore, the contexts shared the properties of plateaus elicited by activation of the parasympathetic proerectile outflow in anesthetized rats, suggesting that this parasympathetic activity was present in conscious rats.

Plateaus lasted several seconds, and in anesthetized rats the ICP increase elicited by stimulation of parasympathetic efferents lasts as long as the stimulation is applied. We infer that in conscious rats plateaus of ICP increase may be supported by the activation of parasympathetic efferents. According to our results, this activation would last for several seconds in response to either peripheral or central information.

In conscious rats, tonic retraction of the preputial sheath elicits reflex responses occurring as clusters of penile erection (15, 29). Plateaus of ICP increase accompany each cluster, and ICP peaks accompany each erection (Ref. 5 and present study). In anesthetized rats, electrical stimulation of the dorsal penile nerve, recruiting sensory afferents from the genitalia, elicits a reflex increase of ICP in the form of a plateau (22, 24, 33). The reflex response can be abolished by switching off the sacral parasympathetic outflow with a bilateral section of the pelvic nerves and remains unchanged after curarization (24). These findings suggest that plateau increases recorded in conscious rats during reflexive erections are supported by the reflex activation of autonomic outflow.

In anesthetized rats, ICP increases occur in response to a variety of stimulations applied to the hippocampus, the paraventricular nucleus (PVN), or the medial preoptic area (MPOA) (6, 7, 10, 18). The ICP rise in response

Table 2. Characteristics of ICP peaks recorded during penile reflex tests and mating tests

<table>
<thead>
<tr>
<th>Context</th>
<th>n</th>
<th>Erectile Response</th>
<th>n/Rat</th>
<th>Duration, s</th>
<th>Amplitude, mmHg</th>
<th>Area, mmHg·s</th>
</tr>
</thead>
<tbody>
<tr>
<td>Reflexive</td>
<td>5</td>
<td>Glans Erection</td>
<td>17.6 ± 7.9</td>
<td>2.0 ± 0.1</td>
<td>140 ± 32</td>
<td>45 ± 17</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Cup</td>
<td>4.2 ± 0.6</td>
<td>1.7 ± 0.2</td>
<td>170 ± 41</td>
<td>47 ± 20</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Flip</td>
<td>15.6 ± 6.8</td>
<td>1.4 ± 0.1</td>
<td>299 ± 61*</td>
<td>146 ± 49*</td>
</tr>
<tr>
<td>Copulation</td>
<td>7</td>
<td>Mount</td>
<td>9.4 ± 3.3</td>
<td>3.6 ± 0.7</td>
<td>297 ± 43†</td>
<td>203 ± 52</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Intromission</td>
<td>19.4 ± 4.5</td>
<td>2.8 ± 0.7</td>
<td>714 ± 188</td>
<td>331 ± 79</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Ejaculation</td>
<td>0.57 ± 0.2</td>
<td>4.7 ± 1.5</td>
<td>781 ± 138</td>
<td>633 ± 247</td>
</tr>
</tbody>
</table>

Values are means ± SE; n = no. of rats, n/Rat, no. of responses per rat. *Statistically different from values measured for glans erection and cups (P < 0.05); †statistically different from values measured for intromission and ejaculation (P < 0.05).
Table 4. Range (minimum–maximum) of systolic and diastolic BP and HR measured before copulation and during mount, intromission, and ejaculation in 3 rats

<table>
<thead>
<tr>
<th></th>
<th>Systolic BP, mmHg</th>
<th>Diastolic BP, mmHg</th>
<th>HR, beats/min</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male alone</td>
<td>139–220</td>
<td>91–193</td>
<td>380–408</td>
</tr>
<tr>
<td>Female present</td>
<td>163–235</td>
<td>117–210</td>
<td>420–720</td>
</tr>
<tr>
<td></td>
<td>120–224</td>
<td>109–181</td>
<td>565–639</td>
</tr>
<tr>
<td>Mount</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intromission</td>
<td>160–244</td>
<td>131–186</td>
<td>525–674</td>
</tr>
<tr>
<td>Ejaculation</td>
<td>187–217</td>
<td>147–196</td>
<td>561–714</td>
</tr>
</tbody>
</table>

BP, blood pressure; HR, heart rate.

It is noteworthy that 1) the amplitude of the plateau and 2) the ICP increase to and decrease from the plateau to basal levels did not differ among reflexive, noncontact, and apomorphine-induced erections. These similarities suggest that the pattern of activation of spinal autonomic nuclei is largely independent of the various stimuli at the origin of the response. This widens and enriches the concept of a spinal generator previously introduced from observations conducted in conscious rats that were spinalized surgically (14, 29) or after spinal anesthesia induced by tetracaine (28). Plateaus during noncontact erections last longer than those during reflexive erections, suggesting that activation of the spinal cord by supraspinal nuclei lasts longer than reflexively elicited activation. The difference in plateau duration between noncontact and apomorphine-induced erections may mean that the activation of spinal autonomic nuclei by supraspinal structures lasts longer when the stimulus is physiological (noncontact condition) rather than pharmacological (apomorphine condition). In the present experiment, apomorphine was delivered at a single dose of 60 µg/kg. This dose was selected on the basis of previous experiments in which it yielded the maximum probability of erection (27). However, other doses may have resulted in different values of ICP that may have elicited responses whose characteristics would have been more similar to measures of noncontact erections. Finally, apomorphine may act in different brain nuclei, some of which may exert antierectile influence. In humans, for example, apomorphine-induced nausea has impeded the use of this drug to correct erectile dysfunction.

Table 3. Characteristics of ICP peaks recorded during noncontact and apomorphine-induced erections

<table>
<thead>
<tr>
<th>Context</th>
<th>n</th>
<th>Erectile Response</th>
<th>n/Rat</th>
<th>Duration, s</th>
<th>Amplitude, mmHg</th>
<th>Area, mmHg·s</th>
</tr>
</thead>
<tbody>
<tr>
<td>Noncontact erections</td>
<td>4</td>
<td>Glans Erection Like</td>
<td>6 ± 3</td>
<td>3.5 ± 1.2</td>
<td>56 ± 7a,c,e</td>
<td>86 ± 26d</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Cup Like</td>
<td>9 ± 2</td>
<td>1.4 ± 0.4</td>
<td>153 ± 35c</td>
<td>46 ± 20</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Flip Like</td>
<td>0.4 ± 0.1</td>
<td>131 ± 29e</td>
<td>18 ± 2e</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Other</td>
<td>0.5 ± 0.2</td>
<td>2.5 ± 0.7</td>
<td>350 ± 44a,b,d</td>
<td>404 ± 23a,b,d</td>
</tr>
<tr>
<td>Apomorphine-induced erections</td>
<td>5</td>
<td>Glans Erection Like</td>
<td>4 ± 1</td>
<td>2.6 ± 0.7</td>
<td>32 ± 7a</td>
<td>17 ± 10</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Cup Like</td>
<td>3 ± 1</td>
<td>0.5 ± 0.1b</td>
<td>108 ± 8b</td>
<td>16 ± 4</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Flip Like</td>
<td>3 ± 1</td>
<td>0.3 ± 0.1a</td>
<td>170 ± 14b</td>
<td>13 ± 4</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Other</td>
<td>0.5 ± 0.3</td>
<td>1.1 ± 0.1a</td>
<td>272 ± 18b</td>
<td>108 ± 25a</td>
</tr>
</tbody>
</table>

Values are means ± SE; n = no. of rats, n/Rat = no. of responses per rat. Different letters indicate statistically significant differences (P < 0.05) from other responses that are similarly identified within same context.
ICP Peaks

ICP recordings displayed peaks superimposed on plateaus in each erectile context. Such intrapenile pressure peaks rising above plateaus to suprasystolic values have been recorded in other species during copulation (3, 4). Anesthesia of the perineal muscles abolished the suprasystolic rises, demonstrating the participation of these muscles to the pressure changes. In anesthetized rats, ICP exceeded BP only when stimulation of the motor pudendal nerve was added to the stimulation of the cavernous nerve. Curarization abolished the suprasystolic rises (13), demonstrating that in rats, too, the striated penile muscles cause the peaks. Plateaus surmounted by peaks have also been recorded in the corpus spongiosum of rats during reflexive and sleep-related erections, and the peaks were accompanied by intense electromyographic activity of the perineal bulbospongious muscles (31, 32). It is therefore likely that the peaks that we recorded are caused by the contraction of perineal muscles acting on an erect penis.

The question arises, however, whether plateaus are a prerequisite for peaks to occur. We observed that plateaus started before peaks during reflexive, noncontact, and apomorphine-induced erections but not during copulation. Other species exhibit plateaus before peaks during copulation (3, 4). Although our experiments are not conclusive on this question, we believe that in most contexts, activation of the spinal autonomic proerectile pathways takes place before that of motoneurons innervating the penial muscles. Our observation that only peaks are present during copulation does not imply an absence of autonomic activity, but rather a very tight coupling between autonomic and somatic outflows, leading to a single pressure rise. Therefore, autonomic and somatic mechanisms are apparently coordinated for the very rapid onset of erection. A major question arises as to whether the penile vasculature could respond sufficiently rapidly for this mechanism to occur. In anesthetized dogs and monkeys, stimulation of the sacral parasympathetic outflow elicited a transient increase in arterial blood flow, with no concurrent change in penile pressure. Then ICP rose to BP levels (1). Perhaps during copulation in rats there is a similar early change in the blood flow to the penis (e.g., during thrusts preceding intromission) that is not translated into a detectable change in penile pressure. This hypothetical vascular mechanism for local changes occurring in the rat penis during copulation should also be present in other erectile contexts. It may be that differences in the latency between vascular changes on one hand and local penile relaxation and striated muscle contractions on the other hand vary with the erectile context.

One should keep in mind that not only does the autonomic sacral parasympathetic outflow play a role in penile erection. The sympathetic innervation to the penis is classically considered antierectile. Sympathetic activity has been related to flaccidity and subsidence of erection. Although the present experiment did not directly investigate the respective contribution of the parasympathetic and sympathetic activation to the ICP increases recorded, the presence of very rapid increases and decreases, e.g., during copulation, may suggest that in this context a good coordination between these two autonomic outflows also occurs. Given the intraspinal location of their motoneurons, a very efficient integration of peripheral and supraspinal information occurs during copulation to coordinate their activity.

Pressure recordings evidenced differences in peaks both within and between contexts. Differences between peaks occurring within a context, e.g., during penile reflex tests, as evidenced by their different amplitude and duration, very likely reflect the different contribution of perineal striated muscles. This inference is based on data from electromyographic recording of the activity of the perineal striated muscles in rats (31) and other mammals (3, 4). These data suggest that within a context, i.e., copulation and reflexive erection, there exist different patterns of activity of pudendal motoneurons. Such experiments are lacking concerning noncontact and apomorphine-induced erections. Within a context, the force developed by the contraction of the perineal muscles, leading to different peak profiles, would depend on the number of pudendal motoneurons active at the same time and the duration of their activity. Between contexts, similarities between peaks may reflect a similar pattern of activation of pudendal motoneurons. In contrast, differences may be due to the nature (peripheral, supraspinal, or a combination of both) of information that activates the motoneurons.

Recruitment of afferents from the genitalia by either stimulation of the glans penis or dorsal penile nerve in humans and animals elicits reflexive contractions of the penial muscles (9). Similar stimulation occurring during mounts and intromissions in conscious rats could, by contracting the perineal muscles, reinforce the ICP rise. This inference is supported by the observation that the greatest peak amplitude was recorded during copulation, relative to reflexive, noncontact, and apomorphine-induced erections. It is noteworthy that reflexive erections lack such a reinforcement from glans stimulation. ICP peaks during intromissions were greater than during mounts without intromission, perhaps because of the stimulation of the engorged penis by the vagina during intromission, resulting in a greater ICP rise.

In conclusion, ICP changes recorded from conscious rats revealed both similarities and differences among erectile contexts, i.e., reflexive, noncontact, and apomorphine-induced erections. The similarities suggest a common activation of neural proerectile pathways. The spinal cord, containing autonomic and somatic motoneurons controlling penile erection, is the recipient of proerectile information from peripheral and supraspinal origins. The convergence of information from these different origins, such as that occurring during copulation, would lead to a better synergy between autonomic and somatic outflows. Differences in ICP increases, such as those occurring between copulation and the
other contexts, may depend on different time correlations of the intraspinal activation of the various neural pathways involved in erection as well as a different balance between the activation of pro- and antierectile neural pathways.

Perspectives

Published results already exist on intraspousiomuscular pressure changes in rats during erection (31, 32). Similarities between the pressure rises recorded by these authors and our results suggest that the technique of telemetry recordings is well suited to study the neural control of penile erection. Simultaneous recording of cavernous and spongiosal corporal pressures could advance our understanding of how erection is coordinated in the two penile bodies. Recent studies on the control of erection using, e.g., pharmacological, endocrine, and molecular genetic approaches, could have benefited from the use of the telemetric technique. Finally, the model should be very promising in promoting understanding of the pathophysiology of erectile dysfunction.

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