Hypothalamic Temperature and Deep Body Temperature During Copulation in the Male Rat

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BLUMBERG, M. S., J. A. MENNELLA AND H. MOLTZ. *Hypothalamic temperature and deep body temperature during copulation in the male rat* PHYSIOL BEHAV 39(3) 367–370, 1987.—The medial preoptic area (MPOA) of the hypothalamus is involved in both the expression of male sexual behavior and the regulation of physiological temperature. This duality of function led us to ask whether arousal, intromission, and ejaculation are accompanied by a distinctive temperature profile. Using telemetric thermosensors, we monitored MPOA temperature and deep body temperature during copulation in the male rat. Changes in MPOA temperature were highly uniform, more so than changes in body temperature. The MPOA heated prior to ejaculation, cooled rapidly following ejaculation and then began to heat again coincident with the termination of the post-ejaculatory refractory period. These changes could not be related to variations in general activity. The most striking change in MPOA temperature, rapid cooling following ejaculation, was explained in terms of certain behaviorally-induced hemodynamic events.

Thermoregulation   Medial preoptic area   Male sexual behavior

THE medial preoptic area (MPOA) of the male rat integrates thermal information from other areas of the central nervous system as well as from the skin and viscera and generates output signals that direct heat-gain and heat-loss effector mechanisms to maintain physiological temperature [17–19, 23]. The MPOA of the male also processes sensory information reflecting the estrous condition of the female and, in the presence of testosterone, it mediates arousal, intromission and ejaculation [9,10]. Noting this two-fold function of the MPOA, Silva and Boulant [22] asked whether there are thermosensitive MPOA neurons that increase their firing rate when exposed to testosterone. Fully one-third of those tested did increase their firing rate, indicating a population of neurons within the MPOA sensitive to both thermal and androgenic influence. Accordingly, Silva and Boulant suggested that thermoregulation and copulation are not only mediated by the MPOA, but that they interact within the MPOA. If the two systems do interact, then perhaps a distinctive temperature profile characteristically accompanies male sexual behavior. We explored this possibility by monitoring MPOA temperature (T_{hy}) and deep body temperature (T_b) in male rats from the moment a receptive female was introduced until sexual satiation was reached.

METHOD

We used eight sexually experienced male Wistar rats that were between 125 and 160 days of age. These males were housed individually in standard laboratory cages under a 12L:12D lighting schedule.

Prior to the beginning of the experiment, each male was anesthetized with ketamine hydrochloride (87 mg/kg) and xylazine hydrochloride (13 mg/kg) and "equipped" with two battery-operated telemetric thermosensors (Mini-Mitter, Inc., Sunriver, OR). One thermosensor was placed in the peritoneal cavity while another was implanted stereotaxically in the MPOA using the atlas of Paxinos and Watson [14]. The coordinates were 0.6 mm posterior to bregma, 0.5 mm lateral to the midsagittal suture and 8–9 mm below the surface of the horizontal skull. After it was positioned in the MPOA, the thermosensor was attached to the skull using dental cement and two skull screws. Our observations began at least one week following surgery, by which time each animal had regained its preoperative weight.

Each thermosensor was calibrated prior to surgery and then again at the conclusion of the experiment. Signals from the thermosensor in the peritoneal cavity were received by an FM radio and those from the thermosensor in the MPOA by an AM radio. The signals were then processed to remove noise and fed into frequency counters. Use of the system enabled us to detect temperature changes in intervals of 0.03 to 0.06°C.

Each male was habituated to a semi-circular arena prior to the beginning of the observation period. Our observations began when a female in natural proestrus was placed in the arena. Using standard scoring procedures [5], we recorded the male's sexual behavior until he reached satiation, defined as 20 minutes without a mount. All observations were carried out under red illumination during the dark phase of the prevailing 12 L:12 D lighting schedule. The ambient temperature was 21°–23°C at a relative humidity of 30–50%.

A Zenith Personal Computer with a specially-written pro-
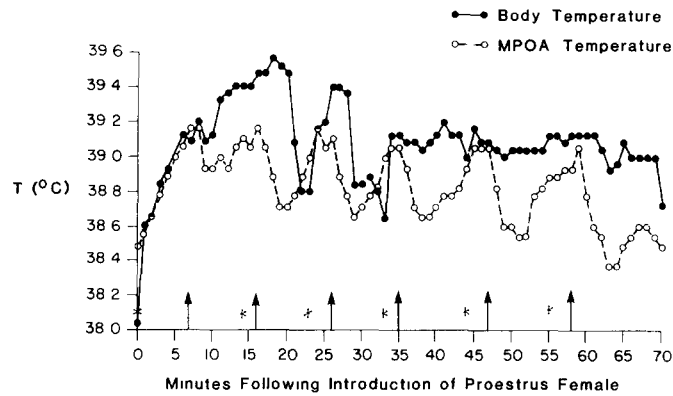
FIG. 1. MPOA temperature and body temperature during copulation
in a single male Arrows indicate time of ejaculation and asterisks
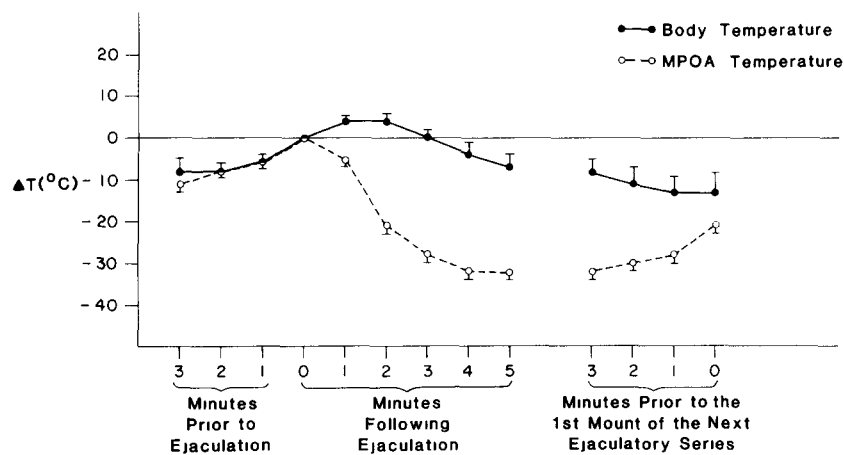indicate time of first intromission of each ejaculatory series

FIG 2 Mean changes in MPOA temperature relative to MPOA temperature at the minute
of ejaculation and mean changes in body temperature relative to body temperature at the
minute of ejaculation for 41 ejaculations across all animals (mean±SE)

gram was used to record the number of mounts and the number of intromissions during each minute and whether or not, during any given minute, an ejaculation had occurred. Both T_{hy} and T_b were also entered minute-by-minute, making it possible to relate temperature to sexual behavior throughout the observation period. All temperature data were converted by the computer to degrees Celsius using a regression equation derived from the calibrations for each thermosensor.

Because the ejaculation-related 22 kHz vocalization has been considered an important aspect of male sexual behavior, we decided to include such data in our minute-by-minute profile. To accomplish this, we used two Mini Bat Detectors (QMC, Ltd., London) tuned to a range of 20–30 kHz, and we entered the number of 22 kHz bouts/minute into the computer. We defined a "bout" as the occurrence of a 22 kHz vocalization within a 6-second interval.

At the conclusion of the experiment, each male was given an overdose of sodium pentobarbital and perfused with 0.9% saline followed by 10% formalin. The brain was removed, sectioned serially and stained with cresyl violet. Proper

placement of the MPOA thermosensor was confirmed for all eight animals.

RESULTS AND DISCUSSION

Figure 1 is the record of temperature changes in the MPOA and core of a single male both prior to and following six ejaculations. Figure 2 shows, for all animals across at least four ejaculations for each animal, mean changes in MPOA temperature relative to MPOA temperature at the minute of ejaculation. Figure 2 also shows mean changes in body temperature relative to body temperature at the minute of ejaculation.

It is evident from Fig. 1 that the temperature of the MPOA began to increase within one minute after the female was introduced. This increase continued until the first ejaculation, whereupon there was a rapid fall in T_{hy}. After the MPOA stopped cooling, the first intromission of the next series occurred. This pattern of MPOA heating up to the minute of ejaculation and MPOA cooling following ejaculation was evident throughout the copulatory series. In con-
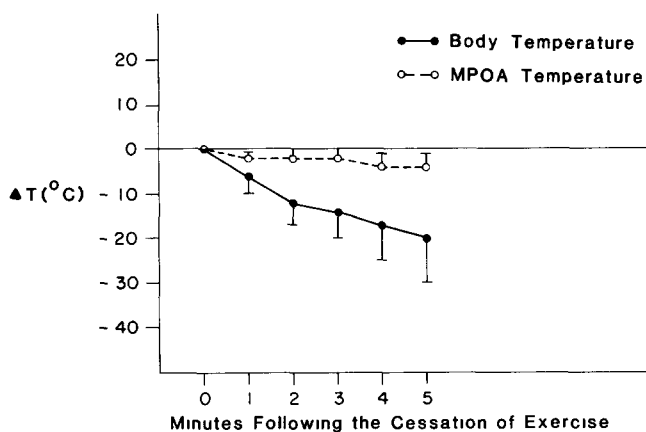
FIG 3 Mean changes in MPOA temperature relative to MPOA temperature at the end of exercise and mean changes in body temperature relative to body temperature at the end of exercise The data represent a total of 16 exercise bouts, the average bout lasting 15.5 minutes (mean±SE).

strast, changes in body temperature were less uniform than changes in MPOA temperature and, indeed, on some post-ejaculatory occasions body temperature remained the same or increased.

The composite data shown in Fig. 2 underscore the picture just presented. MPOA temperature increased up to the time of ejaculation and then decreased progressively during the succeeding four minutes. After a period of stability, during which the temperature of the MPOA remained low relative to its temperature at ejaculation, the MPOA began to heat. This increase became evident just prior to the first mount initiating the next ejaculatory series. In brief, Fig. 2 reveals that the MPOA heats prior to ejaculation, cools immediately following ejaculation, and then begins to heat again coincident with the termination of the post-ejaculatory refractory period. Figure 2 also shows that changes in core temperature were clearly less pronounced than changes in MPOA temperature.

To determine if the MPOA temperature profile just described reflects merely the heightened activity of copulation and then the relative quiescence that follows ejaculation, we ran our animals on a motor-driven wheel at a speed of 6.2 m/min. Although the running was sufficiently strenuous to cause two animals to become so exhausted that they were unable to keep pace with the wheel, nonetheless the mean increase in MPOA temperature over baseline tended to be less than the mean increase during copulation (exercise: $0.75±0.13°C$; copulation $1.00±0.07°C$; $t=1.70$, $p<0.10$). Moreover, we did not observe rapid cooling of the MPOA following running; as Fig. 3 shows. T_{hy} changed little during the first five minutes of post-exercise rest. Clearly, the copulation-related heating and cooling of the MPOA cannot be explained simply as an "exercise effect."

To our knowledge there is only one report in the literature that addresses the question of brain temperature in relation to male sexual behavior. Using rats, Hull et al. [11], implanted thermistors in the lateral convexity of the cerebral cortex and found that cortical temperature following ejaculation "slowly decreased for varying periods until the rat again initiated sexual activity." Evidently, not every area of rat brain shows the rapid post-ejaculatory cooling of the MPOA. The obvious question is, "How does the rat effect rapid MPOA cooling?"

The rat neither pants nor sweats and, unlike artiodactyls and carnivores, it does not have a carotid rete to cool arterial blood flowing to the brain. Of course the body could have functioned as a "heat sink," and indeed the body of the rat can cool rapidly because of its large surface-to-volume ratio. But following ejaculation, it was the MPOA that cooled rapidly, not the body and of the 49 post-ejaculatory periods we monitored, T_{hy} was the same as or lower than T_b more than 75% of the time. It seems unlikely that the MPOA cooled by losing heat to the body.

We think that the rat cools its MPOA through venous blood draining the nasal mucosa and facial cutaneous surfaces. This blood, as Caputa [6] and Caputa et al. [7,8] have shown for the rabbit, is evaporatively cooled and, because it then collects in the cavernous sinus at the base of the brain, it cools the brain through conduction. That there is an intracerebral thermal gradient [6] makes it easy to understand why the MPOA, located just above the sinus, shows a sharper reduction in temperature than brain sites more distal to the sinus. But of course anatomical location does not explain why the MPOA cooled rapidly following ejaculation and why it cooled slowly following exercise. Such an explanation requires attention to certain respiratory and hemodynamic events.

During the post-ejaculatory period, but not during rest after exercise, the male rat often generates bouts of nearly pure tones at a frequency of 22 kHz [1–4]. Such ultrasonic vocalizations are produced by compression of the thoracic cavity and constriction of the larynx, forcing the expulsion of air at high pressure [15,16]. To determine whether or not the MPOA of the rat cools when the male is emitting his post-ejaculatory vocalization, we correlated the decrease in T_{hy}/min and the number of 22 kHz bouts/min during the first six minutes following ejaculation. The correlation was 0.90 ($p<0.01$).

We suggest that the thoracic-laryngeal maneuver underlying production of the "song" has essentially the same hemodynamic effects as cough syncope in man [12,21] and repetitive sneezing in squirrel monkeys [20]: by producing a rise in cerebrospinal-fluid pressure it "squeezes" blood out of the brain into the nasal mucosa and then into the cavernous sinus. Freshly cooled, this blood cools the brain, particularly the ventral brain, through conduction.

Brain tissue is highly sensitive to heat. Polyribosomes begin to disaggregate when the cerebrum reaches 40–41°C and above 41°C marked destruction of mitochondria occurs [6,13]. We now know that at the time of ejaculation the temperature of the MPOA may reach almost 40°C. Our hypothesis is that a distinctive thoracic-laryngeal maneuver follows ejaculation and that it functions to cool the hypothalamus. We think the attendant song is epiphenomenal and that the communicative value of the song, if indeed it has communicative value, is secondary (cf. Thiessen and Kittrell [24]). In this regard, we should emphasize that the song does not always occur after an ejaculation; our observations as well as those of Adler and Anisko [1] and Barfield and Geyer [3,4], indicate that approximately 20% of the post-ejaculatory periods are "silent." In contrast, hypothalamic cooling seems to be an invariant sequela of ejaculation; it was evident in every one of the 49 post-ejaculatory periods we monitored.

We do not know why the male sometimes fails to produce the song after he ejaculates. Perhaps on such occasions he does not present the laryngeal configuration, or does not form what Roberts [15,16] called the "whistle mechanism,"

needed to generate a 22 kHz vocalization. Whatever the reason, we think the male nonetheless compresses his thorax and constricts his larynx. And as already mentioned, we think this maneuver elevates cerebrospinal-fluid pressure to promote hemodynamic changes that cool a heat-threatened hypothalamus. It would be of interest to compare cerebrospinal-fluid pressure during post-ejaculatory episodes of singing and non-singing. Our expectation, of course, is that an elevation of pressure will occur irrespective of the presence of the song.

Finally, it is not clear what role changes in MPOA temperature play in the temporal patterning of sexual behavior Must the MPOA heat to some threshold value before the

male ejaculates? And must he then cool the MPOA before initiating the first mount of the next ejaculatory series? Work is underway in the authors' laboratory to answer these questions.

REFERENCES

1 Adler, N. and J Anisko The behavior of communicating An analysis of the 22 kHz call of rats *(Rattus norvegicus) Am Zool* **19:** 493–508, 1979.

2 Barfield, R J , P. Auerbach, L A Geyer and T K McIntosh Ultrasonic vocalizations in rat sexual behavior. *Am Zool* **19:** 469–480, 1979

3 Barfield, R J. and L A Geyer Sexual behavior Ultrasonic postejaculatory vocalization song of the male rat. *Science* **176:** 1349–1350, 1972

4 Barfield, R. J and L A. Geyer. The ultrasonic postejaculatory vocalization and the postejaculatory refractory period of the male rat *J Comp Physiol Psychol* **88:** 723–734, 1975

5 Beach, F. A and L. Jordan Sexual exhaustion and recovery in the male rat. *Q J Exp Psychol* **8:** 121–133, 1956

6 Caputa, M Selective brain cooling An important component of thermal physiology. In *Satellite Symposium of the 28th International Congress of Physiological Sciences*, edited by Z Szelenyi and M. Szekely. New York Pergamon Press, 1981, pp 183–192.

7 Caputa, M , W. Kadziela and J Narebski Significance of cranial circulation for the brain homeothermia in rabbits 1. The brain-arterial blood temperature gradient *Acta Neurobiol Exp* **36:** 613–624, 1976

8 Caputa, M , W. Kadziela and J Narebski Significance of cranial circulation for the brain homeothermia in rabbits. II The role of the cranial venous lakes in the defence against hyperthermia *Acta Neurobiol Exp* **36:** 625–638, 1976

9 Edwards, D A. and L C Einhorn Preoptic and midbrain control of sexual motivation *Physiol Behav* **37:** 329–335, 1986

10 Hart, B L and M G Leedy Neurological bases of male sexual behavior In *Handbook of Behavioral Neurobiology, Vol 2. Reproduction*, edited by N Adler, D Pfaff and R W. Goy New York Plenum Press, 1985, pp 373–422

11 Hull, C D , J Garcia and E. Cracchiolo Cerebral temperature changes accompanying sexual activity in the male rat *Science* **149:** 89–90, 1965

12 McIntosh, H D , E H Estes and J. V. Warren. The mechanism of cough syncope *Am Heart J* **52:** 70–82, 1956

13 Murdock, L L , S Berlow, R E Colwell and F. L Siegel. The effects of hyperthermia on polyribosomes and amino acid levels in infant rat brain. *Neuroscience* **3:** 349–357, 1978

14 Paxinos, G and C Watson *The Rat Brain in Stereotaxic Coordinates* New York Academic Press, 1982

15. Roberts, L H Correlation of respiration and ultrasound production in rodents and bats *J Zool Lond* **175:** 439–449, 1972

16 Roberts, L H Evidence for the laryngeal source of ultrasonic and audible cries of rodents *J Zool (Lond)* **175:** 243–257, 1975

17 Roberts, W W and R D. Mooney Brain areas controlling thermoregulatory grooming, prone extension, locomotion and tail vasodilation in rats *J Comp Physiol Psychol* **86:** 470–489, 1974

18 Satinoff, E Neural organization and evolution of thermal regulation in mammals *Science* **201:** 16–22, 1978

19 Satinoff, E , J Liran and R Clapman Aberrations of circadian body temperature rhythms in rats with medial preoptic lesions *Am J Physiol* **242:** R353–R357, 1982

20 Schwartz, G G. and L A Rosenblum Sneezing behavior in the squirrel monkey and its biological significance In *Handbook of Squirrel Monkey Research*, edited by L A Rosenblum and C L Coe New York Plenum Press, 1985, pp. 253–269.

21 Sharpey-Schafer, E. P Effects of coughing on intrathoracic pressure, arterial pressure and peripheral blood flow *J Physiol* **122:** 351–357, 1953

22 Silva, N L and J A Boulant Effects of testosterone, estradiol, and temperature on neurons in preoptic tissue slices *Am J Physiol* **250:** R625–R632, 1986.

23. Simon, E , F K Pierau and D. C M Taylor. Central and peripheral thermal control of effectors in homeothermic temperature regulation. *Physiol Rev* **66:** 235–300, 1986

24. Thiessen, D E. and E M W Kittrell Mechanical features of ultrasound emission in Mongolian gerbil, *Meriones unguiculatus Am Zool* **19:** 509–512, 1979