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How the Nose Cools the Brain During Copulation in the Male Rat

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BLUMBERG, M. S. AND H. MOLTZ. *How the nose cools the brain during copulation in the male rat.* PHYSIOL BEHAV **43**(2) 173–176, 1988.—Copulation in the male rat is accompanied by a progressive increase in both body temperature and hypothalamic temperature and, soon after ejaculation, by a rapid and selective decrease in hypothalamic temperature. We hypothesized that two changes occur in tandem within the vasculature of the nasal mucosa that contribute, respectively, to hypothalamic heating and hypothalamic cooling. The first takes place prior to ejaculation and involves mucosal vasoconstriction and warm venous blood flowing from the nose to the base of the brain. We thought of such warm blood as retarding heat loss from the hypothalamus. The second takes place immediately following ejaculation and involves the same venous blood, but now cool owing to an abrupt dilation of nasal blood vessels. We hypothesized that such cool venous blood is largely responsible for the observed postejaculatory reduction in hypothalamic temperature. To test our hypothesis, we measured temperature at the surface of the nasal mucosa and in the hypothalamus during successive copulatory bouts. In accord with prediction, we found a reduction in mucosal-surface temperature prior to ejaculation (reflecting vasoconstriction and heat retention) and a substantial rise in mucosal-surface temperature following ejaculation (reflecting vasodilation and heat dissipation). Accompanying these changes in nasal vasomotor tone was a progressive preejaculatory rise in hypothalamic temperature and a rapid postejaculatory decrease. We conclude that nasal venous blood modulates the temperature of the ventral brain through conductive heat exchange and that such heat exchange is conspicuous during sexual behavior.

Nasal mucosa Thermoregulation Hypothalamus Sexual behavior Male rat Ultrasound

COPULATION in the male rat is accompanied by a progressive increase in body temperature as well as hypothalamic temperature. With the occurrence of ejaculation, however, the increase quickly abates and the hypothalamus relative to the body then undergoes rapid cooling [4]. This selective reduction in hypothalamic temperature is puzzling insofar as the rat does not pant and does not have a carotid rete that cools arterial blood flowing to the brain, as do artiodactyls and carnivores [6].

In searching for an explanation of hypothalamic cooling in the rat, our attention was drawn to the 22 kHz vocalization that the male emits in discontinuous, 1–3 sec bursts beginning soon after ejaculation. He produces this species-specific vocalization by compressing his thoracic cavity and constricting his larynx, thereby forcing the expulsion of air at high pressure [13,14]. We thought that such a thoracic-laryngeal maneuver might cool the ventral brain in one or both of the following ways. First, it might produce a rise in cerebrospinal-fluid pressure which would "squeeze" blood out of the brain, forcing it into the mucosa of the nose. If this "squeezed blood" were under sufficient pressure, it would induce venous dilation and blood draining the nose would cool convectively. Such cooled blood, reaching the cavernous sinus, would then draw heat from the ventral brain. And second, the thoracic-laryngeal maneuver underlying the 22 kHz vocalization might cool the ventral brain by forcing air from the narrow passages of the trachea and larynx into the larger spaces of the upper respiratory tract. When entering these larger spaces, the compressed air would expand rapidly, and by expanding, would cool adiabatically. This cool air, passing over the surfaces of the oral and nasal mucosa, might effectively lower hypothalamic temperature.

As yet, we do not have evidence to determine whether one or both of the mechanisms just sketched functions normatively during the emission of the 22 kHz vocalization. We do have evidence, however, that the vocalization itself is affected by hypothalamic temperature [5]. Specifically, we found that the elevation of hypothalamic temperature that follows the intracerebroventricular infusion of prostaglandin E_2 was accompanied by the vocalization even when the male was isolated. We also found that when he was copulating at a lower-than-normal hypothalamic temperature owing to the prior injection of sodium salicylate, the postejaculatory vocalization was virtually abolished. These data, in addition to showing that the vocalization is sensitive to hypothalamic temperature, suggest that the vocalization, or more precisely the thoracic-laryngeal maneuver underlying it, may function to cool the ventral brain. But then, what of postejaculatory hypothalamic cooling? Does the maneuver play a critical role in effecting this abrupt loss of heat, or is its role auxiliary to that of some other thermolytic mechanism?

We knew from the observations of Adler and Anisko [1] and Barfield and Geyer [3] that 20–30% of the postejaculatory intervals are not accompanied by the 22 kHz vocalization. Nonetheless, our own observations indicated that the hypothalamus can cool rapidly even when the male

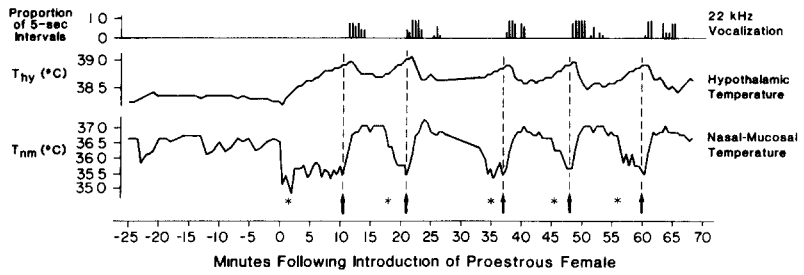

FIG. 1. Hypothalamic temperature and nasal-mucosal temperature during copulation in a single male Also indicated is proportion of 5-sec intervals in which the 22 kHz vocalization was detected. Arrows indicate time of ejaculation and asterisks indicate time of first intromission of each ejaculatory series Note the different scales for hypothalamic and nasal-mucosal temperatures

is "silent." To determine whether the maneuver occurs on such occasions, but for some reason fails to produce the vocalization, we monitored the respiration of copulating male rats using the impedance pneumograph technique (Blumberg and Moltz, unpublished data). Our thinking was that if the vocalization is a variable by-product of the maneuver, the high-amplitude respiratory movements, indicative of heightened thoracic-laryngeal activity, should fail occasionally to give rise to 22 kHz "singing." As it turned out, we never observed a high-amplitude respiratory movement that was not accompanied by singing. The vocalization, in other words, did not appear as a variable by-product of the thoracic-laryngeal maneuver. On the contrary, it was the maneuver that appeared erratically and, in recognizing that its occurrence was erratic, we came to think of the maneuver as playing only an auxiliary role in postejaculatory hypothalamic cooling. At this point the data of Caputa *et al.* [7–9] on the rabbit and guinea pig came to mind, data we had considered as only marginally relevant to postejaculatory hypothalamic cooling in the rat.

The temperature of the ventral brain in the rabbit and guinea pig is significantly affected by nasal vasomotor tone. When nasal-mucosal blood vessels constrict, heat is retained within the mucosa and, as a consequence, nasal-venous blood is warmed. Such warmed blood, when it reaches the cavernous sinus via the internal jugular system, retards heat dissipation from the ventral brain. In contrast, when nasal blood vessels dilate, mucosal heat is lost convectively and venous blood draining the nose is cooled. This blood, once it collects in the cavernous sinus, cools the ventral brain through conductive head exchange.

The rat's successive intromissions, as we have already mentioned, are accompanied by a prominent increase in hypothalamic temperature and, after ejaculation, by a rapid decrease. This decrease does not follow any characteristic alteration in body temperature [4]; on the contrary it is an example of what, in the heat-stressed rabbit and guinea pig, has been referred to as "selective brain cooling" [6]. Thus, thinking of the rabbit and guinea pig, we decided to monitor changes in the mucosal-surface temperature of the male rat both prior to and following ejaculation. We predicted a decrease in mucosal-surface temperature (reflecting vasoconstriction and heat retention) prior to ejaculation and an increase in mucosal-surface temperature (reflecting vasodilation and heat dissipation) following ejaculation.

METHOD

We used five sexually experienced male Wistar rats, 140–190 days old at the time of surgery. These males were housed individually in standard laboratory cages under a 12 L:12 D lighting schedule.

Each male was anesthetized with ketamine hydrochloride (87 mg/kg) and xylazine hydrocloride (13 mg/kg). A battery-operated telemetric thermosensor (Mini-Mitter, Inc., Sunriver, OR) was implanted stereotaxically in the rostral hypothalamus using the atlas of Paxinos and Watson [12]. 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. The transmitter was attached to the skull using two skull screws and dental cement.

Each thermosensor was calibrated in a temperature-controlled water bath both prior to surgery and then again at the conclusion of the experiment. Signals from the thermosensors were received by an AM radio, processed to remove noise and fed into a frequency counter set to the period mode. Data from the frequency counter were expressed in a form later converted to degrees Celsius using a regression equation derived from the calibrations for each thermosensor. With this system we were able to detect temperature changes of 0.03 to 0.06°C.

Immediately after the thermosensor was implanted and while the male was still anesthetized, a hole was drilled into the nasal bone, approximately half way between the eyes and the opening of the nares. A polyethylene tube (PE-60) was then inserted into the hole to serve as a guide cannula for a small-diameter thermistor probe (Yellow Springs Instruments No. 511). When the probe was in place, its tip rested on the ventral surface of the nasal mucosa. A thin cable ran from the probe to a digital thermometer that enabled us to measure nasal-mucosal temperature to 0.1°C. An elastic band attached to a horizontal bar suspended the cable above the animal, allowing the animal freedom of movement. Habituation trials, begun several days before the start of testing, accustomed the animal to the nasal-mucosal probe.

All tests were conducted under red-light illumination during the dark phase of the 12 L:12 D cycle. Immediately following the insertion and attachment of the nasal probe, the animal was placed individually in a rectangular observation arena and nasal-mucosal and hypothalamic temperatures were recorded each minute until both temperatures

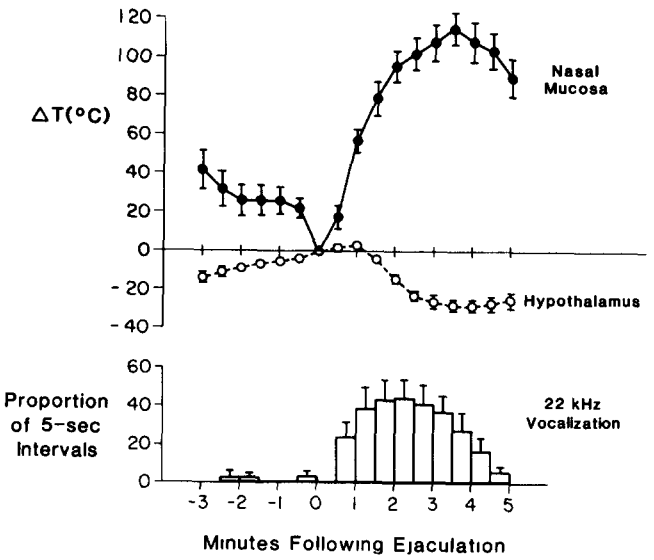

FIG. 2. Mean changes in hypothalamic temperature relative to hypothalamic temperature at ejaculation and mean changes in nasal-mucosal temperature relative to nasal-mucosal temperature at ejaculation. Also indicated is proportion of 5-sec intervals in which the 22 kHz vocalization was detected (mean±SEM).

stabilized. This usually took about 15 min. A female in natural proestrus was then introduced into the arena, and thereafter nasal-mucosal and hypothalamic temperatures were recorded every 30 seconds until the male reached a minimum of three or a maximum of five ejaculations.

Because of our interest in the postejaculatory 22 kHz vocalization as a thermoregulatory behavior, albeit an auxiliary one, we monitored the vocalization to assess its relation to changes in nasal-mucosal temperature. To accomplish this, we used two Mini Bat Detectors (QMC Ltd., London) tuned to a range of 20–30 kHz, and we recorded the number of 5-sec intervals in which the 22 kHz vocalization occurred for each 30-second period of observation.

RESULTS AND DISCUSSION

Figure 1 is a record of temperature changes in both the rostral hypothalamus and the nasal mucosa of a single male prior to and following five ejaculations. Figure 2 also represents mucosal and hypothalamic temperatures, but for all animals across 20 ejaculations. The means shown were calculated for every 30-sec interval and are expressed relative to the corresponding mean value at the time of ejaculation. Also pictured in Figs. 1 and 2 are data concerning the 22 kHz vocalization.

It is apparent from Fig. 1 that mucosal-surface temperature was reduced soon after the female was introduced and that this reduction remained in evidence until the first ejaculation. Then, virtually coincident with the ejaculation, there was a sharp reversal: mucosal-surface temperature rose and quickly reached a peak level. This pattern of reduced mucosal-surface temperature up to the moment of ejaculation (reflecting heat retention) and increased mucosal-surface temperature immediately following ejaculation (reflecting heat loss) was repeated throughout the copulatory series.

Figure 1 also represents hypothalamic temperature and reveals that hypothalamic temperature changed inversely with mucosal-surface temperature. Thus, the hypothalamus began to gain heat soon after the female was introduced and it continued to heat until the time of ejaculation. Following ejaculation, as Fig. 1 shows, the hypothalamus quickly cooled.

Prior to a given ejaculation, the male repeatedly pursues and mounts the female. In doing so, he generates a high trunk temperature, causing an above-normal amount of heat to flow to the brain [4]. In comparison, vasoconstriction and heat retention in the nasal mucosa probably affect the observed preejaculatory rise in hypothalamic temperature only modestly. Then, of course, the male ejaculates, and we suggested that at or soon after the ejaculation the nasal mucosa exhibits a pronounced vasomotor change that results in a selective reduction in hypothalamic temperature. Figure 2 supports this suggestion. Increased heat loss from the surface of the mucosa was evident within 30 seconds following ejaculation, and within 90 seconds hypothalamic temperature began to fall. By 3.5 minutes, mucosal-surface temperature had reached a peak and by 3.5 minutes hypothalamic temperature had reached a nadir. It now seems likely that the rat, in common with the rabbit and the guinea pig, uses the nose to cool the brain.

Figures 1 and 2 also represent the 22 kHz vocalization. Clearly, the vocalization was emitted during the postejaculatory period, and its emission accompanied nasal vasodilation and hypothalamic cooling. What is not evident, however, is the individual variability: one male did not vocalize at all and another vocalized after only two of four ejaculations. A total of six (30%) postejaculatory periods failed to witness the vocalization; nonetheless, during all but one of those periods the hypothalamus cooled rapidly. In contrast, nasal vasodilation occurred during every postejaculatory period and all but two (10%) such periods were followed by a rapid reduction in hypothalamic temperature. Thus, while nasal vasodilation sometimes failed to induce hypothalamic cooling, hypothalamic cooling never occurred in the absence of nasal vasodilation. These data reinforce our hypothesis that nasal vasodilation is the principle mechanism in postejaculatory hypothalamic cooling and that the vocalization plays an auxiliary thermolytic role.

Finally, there is the question of what neural mechanisms underlie the sequential constriction and dilation of the nasal mucosa. It is well known that the mucosal vasculature is innervated by the autonomic nervous system and that sympathetic excitation induces mucosal vasoconstriction and parasympathetic excitation induces mucosal vasodilation (e.g., [11]). If, as recent evidence suggests [2], there is sympathetic dominance during arousal and penile stimulation and parasympathetic dominance during and immediately following ejaculation, then one might expect nasal vasoconstriction to be prominent during the "excitement" stage of the copulatory sequence and nasal vasodilation to be prominent during the "consummatory" stage. Interestingly, there are clinical data in humans that match such a vasomotor picture: men suffering from vasomotor rhinitis report alleviation of nasal congestion during sexual excitement and a return to the congestive condition following ejaculation [10].

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