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Thermal Panting in Dogs: The Lateral Nasal Gland, a Source of Water for Evaporative Cooling

Abstract. Two lateral nasal glands appear to provide a large part of the water for evaporative cooling in the panting dog; their function is analogous to that of sweat glands in man. Each gland drains through a single duct which opens about 2 centimeters inside the opening of the nostril. This location may be essential to avoid desiccation of the nasal mucosa during thermal panting. The rate of secretion from one gland increased from 0 to an average of 9.6 g (gland \cdot hour)⁻¹ as air temperature was increased from 10° to 50°C. Evaporation of the fluid from the paired glands could account for between 19 and 36 percent of the increase in respiratory evaporation associated with thermal panting. The fluid secreted by the gland was hypoosmotic to plasma.

Schmidt-Nielsen et al. found that, during normal open-mouth thermal panting in the dog, most of the air enters the nose and leaves the mouth (1). The nasal passages are, therefore, the primary site of evaporation. The authors suggested that a large serous type gland which is found in the nasal cavities might be a major source of the water for evaporation. This gland was first described by Steno in 1664 (2). It is found in a variety of animals which utilize thermal panting for evaporative cooling (dog, cat, pig, sheep,



Fig. 1. Weight of fluid collected from one chronically cannulated lateral nasal gland as a function of air temperature. Each point is an average weight of nine measurements from three dogs. Each vertical bar is twice the standard error of the mean.

goat, and small antelopes) (3). In such typical "sweaters" as man, horse, and cattle, the gland is either absent or of microscopic proportions (3). We wanted to know whether these glands are an important source of water for evaporation during thermal panting.

There are two glands, one in each maxillary recess. Each gland empties through a single duct (4) which opens about 2 cm inside the nostril (5, 6). One gland was chronically cannulated under general pentobarbital anesthesia in each of three 25-kg dogs. An incision was made slightly lateral to the nasal septum, and the lateral wall of the nose was reflected to expose the orifice of the duct to the lateral nasal gland. A PE 60 cannula was sutured into the orifice. The cannula extended approximately 2 cm anterior to the orifice of the duct so that it was just visible through the external nares. The wound was then closed.

The rate of secretion from these glands increased markedly with increasing ambient temperature (Fig. 1). No secretion was observed at 10°C. The gland began to secrete as air temperature was increased from 20° to 30°C, and an average of 9.6 g (gland · hr) $^{-1}$ was collected at 50°C.

In order to evaluate the importance of this secretion for evaporative cooling, we compared the rate of secretion from both glands with the increment

in respiratory evaporation associated with thermal panting. We trained the dogs to wear ventilated masks and determined the amount of water added to the air flowing through the mask (7). Saliva was observed dripping from the tongue of two dogs at high air temperatures, but not from the third (Fig. 2). This water would appear as respiratory evaporation in our collection system, even though it played no role in evaporative cooling. To correct this error, we collected the saliva which dripped from the tongue of each dog in separate experiments at each temperature. This drooling was copious in two dogs and as much as $100 \text{ g} \cdot \text{hr}^{-1}$ was collected at 50°C (Fig. 2).

The mean value for salivary dripping from each dog at each temperature was subtracted from the observed respiratory water loss in the previous experiments to obtain respiratory evaporation. To check the validity of this correction, we investigated the heat balance of the animal. In the steady state, heat production must equal heat loss. The three avenues of heat loss are evaporation, conduction, and radiation. We selected a steady-state situation in which air and wall temperatures were approximately the same as the body temperature of the dog, thereby nearly eliminating conduction and radiation as means of heat dissipation. Heat loss by evaporation, therefore, equaled heat production. When the ambient temperature was 40.0°C and rectal temperature was 39.1°C, the heat production equaled 2.70 kcal (kg hr) $^{-1}$ and calculated evaporative heat loss equaled 2.90 kcal (kg hr) $^{-1}$. Thus we have



Fig. 2. Grams of saliva which dripped from the tongue as a function of air temperature. This was extremely variable from dog to dog, and none was collected from dog 3 (even at 50°C). Each point represents the mean of six to eight measurements, and each vertical bar represents twice the standard error.

some confidence that our correction is valid.

Using this correction, we calculated the percentage of the increment in respiratory evaporation above that observed at 20°C which could be accounted for by the volume of fluid secreted by both lateral nasal glands. The percentages were 33 at 31°C, 19 at 40°C, and 36 at 50°C. The differences between these figures are not significant, and we conclude that the lateral nasal gland accounts for about 30 percent of the increment.

The fluid secreted by the lateral nasal glands was hypoosmotic to plasma and contained less than 0.1 mg of protein per 100 cm³ (8). There was a slight increase in Na+ concentration and osmolarity with increasing rate of secretion; however, this was not statistically significant in our experiments. The rates of secretion and the compositions of the fluid secreted at various temperatures were: 2.6 g (gland \cdot hr)⁻¹, 18.7 meq Na⁺ per liter, 20.7 meq K⁺ per liter, 75.7 milliosmols per liter, at 30° C; 4.5 g (gland \cdot hr)⁻¹, 21.4 meq Na⁺ per liter, 20.1 meq K⁺ per liter, 80.7 milliosmols per liter, at 40°C; and 9.6 g (gland \cdot hr)⁻¹, 35.3 meq Na⁺ per liter, 18.6 meq K⁺ per liter, 103.3 milliosmols per liter, at 50°C.

We conclude that (i) the rate of secretion from the lateral nasal gland increases with increasing respiratory evaporation as a result of thermal panting; (ii) between 20 and 40 percent of the increment in respiratory evaporation at air temperatures between 30° and 50°C can be accounted for by this secretion; and (iii) the location of the orifice of the single duct anterior to the turbinates may be essential to avoid desiccation of nasal mucosa during thermal panting.

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7. Air was metered through the mask at a rate of 60 to 150 liter/min STP. A sample of this air was metered through drying tubes immersed in an alcohol bath at -70° C. All flow meters were calibrated to better than ± 1 percent accuracy with a Brooks Volumeter. A blank value was obtained from a stream of room air drawn simultaneously through drains these set identical terms. through drying tubes at identical rates of flow. The amount of water frozen in the drying tubes was determined by weighing on a Mettler balance (model H-10). To determine the accuracy of this method, water was evaporated into the mask at known rates

equivalent to those encountered experimental-Recovery was between 98.7 and 101.8 percent.

- 8. Osmolarity was measured with an Advanced Osmometer (model 65-31), sodium and potas-sium were measured with an Instrumentation Lab flame photometer (model 343), and protein was measured by the method of R. J. Henry, C. Sobel, and S. Berkman [Anal. Chem. 29, 1491 (1957)].
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Chromosome Banding Patterns in Preimplantation Mouse Embryos

Abstract. The chromosomes of first cleavage mouse embryos show the same banding patterns after quinacrine mustard staining as do chromosomes of differentiated mouse cells. Whatever feature of chromosome structure the banding pattern reveals thus appears not to be altered during development and differentiation.

No tissue-specific differences in the banding patterns displayed by chromosomes after quinacrine mustard (QM) staining have yet been demonstrated. Mouse fibroblast chromosomes (1) show the same patterns as chromosomes of mouse bone marrow cells (2), and the chromosomes of human peripheral leukocytes (3) show the same patterns as do those of human primary spermatocytes (4). This is not unexpected if the QM bands reflect some feature of DNA composition (5), but they may reflect instead the distribution of a protein or proteins along the chromosomes. Thus the same bands as seen after QM staining can be induced by treatments known to be active toward protein rather than DNA, such as trypsinization (6) and treatment with sodium dodecyl sulfate, mercaptoethanol, and urea (7). Also it is possible that the acetic-saline-Giemsa technique, widely assumed to involve denaturation and renaturation of chromosomal DNA (8), could produce banding by selective protein elution from the chromosomes. If the bands reflect the distribution or types of proteins bound to DNA, or both these factors, then developmental alterations in the banding patterns are at least a formal possibility. We therefore



Fig. 1. Chromosomes of late prophase of first cleavage. In each pair the less condensed, paternal chromosome has been placed on the left. The arrangement of the karyotype is according to the recommendation of the Committee on Standardized Genetic Nomenclature for Mice (12).