THE PANTING RESPONSE OF NORMAL UNANESTHETIZED
DOGS TO MEASURED DOSAGES OF DIATHERMY HEAT

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Animals such as the dog, cat and rabbit, which have a deficiency of
sweat glands, when heated develop a type of respiration called “panting,”
“heat polypnea” or “heat tachypnea.” When panting commences there
is a distinct change in the type of respiration which is characterized by a
marked increase in rate and a reduction of tidal volume. Quantitative
measurements on the changes which occur in respiration before and after
panting are few. This is due possibly to the mechanical difficulties in-
volved where the respiratory rate is high. With rates of 200 to 300 per
minute the errors of moving mechanical systems due to starting inertia
are so great that customary methods of measuring ventilation rate and
tidal volume are useless for quantitative measurements. The few inves-
tigations made on this problem have been made on anesthetized animals
in which tracheal cannulas were used. Anesthetics produce varying de-
grees of respiratory depression and seriously disturb the temperature reg-
ulating mechanism. In addition to the difficulty encountered in matching
the dead space a tracheal cannula used to study panting has a more serious
objection. In normal panting the respired air is blown over the moist
surfaces of tongue, mouth, and pharynx from which evaporation for cooling
purposes takes place. When a tracheal cannula is used the respired air
does not pass over these moist surfaces but through the cannula. A can-
nula thus deprives an animal of a considerable part of the evaporating
surface. Since there are no data on the changes in the type of respiration
of normal unanesthetized dogs breathing in a normal manner without
masks or cannulas the following experiments were performed. Attention
has been directed particularly to the changes of respiration before the
onset of panting and the type of breathing which results from continued
heating.

METHODS AND PROCEDURE. To measure ventilation rate and tidal vol-
ume a body plethysmograph of the Haldane (1935) type was used. A
trained dog lay in a closed plethysmograph with head protruding through a

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seal at the neck. Low inertia valves permitted air to pass through the plethysmograph during respiration. The outlet valve discharged into a 150 liter closed tank. To the outlet tube from this tank there was connected a small aluminum spirometer and a recording gas meter. When air was discharged from the plethysmograph into the tank the increase in pressure was indicated on the spirometer. Suction was then applied through the gas meter until the spirometer returned to its base line. The large air volume, i.e., 150 liters, behaved as a pneumatic cushion, and a continuous pressure increase was produced rather than a pulsating pressure at high respiratory rates.  

Respiratory rates were measured by a small tambour whose natural frequency exceeded the highest respiratory rate. A kymograph record of the recording gas meter (top tracing), the respiratory rate (middle tracing) and a 5 second signal magnet (lowest tracing) is shown in figure 1.

Fig. 1

2 Details of this plethysmograph to be published in “Science.”
In some experiments where changes in respiration rate and body movement were to be determined a thread was stretched over the thorax, abdomen and hip of a quiet, recumbent dog. These threads were attached to levers for kymographic recording. The two lower tracings of figure 1 were obtained by this method.

In order to obtain uniform and reproducible conditions of heating, the plethysmograph and room were maintained at 30-31°C with a relative humidity of 50 ± 10 per cent. The dogs were heated by diathermy current from a machine described by Hemingway and Witts (1936). Using this method the amount of heat received by the dogs could be computed from the high frequency voltage and current, as described by Hemingway and McClendon (1933). The heating rates were made equal to and twice the b. m. r., computed from the metabolism determinations of Kitchen (1923), and the treatment continued for 3 hours. The dogs rested two hours in the plethysmograph before being heated. The temperatures were measured by thermocouples.

RESULTS. Ten experiments were performed on 5 dogs, each dog being heated at a rate of 1.0 and 2.0 b.m.r. units on different days. Figure 2 shows how the tidal volume, ventilation rate and respiratory rate vary during a 3 hour diathermy treatment. This graph is typical but each dog has individual peculiarities of respiratory response. For convenience the respiratory response has been divided into the following parts: the prepanting interval, the onset of panting and the period of panting. The prepanting interval can be divided into two subdivisions which may be designated as part I, wherein the low rates of the resting period are main-
tained or become even lower, and part II where the respiratory rate progressively increases until panting starts. Figure 3 may be considered as an atypical response since part II of the prepanting interval is absent. The onset of panting in this case was very sudden, there being no preliminary rise of rate before panting commenced. This animal has a respiratory response similar to Anrep's vagotomized dogs.

Table 1 contains the summarized data taken from the 10 respiration-time curves. The basal values are those at the beginning of the heat treatment. The minimum values of the respiratory rate under basal conditions at 30 to 31°C. and 40 to 60 per cent humidity are 8 to 40 per minute. This rate is comparatively low compared to the panting values. The ventilation volume is low and for dog A, which was especially cooperative in his ability to relax, the ventilation rate was 1.6 liters per minute. During part I of the prepanting period the basal values are continued or in some cases the respiration rates become less. During this interval the dog is drowsy and apparently quite comfortable. Such a response resembles that of patients undergoing diathermy treatments who often remark on a feeling of comfort and drowsiness during diathermy treatments. At the beginning of part II of the prepanting period the respiratory rate and ventilation rate commence to rise. There is a progressive increase in both rates until panting starts. During this interval the average increase in ventilation rate is 3.5 fold while the respiratory rate increase is 3.2 fold. The increase of ventilation rate results from an increase in respiratory rate, the tidal volume on the average remaining unchanged. In contrast
with part I of the prepanting period the dog exhibits symptoms of restlessness and discomfort. Untrained or partially trained animals will attempt to stand or struggle. These symptoms of discomfort continue throughout this interval but disappear when panting starts.

The onset of panting is marked by a respiratory rate increase of 2.7 times over the highest prepanting rate while the tidal volume is reduced 25 percent on the average. An object of this investigation was to determine if there is an abrupt change in respiration when panting starts or if there is a merging of the prepanting type into panting by a continuous increase of respiratory rate. The results show that within a few seconds there can be an abrupt increase in respiration rate and that a condition of panting can be diagnosed from respiration rate alone. This is illustrated in the middle kymograph tracing of figure 1, which shows thoracic movements at the onset of panting. It is to be noted in this tracing that the prepanting type of respiration was labored in that the whole body moved as indicated by the record of hip movement of the recumbent dog. When panting started this labored type of breathing disappeared.

After panting has once commenced and while the animal continues to be heated the type of respiration resembles that of the lowest tracing of figure 1. There are short intervals of true panting alternating with periods

| TABLE 1 |
|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|
| dog             | HEAT DOSAGE = 1.0 B.M.R. FOR 3 HOURS | HEAT DOSAGE = 2.0 B.M.R. FOR 3 HOURS |
|                 | A    | B    | C    | D    | E    | A    | B    | C    | D    | E    |
| Weight of dogs (kilos) | 17.2 | 19.1 | 15.0 | 17.3 | 12.1 | 35.0 | 37.0 | 35.0 | 37.5 | 37.9 |
| B.M.R. (per dog) watts | 35.1 | 42.4 | 40.0 | 38.7 | 26.5 | 35.0 | 37.0 | 35.0 | 37.5 | 37.9 |
| Basal rectal temp | 37.7 | 37.9 | 35.2 | 37.3 | 35.4 | 35.0 | 37.0 | 35.0 | 37.5 | 37.9 |
| Rectal temp. increase | 1.15 | 0.90 | 0.3 | 0.9 | 0 | 0.85 | 1.40 | 1.0 | 1.3 | 0.9 |
| Humidity | 50 | 45 | 55 | 57 | 50 | 50 | 45 | 40 | 90 | 45 |
| Basal resp. rate | 19 | 39 | 46 | 37 | 34 | 39 | 37 | 14 | 71 | 8 |
| Basal tidal volume | 72 | 106 | 119 | 124 | 73 | 66 | 149 | 101 | 90 | 103 |
| Basal resp. rate | 1.4 | 6.1 | 5.8 | 4.6 | 2.6 | 1.9 | 2.6 | 2.2 | 6.1 | 0.82 |
| Final prepanting resp. rate | 111 | 95 | 118 | 75 | 71 | 157 | 199 | 58 | 86 | 86 |
| Final prepanting tidal vol. | 83 | 172 | 91* | 115 | 75 | 80 | 120 | 170 | 100 | 100 |
| Final prepanting vent. rate | 4.1 | 19 | 31.7 | 11.4 | 7.0 | 3.9 | 19.5 | 17.9 | 0.2 | 5.4 |
| Initial panting resp. rate | 230 | 204 | 222 | 250 | 236 | 204 | 336 | 296 | 203 | 270 |
| Initial panting tidal vol. | 53 | 140 | 66 | 59 | 58 | 123 | 56 | 58 | 57 |
| Initial panting vent. rate | 21.9 | 15.4 | 13.5 | 12.1 | 24.5 | 19.0 | 12.1 | 15.7 |
| Average panting resp. rate | 277 | 251 | 256 | 275 | 255 | 246 | 300 | 320 | 293 |
| Average panting tidal vol. | 74 | 113 | 72 | 52 | 55 | 101 | 50 | 48 | 51 |
| Average inter-panting resp. rate | 145 | 104 | 109 | 155 | 225 | 125 |
| Average inter-panting tidal vol. | 150 | 96 | 53 | 125 | 89 | 75 |
| Average vent. rate after onset of panting | 16.0 | 22.7 | 16.0 | 9.7 | 14.9 | 22.8 | 17.8 | 14.0 | 12.3 |

* Rapid respiration without panting. These are average values for the period remaining after maximum respiration and ventilation rate were reached.

be an abrupt increase in respiration rate and that a condition of panting can be diagnosed from respiration rate alone. This is illustrated in the middle kymograph tracing of figure 1, which shows thoracic movements at the onset of panting. It is to be noted in this tracing that the prepanting type of respiration was labored in that the whole body moved as indicated by the record of hip movement of the recumbent dog. When panting started this labored type of breathing disappeared.

After panting has once commenced and while the animal continues to be heated the type of respiration resembles that of the lowest tracing of figure 1. There are short intervals of true panting alternating with periods
of a type of breathing resembling the prepan ting type which is designated as an interpanting. During the interpanting interval the rate is relatively low and the tidal volume high. During the panting intervals the respiratory rate varied from 200 to 350 respirations per minute and the tidal volume decreased as the rate increased.

With a heat dosage equal to the b.m.r. dog C did not pant but maintained a high respiratory rate of about 150 once this value was reached. With dog A there was no appreciable respiration during the interpanting interval. This interval became a momentary pause.

**DISCUSSION.** It was formerly believed as a result of the experiments of Uyeno (1923) that during panting the breathing becomes very shallow with tidal volumes being reduced to about one-sixth to one-eighth of the basal values. This finding of Uyeno was believed to add support to the theory of panting see (Bazett, 1927), that a shallow rapid respiration favored evaporation by air movement over the moist surfaces of mouth, nose and pharynx without creating too great a stirring of the alveolar air with loss of carbon dioxide. Anrep and Hammouda (1932) using anesthetized dogs and tracheal cannulas in experiments similar to Uyeno's, did not find such low tidal volumes during panting but found a reduction of tidal volume to about 50 per cent of the basal values. Anrep and Hammouda on repeating Uyeno's results identically found that the low tidal volumes of Uyeno were due to the use of Muller valves which did not respond to the rapid pressure changes of panting. Our results on tidal volume changes agree in general with the results of Anrep and Hammouda and lead to the conclusion that very shallow breathing in panting does not occur.

There is, however, another observation which lends support to the theory that panting is adopted to prevent too great a disturbance of alveolar air while increasing the fanning movement of air through the mouth. The disturbance of alveolar air is determined by the ratio of tidal air, \( \Delta V \), to total air in the lungs, \( V \). A low ratio of \( \Delta V/V \) would tend to minimize the disturbance of alveolar air and this ratio would be lowered by a low tidal volume \( \Delta V \). Another method of reducing this ratio would be to increase \( V \). From records of abdominal and thoracic movements as shown in the middle tracing of figure 1 it is to be noted that panting consists of a thoracic movement superimposed on a state of abdominal inspiration. In other words at the outset of a panting interval the lungs are filled with air by abdominal inspiration and this is maintained throughout the interval of thoracic panting. At the end of the panting interval there is abdominal expiration which continues throughout the interpanting interval. Hence during panting \( V \) is increased and the ratio \( \Delta V/V \) is decreased partially by reducing \( \Delta V \) and also by increasing \( V \). This state of inspiration during panting was also observed on records made by connecting a sensitive spirometer directly to the closed plethysmograph. A
kymograph record from such a spirometer, while not responding quantitatively to the rapid panting rate, does show the slower respiration on which the rapid breathing is superimposed.

It is of interest in determining the effect of anesthetics on the panting response to compare the results here reported with those of Anrep and Hammouda (1932) who used chloralose-urethane anesthesia. These authors designate as "mild panting" a respiratory rate of 120 to 150 per minute and a tidal volume reduced from a basal value of 42 ml. to a panting value of 25 ml. They call "severe panting" the respiratory movements when the rate reaches 200–350 per minute, but with these high rates the tidal volume increased from a basal of 42 ml. to values of 80 to 90 ml. With our anesthetized dogs there was no panting with respiratory rates less than 200. Only when panting started at rates of 200 to 350 per minute was the tidal volume reduced. In none of the experiments did we observe an increase of tidal volume of the magnitude described by Anrep and Hammouda. It seems that the urethane chloralose anesthesia 1, depresses the ability to lower tidal volume with the high respiratory rates, and 2, lowers the respiratory rate at which panting starts.

Doubling the heat dosage did not appreciably change the respiration response. One would expect increased ventilation and possibly respiratory rate with an increased heat dosage. No such change was found.

It is a pleasure to acknowledge the interest, cooperation and assistance of Dr. H. G. Barbour, who followed the course of this problem in detail. We wish to thank Dr. R. W. Clark for useful suggestions and the loan of apparatus.

SUMMARY

Trained normal dogs have been heated with diathermy, receiving heat dosages equal to, and double the b. r. at 30 to 31° room temperature and with a humidity of 40 to 60 per cent. The respiratory rate, tidal volumes and ventilation rates have been measured with a recording body plethysmograph similar to that of Haldane, and with a meter system for measuring ventilation rate designed in a special way for high respiratory rates.

When an animal is heated by diathermy, the usual response is a gradually increasing ventilation and respiratory rate with no appreciable change in tidal volume. When panting occurs, there is an abrupt increase of two to three times in respiratory rate over the rate observed immediately before panting. The ventilation rate increases to almost double the final prepanting value. Continued heating results in only a slight increase of respiratory and ventilation rates over the initial panting values. When panting occurs, the tidal volume is reduced 20 to 40 per cent. From kymograph records of chest movement and a plethysmograph it has been observed that a dog pants by thoracic movements during a state of inspira-
tion maintained by the abdominal muscles. Panting with the lungs filled with air would tend to reduce the disturbance of alveolar air resulting in a lowered CO₂ tension.

Comparing these results with those of Anrep and Hammouda (1932) who used urethane-chloralose anesthesia, it has been shown that this type of anesthesia does not permit the lowered tidal volume with the high respiratory rates of 200 to 350 per minute as occurs in normal dogs without anesthesia and which, according to theory, is desirable to prevent loss of carbon dioxide by hyperventilation.

REFERENCES

Uyeno, K. J. Physiol. 67: 203, 1923.