Jackrabbit Ears: Surface Temperatures and Vascular Responses

Abstract. *Blood flow to the ear pinnae is curtailed at ambient temperatures of between 1.4° and 24.0°C, which minimizes heat loss across the pinnae and allows the surfaces of erect pinnae to approach ambient temperature. The pinnae are warmed by steady or pulsatile vasodilation in some animals when the ambient temperature is between 1° and 9°C below body temperature, a response favoring heat loss. When ambient temperature exceeds body temperature by 4° to 5°C, the pinnae are circulated with blood cooler than ambient temperature; this response favors heat influx.*

The large pinnae ("ears") of jackrabbits, estimated to represent 19 percent of the body surface area in *Lepus californicus* and 25 percent in *L. alleni* (*1*), are potentially outstanding sites of conductive, convective, and radiative heat exchange with the environment. The extreme development of the pinnae has been postulated to be related to the special requirements of thermoregulation in the desert (*2*). Wathen *et al.* (*3*) calculated that, if the pinnae are maintained at the same temperature as the body core, convective heat loss across them could account for dissipation of 16 to 66 percent of metabolic heat production at an ambient temperature (T_a) of 35°C and for dissipation of 40 to 161 percent at 30°C (presuming wind speeds of 22 to 224 cm/sec). Correspondingly, when T_a exceeds body temperature, the pinnae could be a significant site of convective heat uptake if they are well circulated. Dawson and Schmidt-Nielsen (*4*) demonstrated that whole-body heat conductance by dry routes (dry heat conductance) (*5*) in *L. alleni* increased as T_a was elevated toward rectal temperature (T_{rec}) but then fell sharply when T_a exceeded T_{rec}. They suggested that changes in blood flow in the pinnae might play a major role in modulating dry heat conductance.

We have determined changes in pinna surface temperature and blood flow during exposure to T_a's of 1.4° to 45.5°C. We hypothesized (i) that in resting animals at low T_a pinna blood flow would be minimal and pinna surface temperature would approach T_a, and (ii) that blood flow would increase as T_a rose toward body temperature and decrease when T_a exceeded body temperature. Such changes would minimize heat loss across the pinnae at low T_a, augment dry heat loss at T_a's only modestly below body temperature, and minimize heat uptake at T_a's exceeding body temperature. Infrared radiography was selected as the method of study because it is noninvasive and can be carried out on undisturbed animals.

Three female *L. californicus* were captured in Fish Lake Valley, Nevada, in late May 1975, and studied within 4 weeks of capture. Food and water were constantly available except during experimentation. Because the animals exhibited differences in behavior and thermal responses, they will be identified individually by number (*6*). At all test T_a's animals 2 and 3 nearly always held their pinnae erect. Animal 1 generally held its pinnae erect when T_a was between 31.0° and 45.5°C but virtually always held them against the thorax and abdomen when T_a was between 1.4° and 24.0°C.

The animals were studied in wire cages (61 by 41 by 34 cm) in a large Webber controlled temperature cabinet at T_a's (± 2°C at most) of 1.4°, 11.3°, 24.0°, 31.0°, 38.7°, and 45.5°C. We assured that the radiant temperatures of all environmental surfaces facing the animals were the same as the air temperature (*7*). Water vapor pressure ranged from 4.4 mm-Hg (at 1.4°C) to 14.8 mm-Hg (at 45.5°C). Wind speed was 10 to 15 cm/sec. Experiments were performed in darkness between 1000 and 2400 E.S.T. Each animal was housed at each T_a for at least 2 hours before data were collected. Then it was observed and photographed by infrared radiography (through a port in the door of the temperature cabinet) for 0.3 to 1.6 hours (mean, 0.8 hour) with an AGA Thermovision system (model 680/102B). Deep body temperature was then determined with a thermistor probe inserted 10 cm rectally. Black-and-white radiographs (Figs. 1 and 2) illustrate general aspects of the thermal response. Surface temperatures were determined from color radiographs that incorporated isotherms of known thermal dimensions (*8*).

In animals 2 and 3 at T_a's of 1.4°, 11.3°, and 24.0°C, T_{rec} was between 37.5° and 40.3°C, but surface temperature (T_s) on the pinnae was close to T_a and blood vessels could never be observed in the pinnae radiographically, which indicated little or no blood flow. On the bases of the pinnae, T_s in these two animals was well above T_a, but the warm basal regions terminated abruptly (Fig. 1A). Over most of the pinna surfaces, T_s was so close to T_a that the pinnae could hardly be perceived radiographically. The abrupt termination of the basal region of elevated T_s suggests vasoconstriction in major arteries supplying the pinnae.

Unlike animals 2 and 3, which always

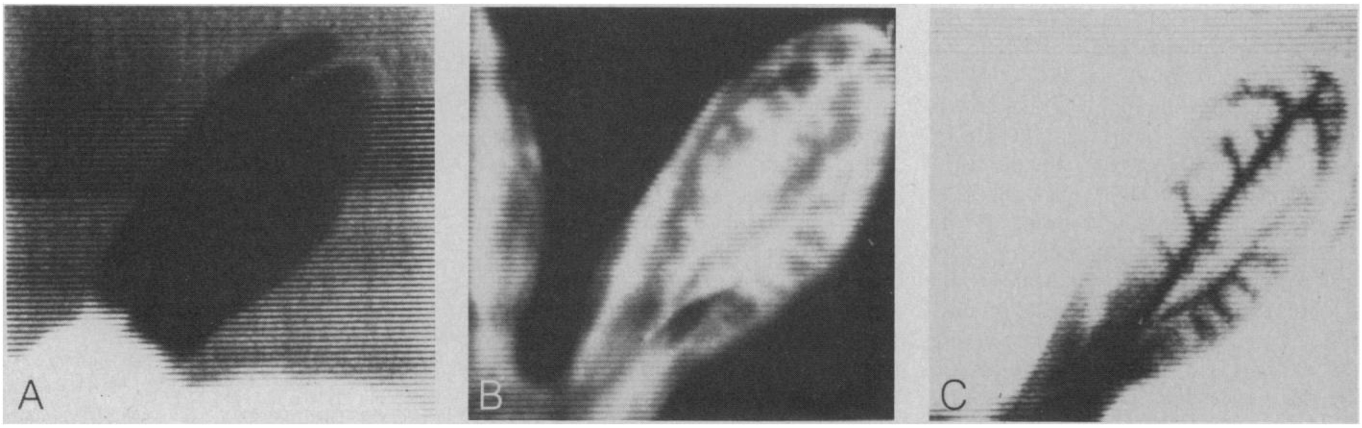

Fig. 1. Infrared radiographs of the pinnae of animal 3 at three ambient temperatures: (A) 11°C, (B) 31°C, and (C) 45°C. In each radiograph, relatively cool surfaces are colored black, relatively warm surfaces are colored white, and surfaces of intermediate temperature are represented in appropriate gray tones. (A) The pinnae were scarcely visible radiographically at 11°C; a brief heat pulse was delivered to the background to silhouette the cold pinnae. The posterior-dorsal aspect of the head appears at the bottom; only the very bases of the pinnae are kept warm at 11°C. Surfaces above the pinna arteries are relatively warm at 31°C (B) and relatively cool at 45°C (C). Radiograph (C) was taken during a period of pulsatile engorgement.

held their pinnae erect, animal 1 virtually always held its pinnae flat against the body between 1.4° and 24.0°C T_a. There was considerable variation in T_s from place to place on the pinnae of animal 1 at such T_a's, its being 10° to 17°C above T_a in certain regions. We believe for several reasons that the pinnae of this animal were warmed through contact with the body and that, as in animals 2 and 3, circulatory influx of heat to the pinnae was curtailed. First, pinna blood vessels were never observed radiographically. Second, parts of the pinnae that did not actually touch the body were cool; on the curl of the medial pinna margin, for example, T_s was sometimes within 1° to 2°C of T_a and never exceeded T_a by more than 6°C. Third, T_s of the pinnae was highest on parts that touched the body and there closely matched that of the thorax and abdomen. The weight of evidence is that circulatory influx of heat to the pinnae was highly limited in all animals at between 1.4° and 24.0°C T_a.

At 31.0°C T_a a dramatic change was observed in animal 3. The arteries of the pinnae were continuously dilated and could be perceived radiographically out to tertiary or quaternary branches (Fig. 1B). Over most of the pinna surfaces, T_s was 2° to 6°C above T_a, and on parts overlying major arteries, it was often 38° to 39°C (T_{rec} = 40.4°C). Animals 1 and 2 behaved differently. Pinna T_s was within 1°C of T_a (the pinnae of animal 1, as well as those of animal 2, were now being held away from the body). Vasodilation was never observed in animal 1 and, during 20 minutes of observation, it was seen in only one brief interval in animal 2 (when T_s above the arteries rose to 34° to 35°C).

The average pinna T_s of animal 3 at a T_a of 31°C, as determined from three radiographs, ranged from 35.7° to 36.5°C (*9*). Thus, even in an individual showing steady vasodilation in the pinnae, convective heat loss across the pinnae is significantly lower than that predicted by Wathen *et al.* (*3*) who assumed T_s to equal T_{rec}. The calculated loss at a wind speed of 22 cm/sec is 22 cal/min (55 percent of that calculated by Wathen *et al.* for similar conditions), and the loss at the average wind speed in these experiments, 12.5 cm/sec, is 16 cal/min. Radiative losses across the pinnae are calculated to be 11 cal/min, and total convective and radiative losses amount to 32 percent of metabolic heat production at a wind speed of 22 cm/sec and 26 percent at 12.5 cm/sec (*10*). When the pinnae are circulated steadily with blood, they seem to dissipate metabolic heat in moderate disproportion to their surface area, which is estimated to be 19 percent of total body surface area (*1*); this finding reflects the fact that T_s is higher on the pinnae than on most parts of the body.

Fig. 2. Infrared radiograph of the head of animal 2 at a T_a of 39°C. The dorsal and laterodorsal surfaces of the snout are cooled.

At a T_a of 38.7°C, the animals, which panted, maintained rectal temperatures of 39.4° to 40.4°C, and T_s over all body surfaces was close to T_a. Animal 3 continued to show steady vasodilation in the pinnae, and T_s over the arteries was 39.6° to 40.0°C (T_{rec} = 40.2°C). Animal 1 exhibited pulsatile vasodilation; the arteries were radiographically invisible most of the time, but they filled once every several minutes. Animal 2 showed pulsatile vasodilation of much higher frequency; filling often occurred as often as twice per minute and averaged about once per minute. In both animals 1 and 2, filling progressed in stages, with the major basal arteries appearing as heat images first and the more distal longitudinal arteries and their branches appearing shortly thereafter. Once filled, the vascular tree remained so for 10 to 20 seconds, then emptied in stages.

Although high in the thermoneutral zone (*1*), T_a's of 31° and 38.7°C are below deep body temperature. Thus heat loss would be favored by vasodilation in the pinnae. Animal 3 exhibited the steady vasodilation we had predicted, but animals 1 and 2 yielded different and unexpected results. At a T_a of 38.7°C, vasodilation occurred so frequently in animal 2 that it must have contributed significantly to dry heat loss, but it occurred at such a low frequency in animal 1 as to be of questionable significance for heat loss.

At a T_a of 45.5°C, the animals panted vigorously and maintained T_{rec}'s of 40.9° to 41.4°C. All animals exhibited similar and unexpected pinna responses. The arteries were nearly always visible radiographically as thin lines (the surfaces above them were relatively cool because blood temperature was below T_a). Once every several minutes the arteries would dilate more fully for 10 to 20 seconds (Fig. 1C). On the pinnae, the surface temperature was typically 42° to 46°C and fell to as low as 41°C over the arteries during pulsatile engorgement. Given that T_s over large areas of the pinnae was typically below T_a, heat influx across the pinnae was favored. Ten radiographs taken predominantly during arterial engorgement showed average pinna T_s to be 0.5° to 3.8°C (mean, 2.4°C) below T_a (*9*); convective and radiative heat gains across the pinnae were calculated to average 14 cal/min at a wind speed of 12.5 cm/sec and 17 cal/min at 22 cm/sec (*10*). From measures of evaporative water loss near a T_a of 45.5°C (*1, 4*), whole-body heat gain from the environment seems to reach a rate equivalent to about 20 percent of metabolic heat production, or about 30 cal/min for a 2.3-kg animal (*1*). Thus, at times of arterial engorgement, the pinnae account for 47 to 57 percent of the average total heat gain. Because we did not take radiographs systematically over the entire cycle of arterial engorgement and disengorgement, we cannot compute a rigorous estimate of the temporally averaged rate of heat gain across the pinnae, a rate that would be lower than that computed for periods of engorgement alone. Clearly, however, heat gain across the pinnae can be appreciable.

The apparently steady circulation of the pinnae at a T_a of 45.5°C and the periodic engorgement call into question the magnitude of the role of pinna vasomotor control in reducing dry heat conductance at high T_a (*4*). Whereas blood flow in animal 3 appeared to be reduced when T_a was 45.5°C by comparison to 31° to 39°C, that in animal 1 was probably enhanced. The steady circulation and periodic engorgement observed at a T_a of 45.5°C are particularly puzzling from the point of view of thermal exchange because we know, from the results at low T_a, that blood flow to the pinnae can be curtailed abruptly at their bases and limited steadily for hours. High tissue temperatures in the pinnae at high T_a may impose demands for oxygen delivery, nutrient supply, and waste removal that obligate steady circulation in the pinnae despite the implications for heat exchange.

When T_a was 38.7° and 45.5°C, we observed that the pinnae consistently vibrate during panting, as Wathen *et al.* (*3*) suggested they might. These vibrations would be expected to augment convective heat exchange with the air, an advantage when T_a is 38.7°C and a disadvantage when it is 45.5°C. Strikingly,

T_s on the dorsal and laterodorsal aspects of the snout was relatively low during panting (Fig. 2), which indicates that cooling of the nasal passages is transmitted to the body surface through the intervening bone and skin (the total thickness of these tissues is less than 2 mm). At a T_a of 45.5°C, T_s on the cheeks was 42° to 45°C, whereas T_s on the coolest parts of the snout was 40° to 41°C.

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5. Dry heat transfer includes transfer by conduction, convection, and radiation, but not transfer by evaporation.
6. Animal 1 was a quiet animal that was in late pregnancy at the time of study. Animal 2 was agitated and had given birth to a premature and stillborn litter 1 week before study. Animal 3 seemed to be a young animal, was not pregnant at the time of capture, and was the least affected by human activity. Body weights (measured postpartum in the cases of animals 1 and 2) were 1.4 to 1.9 kg.
7. Sheets of cloth coated with infrared-black paint (emittance .98 between 1 and 20 μm) were suspended freely in the air between the animal cage and the top and sides of the temperature cabinet, and the platform on which the cage rested was coated with the same paint.
8. We analyzed dried pinnae from two animals that were born to animal 1, grew nearly to adulthood, and later died, for spectral total hemispheric reflectance and spectral transmittance in the range of 2.8 to 20 μm with a reflectance spectrophotometer (Cary-White 90) and a transmittance spectrophotometer (Perkin-Elmer 621). Reflectance varied with wavelength between .01 and .13, and transmittance varied between .00 and .04. Integrated emittance over the range of sensitivity of the AGA Thermovision system was .89, calculated according to the methods of R. Siegel and J. R. Howell [*Thermal Radiation Heat Transfer* (McGraw-Hill, New York, 1972)]. We determined surface temperatures using the integrated emittance according to formulas in AGA Operating Manual 7202, section 8. We analyzed 72 color infrared radiographs.
9. To calculate the average surface temperature in a given radiograph, the proportion of the total pinna surface covered by each isotherm in the radiograph was determined by polar planimetry. The proportions were then multiplied by the respective average temperatures represented by the isotherms, and the products were added.
10. We calculated convective and radiative losses or gains by the methods of Wathen *et al.* (*3*), using their field values for the convection coefficient, their value of 0.8 for the radiative view factor, and 0.95 for the overall infrared emittance of the pinnae. Calculations were carried out for the average 2.3-kg animal as reported in Schmidt-Nielsen *et al.* (*1*). Total pinna surface area was thus taken to be 332 cm^2, and comparisons of heat exchange across the pinnae were made to metabolic data and overall heat exchange data reported in Schmidt-Nielson *et al.* (*1*).
11. We thank D. M. Lay for procuring the jackrabbits and L. Blaine for making available the spectrophotometers of the Goddard Space Flight Center, Greenbelt, Md. We are grateful for use of the facilities of the 6570th Aerospace Medical Research Laboratory, Wright-Patterson Air Force Base.

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The Amnesia Gradient: Inadequate as Evidence for a Memory Consolidation Process

Abstract. *Rats were conditioned to fear a tone paired with shock to the feet. Retention tests 4 days later showed that consolidation had occurred. Other animals were not tested for retention at 4 days, but the tone was presented in order to reactivate their memories of the conditioning. An amnesia gradient was generated by low-intensity electrical stimulation of the amygdaloid complex at different intervals after the tone, but stimulation was without effect either when given to rats not previously conditioned or when given to conditioned rats without preceding memory reactivation. Thus, stimulation of the amygdaloid complex can affect memory retrieval. Moreover, the data call into question the assumption that an amnesia gradient indicates that the memory consolidation process has been modified.*

A variety of treatments, including specific, low-intensity stimulation of some regions of the brain, produce retrograde amnesia (*1*), which is shown experimentally when different groups of animals are treated at various intervals after a training trial. In the resulting "gradient of amnesia" for the training, the degree of amnesia varies inversely with the interval between training and treatment until the treatment no longer has an effect. The presence of such an amnesia gradient has long been considered to be strong evidence that the amnesic treatment disrupts memory consolidation (*1*, *2*).

However, we have found that low-intensity stimulation of the amygdaloid complex (AC) given at different intervals after the reactivation of an old, well-consolidated memory can effect an amnesia gradient. The generation of an amnesia gradient can thus no longer serve as undisputed evidence of a modified consolidation process.

Male Long-Evans rats between 90 and 120 days of age had bipolar electrodes stereotaxically implanted unilaterally into the AC (*3*). After a 5- to 7-day recovery period, the rats adapted for several days to various aspects of the experimental procedure, for example, by drinking water while in the training-testing apparatus and by having the stimulation cable attached. Some rats were then conditioned in the training-testing apparatus by a single pairing of a tone (15 seconds, 12,000 hertz, 90 db) with shock to the feet (1.6 ma) administered through the grid floor of the apparatus during the last 3 seconds of the tone. Other rats received noncontingent shock to the feet in an apparatus distinctly different from the training chamber to control for any systemic effects of shock per se. Four days after conditioning or noncontingent shock some animals from both groups were tested for retention.

In the retention test, the rats, deprived of water for 24 hours, were placed in the training-testing chamber and allowed access to a drinking tube. Through a drinkometer circuit and programming equipment, the conditioning tone was automatically presented after the rat had completed 50 seconds of tube contact. Both the response time (in seconds) to complete the initial 50 seconds of tube contact and the latency from the onset of the tone to the completion of an additional 5 seconds of tube contact by the rat were converted to logarithms. Long drink latencies during the presentation of the tone were considered evidence of retention, and short drink latencies, of amnesia. Details of the apparatus and the training-testing procedure have been described (*4*).

Other rats were not tested for retention but were individually placed in the training-testing chamber and presented with the conditioning tone without the shock, as a memory reactivation treatment (*5*). Rats previously given noncontingent shock but not tested were also presented with the tone as a control for the reactivation procedure. The AC was stimulated (*6*) either immediately, 30 minutes, 60 minutes, or 240 minutes after the termination of the tone. Only animals in the immediate stimulation groups had the stimulation cable attached and received stimulation in the training-testing chamber. Animals in the other stimulation conditions were returned to their home cages for the appropriate interval and were then taken to a different experimental room where the stimulation cable was attached and the AC was stimulated. One group of conditioned animals (TS-C-NS) received no stimulation of the AC but were given the memory reactivation treatment and handled identically to stimulated animals. Another group of conditioned animals (TS-NC-S) were not given memory reactivation treatment but were placed in a different box and given AC stimulation to determine the effects of the stimulation alone. The animals given memory reactivation treatment, AC stimulation, or both, 4 days after training or noncontingent shock were tested, 24 hours water deprived, the next day. The