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Brain Temperature in Pigeons: Effects of Anterior Respiratory Bypass

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Summary: During heat stress in domestic pigeons (*Columba livia*, mean mass 0.43 kg) brain temperature (T_B) varied in parallel with colonic temperature (T_C). The difference between these ($T_C - T_B = \Delta T$) averaged 0.7 °C and was not significantly altered when the animal breathed through a trachael cannula bypassing the buccopharyngeal cavity. When we sealed the nares and beak in bypass animals, ΔT was significantly reduced but was nevertheless maintained at 0.4 °C. When the eyes were sealed as well, however, ΔT was reversed, amounting to -0.4 °C. Conversely, with eyes sealed but beak and nares open, ΔT was indistinguishable from that in controls. These results suggest a role for the cornea in evaporative cooling, at least when respiratory evaporation is impaired, and are consistent with the hypothesis that buccopharyngeal and corneal evaporation are coupled to brain cooling. The probable mechanism for this coupling is the flow of venous blood from evaporative surfaces through the *retia mirabilia* in the temporal areas. Here heat is transferred from the warmer arterial blood flowing through the *retia* toward the brain to the centrally flowing, cooler venous blood.

Introduction

All birds so far investigated maintain the temperature of the anterior hypothalamus significantly below that of the body core during heat stress (Richards, 1970; Scott and van Tienhoven, 1971; Kilgore et al., 1973, 1976), and possess a well developed, extensive *rete mirabile ophthalmicum* in the temporal region of the skull. The *rete* consists of multiple branches of the external ophthalmic artery in intimate contact with a venous network whose supplying vessels originate in the orbit and buccopharyngeal cavity (Wingstrand and Munk, 1965; Richards, 1970; Kilgore et al., 1973, 1976). The anatomy of the *rete* strongly suggests that it acts as a countercurrent heat exchanger permitting warm blood flowing toward the brain to lose heat to cooler venous blood returning from evaporative surfaces of the head (Kilgore et al., 1973).

In spite of the suggestive vascular anatomy, no physiological data were available regarding the effect of the network on brain temperature until Kilgore et al. (1978) measured brain temperature in heat-stressed pigeons after bilateral occlusion of the temporal *rete*. The results of this experiment, a loss of ability to maintain the body-to-brain temperature difference, strongly support the hypothesis of a role for the *rete* in maintaining brain temperature during heat stress.

The hypothesis relies on the effectiveness of cranial evaporative water loss in cooling the venous blood about to pass through the *rete*. In this paper we report the results of experiments in which we partially or completely prevented such evaporative cooling in pigeons having intact temporal *retia*, and measured the effect on brain temperature. The results, like those of Kilgore et al. (1978), are in concert with the hypothesis.

Material and Methods

Simultaneous measurements of brain, colonic, and ambient temperatures were obtained in a total of 24 domestic pigeons (*Columba livia*, mean mass 0.43 kg) obtained from commercial suppliers and maintained for at least two weeks prior to experimentation in a windowless room at an air temperature of 23 °C, an ambient water vapor pressure of 6 millibars, and with food and water available ad libitum.

Thermocouple placement, temperature measurements, and experimental procedures were as described in Kilgore et al. (1976). Welded copper-constantan thermocouples (0.12 mm wire diameter) were coated with polyvinyl to a final diameter of 0.3 mm. After 1.0 mm diameter holes were drilled in the top of the skull under local anesthesia (Lidocaine, 1%), the probe was implanted in the preoptic region of the hypothalamus, and held to the skull with dental cement. Post-mortem examination after each experiment verified thermocouple positions. The edges of the incision were sutured about the exterior portion of the thermocouple in a manner simulating as closely as possible the natural contours of the scalp in the intact animals. After recovery from surgery (12–24 h) a second thermocouple was inserted to a depth of 5 cm in the colon to permit simultaneous recording of brain and colonic temperatures. The reference juntions were placed in a covered Dewar flask containing water at a constant temperature of approximately 23 °C, as measured by a mercury-in-glass thermometer having an accuracy of ±0.1 °C, traceable to the U.S. National Bureau of Standards (NBS). Leads were connected to a multiplexer which connected each thermocouple in turn, at 1 s intervals, to an amplifier having a gain of 1000. The output of the amplifier was displayed on a potentiometric recorder after most of the output was nulled by a bucking voltage supply. The outputs of the latter were determined with a digital multimeter calibrated with an NBS-certified Eppley standard cell. The standard cell was also used for calibration of the recording system, which had an accuracy of ±0.025 °C.

At the beginning of an exeriment birds were lightly restrained in a manner which permitted normal panting and other respiratory movements. They were then placed in a temperature controlled chamber (±0.5° C) at ambient water vapor pressures between 4 and 9 millibars, and exposed to each of several ambient temperatures from 30 to 54° C. At each temperature brain and colonic temperatures were permitted to stabilize for 1 to 2 h. Readings were then taken over a period of about 30 min. All experiments were performed at approximately the same time of day.

Birds were divided into five experimental groups. In the first (6 birds), the experiments reported by Kilgore et al. (1976) were repeated; brain and colonic temperatures were recorded in animals intact but for the presence of the thermocouples. In the second group (6 birds), in addition to thermocouple implantation, a tracheotomy was performed under local anesthesia (Lidocaine, 1%), and a stainless steel tube tied into the trachea so as to conserve normal respiratory dead space. We have termed this procedure an anterior respiratory bypass (ARB). Recovery from this surgery was also 12–24 h. During the experiment the animal breathed through the tracheotomy tube; frequencies of both breathing and gular flutter movements were similar both in ARB and in intact birds. ARB procedures were performed on all members of the third, fourth, and fifth groups, as well. In addition, in the third group (3 birds), the eyes were held closed by a coating of sheet paraffin held firmly in place over the closed eyelids by surgical gauze and tape. In the fourth group (5 birds), the eyes remained opened but the nares were plugged and the mouth taped in a closed position to prevent evaporation. Finally in the fifth group (4 birds), the eyes, nares, and mouth were all held in closed positions.

Results

As shown in Figure 1, anterior respiratory bypass (ARB) had no effect on colonic temperature. Whether the eyes were opened or closed seemed likewise to have no effect, although when the mouth was closed, the variability of body temperature responses to air temperature was increased.

The relationships between brain and colonic temperatures are shown in Figure 2. The control experiments of the present study (intact pigeons, Fig. 2B) gave results indistinguishable from those of corresponding experiments (Fig. 2A) reported by Kilgore et al. (1976). The slopes of the least-squares, linear regression lines relating brain temperature to colonic temperatures in all experiments were not statistically different from 1.0 ($P > 0.05$).

The results shown in Figure 3 indicate that anterior respiratory bypass had no statistically discernible effect upon the mean difference between colonic and brain temperatures, in animals permitted to keep their beaks open (Fig. 3C, D). ARB accompanied by blockage of the nares and closure of the beak, however, resulted in significant alterations in the colonic-brain temperature difference. With the eyes open (Fig. 3E) the temperature difference was statistically significantly reduced ($P < 0.01$) from the control value of 1.07 °C to 0.39 °C.

Closure of the eyes as well (Fig. 2F) resulted in a complete and statistically significant ($P < 0.001$) re-

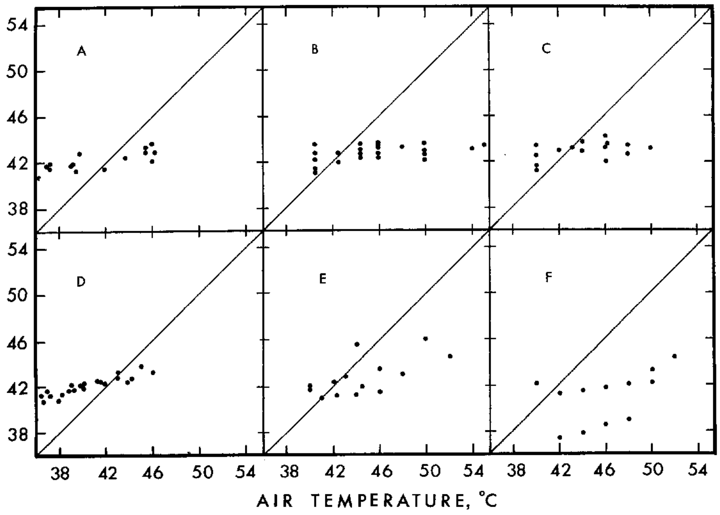

Fig. 1 A–F. The relationships between colonic and ambient temperatures in control and experimental pigeons during exposure to heat stress.
A Data for intact animals from Kilgore et al. (1976).
B Data for intact pigeons obtained under conditions nearly identical to those utilized by Kilgore et al. (1976).
C Pigeons with anterior respiratory bypass (ARB).
D Pigeons with ARB and with eyes closed and sealed.
E ARB pigeons with beak and nares closed and sealed.
F ARB pigeons with eyes, nares, and beak closed and sealed

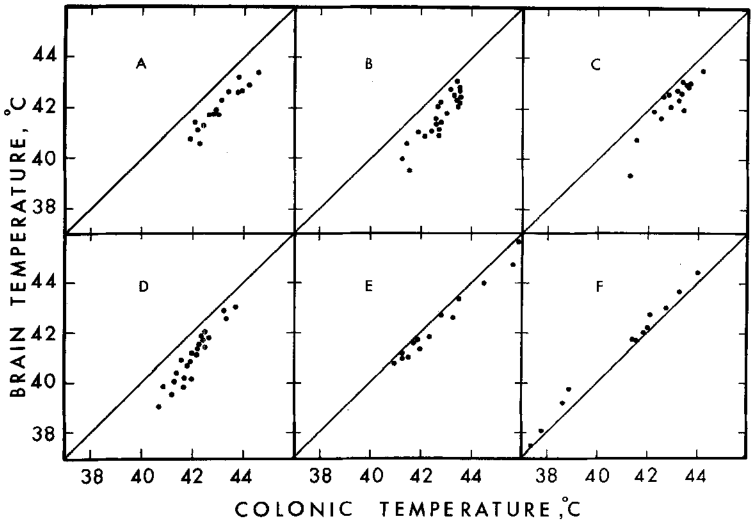

Fig. 2A–F. Relationships of brain to colonic temperature in control and experimental pigeons during heat stress. Letters **A–F** as in Figure 1

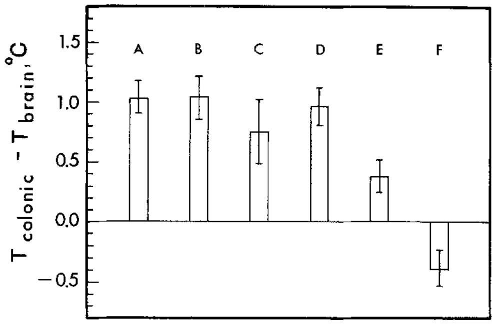

Fig. 3. Difference between colonic and hypothalamic temperatures in control and experimental pigeons during heat stress. Data from Figure 2. Length of bar represents mean. Vertical lines extend 2 standard errors either side of the mean. Letters *A–F* as in Figure 1

versal of the temperature difference between body and brain; brain temperature was always higher than colonic temperature, with a mean colonic-brain temperature difference of −0.40 °C.

Discussion

The results shown in Figure 1 were tested by an analysis of variance, the results of which suggest that the treatment of the animals in all experimental groups did not appreciably alter the relationship between colonic and ambient temperature ($P > 0.05$). Furthermore, as shown in Figures 2 and 3, the relationship between brain and colonic temperatures was not affected by ARB alone. This result suggests that if evaporative cooling in the buccopharyngeal cavity is necessary to the maintenance of brain temperature below body temperature, then such cooling must continue even during bypass. This is not surprising in light of the vigorous gular flutter response of heat stressed pigeons. Although gular flutter undoubtedly contributes greatly to evaporative cooling (Weathers and Schoenbaechler, 1976), the extent to which it can effect buccopharyngeal ventilation remains unknown.

When the nares and beak were closed in the ARB birds, thus preventing gular flutter, the colonic-brain temperature difference remained positive, though reduced; when the eyes were closed as well, the difference became negative (Fig. 2E, F). These results strongly suggest that the corneal surface can be an important avenue for evaporative water loss associated with the maintenance of colonic-brain temperature differences during heat stress in pigeons. The importance of the corneal evaporative route can apparently vary quite widely, however. When the animal was permitted to gular flutter with the mouth open after ARB, the temperature difference was little affected by whether the eyes were opened or closed (Figs. 2C, D; 3). In view of these results, it is tempting to speculate that blood flow to and from the orbit and buccopharyngeal surfaces can be selectively regulated according to the animal's need for cranial cooling. Magilton and Swift (1969), have demonstrated controlled variation of flow in the venous return from nasal heat loss regions in dogs.

That brain temperature did not simply become equal to colonic temperature, but was higher in this experiment, has at least three possible explanations. First, brain metabolic heat production might be so high as to result in temperature elevation above the rest of the body under the experimental conditions. Second, heat transfer from the hot environment may be greater to the head (larger surface-to-volume ratio) than to the rest of the body. Third, the location, contents, or activity of the colon may result in temperatures unrepresentative of other parts of the body. In this case, several temperatures would be required to obtain a "mean" body temperature.

The results of this study are consistent with two possible mechanisms for cooling of brain tissue below the temperature of the body. The first of these is that the evaporative surfaces of the soft and hard palate and perhaps of the cornea are at lower temperatures than that of the adjacent nervous tissue, and thus provide a heat sink for direct conduction of heat. The second explanation involves countercurrent heat exchange in the temporal *retia*, as described above. The present data do not exclude either of these hypotheses; indeed the possibility of buccopharyngeal and corneal surfaces acting to some extent as a heat sink needs further study. However, the thermal conductivity of the bone, connective tissue, and integument of the palate is low, and the distance for heat transfer from the brain to the cornea is large. It seems likely, therefore, that the most important mechanism is evaporative cooling of blood perfusing the moist, richly vascularized surfaces of the buccopharyngeal cavity, and the transfer of heat from arterial blood to this cooler blood in the temporal *rete*. Prevention of evaporation results in a diminution of the cloacal-brain temperature difference in a manner consistent with this hypothesis.

In ARB birds with eyes as well as nares and beak closed, the relationship between brain and cloacal temperature is virtually identical to that presented for otherwise intact pigeons in which the temporal *retia* had been bilaterally occluded (Kilgore et al., 1978). The gratifyingly similar data shown in our Fig. 2 and in Fig. 2 presented by Kilgore et al. (1978) strongly support the hypothesis that the temporal *rete* acts to cool blood traveling toward the brain.

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