Sweating in the kangaroo: a cooling mechanism during exercise, but not in the heat

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Materials and methods

Animals

Two red kangaroos, Megaleia rufa (both females, avg weights 28 and 18 kg), were used in the heat balance experiments. The two females and a male (avg weight 42 kg) were used in the investigation of the control of sweating. The kangaroos were hand-reared in Australia at the University of New South Wales and airfreighted to our laboratory as adults.

Heat Balance

A complete heat balance was measured both in resting and in exercising animals. In the resting studies, heat balance was measured over a 30-min interval at an air temperature of 24°C. The animals were exposed to the experimental air temperature for 3–4 h before the measurements were begun. In the exercise studies the animals ran on a treadmill at 4 km h⁻¹ until they began to salivate and drool into the mask (18–32 min). We terminated the experiments at this time because the drooling resulted in serious errors in our measurements of evaporation. Air temperature was 24°C and wind speed was approximately matched to treadmill speed.

We measured heat production, heat storage, and total evaporative heat loss. Nonevaporative heat loss was calculated by subtracting heat storage plus heat loss by evaporation from heat production using the heat balance equation: heat production = heat loss by evaporation ± nonevaporative heat loss ± heat storage.

Heat production was calculated from measurements of oxygen consumption. We used 4.8 kcal (liters O₂)⁻¹ as an energetic equivalent. The animals wore a ventilated mask through which air was metered at a fixed rate between 150 and 350 liters (min)⁻¹ STP. An aliquot of the air leaving the mask was dried and passed through a paramagnetic oxygen analyzer (Beckman model F-3, sensitivity 20–21% or 20.5–21% oxygen for a full-scale deflection) to determine the concentration of oxygen. Flowmeters were calibrated to better than 1% accuracy using gas-flow calibrators (Brooks Vol-U-Meters). The accuracy of the oxygen determination was measured by flowing nitrogen at known rates into the mask (diluting the oxygen in room air much the same way an animal does) and determining the change in oxygen concentration of air flowing through the mask. The
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case in eutherian mammals. A single splanchnic nerve
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nerve was retroperitoneal, and the incisions were parallel and
sectioned at midneck level. This nerve was contained
within the carotid sheath, but it was discrete and easily
distinguished from the vagus nerve.

Sodium and maintained with halothane in closed circuit.

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The manner in which the exercising kangaroo handled
the relatively large amounts of heat it produced depended
a great deal on its body temperature when it started to hop
and on the experimental procedures. We were unable to
measure evaporation accurately when the animals drooled.
Therefore, we began our experiments when body tempera-
ture was low (36.7 ± 1.7°C) and terminated them when the
animal began to salivate. A small amount of saliva prob-
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could be terminated, resulting in a slight overestimate of
respiratory and total evaporation and a slight underesti-
mate of nonevaporative heat loss. Under these conditions,
heat storage accounted for about 43%; evaporation ac-
counted for about 43%; and nonevaporative heat loss
accounted for about 14% of the heat production (Fig. 1).

The amount of heat stored in these runs was greater and
cutaneous evaporation was less than that observed in runs
where the body temperature was higher at the beginning
of the run. Heat storage, however, remained an important
element in the heat balance of the exercising kangaroo even

RESULTS
Heat Balance

Heat production. In a previous study, it was found that
oxygen consumption of the red kangaroo increased rapidly
as the animal’s speed increased up to 4–6 km·h⁻¹ and then
remained unchanged with further increases in speed up to
99 km·h⁻¹, the highest speeds experimentally obtainable
(3). This was convenient for heat balance studies, since
data obtained at an one speed are applicable over a wide
range of speeds. In this study heat production at a speed
of 4 km·h⁻¹ (air temperature 24°C) was about 8 times the
observed resting levels (Fig. 1) and 16 times the standard
metabolic rate observed by Dawson and Hulbert (3) for
this species. During our experiments the animals were
often restless, and no attempt was made to obtain minimal
resting values. In other experiments we did obtain resting
levels close to the standard metabolic rate.

Heat loss. Two-thirds of the heat produced by the resting
animal was lost nonevaporatively and one-third was lost by
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Drugs

The following drugs were used in these experiments:
adrenaline hydrochloride, atropine sulfate, bethanidine
sulfate, and phenoxbenzamine hydrochloride. Drugs were
administered intravenously through a polyethylene canula
inserted into the lateral tail vein.

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Sympathetic Deneration of Skin and Adrenal Glands

All surgery was performed after premedication with
atropine sulfate and ketamine hydrochloride. Anesthesia
was induced by intravenous administration of thiamylyl
sodium and maintained with halothane in closed circuit.

The sympathetic nerve supplying one side of the head
was sectioned at midneck level. This nerve was contained
within the carotid sheath, but it was discrete and easily
distinguished from the vagus nerve.

Bilateral adrenomedullary denervation was performed in
a single operation by removal of 0.5 cm of the splanchnic
ergve and section of the branches to the adrenal gland from
the lumbar sympathetic ganglia. The surgical approach
was retroperitoneal, and the incisions were parallel and
ventral to the sublumbar muscles. In the kangaroo the
sympathetic supply to the abdominal viscera originates
largely from the thoracic paravertebral ganglia, as is the
case in eutherian mammals. A single splanchnic nerve
passed from the thoracic to the abdominal cavity near the
crura of the diaphragm. It forms a plexus close to the disc-
like adrenals. A few small branches enter the plexus from
the lumbar paravertebral ganglia. The fine fibers of the
splanchnic nerves radiate out toward the plexus: on the
right side the radiation occurs at the level of the diaphragm;
on the left side it occurs after the nerve has entered the
abdominal cavity.

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when body temperature was 39.5°C at the beginning of a run, amounting to 32% of the heat produced. Rectal temperatures up to 41°C were observed at the end of a run.

The onset of sweating occurred sooner after the initiation of exercise in the heat balance experiments (where the animals were weighed and masks and thermocouples were attached at the beginning of the experiment) than when the animal started to exercise without prior handling. Presumably heat storage was decreased and cutaneous evaporation increased as a result of handling. From these observations it seems clear that the relative roles of cutaneous and respiratory evaporation and heat storage in the heat balance of the exercising animal is inversely related and quite variable, with heat storage being particularly important in the initial stages of exercise.

Respiratory evaporation and nonevaporative heat loss from the exercising kangaroo were not greatly influenced by body temperature or experimental procedures. Respiratory evaporation increased by approximately the same amount as oxygen consumption (9.6 and 8.0 times resting levels, respectively). Thus, the increase in respiratory evaporation appears to be mainly the result of an increased ventilation associated with the higher oxygen consumption. Respiratory evaporation, however, accounts for 17% of heat production and 40% of the total evaporation during exercise; and within a short period the rate returned to the same high levels as previously observed (Fig. 2).

Surgical denervation experiments. Sympathetic denervation of one side of the face abolished sweating from that side of the face, while having no effect on sweating from the other side (Fig. 3). A single intravenous injection of adrenaline values agree well with those obtained by Dawson (2) under similar conditions. Using ventilated capsules we observed sweating rates up to 370 g (m²·h⁻¹) in exercising animals. The values obtained in the heat balance experiments were lower because they reflected an average of the entire exercise period, and there was a delay after the animal started to hop before sweating commenced.

Salivation often begins while an animal hops; however, it plays no role in evaporative cooling until the animal stops. The saliva drools from the mouth of the hopping animal and is lost. When the animal stops, however, it immediately begins to lick primarily the highly vascularized foreleg (11). Under these circumstances, salivation appears to play a significant role in cooling, and during recovery from exercise we found rates of total evaporation 2.9 times that observed during exercise. Body temperature fell as rapidly as 2.3°C in 30 min during recovery.

Patterns and Control of Sweating

Effect of heat exposure. Resting kangaroos did not sweat in the heat even when exposed to an ambient temperature of 55°C for 4 h. Cutaneous evaporation under these conditions varied between 7 and 20 g H₂O (m²·h⁻¹). These values are similar to those observed by Dawson (2) and by Gubbins and Johnson (7) at 45°C. The kangaroo was able to maintain a constant body temperature of about 38°C when ambient temperature was 55°C and showed no signs of distress. It increased evaporation both by spreading saliva and by panting at rates in excess of 200 respirations/min.

Effect of exercise. The onset of sweating occurred between 2 and 32 min after the onset of exercise at 4 km·h⁻¹. Sweating increased in a series of steps (Fig. 2) and fell off rapidly after the animal stopped hopping, returning to the initial level within 10–15 min. If the animal began to exercise again before sweating rates had returned to the initial levels, then there was no further decline in sweating rate and within a short period the rate returned to the same high levels as previously observed (Fig. 2).

FIG. 1. Heat balance of 2 red kangaroos at rest and while travelling at 4 km·h⁻¹ on a treadmill. Air temperature was 24°C and wind speed was approximately matched to treadmill speed. Data are an average of 8–12 measurements under each condition and vertical lines represent ± twice SE. Entire bar represents total heat production; heavy diagonally shaded area represents heat storage by cutaneous evaporation; lightly diagonally shaded area represents nonevaporative heat loss; unshaded area represents heat storage.

FIG. 2. Sweating of a red kangaroo in response to travelling at 4 km·h⁻¹ on a treadmill. Sweating fell off rapidly when the animal stopped; however, this decline was halted immediately if exercise started again and sweating rate rapidly returned to higher levels. Measurements were made with a ventilated capsule attached to middle of the back. Air temperature was 24°C and wind speed was approximately matched to treadmill speed.
the capability of the animal to exercise.

Effects of drugs. Kangaroos sweated in response to a single intravenous injection of adrenaline hydrochloride (5 mg/kg body wt). Phenoxynbenzamine hydrochloride, which blocks adrenergic α-receptors, blocked exercise-induced and adrenaline induced sweating when administered at a dose of 3 mg/kg body wt.

An intramuscular injection of atropine sulfate, which blocks cholinergic receptors, at a dose of 0.15 mg/kg body wt did not block exercise-induced sweating although it did block salivation.

Bethanidine sulfate, which blocks adrenergic neurons, did not block sweating either before or after denervation of the adrenal glands when administered intravenously in doses up to 4 mg/kg body wt. It did, however, produce symptoms of bronchoconstriction which markedly limited the capability of the animal to exercise.

DISCUSSION

It seems clear from these results that the red kangaroo has adopted separate evaporative cooling mechanisms for use during rest and during exercise. The resting kangaroo pants and selectively spreads saliva to increase evaporative cooling but does not sweat. The exercising kangaroo, on the other hand, is unable to spread saliva and uses an alternative system of evaporative cooling, sweating.

It is interesting that sweating occurred only during exercise and that when the animal stopped hopping it began to pant rapidly and spread its saliva and the sweating stopped. Thus, as one mechanism becomes operative, the other is “turned off.”

Thermal panting is an important cooling mechanism in many animals. There are three main types of thermal panting in mammals. In the first type, the mouth is closed and the air enters and exits through the nose; thus, the nasal mucosa is the site of evaporation. This is the principal form of evaporative cooling in resting kangaroos (2) and in many other species. To increase respiratory evaporation, animals may switch to the second type of panting where the mouth is open and air enters the nose and exits primarily from the mouth, bypassing a countercurrent recondensation of water in the nose (15). Again the nasal mucosa is the site of evaporation. In these two forms of panting, respiratory alkalosis does not develop because tidal volume is low (4, 8–10). Respiratory evaporation is still greater in the third form of panting, “second phase,” or deep open-mouth panting where the air enters both through the nose and mouth and exits both through the nose and mouth. Thus, the nasal mucosa and the pharyngeal region are both sites of evaporation. Severe blood acid-base problems may arise during second-phase panting because of increased alveolar ventilation (4, 8–10).

During the first two types of “shallow panting,” respiratory frequencies reach maximum values and respiratory ventilation (and probably also evaporation) increases by only about fourfold, threefold, and fivefold over resting values in the dog (6), sheep (10), and ox (9), respectively. During “deep or second-phase panting,” however, respiratory ventilation increases by about 14-fold, fivefold, and sevenfold in these same animals, and additional evaporative surfaces are involved as well as larger ventilation volumes. We observed a ninefold increase in respiratory evaporation in the exercising kangaroo. Breathing was deep and open-mouthed and although the increased ventilation was probably primarily a response to the increased demands for oxygen, its effect on water loss might well be at least considered equivalent to the high rate of evaporation of the deep panting associated with extreme thermal loads in resting animals. Exercising kangaroos seem to have reached the upper limits of evaporation from the nasal mucosa and the pharyngeal region, and sweating then offers an additional evaporative surface and gives the potential of still further increases in evaporation.

Exercise heat production presents the kangaroo with a heat load about twice as great as it might encounter in a hot desert (16). It is unable to spread saliva while running, and sweating together with an increased respiratory cooling appear to be the alternative mechanisms. In spite of these mechanisms, the kangaroo appears unable to dissipate all of the heat it produces at speeds between 4 and 22 km/h. If it hopped continually for 1–2 h, it would eventually reach a lethal temperature. In practice, kangaroos do occasionally stop and spread the copiously produced saliva, and this would partially alleviate the problem of heat storage.

The effeent control of sweating is obviously by means of sudomotor nerves since cutaneous sympathetic denervation abolished the sweating of exercise. The nerves are adrenergic since: 1) kangaroos sweat in response to intravenous adrenaline; 2) sweating can be blocked by the adrenergic α-receptor antagonist, phenoxybenzamine, and 3) sweating is not inhibited by the cholinergic blocking drug atropine. The effective blockade of both adrenaline-induced and exercise-induced sweating by the adrenergic α-receptor
antagonist phenoxybenzamine demonstrates an α-receptor-mediated effect, in common with the Bovidae, but in contrast to the Equidae where the receptors are of the β variety. This conclusion is supported by the observation of Gubbins and Johnson (7) who noted that the β-agonist isoprenaline had only a slight sudomotor effect compared to adrenaline.

The adrenergic neuron-blocking agent, bethanidine, however, failed to inhibit sweating. This drug has proved effective in preventing sweating in other species such as cattle (6) and equids (13) where sweating is under adrenergic neurone control. At high rates of nerve stimulation, the blocking action of bethanidine can be overcome, although at high doses (in excess of 3 mg/kg) blockade is virtually complete (1). Presumably, in the present experiments either sudomotor nerve activity was high enough to overcome bethanidine blockade or the rate of metabolism of the drug within the sudomotor nerve terminals was greater in this species than others. There appeared to be some effect on the bronchial musculature; the bronchoconstriction reduced the animal’s capacity to exercise and was sufficient to preclude us from increasing the dosage in order to achieve adrenergic blockade.

REFERENCES