Journal of Physiology (1993), **471**, *pp.* 679–692
With 7 figures
Printed in Great Britain

SELECTIVE BRAIN COOLING IN GOATS: EFFECTS OF EXERCISE AND DEHYDRATION

BY M. A. BAKER AND M. J. M. NIJLAND

From the Division of Biomedical Sciences, University of California, Riverside, CA 92521–0121, USA

(*Received 5 January 1993*)

SUMMARY

1. Measurements of brain and central blood temperature (T_{br} and T_{bl}), metabolic rate (MR) and respiratory evaporative heat loss (REHL) were made in trained goats walking on a treadmill at 4·8 km h^{-1} at treadmill inclines of 0, 5, 10, 15 and 20 % when they were fully hydrated and at 0 % when they had been deprived of water for 72 h.

2. In hydrated goats, exercise MR increased progressively with increasing treadmill incline. Both T_{bl} and T_{br} rose during exercise, but T_{bl} always rose more than T_{br}, and selective brain cooling (SBC = $T_{\mathrm{bl}} - T_{\mathrm{br}}$) increased linearly with T_{bl}. Significant linear relationships were also present between REHL and T_{bl} and between SBC and REHL. Neither the slope of the regression relating SBC to T_{bl} nor the threshold T_{bl} for onset of SBC was affected by exercise intensity. Manual occlusion of the angularis oculi veins decreased SBC in a walking goat, while occlusion of the facial veins increased SBC.

3. Dehydrated goats had higher levels of T_{bl}, T_{br} and SBC during exercise, but the relationship between SBC and T_{bl} was the same in hydrated and dehydrated animals. In dehydrated animals, REHL at a given T_{bl} was lower and SBC was thus maintained at reduced rates of REHL.

4. It is concluded that SBC is a linear function of body core temperature in exercising goats and REHL appears to be a major factor underlying SBC in exercise. The maintenance of SBC in spite of reduced REHL in dehydrated animals could be a consequence of increased vascular resistance in the facial vein and increased flow of cool nasal venous blood into the cranial cavity.

INTRODUCTION

In panting ungulates and carnivores the brain can be cooled below deep body temperature during heat stress. In these animals, arterial blood destined for the brain traverses the carotid rete where it loses heat to venous blood draining the nasal passages (Baker, 1982). The magnitude of this selective brain cooling (SBC) is usually seen to be related directly to the rate of respiratory evaporative heat loss (REHL) and to the rate of blood flow through the upper respiratory passages (Baker & Hayward, 1968; Jessen & Pongratz, 1979; Baker, 1982; Bamford & Eccles, 1983). Selective brain cooling may also be affected by muscular venous sphincters which can change the direction of flow of blood draining the nasal passages (Johnsen, Blix, Mercer & Bolz, 1987; Nijland, Mitchell & Mitchell, 1990).

Selective brain cooling has been viewed as a mechanism which can protect the brain from overheating (Carithers & Seagrave, 1976) and extend the range of body core temperature over which an animal can function in hot environments and during exercise (Taylor & Lyman, 1972). However, the observation that goats can withstand brain temperatures of 42·5 °C without apparent deleterious effect (Caputa, Feistkorn & Jessen, 1986) suggested that the vulnerability of the brain to thermal damage might not be as important as once believed (Burger & Fuhrman, 1964). Recently, Kuhnen & Jessen (1991) showed that SBC occurs in the normothermic range of body temperatures in goats and proposed that SBC is 'a thermoregulatory effector mechanism like shivering or panting', with thermostasis of the head rather than of the general body core as the net result. In support of this concept, they presented SBC as a function of aortic blood temperature and showed a point of onset (threshold) and a region of positive slope. In addition, by independently manipulating brain and blood temperature through the use of intravascular heat exchangers, Kuhnen & Jessen (1991) observed that SBC could be dissociated from REHL. These investigators hypothesized that SBC may function to increase the range of core temperatures over which both metabolic rate and respiratory evaporation are at a minimum, thereby decreasing the cost of thermoregulation. We were intrigued by these results, and have conducted experiments to further analyse selective brain cooling as a thermoregulatory effector function.

We first wanted to establish how SBC is related to body core temperature in goats without thermal manipulations by implanted heat exchangers. To accomplish this we used light exercise to raise core temperature through the range of temperatures reported by Kuhnen & Jessen (1991). We also wanted to know how exercise hyperthermia and exercise intensity affect the relationship between SBC and core temperature, and whether SBC can be dissociated from REHL in exercising goats. Finally, the possibility that SBC might allow the conservation of water by delaying the onset of thermoregulatory evaporation led us to investigate how SBC is affected by dehydration.

METHODS

We trained six adult Alpine–Toggenberg wethers (71 ± 5 kg) to walk at 4·8 km h^{-1} on a motor-driven treadmill and exercised them 2–3 times a week for several months before these experiments began. The goats were housed indoors (12 h light–dark; ambient temperature (T_a) 23 °C) overnight and in outdoor pens during the day and were fed alfalfa hay at 08.30 and 16.30 h each day. They had free access to water throughout the study, except during dehydration when drinking water was removed.

Surgical procedures

A re-entry tube for measurement of brain temperature was surgically implanted in each animal at least 10 days before the measurements began. Before the surgery, each animal was first anaesthetized using thiopentone sodium (15–20 mg kg^{-1}, I.V.) and an endotracheal tube was placed through the mouth using a specially constructed laryngoscope with a long blade. Surgical anaesthesia was maintained with halothane and oxygen. Using sterile surgical technique, a blind-ended stainless-steel tube (21 gauge, 53 mm long) was placed in the rostral, ventral brain-stem, aimed at the hypothalamic region with the tip 2–4 mm above the base of the brain. Placement of the tube was done using bony landmarks and measurements made from dissected goat heads. The tube was attached to the skull with stainless steel screws and dental acrylic and was closed with a stylet when not in use.

Experimental protocol

Each experiment was composed of three time segments. A 15 min rest period preceded and followed a period of 20–60 min of exercise. The exercise period was terminated when one of the following criteria was met: exercise duration reached 60 min, central blood temperature reached 42·5 °C, or the animal refused to continue walking voluntarily without pulling on the tether attached to its halter.

On the day of an experiment, the goat was brought from the animal quarters to the laboratory in a cart. Under local anaesthesia (lignocaine hydrochloride) a copper–constantan thermocouple in polyethylene tubing (1 mm o.d.) was inserted percutaneously into an external jugular vein through a hypodermic needle to the level of the right atrium for measurement of body core blood temperature (T_{bl}). A second thermocouple was positioned at the tip of the brain tube for the measurement of brain temperature (T_{br}). The goat was then led into a climate chamber (T_{a} $23 \pm 0{\cdot}2$ °C) where it stood on the stationary treadmill. All thermocouples were connected via an ice-point reference junction to an ADC–1 analog-to-digital converter (Remote Measurement Systems, Seattle, WA, USA) and Zenith AT personal computer data acquisition system. The thermocouple system was calibrated against a mercury thermometer readable to 0·05 °C. Temperatures were measured at 30 s intervals.

Five animals were trained to wear a light plastic mask for measurement of oxygen consumption ($\dot{V}_{\mathrm{O_2}}$) and respiratory evaporation in an open-circuit system, ventilated at 500 l min^{-1} (Nijland & Baker, 1992). One goat refused to wear the mask. The change in oxygen content of air flowing through the mask was measured with an S–3A Oxygen Analyser (Applied Electrochemistry) and the change in water content with a resistance hygrometer (Vaisala, HMI 32). Respiratory evaporative heat loss (REHL) was calculated assuming the latent heat of vaporization of water to be 2·411 kJ g^{-1}, and expressed as W kg^{-1}. $\dot{V}_{\mathrm{O_2}}$ was converted to metabolic rate (MR, W kg^{-1}), assuming a respiratory quotient of 0·85 and a calorific equivalent for oxygen of 20·349 kJ l^{-1}. Measurements of REHL and $\dot{V}_{\mathrm{O_2}}$ were made for 3 min at the beginning and end of the rest periods and at 10 min intervals during exercise. The mask was placed over the nose and mouth of the animal for the measurement periods and removed after each measurement.

Exercise workload was varied by changing the incline of the treadmill from 0 to 20 % in 5 % increments in different experiments. All animals were capable of walking at inclines of up to 10 %, but only three could walk at 15 and 20 %.

Dehydration was achieved by removal of drinking water for 72 h combined with daily 30 min bouts of exercise at $T_{\mathrm{a}} = 35$ °C and 10 % incline. A single workload (0 % incline) was used in the dehydration studies. Body weights of the dehydrated animals were returned to hydrated levels with weighted ‘saddlebags’ to ensure that MR was the same in hydrated and dehydrated animals.

In one animal, two additional experiments were performed to determine the effect on SBC of occlusion of the veins draining the nasal cavity in an exercising goat with an elevated body temperature. T_{bl} and T_{br} were measured while the angularis oculi veins or the buccal segments of the facial veins were occluded manually in a goat walking at a treadmill incline of 10 %.

Data analysis

Selective brain cooling (SBC) was calculated as the difference between T_{bl} and T_{br} at each 30 s time interval. T_{bl}, T_{br} and SBC of each animal were numerically integrated over 5 min periods before being grouped together for statistical analysis. All points depicted with error bars are the means ± S.E.M. for the group of animals. Two-way analysis of variance with repeated measurements was used to describe time and dehydration effects, or time and workload effects on the parameters measured. Linear regression analysis and analysis of covariance were used where applicable, using 5 min data averaged for all goats. Statistical significance was tested at $P = 0{\cdot}05$.

RESULTS

Selective brain cooling at blood temperatures below 40·5 °C

Walking at 4·8 km h^{-1} on a 0 % incline for 60 min increased T_{bl} from $38{\cdot}8 \pm 0{\cdot}1$ to $40{\cdot}2 \pm 0{\cdot}2$ °C and T_{br} from $39{\cdot}0 \pm 0{\cdot}1$ to $39{\cdot}5 \pm 0{\cdot}1$ °C above resting levels (Table 1;

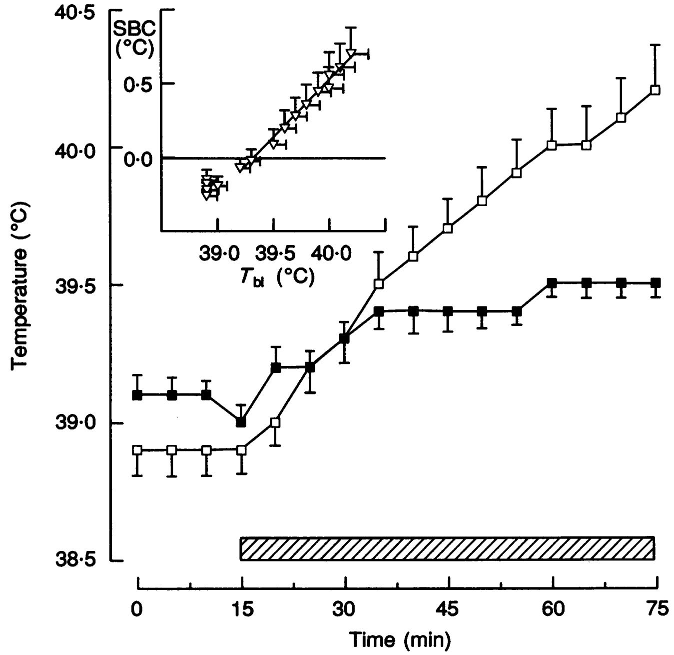

Fig. 1. Central blood temperature (□) and brain temperature (■) of 6 goats at rest and while walking on a level treadmill at 4·8 km h^{-1} for 60 min. The hatched bar delimits the exercise period. Inset, selective brain cooling (SBC) as a function of central blood temperature (T_{bl}). The fitted line represents data where SBC $\geqslant$ 0.

TABLE 1. Responses of hydrated goats to exercise at 4·8 km h^{-1} at different treadmill inclines

	Treadmill incline				
	0 %	5 %	10 %	15 %	20 %
Exercise (min)	60	60	60	45	20
Animals	6	6	6	3	3
MR (W kg^{-1})	4·8 ± 0·2	6·4 ± 0·2	7·9 ± 0·2	8·2 ± 0·1	10·6 ± 0·1
T_{bl} range (°C)	38·8–40·2	38·9–40·4	38·9–41·3	38·8–41·5	38·8–40·8
T_{br} range (°C)	39·0–39·5	39·0–39·6	39·0–39·8	39·0–39·8	39·1–39·8
SBC as a function of T_{bl}					
Slope	0·81	0·69	0·71	0·78	0·63
Threshold T_{bl}	39·3	39·3	39·2	39·3	39·2
R^2	0·99	0·99	0·99	0·98	0·99
P value	< 0·001	< 0·001	< 0·001	< 0·001	< 0·001
REHL as a function of T_{bl}					
Slope	1·00	0·85	0·92	1·03	*
R^2	0·99	0·98	0·97	0·87	
P value	< 0·001	< 0·001	< 0·001	< 0·01	
SBC as a function of REHL					
Slope	0·78	0·79	0·76	0·87	*
R^2	0·99	0·93	0·96	0·95	
P value	< 0·001	< 0·01	< 0·001	< 0·01	

Linear regression analysis for SBC $\geqslant$ 0 throughout.
*$n = 2$. No regression analysis was performed.

Fig. 1), and SBC reached a maximum of 0·7 ± 0·2 °C. Expressing SBC as a function of T_{bl} (Fig. 1 inset) revealed a significant linear relationship with a slope of 0·81 and a threshold (T_{bl} at onset) of 39·3 ± 0·1 °C (Table 1).

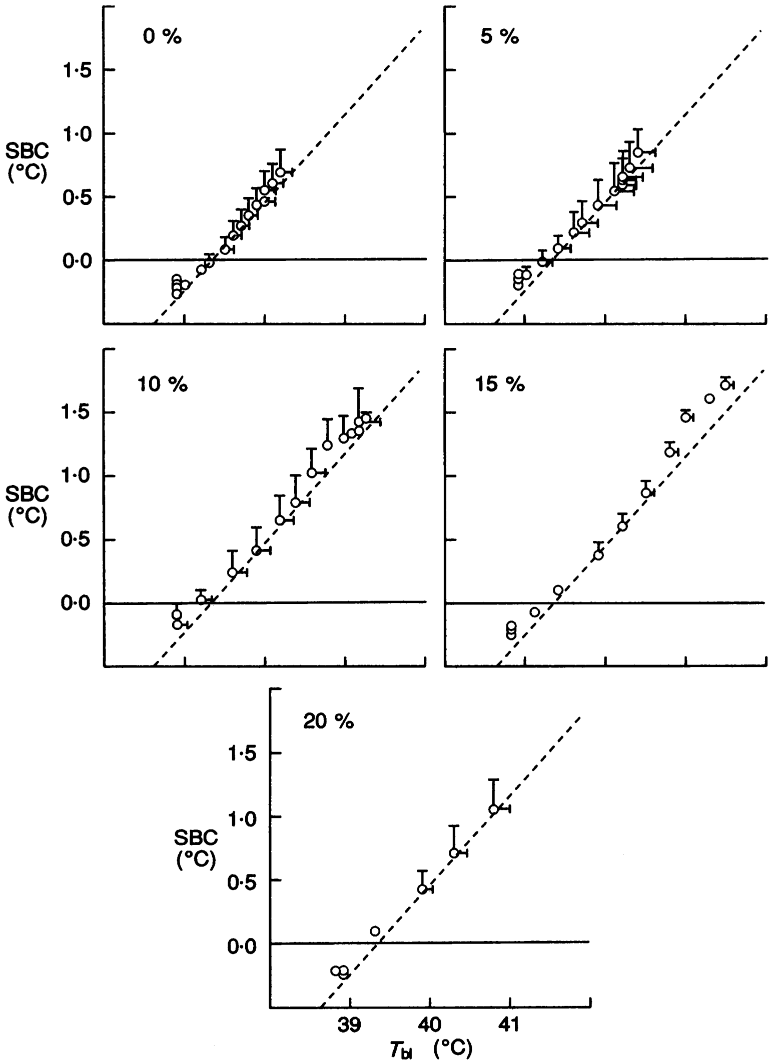

Fig. 2. Selective brain cooling (SBC) as a function of central blood temperature (T_{bl}) at rest and during exercise at 0, 5, 10, 15 and 20 % treadmill inclines. The dashed line is the common regression line generated using all data where SBC ⩾ 0.

Selective brain cooling at elevated workloads

The resting MR of these six animals was 1·4 ± 0·1 W kg^{-1}, a value which is close to the standardized metabolic rate for animals of this size (Kleiber, 1947). Walking at treadmill slopes of 0, 5, 10, 15 and 20 % increased MR to 3·4, 4·6, 5·6, 5·9 and 7·6 times resting MR, respectively (Table 1). These rates range from about 29 to 63 %

of maximal metabolic rate, which is around twelve times the resting rate for goats (Taylor, Karas, Weibel & Hoppeler, 1987).

Analysis of the temperature response trends at the various inclines revealed that exercise significantly increased T_{bl}, T_{br} and SBC above resting levels in all experiments ($P < 0.001$). An increase in incline from 0 to 5 % did not alter the responses in T_{bl}, T_{br} and SBC found during exercise. Further 5 % increases in treadmill incline showed significant elevations in all three parameters ($P < 0.02$), however, except when the incline increased from 15 to 20 %, where T_{br} responses were the same. When compared to the responses found while walking at 0 %,

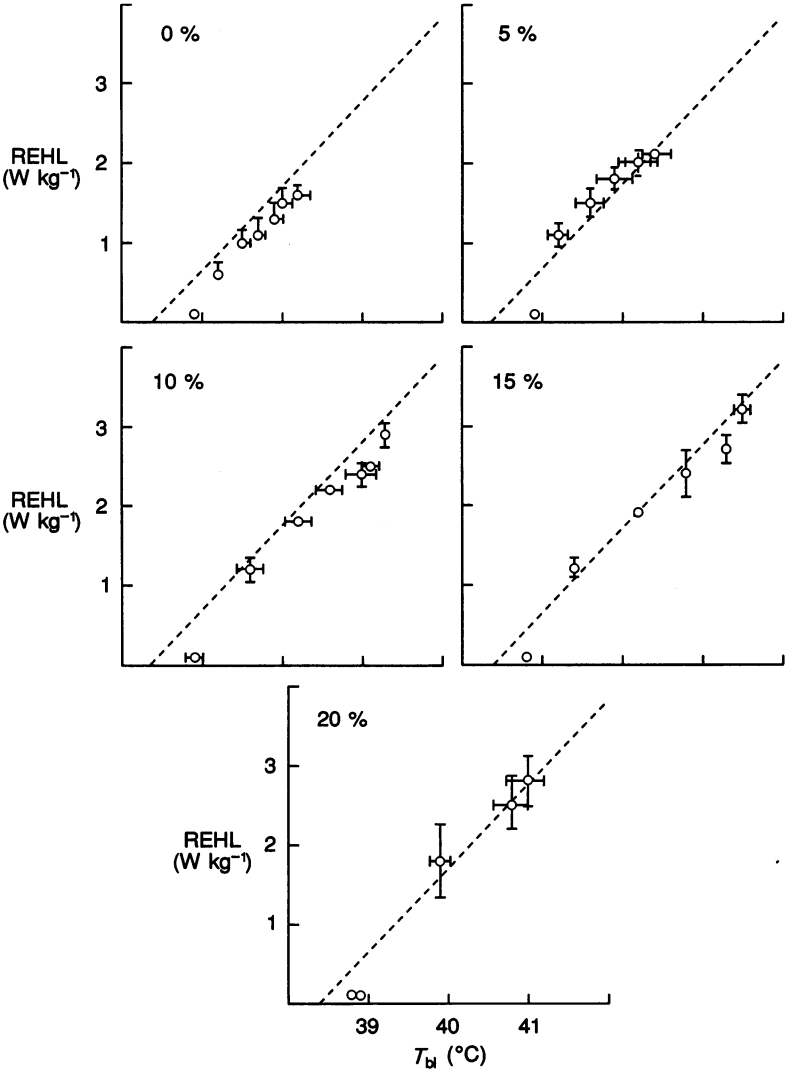

Fig. 3. Respiratory evaporative heat loss (REHL) as a function of central blood temperature (T_{bl}) at rest and during exercise at 0, 5, 10, 15 and 20 % treadmill inclines. The dashed line is the common regression line generated using data from all exercise periods at 0–15 % inclines.

however, successive inclines above 5 % significantly increased T_{bl}, T_{br} and SBC (10 %: $P < 0{\cdot}001$; 15 %: $P < 0{\cdot}003$; 20 %: $P < 0{\cdot}001$). Despite these workload related increases in temperature and the larger $T_{bl}-T_{br}$ temperature differences, ANCOVA of SBC as a function of T_{bl} could detect no progressive workload-induced change in

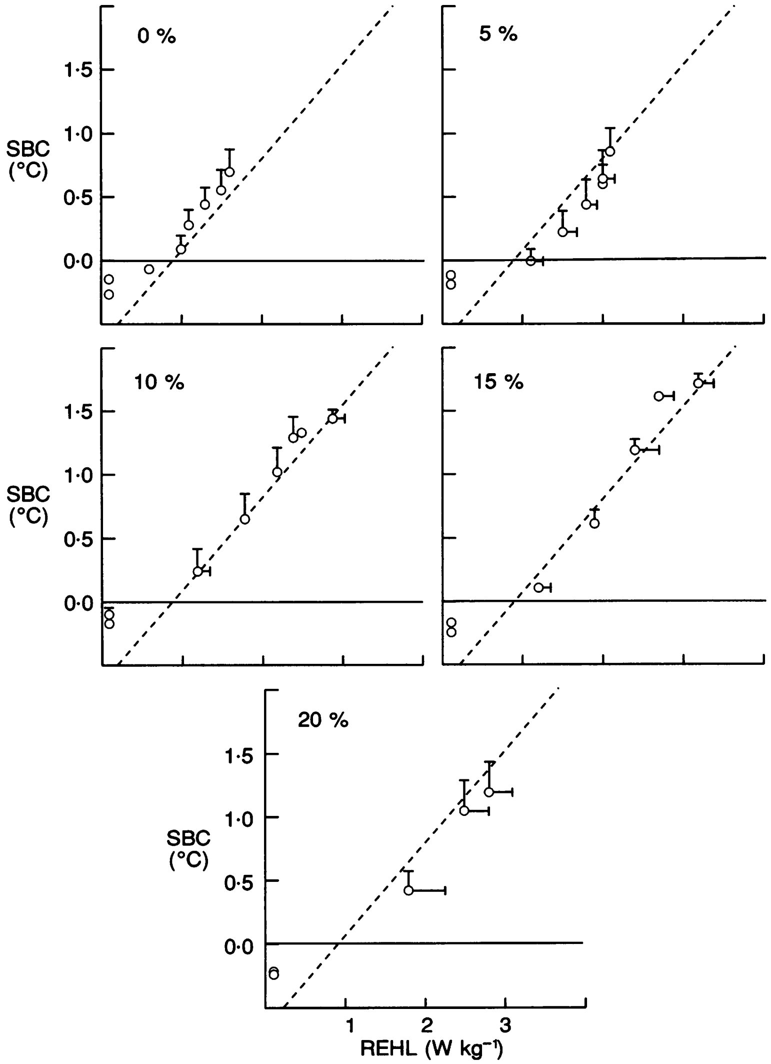

Fig. 4. Selective brain cooling (SBC) as a function of respiratory evaporative heat loss (REHL) at rest and during exercise at 0, 5, 10, 15 and 20 % treadmill inclines. The dashed line is the common regression line generated using all data from experiments at 0–15 % inclines where SBC ≥ 0.

the slope of the regression line or in the T_{bl} at the onset of SBC (Table 1, Fig. 2). Pooling the results from all workloads gives the common regression line:

$$\mathrm{SBC} = -28{\cdot}85 + 0{\cdot}73\ T_{bl} (R^2 = 0{\cdot}99;\ P < 0{\cdot}001).$$

Respiratory evaporation in exercise

REHL was strongly related to T_{bl} at each incline used (Table 1, Fig. 3). ANCOVA revealed differences in slopes between different workloads, but there was no progressive effect of increasing workload (Table 1). Measurements of REHL during exercise at a 20 % incline were omitted from the analysis as only two animals could wear the respiratory mask and exercise at this intensity. Nevertheless, it appears from Fig. 3 that the REHL–T_{bl} relationship apparent at lower work intensities is also present at the highest workload. The common regression line relating REHL to T_{bl} is as follows:

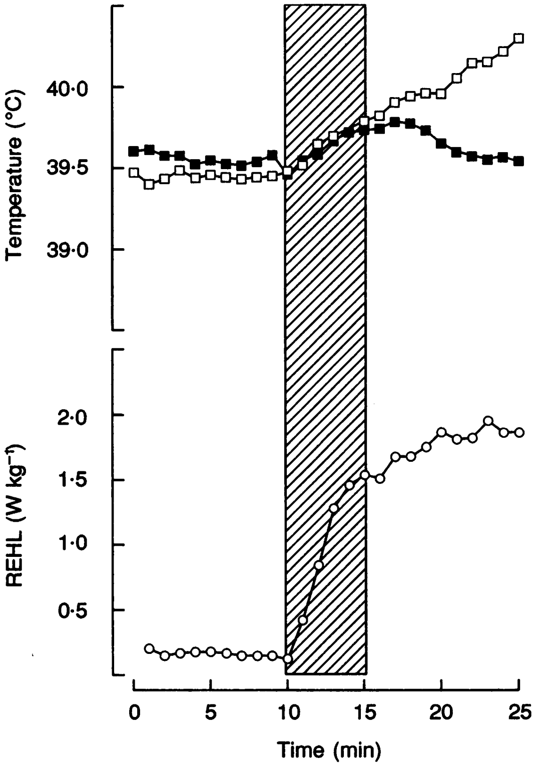

Fig. 5. Central blood temperature (□), brain temperature (■) and respiratory evaporative heat loss (REHL, ○) in one goat at rest and during the first 15 min of exercise at a 10 % incline. Exercise begins at 10 min. Points represent 1 min averages. The hatched bar marks the time period where REHL and SBC are dissociated from one another.

$$\text{REHL} = -33{\cdot}96 + 0{\cdot}89\ T_{bl}\ (R^2 = 0{\cdot}99;\ P < 0{\cdot}001).$$

Respiratory evaporation and selective brain cooling

The linear correlations between SBC and T_{bl} and REHL and T_{bl} suggested that SBC and REHL are similarly related. In Fig. 4, SBC is presented as a function of

REHL. At all levels of SBC above threshold, a positive linear relationship between SBC and REHL was found at treadmill inclines between 0 and 15 % (Table 1). A similar relationship appears at the 20 % incline, but insufficient data prevented statistical analysis. ANCOVA again revealed some differences between regression

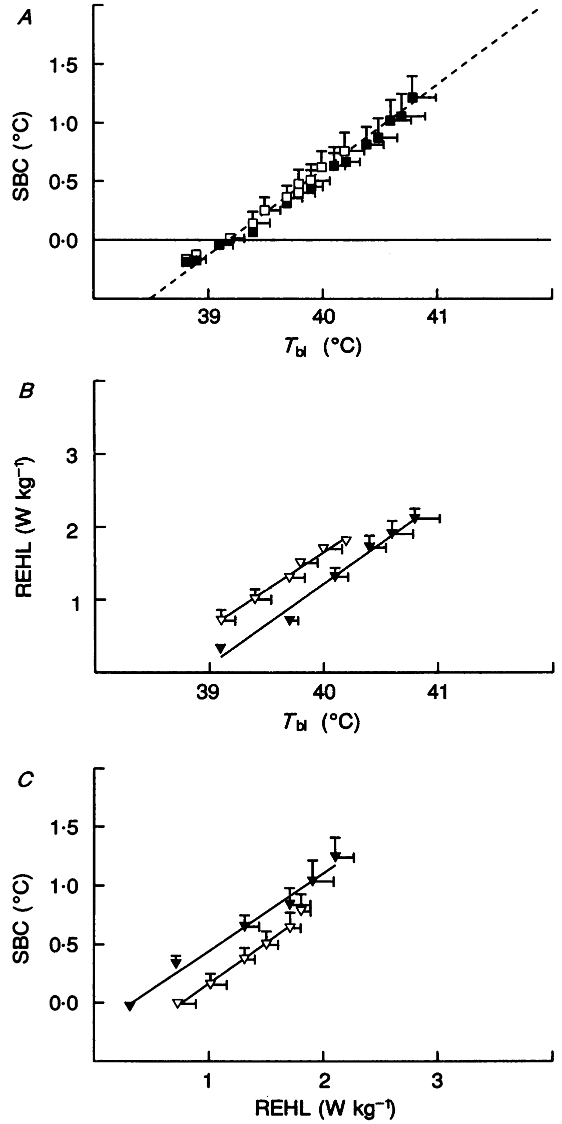

Fig. 6. *A*, selective brain cooling (SBC) as a function of central blood temperature (T_{bl}) in 6 goats at rest and walking at 0 % incline when they were hydrated (□) and when they were dehydrated (■). The dashed line is the common regression line generated using data where SBC ≥ 0. *B*, respiratory evaporative heat loss (REHL) as a function of T_{bl} during exercise in 6 hydrated (▽) and dehydrated (▼) goats in the same experiments as shown in *A*. *C*, SBC as a function of REHL during exercise in 6 hydrated (▽) and dehydrated (▼) goats in the same experiments as shown in *A* and *B*.

lines at the different workloads, but there was no trend related to increasing workload (Table 1). The regression line from the pooled data relating SBC to REHL is as follows:

$$\mathrm{SBC} = -0{\cdot}83 + 0{\cdot}82\ \mathrm{REHL}\ (R^2 = 0{\cdot}97;\ P < 0{\cdot}001).$$

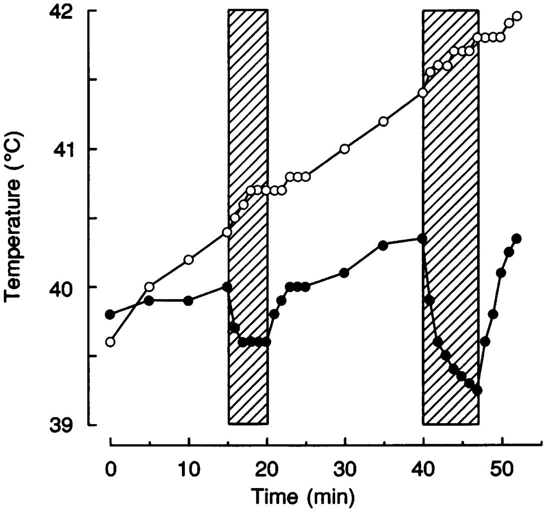

Fig. 7. Central blood temperature (○) and brain temperature (●) in 1 goat exercising at a 10 % treadmill incline. The hatched areas represent two periods during which the buccal segments of both facial veins were manually occluded by an experimenter.

Selective brain cooling appeared after the onset of exercise at all work intensities. The time between the beginning of exercise and the onset of SBC shortened with increasing workload. We examined this period by measuring REHL continuously at the beginning of exercise (10 % incline) in one animal while T_{bl} and T_{br} were measured at 30 s intervals (Fig. 5). It is apparent that there was a time when REHL increased rapidly prior to the appearance of SBC. There was therefore a brief dissociation of REHL and SBC at the onset of exercise. The 10 min measurement protocol used in the other experiments would have missed this period in all but the lowest workload.

Selective brain cooling in dehydrated animals

Each goat was studied walking on a 0 % incline when hydrated and then again after water deprivation. The body weight of the goats decreased by $9{\cdot}2 \pm 0{\cdot}3$ % over the dehydration period. Metabolic rate before and during walking was not different in the hydrated and dehydrated animals.

Water deprivation elevated both T_{bl} and T_{br} responses to exercise ($P < 0{\cdot}002$) while SBC attained higher levels in the dehydrated animals ($P < 0{\cdot}001$). When expressed as a function of T_{bl}, however, SBC was unaffected by dehydration (Fig. 6*A*), the common regression line being:

$$\mathrm{SBC} = -29{\cdot}85 + 0{\cdot}76\ T_{\mathrm{bl}}\ (R^2 = 0{\cdot}99;\ P < 0{\cdot}001).$$

The REHL–T_{bl} relationship, on the other hand, was shifted to the right in the dehydrated goats (Fig. 6*B*; $P < 0{\cdot}01$), indicating reduced REHL at each level of T_{bl}. The relationship between SBC and REHL was also affected by dehydration. Analysis of SBC as a function of REHL revealed highly linear functions for both hydrated ($R^2 = 0{\cdot}99$, $P < 0{\cdot}001$, Table 1) and dehydrated ($R^2 = 0{\cdot}98$, $P < 0{\cdot}001$) animals, with the regression line for dehydrated animals parallel to and shifted to the left of the line for hydrated animals (Fig. 6*C*; $P < 0{\cdot}05$).

Effect of venous occlusion on SBC

We measured T_{bl} and T_{br} in one exercising animal when it was fully hydrated to determine the effects of temporary occlusion of the angularis oculi veins or the facial veins on SBC. The veins were clearly visible and could be occluded manually by the experimenter while the animal continued to walk. Occlusion of both angularis oculi veins for 5 min raised T_{br} from 39·9 to 40·6 °C, while T_{bl} changed from 41·2 to 41·3 °C. SBC dropped from 1·3 °C immediately before the angularis oculi occlusion to 0·7 °C after 5 min of occlusion and began to rise when the occlusion was released. This result is similar to that reported by Johnsen *et al.* (1987) in hyperthermic reindeer and indicates that the angularis oculi veins play a role in SBC in goats.

The opposite effect was observed when the facial veins were occluded. Two periods of manual compression of the buccal segments of both facial veins produced a reversible fall in brain temperature and an increase in SBC (Fig. 7).

DISCUSSION

These experiments demonstrate that the rate of selective brain cooling is a linear function of body core temperature in exercising goats from a threshold of 39·3 to 42·5 °C, the highest core temperature which we observed, and that the relationship of SBC to T_{bl} is not affected by increasing exercise intensity or by the hydration state of the animals. These findings confirm and extend the measurements of Kuhnen & Jessen (1991) who found a similar linear relationship from 38·8 to 40·5 °C in resting goats when core temperature was elevated with intravascular heat exchangers. The slope of the regression line describing the relationship between SBC and T_{bl} in our animals is similar to the one reported by Kuhnen & Jessen (1991), but the threshold T_{bl} for SBC in our experiments is higher by 0·5 °C. Whether this difference represents an effect of exercise on the threshold for SBC or merely a difference between the two groups of animals would have to be tested by measuring threshold at rest and during exercise in the same group of animals.

The finding of a positive, highly significant relationship between SBC and REHL at every workload which we studied is strong evidence that upper respiratory evaporation is a major factor underlying SBC in exercising goats. Although this conclusion has been inferred from a number of earlier studies in both resting and exercising panting animals (Baker & Hayward, 1968; Baker, Chapman & Nathanson, 1974; Jessen & Pongratz, 1979; Laburn, Mitchell, Mitchell & Saffy, 1988), this is the first analysis of the relationship over a wide range of body core temperatures and evaporative rates. Kuhnen & Jessen (1991) found a positive relationship between SBC and REHL in resting goats when heat exchangers were used to produce parallel increases in temperature of the blood perfusing the head and the body core, i.e. a condition which is present in the normal heat-stressed or exercising animal. However, when they controlled the temperatures of head and trunk differentially, with one temperature clamped and the other increasing, SBC and REHL could be dissociated from each other.

In the present experiments, there were only two conditions when the SBC–REHL relationship varied from that which was present in the hydrated animals after the first 10 min of exercise: at the onset of exercise, when REHL increased faster than SBC, and in the dehydrated exercising animals, when the regression of SBC on REHL was shifted to the left, indicating an increase in SBC at a given rate of REHL. We can only speculate about the mechanisms which could account for these variations in the relationship between SBC and REHL. A 'mismatch' between REHL and nasal mucosal blood flow could lead to dissociation between SBC and REHL, although measurements in dogs suggest that the rate of upper respiratory blood flow is co-ordinated closely with the rate of REHL in both resting and exercising animals (Pleschka, Kuhn & Nagai, 1979; Baker, Hawkins & Rader, 1982; Baker, 1984). However, a delay in the increase of blood flow with relation to the increase in respiratory evaporation has been observed in dogs at the beginning of exercise (Baker, 1982).

Another factor which could affect the relationship between REHL and SBC is the distribution of nasal venous return via the superficial vasculature of the face and head. In a number of panting species, veins draining the nasal mucosa communicate with both the angularis oculi vein and the facial vein. Blood in the angularis oculi flows into the cavernous sinus and exchanges heat with arterial blood in the carotid rete, while nasal blood in the facial vein flows directly to the heart via the external jugular vein and the proportion of nasal venous blood which flows into the angularis oculi or the facial depends upon the relative resistances of the two pathways (Johnsen & Folkow, 1988). Anatomical and pharmacological studies in dogs (Magilton & Swift, 1969), rabbits (Pegram, Bevan & Bevan, 1976), sheep (Khamas & Ghoshal, 1982), reindeer (Johnsen *et al.* 1987) and camels (Elkhawad, Al-Zaid & Bou-Resli, 1990) have demonstrated a muscular segment of the buccal facial vein which has been called a 'sphincter' by some investigators. Both the angularis oculi and the facial veins are innervated by sympathetic nerve fibres. In reindeer, the buccal facial vein contains β-adrenergic receptors while the angularis oculi contains α-adrenergic receptors (Johnsen & Folkow, 1988). In the only study of the activity of these venous structures in intact animals, Johnsen *et al.* (1987) showed in reindeer that the angularis oculi vein is constricted in cool conditions and dilates when body temperature rises, while the facial sphincter is open in normothermia and constricts in hyperthermia. These authors also found that T_{br} increased with no change in T_{bl} when the angularis oculi was occluded manually in hyperthermic reindeer, a finding which we have confirmed in the goat.

Our observation that manual occlusion of the facial vein increased SBC in an exercising goat with elevated T_{bl} indicates that the vein was not fully constricted before the occlusion. The structure of the facial vein has not been studied in goats, but if we assume that a muscular sphincter is present there, then it is possible that exercising goats could maintain SBC even at reduced levels of REHL by constricting the sphincter and directing a greater proportion of nasal venous blood to the cranial cavity. Increased tone in the facial sphincter is a feasible mechanism for the small shift in the relationship between SBC and REHL which we observed in dehydrated exercising animals.

Dehydrated mammals can save water by reducing thermoregulatory evaporation and allowing the body temperature to rise during heat stress (Schmidt-Nielsen, Schmidt-Nielsen, Jarnum & Houpt, 1957). One mechanism for this readjustment of thermoregulation has been thought to be an osmotically induced reduction in the sensitivity of the hypothalamus to increased temperature (Baker & Doris, 1982). Keeping the brain cool by maintaining SBC at hydrated levels even with elevated T_{bl} could also help the dehydrated animal save water, especially if REHL can be maintained at or below hydrated levels. Kuhnen & Jessen (1991) pointed out that an important consequence of SBC is to reduce the drive on thermoregulatory responses which are driven by thermal inputs from both the body core and the brain.

Goats use both panting and sweating for evaporation in heat stress and, while it is known that panting in goats is controlled by both brain and core thermoreceptors (Jessen & Feistkorn, 1984), the thermal factors controlling sweating have not been studied. Dehydrated goats show a marked reduction in sweating when they are resting in hot environments (Robertshaw & Dmi'el, 1983; Baker, 1989) and an elevation in the core temperature threshold for sweating during exercise (Nijland & Baker, 1992). Studies of the effect of dehydration on REHL in goats suggest that the relationship between REHL and body core temperature may shift slightly in the direction we have observed here, i.e. reduced REHL at a given body temperature (Baker, 1989) in mild heat stress, or may not change from the hydrated state with more severe thermal loads (Nijland & Baker, 1992). Further studies are needed to clarify how SBC and REHL are affected by different thermal loads in resting and exercising animals and whether the activity of the facial venous system plays a significant role in maintaining SBC in dehydrated animals.

Part of this work has been published in abstract form (Baker & Nijland, 1992). M. J. M. N. was a Fellow of The American Heart Association, California Affiliate.

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