A COUNTER-CURRENT HEAT EXCHANGE SYSTEM IN THE TAIL OF THE VERVET MONKEY, *CERCOPITHECUS PYGERYTHRUS* (PRIMATA : CERCOPITHECIDAE)

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ABSTRACT

Lightly anaesthetized vervet monkeys can maintain their body core-temperature by skin vaso-constriction and shivering when the environmental temperature is moderately lowered.

Under such conditions the arterial blood supplying the tail skin is several degrees cooler than the core temperature and thus heat loss from the tail is reduced.

The core-caudal artery temperature difference is most probably due to counter-current heat exchange between the median sacral and caudal artery and the median caudal veins above the sixth postsacral tail segment.

The medial caudal veins are small compared with the dorsolateral caudal veins which run a superficial course, but the arrangement of valves permits movement of blood between them. The balance of blood flow in the two systems will determine the extent of heat exchange with the arterial inflow. The properties of the dorsolateral veins and the structural arrangements increase the proportion of blood returning by the median system under cool conditions.

The functional integrity of the sympathetic nervous system is necessary for effective control of the heat exchange system.

INTRODUCTION

A thermoregulatory function for the vervet monkey tail has been suggested from observations on the changes in blood flow produced by alterations in deep body or environmental temperature (Hongo & Luck 1953; Wright 1959). Under conditions which produce a low blood flow, contractile activity occurs in the dorsolateral veins. This promotes venous return and reduces stagnation in an organ in which gravity will further aggravate matters when the animal is at rest. Such an adaptation is consonant with a thermoregulatory function.

Though the two dorsolateral veins are the larger vessels draining the tail circulation, the anatomical arrangement of the smaller medial vein and the caudal artery suggests that a counter-current heat exchange system may exist in the upper third of the organ (Wright 1977). The efficiency of such an arrangement in conserving heat will depend upon the relative blood flows in the two vessels. The influence of venous blood flow in the medial vessels on the temperature of arterial blood entering the tail vasculature has now been tested during environmental temperature changes in lightly anaesthetized animals.

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MATERIAL AND METHODS

Adult vervet monkeys of both sexes and weighing between 3,6 and 4,7 kg were initially anaesthetized by an intramuscular injection of 10 mg. kg^{-1} ketamine (Parke-Davis). A fine silicone catheter was then introduced into the saphenous vein through a small skin incision and 25 mg. kg^{-1} choralose (Kuhlmann) and 250 mg. kg^{-1} urethane (BDH) dissolved in 0,9% non-pyrogenic saline was injected to maintain light anaethesia.

Hair on the tail was clipped and a small incision (4 mm) was made through the ventral skin and connective tissue of the sixth postsacral segment to expose the caudal artery as it emerged from the last haemal arch. The tip of a tiny thermistor (ITT type U) was positioned on the artery and secured in place by a small polystyrene bridge held with adhesive tape or silicone adhesive. This arrangement completely insulated the vessel and thermistor from the environment.

Body core temperature was measured via a thermistor (ITT type F) in the oesophagus at heart level. The volume of a tail segment was recorded using a water-filled plethysmograph attached with a silicone and talc paste. The plethysmograph was enclosed in a water jacket so that the environmental temperature of the segment could be altered along with the environmental temperature. The plethysmograph volume was measured by means of a gravimetric technique which imposed no external pressure upon the tissues.

Shivering was monitored by means of an electromyogram sampled with a monopolar electrode in the gluteus muscle. All recordings were made with a Honeywell 2106 Visicorder. The surface area measurements were made by covering marked areas of the shaved skin with aluminium foil and then weighing the foil. The animal was laid upon an open mesh platform in an environmental chamber through which heated or cooled air could be circulated.

RESULTS

The response to environmental cooling.
The light anaesthesia employed during these experiments interfered minimally with thermoregulation because the core temperature was maintained with a neutral environmental temperature of about 25° to 30°. Shivering usually occurred when the temperature was lowered to 20° or less and this often resulted in an increase in core temperature above the initial level.

Typical records are illustrated in Figures 1 and 2. With a neutral ambient temperature of 25° to 30° the body core temperature had fallen slightly from an initial 36° but, with slight shivering, was maintained at about 35,3°. The caudal artery temperature was 1,0° to 1,1° lower and this temperature difference can only be due to counter-current heat exchange between the caudal and median sacral artery and the median caudal veins above the level of the thermistor.

In Figure 1 when the ambient temperature was lowered from 30° to 20° over 14 minutes

the caudal artery temperature progressively decreased by 3,5° and there was a 2,7% decrease in tail segment volume superimposed on, what appeared to be, rapid volume fluctuations. The rapid nature of the response was apparent and after three minutes of cooling it was noticeable that an enhanced general response produced synchronous increases in vasomotor activity and shivering.

Some idea of the delicate nature of this thermoregulatory adjustment can be seen in Figure 2. When the ambient temperature was lowered by 3° to 22° the caudal artery temperature also fell 0,8° and this decrease coincided with the appearance of rapid intermittent volume fluctuations in the plethysmogram and a general decrease of tail segment volume of about 2,3%. Shivering increased and the core temperature was maintained. A further 2° reduction in the ambient temperature, to 20°, caused a further fall of 0,8° in caudal artery temperature, a further reduction in tail volume and violent shivering reactions.

In both experiments raising the ambient temperature reversed these responses. The core temperature now fell by 0,2° and shivering continued at a reduced level until the core temperature was restored after several minutes.
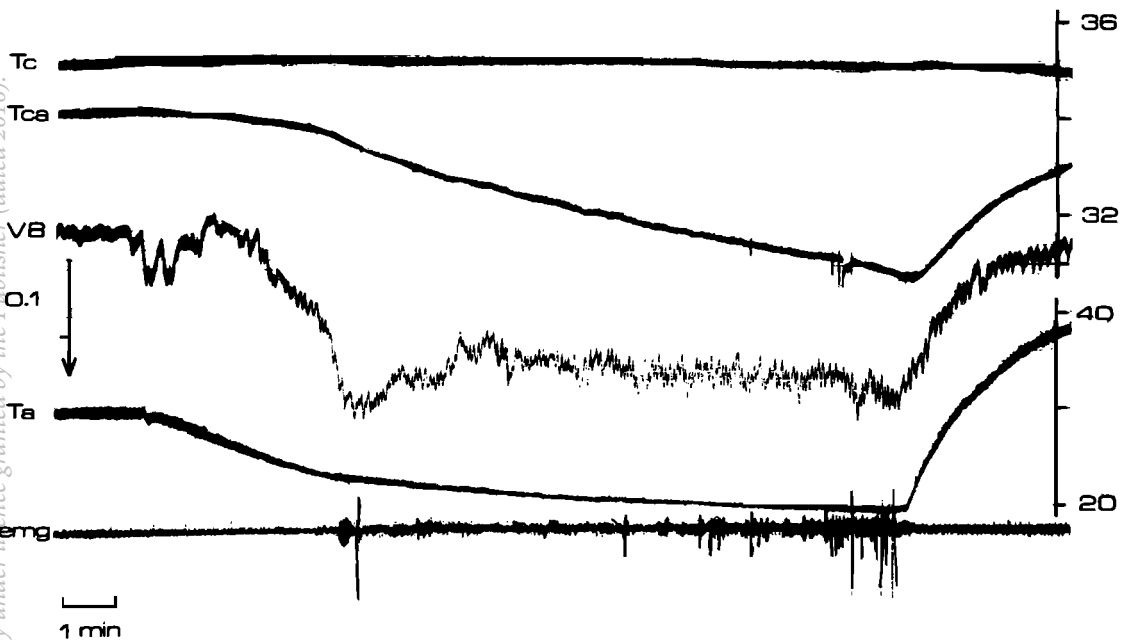

FIGURE I

Effect of changing ambient temperature (Ta) on core temperature (Tc), caudal artery temperature (Tca), volume of eighth postsacral tail segment (V8), and shivering (emg). The calibration of V8 is 0,1 ml = 1,22% total volume change; the arrow indicates volume decrease. Vervet ♂, 4,76 kg, choralose-urethane anaesthesia.

Figure 3 illustrates a similar experiment on an animal from which the sympathetic chains between L5 and L8 (including ganglia L6 and L7) had been removed on both sides 12 months before. At an ambient temperature of 30°, a core temperature of 36,2° was maintained with slight shivering; the caudal arterial temperature was 0,4° lower. Reduction of the ambient temperature to 15° caused a fall in caudal arterial temperature but also a fall in core temperature in spite of some increase in shivering. Rapid volume fluctuations of varying pattern existed before cooling and these increased with cooling. There was a gradual decrease in overall tail segment volume of about 2% over 14 minutes of cooling. Raising the ambient temperature reversed these effects. Again the core temperature continued to fall for several minutes and there was increased shivering.

In none of the experiments illustrated above was cooling prolonged because increasingly vigorous shivering and general limb movements inevitably disturbed the recording instruments; movement artefacts can be seen on the caudal artery temperature record in Figures 1 and 2. In consequence the full extent of the core-caudal artery temperature difference was not realised. In other experiments, where only temperatures were measured, differences of nearly 10° could be established representing a gradient of about 0,5° cm^{-1}. In the experiment illustrated in Figure 4 change from a warm ambient temperature of 36° to 22°
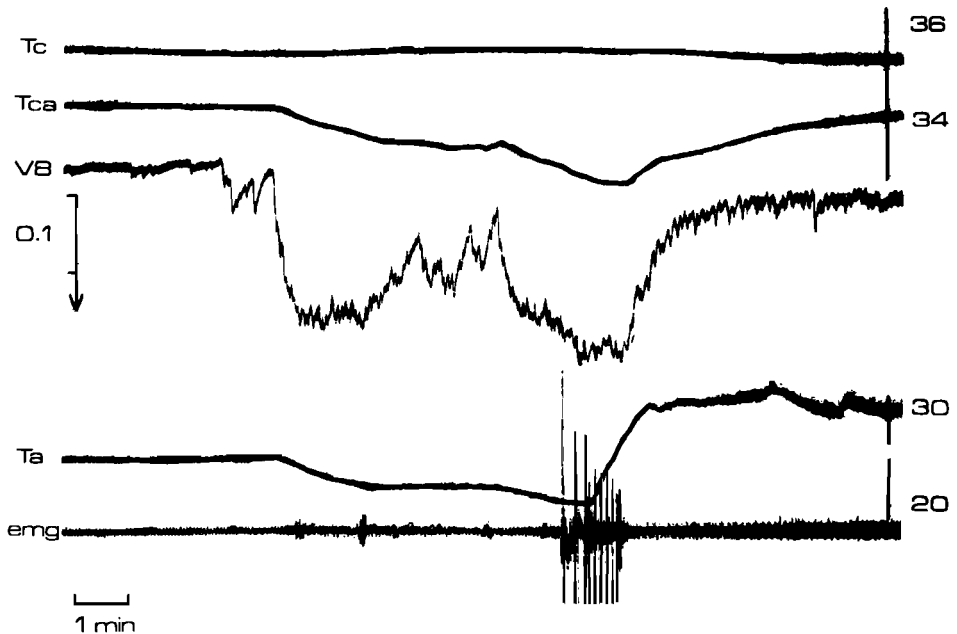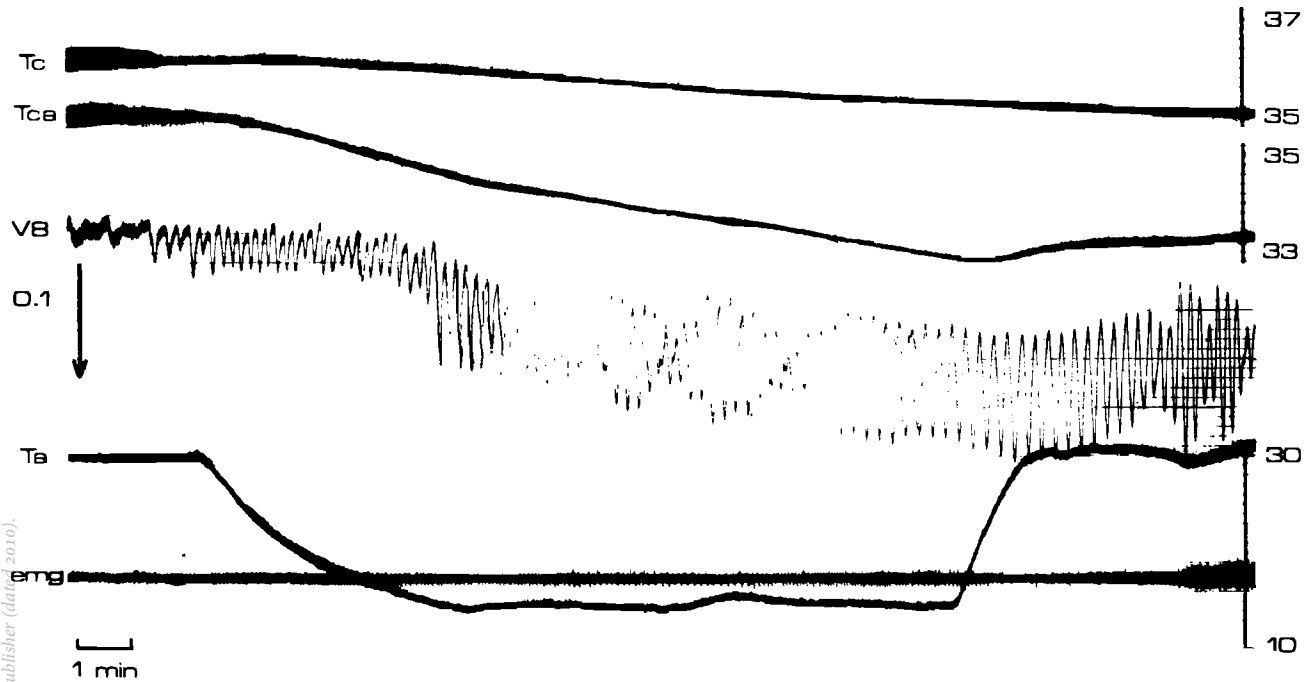

FIGURE 2
As in Figure 1.

FIGURE 3

As in Figure 1 except that Tc and Tca are separately scaled. The calibration of V8 is 0,1 ml = 1,14% total volume change. Vervet ♂, 4,42 kg, chloralose-urethane anaesthesia. The lumbar sympathetic chain from L5 to L8 had been removed bilaterally 12 months before this experiment.

over 18 minutes caused the caudal artery temperature to fall by 4,8° while, due to shivering, the core temperature rose by 0,4°. The core-caudal artery temperature difference thus increased from 3,4° to 8,6°, a change of 0,29° min $^{-1}$ and a longitudinal gradient of about 0,4° cm^{-1}. The rapid reversal of the caudal artery temperature trend on raising the ambient to near core temperature can be seen before and after the cooling period.

Body surface area
The body surface area was measured in five animals with the results shown in Table 1.

TABLE 1

Surface area as percentage of total

No.	Sex	Mass (kg)	Tail	Hands	Feet
1	F	3,5	8,1	4,6	5,6
2	M	3,2	8,4	4,3	6,4
4	M	2,8	7,3	4,8	7,5
5	F	2,8	8,2	3,4	5,8
6	M	5,4	6,8	2,8	5,5
Mean		3,5	7,8	4,0	6,2

DISCUSSION

The blood flow rate in the tail circulation of the vervet monkey was estimated at 20 to 32 ml. 100 g tissue^{-1}. min^{-1} at a neutral environmental temperature of 22° to 28° by Hongo & Luck (1953). They found that it could be varied between less than 2 ml and more than 40 ml. 100 g tissue^{-1}. min^{-1} by manipulating the body environmental temperature. In their pento-barbitone-anaesthetized preparation the flow rate appeared to be more closely related to environmental temperature than rectal temperature and, between 20° and 40°, body ambient rather than tail ambient temperature determined the response. Considering the composition of the tail they suggested that the tail circulation was concerned in temperature regulation and that the venomotion stimulated by a cool environment aided venous return and reduced local heat loss. Wright (1959) came to similar conclusions and demonstrated that sympathetic α - receptor mechanisms influenced both inflow and venomotor activity but that local venomotion was not dependent on intact central connections of the sympathetic system. In all these experiments the tail ambient temperature was maintained around a neutral 25°.

The two large dorsolateral tail veins might be expected to carry the bulk of the venous

return as suggested in one experiment by Hongo & Luck (1953) in which the body environmental temperature was changed from 41° to 24°. This has since been confirmed in experiments in which arterial inflow and lateral venous outflow was measured directly (Wright 1976). As these veins run superficially along the whole length of the tail until they enter the greater sciatic foramina, blood returning along them will continue to lose heat to cooler air. However in a cold environment this would be disadvantageous and in a number of animal species (Schmidt-Nielsen 1963) an alternative route for the returning blood in deep veins associated with the artery provides a counter-current heat trap. Bazett, Love *et al.* (1948) showed that a temperature gradient of 0,3° cm⁻¹ could be established along the brachial and radial arteries in man exposed to a 9° ambient which also produced a fall of about 1° in rectal temperature. Raman & Vanhuyse (1975) studied the distribution of blood in the hand and concluded that blood starts to be shunted to deep veins at an ambient temperature of 25° and this continues to 15°.

Wright (1976, 1977) has examined the vascular anatomy of the vervet caudal circulation in some detail and has suggested that above the last haemal arch the arrangement of the medial caudal venous plexus in relation to the caudal artery and median sacral artery constitutes a heat exchange system. The position of the valves in the dorsolateral and
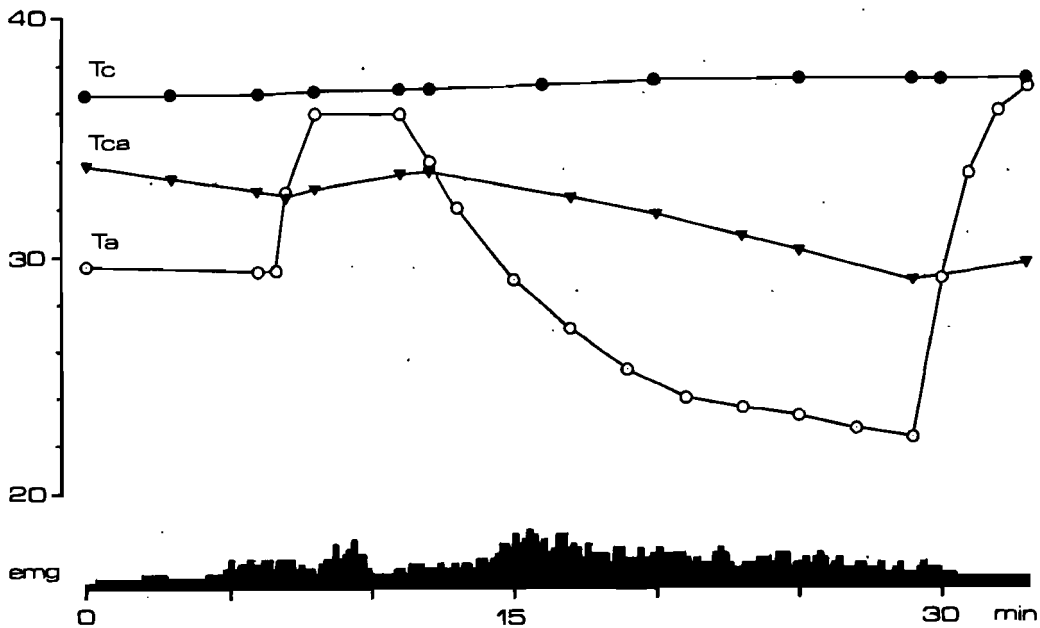

FIGURE 4

Plot of temperatures and electromyogram in a similar experiment to Figure 1. the amount of shivering is roughly quantitated as the area of the electromyogram in each minute. Vervet ♀, 3,0 kg. choralose-urethane anaesthesia.

median veins allows blood to pass between these vessels in each segment and Wright (1976) has suggested that the pattern of dorsolateral venomotion may promote flow to the median venous system. As venomotor activity is most pronounced when blood flow is reduced in response to body cooling, an effective counter-current heat conservation mechanism could exist in spite of the apparent disparity in size of the dorsolateral and median veins.

The core-caudal artery temperature difference now reported, and the rapid increase produced in it in response to a relatively modest reduction in the ambient temperature, demonstrates that a counter-current heat exchange system probably exists, and that it functions effectively to reduce the temperature of blood flowing into the tail circulation. In turn this will reduce heat loss to the environment.

The caudal artery temperature as measured may differ slightly from the blood temperature within the vessel. Bazett, Love *et al.* (1948) found a difference of up to 1° on piercing the wall of the brachial or radial artery in man under cold conditions. However the lightly clad subjects of these experiments had been sitting in a room at 9° for 20 to 120 minutes before observations began. A skin surface-to-artery blood temperature gradient had therefore become established. Pennes (1948) in a detailed analysis of tissue temperature gradients in the human fore-arm found little difference between brachial artery blood temperature and the surrounding deep fore-arm tissue; 0,00° to 0,36° (mean 0,16°) in all subjects at a comfortable environmental temperature of 25° to 27°. The change in arterial blood temperature when the ambient air temperature was changed was comparatively slow in the experiments of Bazett, Love *et al.*; an increase in room temperature from 21° to 34,5° produced an increase in brachial and radial arterial temperatures of 1° to 1,5° over one hour.

Considering the relative thickness of the human fore-arm and vervet caudal arteries at the respective sites of measurement and the rapidity of the temperature changes in the experiments recorded now with moderate environmental temperature changes, I do not consider that any serious error is introduced by the technique used for measuring the caudal artery temperature. Any attempt to introduce even a small detecting device inside a small vessel is likely to impede blood flow with consequent disturbance of temperature as Bazett, Love *et al.* found.

It is well known that anaesthesia interferes with thermoregulation and the overall response to ambient temperature change is distorted at different levels. Under the anaesthetic conditions in the present experiments the animals were able to maintain their core temperature within the normal range by peripheral vasoconstriction and shivering in response to a fall in ambient temperature. Tokura *et al.* (1975) found that unanaesthetized patas monkeys (*Erythrocebus patas*) were able to maintain normal rectal temperatures at environmental temperatures between 10° and 30° and that below 25° they shivered and their oxygen consumption rose. It would appear therefore that in the present study the level of anaesthesia interfered minimally with the response to cooling.

It was shown by Wright (1959) that stimulation of the sympathetic nerve supply to the tail caused arterial vasoconstriction and increased venomotor activity with a resultant decrease in tail segment volume. When the preganglionic outflow to the tail was interrupted the tail

circulation no longer responded to vasomotor reflexes elicited by body stimulation. There was a high arterial inflow and venomotor activity continued in a fluctuating manner. It is noticeable in Figures 1 and 2 that lowering the ambient temperature caused an immediate overall decrease in tail-segment volume accompanied by rapid fluctuations due to veno-motor activity and that the volume changes coincided with an increase in the core-caudal artery temperature difference. This suggests that cooling produced increased sympathetic vasomotor discharge which reduced caudal arterial inflow and venous outflow with the expected effect on the counter-current heat exchange mechanism.

The sympathectomy carried out in the animal used for the experiment in Figure 3 deprived the tail and part of the hind-limbs of preganglionic connections with the central nervous system; the ganglia below L7 remained together with their postganglionic nerves (Wright 1977). There was a high blood-flow rate in the tail and spontaneous fluctuating venomotor activity characteristic of this type of preparation (Wright 1959). In the lightly anaesthetized state the animal was able to maintain its core temperature at an environmental temperature of about 30°. The core-caudal artery temperature difference was only 0,4° under these conditions. Cooling increased this difference to 2,4° after 14 minutes during which time the core temperature fell by 1° in spite of increased shivering. There was a gradual small decrease in tail segment volume and an enhancement of venomotion, which was probably due to a direct effect of cooling on the tail vasculature (Wright, unpublished observations) and of blood-borne catecholamines from the adrenal medulla released as part of the response to cold (Cannon *et al.* 1927). This demonstrates that the effectiveness of the counter-current heat exchange system in the tail depends upon the integrity of the sympathetic nervous system which reduces overall skin blood-flow and probably affects the distribution of the venous return. Abolishing or largely reducing postganglionic sympathetic activity by deepening anaesthesia, by blocking ganglionic transmission with hexamethonium, by blocking ∝ - receptors with phenoxybenzamine (Wright 1959) increases general skin blood-flow so that the core temperature cannot be maintained. As part of this response, tail blood-flow increases and the core-caudal artery temperature difference is almost abolished. This is to be expected as under these conditions most of the high arterial inflow is returned via the large dorsolateral veins.

It is of interest to note that the core temperature fell or continued to fall slightly when rewarming commenced in these experiments. This must reflect the release of tone in the skin blood vessels with the consequent rewarming of the cold outer 'shell' of the body and the return of cold blood. It is a further indication of the satisfactory level of anaesthesia in these preparations and it is pertinent that Bazett, Mendelson *et al.* (1948) commented on similar paradoxical trends during rewarming in unanaesthetized human subjects.

The tail of the vervet monkey constitutes about 3% of the body mass and the proportion of skin to other tissues increases from 21% in the upper third to 24% in the middle third and 37% in the lower third. This changing proportion of skin is similar in the digits in man (Abramson & Ferris 1940) and the extremities play a substantial role in human thermo-regulation (Bazett 1949). The tail skin surface in *C. pygerythrus* is about 7,8% of the total surface area (five animals) with 10,2% for hands and feet together (Table 1). This compares

with 3,2% for the tail (eight animals) and 13,9% for hands and feet in *M. mulatta* (Johnson & Elizondo 1974). Napier & Napier (1967) record tail lengths of between 480 and 1090 mm in 203 specimens of *Cercopithecus (Cercopithecus)* compared with 0 to 686 mm in 196 specimens of *Macaca.*

Considering the high blood flow rate in the tail and the range of its variation demonstrated by Hongo & Luck (1953) and Wright (1959) it is apparent that this organ could make a more significant contribution to thermoregulation in the long-tailed monkeys than is the case in the short-tailed specimens such as the macaques where the vascular anatomy does not appear to be similarly developed (Luck, personal communication).

SUMMARY

In *C. pygerythrus* the anatomical relationship between the median caudal vein and the caudal and median sacral arteries above the fifth postsacral vertebra constitutes a counter-current heat exchange system. The flow relationship of blood in the caudal artery and median veins reduces the temperature of the arterial blood flowing to the tail skin circulation under moderately cool environmental conditions.

The efficiency of the system is dependent upon the functional integrity of the sympathetic nervous system.

ACKNOWLEDGEMENTS

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