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THE INFLUENCE OF DEEP BODY AND SKIN TEMPERATURES ON THERMOREGULATORY RESPONSES TO HEATING OF THE SCROTUM IN PIGS

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SUMMARY

1. The temperature on the surface of the pig's scrotum was increased by circulating water through a pad held over the scrotal surface while the animal was lightly restrained.

2. At an ambient temperature of 25° C there was no change in respiratory frequency even when the scrotum was heated to 42° C, but peripheral blood flow did increase and body temperature fell. At 30° C ambient temperature, respiratory frequency increased when the scrotum was warmed to 42° C. At an ambient temperature of 32° C, the frequency increased at a scrotal temperature of 40° C and was even higher when the scrotum was 42° C, but body temperature did not fall.

3. At a constant ambient temperature the effect on respiratory frequency of heating the scrotum to a given temperature depended on the skin temperature of the trunk which was modified by means of a coat through which water was circulated.

4. In a cold environment, heating the scrotum was accompanied by a fall in body temperature, the arrest of shivering and a decline in oxygen consumption.

5. Cooling a thermode in the hypothalamus or over the spinal cord inhibited the increase in respiratory frequency and peripheral blood flow caused by heating the scrotum. Warming either thermode potentiates the effect of heating the scrotum.

INTRODUCTION

In the ram, heating the scrotum is followed by a marked rise in respiratory frequency which is maintained in spite of a gradual decline in the temperature of the body core of as much as 2° C (Waites, 1961, 1962). Such a finding raises the possibility that the response to thermal stimuli on the scrotum is relatively unaffected by changes in the temperature of thermosensitive regions such as the hypothalamus (Bligh, 1966; Hammel, 1968) or the spinal cord (Thauer, 1971) which lie deep in the body. The temperatures of other regions of the periphery do, however, appear to influence the response, since panting is not induced in the shorn sheep when scrotal temperature is raised. Further investigations of the role of the scrotum in thermoregulation by Hales & Hutchinson (1971) have confirmed Waites's (1962) findings and demonstrated that when the scrotum is heated oxygen consumption tends to be depressed. Changes in peripheral blood flow as judged by skin temperatures on the extremities, on the other hand, were, according to Hales & Hutchinson, 'variable and disorganized'.

In the present study on the pig the interaction of thermal stimuli on the scrotum, hypothalamus, spinal cord and skin of the trunk have been investigated with respect to respiratory frequency, oxygen consumption and quantitative estimates of blood flow in the tail. The use of the pig provides the opportunity to extend the study of the problem to an animal in which the general body surface has little more external insulation than the scrotum itself.

METHODS

Animals. Ten healthy boars (Large White breed) aged between 6 and 12 weeks and weighing 15–20 kg were used. In four animals a thermode was implanted into the preoptic region of the hypothalamus and in two others thermodes were implanted into the cervical region of the spinal cord. In another two pigs, a blind-ended catheter was placed round the carotid artery. The remaining animals were not subjected to surgery.

Thermodes. The thermode implanted into the hypothalamus consisted of a chamber 5 mm in diameter mounted at the end of two stainless-steel tubes with a thermistor attached to the side of the chamber (Baldwin & Ingram, 1967). The thermode implanted along the epidural space consisted of a loop of polyethylene tube inserted in the mid-thoracic region and reaching up to C 1. In addition a blind-ended catheter was implanted alongside the thermode with its end about half way along in the epidural space and this tube received a thermojunction during an experiment (Ingram & Legge, 1971). The operations were performed under general anaesthesia using sterile precautions, and the position of the thermodes were established by means of radiographs.

Carotid catheter. The catheter consisted of a polyethylene tube which was sealed at one end and attached to a polyvinyl cuff. This cuff was sewn round the carotid artery under general anaesthesia and the open end of the catheter passed out through the skin. During an experiment a copper-constantan thermocouple was threaded down the tube to lie close to the wall of the artery (Ingram & Legge, 1970).

Control of scrotal temperature. A series of vinyl tubes of 4 mm outside diameter and spaced at 7 mm intervals were sewn into a pad consisting of a double layer of terylene net and a layer of aluminium foil on the scrotal side of the tubes. The pad, which covered only the scrotum and stopped well clear of the anus, was held in place by means of elastic straps, and the tubes were perfused with water at a controlled temperature. Care was taken to ensure that the tubes carrying water to and from the pad did not touch the tail or alter the skin temperature of parts of the body. The temperature of the skin on the scrotum beneath the pad was measured by means of two thermojunctions (36 S.W.G.) held in place by means of adhesive tape.

Control of skin temperature on the trunk. A coat consisting of water-perfused tubes sewn into terylene net (Ingram & Legge, 1971) was used to control skin temperatures. The limbs, head and tail were outside the coat.

Measurement of skin temperature. Skin temperature was measured by means of thermojunctions (36 S.W.G.) attached to the skin with adhesive tape.

Respiratory frequency. This was measured by counting flank movements.

Blood flow. Blood flow in the tail was measured by means of venous occlusion plethysmography using a mercury-in-rubber strain gauge (Whitney, 1953; Ingram & Legge, 1971).

Oxygen consumption. Pigs were placed in a chamber 1·2 m long by 0·6 × 0·6 m which was ventilated at 50 l./min and housed inside a temperature controlled room. The oxygen content of the exhaust air was then analysed using a Beckman oxygen analyser (Model F3) and the whole apparatus was calibrated by burning a known quantity of alcohol in the chamber.

Experimental procedure. The animals were lightly restrained in a stall inside a temperature-controlled room. All measuring and control apparatus was housed outside the room and observations were made through a window. No experiments were started until the animals had become accustomed to the room and the heating pad. After three or four training periods of 3 hr duration all animals lay down and sometimes closed their eyes.

RESULTS

Effects of peripheral body temperatures on the change in respiratory frequency induced by heating the scrotum

The effects of peripheral stimulation were examined in two pigs. In the first experiment the temperature on the scrotum was raised in a series of steps up to 42° C, held for 30 min and then allowed to return to its previous value. The respiratory frequency determined from the mean of the last three readings taken at 5 min intervals during the heating period was then plotted against scrotal temperature. From the results of this experiment it can be demonstrated (Fig. 1) that the change in respiratory frequency during heating depends both on the ambient temperature and on the temperature of the scrotum. At 25° C there was no change in respiratory rate even when scrotal temperature was 42° C, and it was found that further heating of the scrotum caused the animals to become restless. At 30° C ambient temperature, respiratory frequency was increased at a scrotal temperature of 42° C. When the ambient temperature was 32° C the rate of breathing increased at a scrotal temperature of only 40° C while further heating of the scrotum induced an even greater increase in breathing. When the pad used for heating the scrotum was attached to the abdomen or the back and heated to 42° C there was no increase in respiratory frequency at any of the ambient temperatures.

In another experiment using the temperature-controlled coat the temperature of the skin on the trunk was fixed at either 34, 36 or 38° C while ambient temperature was controlled at 30° C. Under these conditions the response to heating the scrotum to 40° C depended on the temperature of the skin of the trunk (Fig. 2). During cooling of the skin of the trunk to 34° C, the response to heating of the scrotum was equivocal, but at higher skin temperatures the respiratory frequency increased immediately the scrotum was heated.

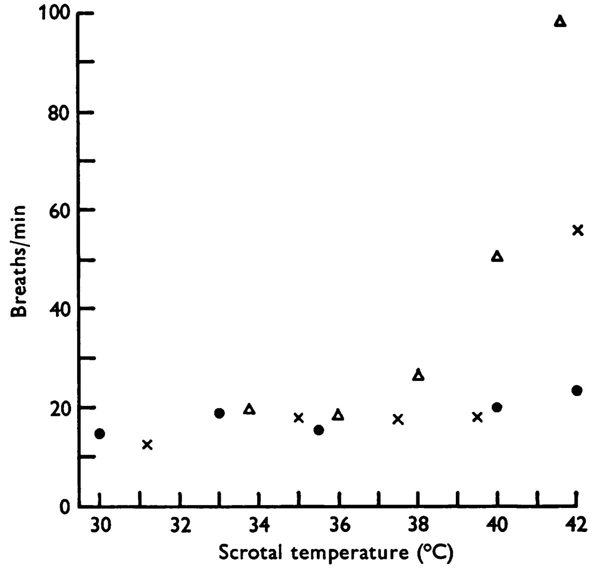

Fig. 1. The effect of warming the scrotum on respiratory frequency in three ambient temperatures of ● = 25° C, × = 30° C and △ = 32° C. Each point is the mean of three readings taken 20, 25 and 30 min after the temperature of the skin of the scrotum had been changed.

Effect of deep body temperatures on the change in respiratory frequency induced by heating the scrotum

The effects of changing the temperature in the hypothalamus and spinal cord were examined in six pigs. At an ambient temperature of 33° C, the scrotum was warmed to 42° C and after panting had begun the hypothalamus was cooled. The result of this cooling was an immediate decline in respiratory frequency, but as soon as the cooling was stopped, respiratory frequency again increased (Fig. 3). Similarly it was found that if the spinal thermode was cooled while the scrotum was being warmed respiratory frequency declined (Fig. 3).

Heating the thermode in the hypothalamus potentiated the effect of heating the scrotum but only when the ambient temperature was warm. At an ambient temperature of 25° C the respiratory frequency did not increase even when both the hypothalamus and scrotum were heated. At 30° C ambient temperature, however, when heating either the scrotum or the hypothalamus alone had no effect, respiratory frequency did increase under the combined stimulus. At an ambient temperature of 32° C heating the hypothalamus alone again had no effect, but when combined with heating the scrotum the response was much greater than when the scrotum alone was heated (Fig. 4).

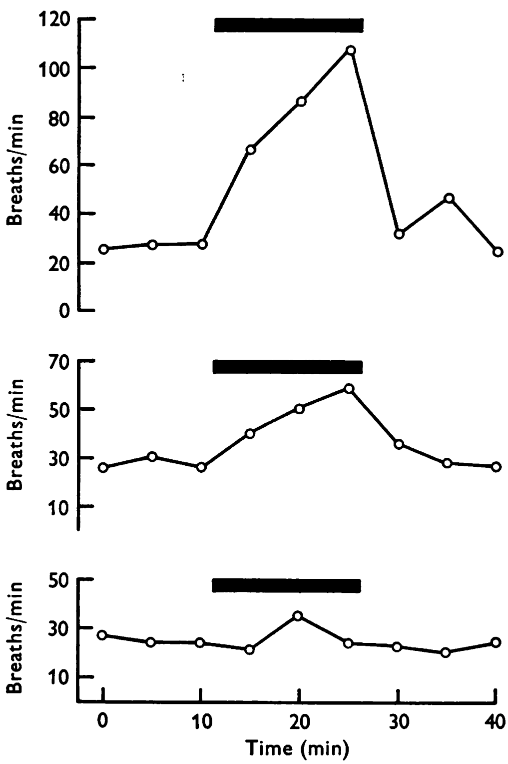

Fig. 2. The effect on respiratory frequency of warming the scrotum to 40° C (black bar) at 30° C ambient temperature and trunk skin temperature controlled by a coat of 38° C (top), 36° C (middle) and 34° C (bottom).

Heating the thermode in the spine also potentiated the effect of heating the scrotum in a manner similar to that which occurred on heating the hypothalamus. Although the effects of changing the temperature of the thermodes suggests that the thermosensitivity of the hypothalamus and spinal cord might have been compared in these experiments, in fact the temperature of the actual thermosensitive cells was not known. For these reasons no such comparisons were attempted.

Effects of heating the scrotum on blood flow in the tail

Blood flow through the tail was measured in three animals. Increasing the temperature of the scrotum to 42° C resulted in a substantial increase in blood flow through the tail at ambient temperatures of 25 and 27° C. At warmer ambient temperatures blood flow was already fairly high, and in cooler environments the animals tended to move about frequently making blood flow measurements difficult or impossible.

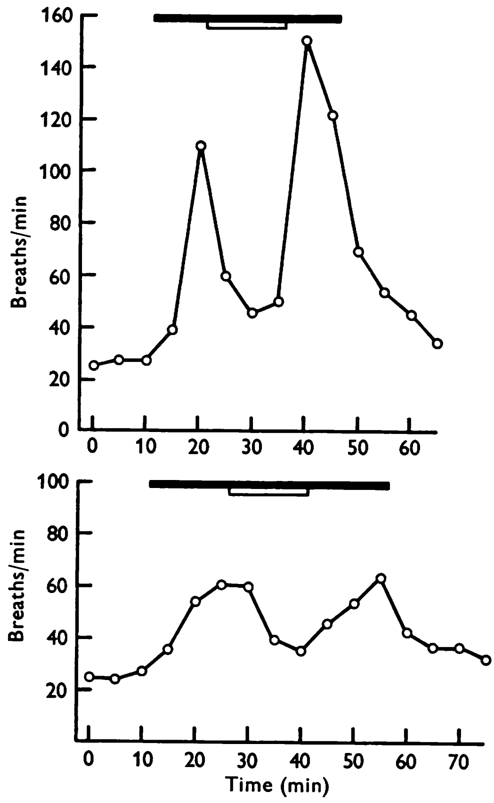

Fig. 3. Top: the effect on respiratory frequency of warming the scrotum to 42° C (black bar) and during part of this period cooling the thermode in the hypothalamus to 20° C (open bar). Ambient temperature 33° C.

Bottom: the effect on respiratory frequency of warming the scrotum to 42° C (black bar) and during part of this period cooling the thermode over the spinal cord to 10° C (open bar). Ambient temperature 31° C.

Cooling either the hypothalamus or the spinal cord while the scrotum was being heated caused blood flow to return again to the previous control level (Fig. 5).

Effects of heating the scrotum on oxygen consumption

When the ambient temperature was 25° C, heating the scrotum had no effect on oxygen consumption as might have been expected since this is a thermoneutral temperature for animals of the age used (Ingram, 1964*b*). At 15° C ambient temperature, heating the scrotum to 42° C resulted in a fall in oxygen consumption of between 5·9 and 7·5 % and abolished shivering.

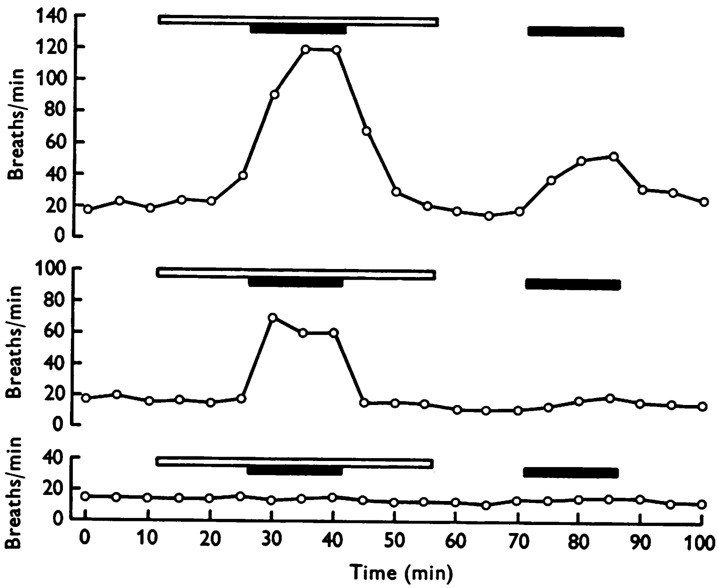

Fig. 4. The effect on respiratory frequency of warming the thermode in the hypothalamus (open bar) to 43° C and warming the scrotum to 40° C (black bar) at ambient temperatures of 32° C (top), 30° C (middle) and 25° C (bottom).

The effect of heating the scrotum on body temperatures

When the temperature on the surface of the scrotum was raised to 42° C at an ambient temperature of 15° C, body temperature as measured on the surface of the carotid artery declined over a period of 30 min by 0·7 to 0·8° C, but there was no change in respiratory frequency. As soon as the heating was stopped the pig began to shiver again. At an ambient temperature near the critical temperature of 25° C, heating the scrotum again caused no change in respiratory frequency, but core temperature fell by 0·4–0·5° C in 30 min. At 32° C, although heating the scrotum did cause panting, body temperature did not decline even after 90 min. Under these conditions core temperature either remained constant or increased by 0·1 to 0·4° C in 30 min. In the absence of any heating of the scrotum, however, body temperature increased by about 0·5° C in 30 min.

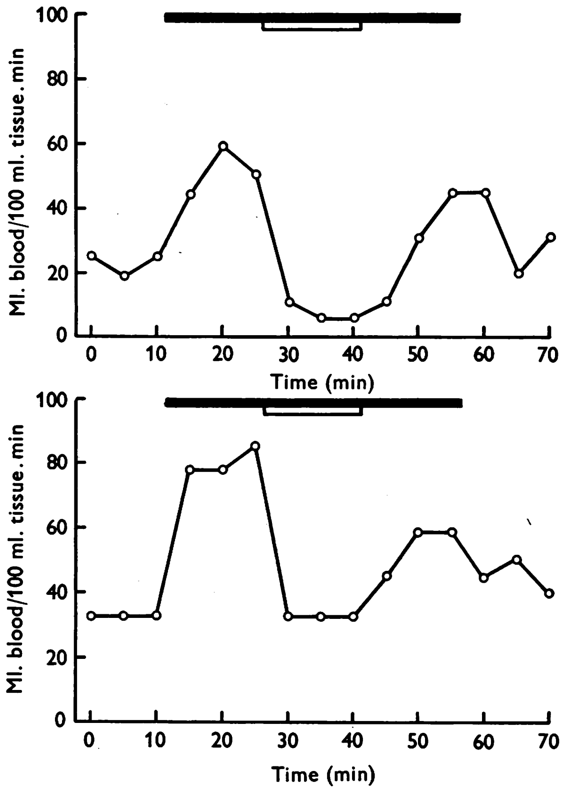

Fig. 5. Top: the effect on blood flow in the tail of warming the scrotum to 42° C (black bar) and during this period cooling the thermode in the hypothalamus to 20° C (open bar). Ambient temperature 25° C.

Bottom: the effect on blood flow in the tail of warming the scrotum to 42° C (black bar) and during this period cooling the thermode over the spinal cord to 10° C (open bar). Ambient temperature 27° C.

DISCUSSION

The results of the present experiment extend the observations of Waites (1961, 1962) to another species, which unlike the sheep does not have a substantial external thermal insulation and might therefore detect temperature changes rapidly by sensors anywhere on the body surface. In sheep the thermoregulatory responses to heating the scrotum are modified by removing the insulation provided by the fleece. A shorn animal does not pant at a neutral temperature when the scrotum is heated and in this respect it resembles the pig which may be regarded as a naturally shorn animal. Replacement of the thermal insulation by putting a coat over the sheep and hence increasing skin temperature, fully restores the reactions to heating the scrotum (Waites, 1962; Hales & Hutchinson, 1971); similarly changing the skin temperature on the trunk of the pig by means of a temperature controlled coat also modifies the animals response to heating the scrotum In the case of the pig the net result of the cold stimulus on the skin inhibiting panting is such that an increase in respiratory frequency can be evoked by heating the scrotum only at ambient temperatures close to those which would cause an increase in respiratory frequency in any event (Ingram, 1964*a*). In this respect the effect of heating the scrotum is similar to the effect of heating the hypothalamus or the spinal cord in the pig, since no increase in the rate of breathing is seen at ambient temperatures below 30° C (Ingram & Legge, 1972).

In contrast to the sheep the induced panting in pigs is not accompanied by a fall in body temperature. At most, the increased ventilation rate prevented core temperature from rising and in some experiments it did not even accomplish this. This species difference is probably accounted for chiefly by the rather inadequate respiratory evaporative heat loss mechanism in the pig as compared with the sheep (Ingram & Legge, 1969). The fall in body temperature during heating of the pig's scrotum in a thermoneutral environment can be accounted for at least partly by the increase in peripheral blood flow. In a cold environment, warming the scrotum stopped shivering and there was a fall in oxygen consumption which accounts for the decline in body temperature.

It is evident from the present results that, in the pig the thermoregulatory responses to heating of the scrotum are also considerably modified by changes in the temperature of either the hypothalamus or the spinal cord. Cooling either of the implanted thermodes reduces the response to heating the scrotum as judged by the change in respiratory frequency, and blood flow. Conversely the response to heating the scrotum was potentiated by warming either thermode. These findings are in agreement with findings on thermal stimulation of the periphery and central warming and cooling in the pig with respect to blood flow (Ingram & Legge, 1971) and respiratory frequency (Ingram & Legge, 1972). In the pig, at least, the thermosensors on the scrotum are influenced by core temperature. It may, however, be that even in sheep the cooling of the central receptors as a result of panting induced by warming the scrotum also reduces the respiratory frequency since the rate of panting tends to decline after prolonged stimulation (Hales & Hutchinson, 1971) as core temperature falls.

The mechanism by which heat loss is activated, or heat production reduced on heating the scrotum could be described either by the sort of model proposed by Stolwijk & Hardy (1966) in which the drive is determined by the multiplication of error load signals from both the periphery and the core, or by the variable set-point concept of Hammel, Jackson, Stolwijk, Hardy & Strømme (1963) in which peripheral temperatures modify the set-point temperature in the core. In the first instance the implication would be that before heating the scrotum the central temperature was already above the set-point giving a positive error load, while the scrotal temperature was below its set-point giving a negative error load. Multiplication of the two signals would then give a negative signal, but as soon as the scrotum was heated both error loads would become positive, and hence give a positive drive. The effects of heating or cooling the hypothalamus or spine would be to manipulate the central error load and hence alter the final signal. In the second model the effect of warming the scrotum would be to lower the central set-point temperature and hence give rise to a signal for additional heat loss or decreased heat production, while heating or cooling centrally placed thermodes would alter the error load directly.

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