J. Physiol. (1968), **198**, *pp.* 517–529
With 4 *text-figures*
Printed in Great Britain

THE INFLUENCE OF HYPOTHALAMIC TEMPERATURE AND AMBIENT TEMPERATURE ON THERMOREGULATORY MECHANISMS IN THE PIG

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(*Received* 18 *December* 1967)

SUMMARY

1. Two types of temperature fluctuation have been recorded from the preoptic region of the conscious pig. One, which is associated with arousal or movement, and another, which is related to rhythms in respiration and blood pressure.

2. When the pigs were subjected to infra-red irradiation at various ambient temperatures it was found that there was no precise temperature of the preoptic region at which the respiratory frequency increased.

3. Local heating of the preoptic region was effective in increasing the respiratory frequency only when the ambient temperature was above 30° C.

4. Even when both the peripheral temperature and central temperatures were increased there was a delay of several minutes before the onset of panting.

5. Cooling the preoptic region of the hypothalamus prevented the onset of panting in a hot environment, and reduced respiratory frequency in an animal which was already panting.

6. Oxygen consumption was reduced in a cold environment when the preoptic region was warmed, and increased when it was cooled. No increase in oxygen consumption occurred when the hypothalamus was cooled in a hot environment.

INTRODUCTION

It has been established that the thermoregulatory effects of changes in deep body temperature can be modified by the environmental temperature and the relative importance of central and peripheral factors in the control of homeothermy have been discussed by Hardy (1961), Bligh (1966) and Hammel (1966). One factor which is likely to be of significance in limiting the influence of the peripheral temperature is the extent to which the hair coat insulates the skin from changes in the external environment. In the sheep, the skin of the scrotum, which is relatively poorly insulated, contains receptors which are particularly sensitive to temperature changes. The warming of this region alone will cause the animal to pant and lower its body temperature while warming an equivalent area elsewhere has little effect (Waites, 1962).

In contrast to the sheep and most other species the pig has a sparse hair coat and would therefore appear to be a particularly suitable animal in which to study the modifying effects of ambient temperature on changes in hypothalamic temperature. Some evidence that this is so has been obtained in experiments on behavioural thermoregulation in which pigs were trained to warm themselves by pressing a switch in order to turn on infra-red heaters and the rate at which they did so observed over a wide range of ambient temperatures (Baldwin & Ingram, 1967*a*). It has been shown that the rate at which pigs turn on extra heating can be increased by cooling the preoptic region of the hypothalamus but when central cooling was carried out at high ambient temperatures the pigs frequently made no attempt to obtain extra heat (Baldwin & Ingram, 1967*b*).

In the present study the responses of physiological thermoregulatory mechanisms to changes in hypothalamic temperatures and ambient temperature have been investigated in the pig: (1) in order to determine the extent to which hypothalamic temperature influences thermoregulatory mechanisms; (2) to find out whether thermoregulatory response can be initiated in the presence of opposite thermal stimuli at the periphery and in the hypothalamus.

METHODS

Animals. Twenty-five pigs of the Large White breed aged between 8 and 12 weeks were used. In some of the animals thermodes had been implanted into the hypothalamus, and in others a thermistor was inserted into the same region.

Anaesthesia and surgery. The pigs were given phencyclodine hydrochloride (Sernyl Parke-Davis) in order to facilitate handling and then anaesthesia was induced with halothane (Fluothane I.C.I.) delivered through an endotracheal tube from a Boyle's apparatus. All surgical procedures were carried out under sterile conditions. The pigs were used in experiments 10 days after operation.

Implantation of thermodes. In thirteen pigs a thermode of the type previously described was implanted into the preoptic region of the hypothalamus within 1 mm of the mid line, between the optic chiasma and the anterior commissure (Baldwin & Ingram, 1967*b*). The thermode was attached to the skull by means of dental cement. Its positioning was assisted by taking a series of radiographs while holding the animal's head in a stereotaxic frame, which was devised in this laboratory for the purpose.

Implantation of thermistors. In five animals a temperature measuring probe was implanted in place of a thermode, its tip being placed between the optic chiasma and the anterior commissure 1 mm from the mid line. The probe consisted of a glass haematocrit tube of 1 mm outside diameter through which were passed two 40 S.W.G. copper wires. A small-head thermistor (Stantell U. 23 u/s) was soldered to the ends of a wire and covered with a thin layer of Araldite (Ciba). The use of a glass rather than a metal tube and of fine wires reduced conduction of heat away from the site at which temperature was being measured and the small thermistor, which was barely covered with Araldite, had a low enough thermal capacity to respond to a change of 1° C within 0·5 sec.

Implantation of heating electrodes. A second method of heating the hypothalamus was used to cover the possibility that the larger region of the brain warmed by diathermy might give different results. The electrodes were implanted in four pigs. They were made of oval silver disks (5 × 3 mm) attached to stainless-steel tubes. All metallic surfaces except the inner face of the disks were coated with Araldite. The disks were 10 mm apart and a thermistor mounted at the end of a stainless-steel tube was placed 3 mm from one electrode (Baldwin & Ingram, 1967*b*). The heaters were inserted into the preoptic region by the same methods used for implanting the thermode. When used for warming the hypothalamus the electrodes were connected to a 2 Mc/s 10 W maximum output radio-frequency generator.

Experiments on anaesthetized animals. In three experiments in which the animals were not allowed to recover, the pig's head was held in the stereotaxic frame and a temperature measuring probe was inserted into the preoptic region. Blood pressure was also measured from the femoral artery by means of a catheter connected to a Statham transducer.

Respiratory frequency. The frequency was measured using a strain-gauge belt. All the recordings were then displayed on a polygraph.

Temperature was measured by means of implanted thermistors and displayed on a meter which could detect changes of 0·1° C; in some experiments temperatures were recorded continuously on the polygraph when changes of 0·05° C could be detected. The surface temperature of the skin at the tip of the ear was measured by means of a 36 S.W.G. copper–constantan thermojunction attached to the skin by means of rubber solution and covered with a thin rubber patch.

Thermode temperature was varied by circulating either cold alcohol or warm water through the tubes. As shown in a previous study (Baldwin & Ingram, 1967*b*), a temperature of 10° C on the surface of the thermode reduced the temperature of the brain 5 mm away by 1–2° C, while a temperature of 43° C on the surface of the thermode raised the brain temperature to 42° C at a distance of 5 mm.

Oxygen consumption was measured by means of a Diaferometer (Kipp & Zonnen, Holland). The animal was restrained in a chamber placed inside a temperature-controlled room and the exhaust air from the chamber sampled continuously by the Diaferometer.

Experimental procedure. The pigs were held in a leather harness by means of which they could be loosely restrained in a metal stand (Baldwin & Ingram, 1967*b*). The stand was placed in a room in which the temperature of the air and walls was controlled to within ± 0·5° C.

RESULTS

Hypothalamic temperature. Five conscious pigs were exposed to various ambient temperatures between − 5° C and + 40° C while their hypothalamic temperature and respiratory frequency were recorded. On exposure to an environmental temperature of − 5° C the pig shivered violently and the temperature of the hypothalamus increased to as much as + 40° C before it declined again to a value in the region of 38·5–39·5° C. At ambient temperatures of 15–30° C the hypothalamic temperature settled between 37·8 and 39·2° C. Exposure to environmental temperatures of 35–40° C was accompanied by a gradual rise in both hypothalamic temperature and respiratory frequency.

At temperatures between − 5 and 30° C the animals did not pant and hypothalamic temperature, as measured by means of the thermistor mounted on a glass probe, showed continuous fluctuations. Two kinds of temperature change were seen. One was a regular oscillation, usually in the range of 0·05–0·15° C, which was obviously related to respiratory movement (Fig. 1*a*) and disappeared when respiratory frequency reached about 50/min. The other consisted of sudden larger changes in temperature and was associated with the animal becoming alert as indicated by the opening of the eyes or the directing of the ears towards the source of a disturbance (e.g. opening of the door to the temperature-controlled room). Such temperature changes were sometimes as great as 1·0° C but usually lasted for only a few seconds (Fig. 1*a*).

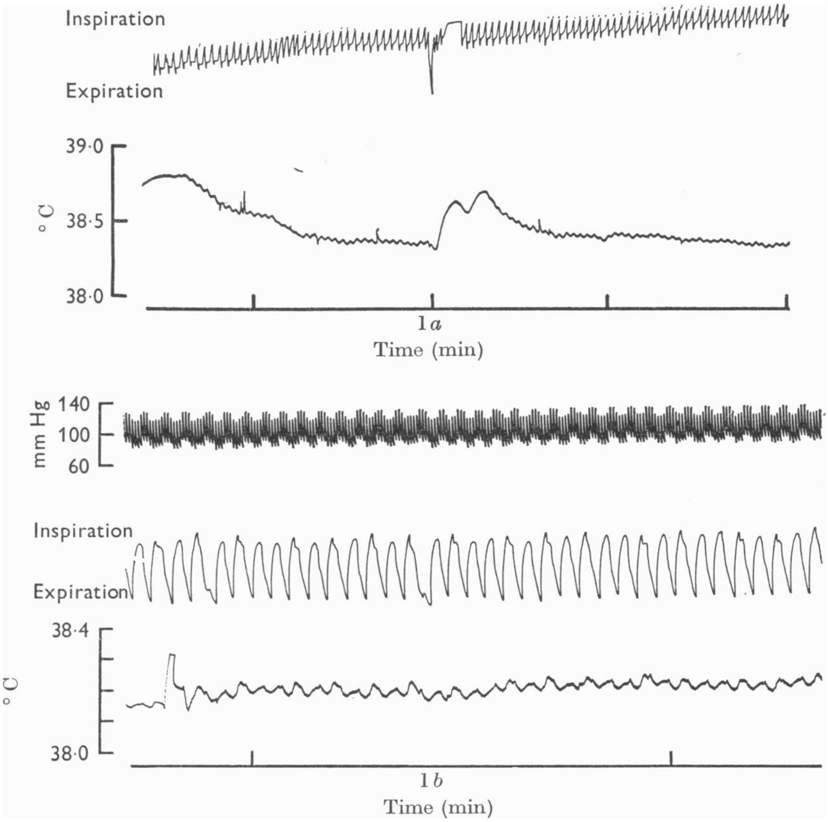

Fig. 1. Relation between respiration and brain temperature in a conscious pig. Two large changes in the temperature of the preoptic region are illustrated. The second change in the middle of the trace was associated with arousal as indicated by the interruption in the respiratory trace. *b*. Relation between blood pressure, respiration and hypothalamic temperature in an anaesthetized pig. The fall in brain temperature is associated with expiration and increased blood pressure.

The temperature oscillations related to respiratory movements were investigated in both conscious and anaesthetized pigs. In anaesthetized animals blood pressure was also recorded from a femoral artery. Figure 1*b* shows the waves in blood pressure associated with respiration from which it can be seen that during expiration mean blood pressure increased and the temperature in the preoptic region fell. When the pig was momentarily prevented from breathing by occlusion of the endotracheal tube, the oscillations in both blood pressure and temperature disappeared until the point when the pig attempted to inspire against the resistance when gross changes in both temperature and blood pressure occurred although no air had passed down the trachea. During apnoea induced by thiopentone sodium the fluctuations in mean blood pressure disappeared and although the heart continued to beat no temperature oscillations were seen. Immediately after death, that is, when the heart stopped beating, rhythmic inflation of the lungs by means of pressure on the thorax did not result in any fluctuations in brain temperature. These temperature fluctuations were not related to the cooling effects of inspired air in the nasal cavity since the animals were breathing through an endotracheal tube.

Effect of radiant heat. The possibility that an increase in respiratory frequency could be initiated by a strong peripheral stimulus unaccompanied by a change in the hypothalamic temperature was investigated. Conscious pigs were exposed to ambient temperatures between 25 and 35° C and then subjected to a sudden increase in radiant heat by switching on a bank of infra-red heaters.

It was found that when the frequency of respiration increased the change was fairly abrupt (Fig. 2) and therefore a sustained frequency of over 40 breaths/min was used as the criterion of an increase. The temperature of the preoptic region at which this increase occurred was noted, but because hypothalamic temperature fluctuated, the mean over a minute, rather than a single value at the time of change in the frequency of breathing, was taken as the true temperature level.

The results from five pigs in twenty-nine experiments were examined. Pigs were exposed to infra-red irradiation at an ambient temperature of 25° C on nine occasions; in five instances the respiratory frequency did not increase even after $1\frac{1}{2}$ hr irradiation, while in four instances there was a marked increase. As shown in Fig. 2, the same animal did not always react in the same manner, but on those occasions when respiratory frequency increased the increase occurred during a period when hypothalamic temperature was increasing, although not all increases in hypothalamic temperature were accompanied by changes in respiratory frequency. At 30° C hypothalamic temperature increased slowly and sometimes remained steady between readings before rising again. With two exceptions the initial increase in respiratory frequency beyond 40 breaths/min occurred during a period when hypothalamic temperature was rising. At 35° C hypothalamic temperature always increased steadily and respiratory frequency also increased.

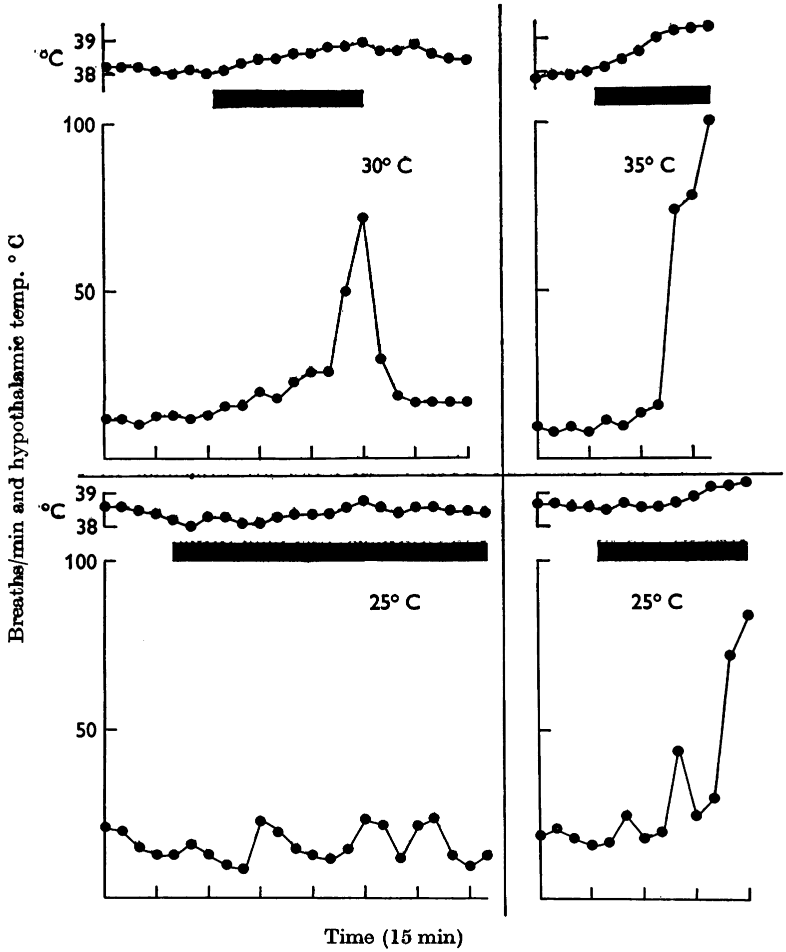

Fig. 2. Hypothalamic temperature and respiratory frequency at various ambient temperatures in the presence of infra-red heat (black bar). The two experiments at 25° C were both on the same pig.

Figure 3 shows the relation between the temperature of the preoptic region and the increase in the frequency of breathing. It gives no evidence to support the idea that the change in respiratory frequency occurs at any constant hypothalamic temperature.

When the infra-red heat was switched off in the above experiments respiratory frequency did not always decrease immediately and in one instance at an ambient temperature of 35° C the pig continued to breath at a frequency of 90/min even though the hypothalamic temperature was only 38·2° C.

Effect of heating the preoptic region of the hypothalamus. At ambient temperatures between 0 and 25° C no change in respiratory frequency was induced by warming the hypothalamus. In two animals exposed to this temperature range the preoptic region was warmed by means of a thermode to 42° C for 30 min periods and in four other pigs it was warmed by means of a radio frequency generator to 42° C for 15 min periods.

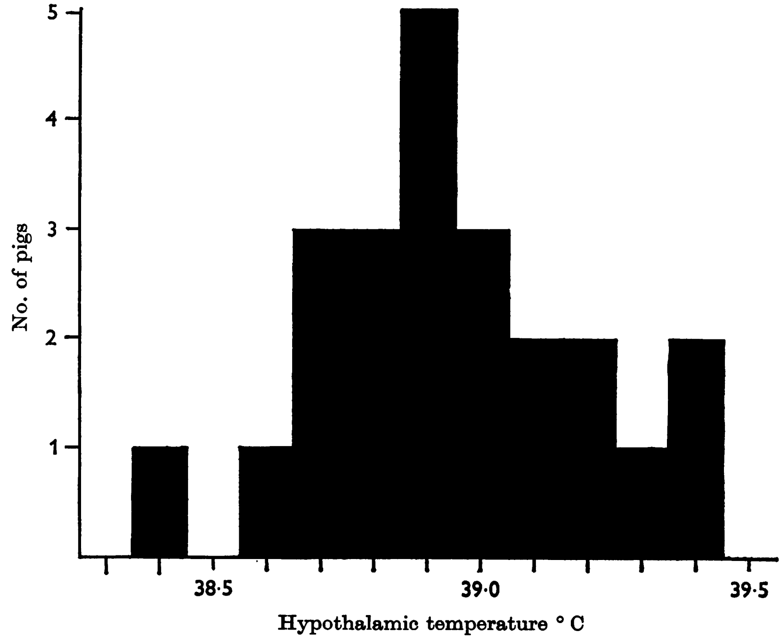

Fig. 3. The frequency distribution of the hypothalamic temperatures at which panting started in the presence of infra-red heating.

At an ambient temperature of 30° C, heating the hypothalamus to 42° C for 15–50 min was followed by an increase in respiratory frequency on only three occasions out of eleven. The experiments were conducted on seven animals, of which four had implanted thermodes and three implanted electrodes for radio frequency heating. Positive results were obtained only with the thermodes and with these it was noted that the same animal sometimes behaved differently on successive occasions.

At an ambient temperature of 35° C, heating the hypothalamus in seven pigs was followed by an increase in respiratory frequency in ten tests out of eleven. Both methods of heating the hypothalamus gave positive results.

The time taken to induce a change in respiratory frequency by heating the hypothalamus was between 1 and 10 min.

Interaction of central and peripheral thermal stimuli. In sixteen experiments on three pigs, the interaction of central and peripheral thermal stimuli was investigated by heating the hypothalamus and irradiating the body surface with infra-red heat at ambient temperatures between 25 and 28° C (i.e. the thermoneutral zone for these animals).

In one set of experiments the animal was subjected to 10 min of infra-red heat and then while continuing the infra-red heating the hypothalamus was heated for a further 10 min. In another set of experiments the hypothalamus was first warmed for 10 min and then while continuing to warm the hypothalamus the infra-red heat was turned on for a further 10 min period. Heating the hypothalamus after 10 min of infra-red irradiation always resulted in panting after 2–3 min. In the converse experiment in which the hypothalamus was heated first infra-red heating resulted in panting after 2–10 min on eight occasions, but on four occasions no panting occurred.

These experiments demonstrate that even when the peripheral and hypothalamic temperature receptors are simultaneously stimulated, panting is not immediate nor inevitable.

Effect of cooling the hypothalamus. In these experiments the hypothalamus was cooled at a time when the pig was exposed to an ambient temperature of 40° C. It was found that if the cooling of the hypothalamus was begun as soon as the pig entered the room at this temperature respiratory frequency remained at about 20/min. After 70 min the rectal temperature was 41° C and when cooling was stopped at this time respiratory frequency increased to 254/min.

In three animals the preoptic region was cooled only after the respiratory frequency had reached a high level (Fig. 4). This treatment reduced the frequency of breathing to within the region of 20/min, but as soon as the cooling was stopped respiratory frequency increased again.

Influence of hypothalamic temperature and ambient temperature on vasomotor control. At ambient temperature below 27° C the surface temperature of the pinna of the ear changes spontaneously from a little above ambient temperature to as much as 37° C, presumably as the arteriovenous anastomoses open fully and blood flow increases. The temperature on either ear may alter independently of the other and of ambient temperature.

At an ambient temperature of 25° C, heating the hypothalamus in two pigs while the ears were cold was followed by an increase in temperature of 8–10° C in five out of five instances, there being a delay of about 7 min before any change occurred. When the heating was stopped the ears became cold again within 10 min.

At 5, 15 and 20° C ambient temperatures, heating the hypothalamus did not result in an increase of ear temperature in five out of five instances. On one occasion before the hypothalamus was heated one ear was already warm, but heating the hypothalamus did not result in an increase in temperature of the other cold ear.

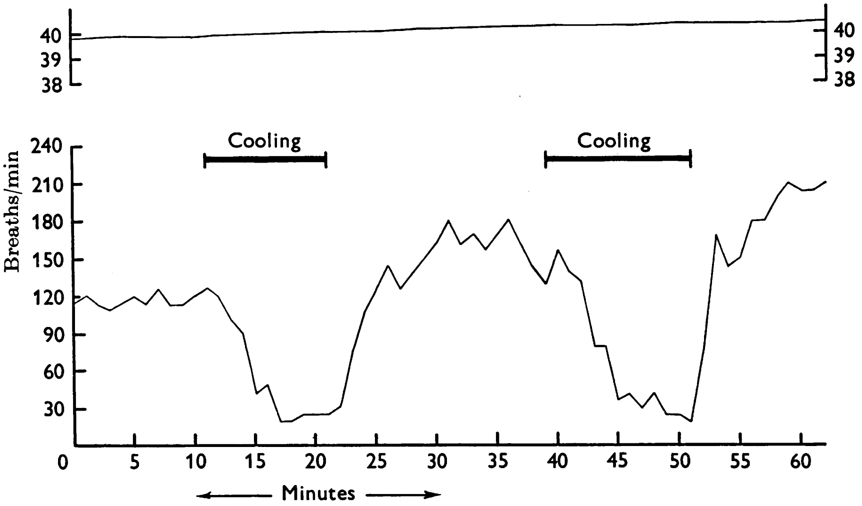

Fig. 4. The effect of cooling the hypothalamus on panting at an environmental temperature of 40° C.

The temperature of the pinna of the ear was measured in six experiments at an environmental temperature of 27° C. In all but one instance the ears were 35–36° C before cooling of the hypothalamus started, and in the remaining experiment only one ear was warm. Cooling the hypothalamus was followed by a reduction in the temperature on one or both ears after about 30 min in all animals except that which already had one cold ear. In this animal cooling had no effect even after 2 hr. When cooling was stopped the ears in all animals became warm within 10 min. Body temperature increased by about 0·5–1·0° C during 1 hr of cooling at an ambient temperature of 27° C.

Effect of heating or cooling the preoptic region on oxygen consumption. The effect on oxygen consumption of cooling the hypothalamus was found to depend on the ambient temperature. At an ambient temperature of 10° C cooling the hypothalamus for 30 min was always followed by an increase in oxygen consumption. At ambient temperatures of 25 and 30° C cooling was associated with a slight increase in oxygen consumption. At an environmental temperature of 35° C cooling had no effect on oxygen consumption (Table 1).

TABLE 1. The effect on oxygen consumption of cooling and warming the hypothalamus for 30 min at various ambient temperatures

Pig no.	Environment (temp. ° C)	Before (ml. O_2/min)	During (ml. O_2/min)	After (ml. O_2/min)	% change in O_2 consumption during cooling
			Cooling		
1940	35	97	97	97	0
1901	35	163	172	180	+6
1940	30	157	210	175	+27
1977	30	159	186	159	+17
1974	25	197	233	197	+18
1694	25	161	211	132	+45
1901	20	202	281	219	+34
1974	10	247	357	256	+42
1940	10	229	405	211	+84
1694	10	237	333	186	+84
			Warming		
2064	20	153	153	153	0
2099	20	131	131	131	0
2064	10	297	297	387	−13
2064	5	435	373	453	−15
2099	5	399	203	310	−43
2100	5	373	282	400	−27

DISCUSSION

The large changes in the temperature of the hypothalamus which were observed when the pig moved or became aroused spontaneously are similar to those observed in the dog and monkey by Rawson & Hammel (1963), Fusco (1963) and Rawson, Stolwijk, Graichen & Abrams (1965). The small changes, usually between 0·05 and 0·15° C, which were associated with respiratory rhythm, do not appear to have been previously described. The significance of both these types of temperature change, which are most likely to be related to blood flow, needs to be considered in the light of the finding of Euler (1964). He reported that, using the technique of the thermal clamp, by which hypothalamic temperatures can be maintained for an hour at a fairly uniform temperature, changes of as little as 0·2° C could elicit sustained thermoregulatory responses in spite of larger changes in other body temperatures. One possibility is that the considerably larger changes in hypothalamic temperature which are associated with arousal do not persist for long enough to make their effect manifest. If on the other hand the heat loss mechanisms are activated only when a critical temperature has been exceeded the small and large fluctuations below this set point would be ineffective.

The experiment involving the application of infra-red heat was designed to test the idea that panting could be initiated by a strong peripheral stimulus in the absence of a rise in hypothalamic temperature. In most instances panting was preceded by a rise in the temperature of the hypothalamus. This result contrasts with the results of similar experiments in the ox (Findlay & Ingram, 1961) in which a rise in respiratory frequency always occurred before there was an increase in brain temperature. In the experiments on the ox both brain and blood temperature sometimes fell when the infra-red heating was applied. A second contrast with the results obtained on the ox and other species is that heating the hypothalamus of the pig at an ambient temperature in the region of or below the thermoneutral zone did not affect respiratory frequency. In the ox (Ingram & Whittow, 1962*a*) the effect of heating the hypothalamus was depressed at low ambient temperatures, but even at 5° C respiratory frequency increased.

Various hypotheses have been postulated to explain the interaction of peripheral and central thermal stimulation. Hammel, Jackson, Stolwijk, Hardy & Strømme (1963) and Hammel (1966) have suggested a 'set point' in the hypothalamus which can be varied by the temperature of the skin. This suggestion is in accord with the findings of Chatonnet, Cabanac & Mottaz (1964), who varied the skin temperature of the dog by immersing the whole animal in a water-bath and found that the hypothalamic temperature at which panting started depended on the temperature of the water. This hypothesis may also explain the result obtained with the ox, since the rise in skin temperature when infra-red heating was applied may have lowered the set point below the hypothalamic temperature. In the pig the failure to cause panting by warming the hypothalamus at low ambient temperatures could be explained by suggesting that the 'set point' in the hypothalamus was set above 42° C. Cooling the hypothalamus on the other hand may have reduced the hypothalamic temperature below the set point even when the animal was panting at an ambient temperature of 40° C. In the experiments using infra-red heat, however, there was no evidence of either a fixed 'set point' or one which varied systematically with ambient temperature.

Another hypothesis proposed by Stolwijk & Hardy (1966) for temperature regulation in man involves a 'set point' in the mean skin temperature and the temperature of the hypothalamus, both of which must be exceeded before heat loss mechanisms are initiated. This hypothesis would explain the results obtained when the pig's hypothalamus was heated, or cooled, but again it would not account for the results obtained using infra-red irradiation.

In the pig there is evidence from the present study that there is a delay in the onset of panting even when the combined stimulus of infra-red heating and local heating of the hypothalamus is applied. A similar delay in response to a peripheral thermal stimulus was observed in the ox by Ingram & Whittow (1962*b*), who found that heating the hind quarters with infra-red lamps was followed after a delay of at least 20 min by vasodilatation of the ears without any change in deep body temperature or blood pressure. More striking is the long delay in the onset of panting in the shorn sheep observed by Bligh (1963). In contrast with normally fleeced animals, shorn sheep do not pant soon after they are exposed to high ambient temperature and the delay in the onset of panting may last over an hour. During this period deep body temperature tended to rise but there was no evidence to suggest any direct connexion between changes in deep body temperature and the onset of panting. Bligh (1963) suggested the delay in panting was probably related to a persistent central nervous block between peripheral warm receptors and the respiratory centres produced by the exposure of peripheral cold receptors. Waites (1962) has shown that panting which can be initiated by warming the scrotum of the ram will persist despite a fall in deep body temperature, to 36° C. The panting in response to warming the scrotum does not occur after removal of the fleece with consequent exposure of the cold receptors.

In the present study cooling the hypothalamus failed to cause an increase in oxygen consumption at an ambient temperature of 35° C. In the rabbit on the other hand Downey, Mottram & Pickering (1964) found that an increase in oxygen consumption could be elicited even at high ambient temperatures when the brain temperature was lowered by cooling the blood of the internal carotid. The thermoregulatory effects of heating and cooling the hypothalamus of the pig differ from those obtained in the other species so far investigated and this suggests that general explanations of the interaction of central and peripheral thermal stimuli in the control of thermoregulatory mechanisms must be based upon a wider range of comparative data than is at present available.

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