Antidiuretic Responses to Thermal Stimulation of Hypothalamus and Spinal Cord in the Conscious Goat

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Summary. At various ambient temperatures the effects of hypothalamus temperature and spinal cord temperature on urine formation and heat production were studied in conscious goats with chronically implanted thermodes. At neutral air temperature cooling hypothalamus or spinal cord induced a fall in urine volume and a rise in urine osmolality. This antidiuretic response was concurrent with a rise in heat production. Simultaneous occurrence of antidiuresis and increased heat production was also found after cessation of hypothalamic warming. At hot ambient temperature cooling hypothalamus affected neither urine formation nor heat production. Since hypothalamic cooling and spinal cord cooling produce identical effects on kidney function it is concluded that this response is linked to the complex cold defence activity as a whole. The predominant change of free water clearance is tentatively interpreted as caused by an increased ADH concentration in the blood during the cold defence activity.

Key words: Urine formation — Hypothalamus — Spinal cord.

INTRODUCTION

Thermosensitivity of the hypothalamus in homeotherms is generally considered to be specifically involved in control of body temperature. However, recent experiments have shown that in some birds a second hypothalamic control mechanism, not related to temperature regulation, is directly influenced by hypothalamic temperature: Cooling the rostral brain stem in Adelie penguins (Hammel et al., 1976a) and in Pekin ducks (Hammel et al., 1976b) inhibits osmoregulatory functions such as nasal salt gland secretion and urine concentration. These results have been tentatively interpreted by assigning non-specific, i.e. non-sensory thermosensitivity to those hypothalamic neurons which are involved in osmoregulation (Simon et al., 1976). The question arises whether such non-specific thermosensitivity of hypothalamic osmoregulatory control mechanisms can also be demonstrated in the mammalian class of homeotherms. Thus, a series of experiments was performed in conscious goats to investigate the effects of altering hypothalamic temperature on osmoregulation, as they can be deduced from changes in urine formation.

The results of these experiments proved it advisable to test whether osmoregulation can also be affected by altering spinal cord temperature. The spinal cord is known to contain thermosensitive structures which are linked to the temperature regulating system (Simon, 1974). Therefore, in a second series of experiments, the effects of spinal cord cooling on urine formation were examined.

METHODS

a) Animals and Preparations. The experiments were performed on 4 young adult female goats whose body weights varied between 30 and 40 kg. Several months before the experiments started, the animals had been prepared by implanting hypothalamic and/or spinal thermodes. For further details see Jessen (1976) and Jessen and Clough (1973b). All animals had been used in previous studies and were familiar with the general experimental procedure. They remained healthy throughout the complete series of experiments.

b) Experiments. In the 4 animals, 20 experiments with 56 periods of hypothalamic or spinal thermal stimulation were performed following a fixed schedule. Twenty-four hours before start of an experiment the animal was deprived of food. Fourteen hours before start the animal was brought into the climatic chamber and exposed to air temperature chosen for the experiment. When exposed to hot ambient temperature, the animal had free access to water. At 8.00 on the day of the experiment a balloon catheter for urine sampling was introduced into the bladder and a polyethylene catheter for blood sampling was placed in a jugular vein. Perfusion system and measuring probes were attached and the animal was given 100 ml of tepid water per kg body weight by gastric tube. Three periods of thermal stimulation were then applied. Each period lasted 30 min,
Table 1. Control values of heat production, rectal temperature and urine formation during 30 min before start of hypothalamic or spinal thermal stimulation

<table>
<thead>
<tr>
<th>Animals</th>
<th>Heat production (M)</th>
<th>Rectal temperature ($T_m$) °C</th>
<th>Urine volume ($V$) ml/min</th>
<th>Urine osmolality ($U_{osmol}$) mosmol/kg</th>
<th>Free water clearance ($C_{H_2O}$) ml/min</th>
<th>Osmolal clearance ($C_{osmol}$) ml/min</th>
</tr>
</thead>
<tbody>
<tr>
<td>$T_a = +20^\circ$ C</td>
<td>46</td>
<td>19.07 ± 0.067</td>
<td>38.69 ± 0.07</td>
<td>7.68 ± 0.39</td>
<td>108.04 ± 4.59</td>
<td>4.85 ± 0.26</td>
</tr>
<tr>
<td>$T_a = +36^\circ$ C</td>
<td>10</td>
<td>1.863 ± 0.111</td>
<td>39.91 ± 0.07</td>
<td>4.12 ± 0.48</td>
<td>52.40 ± 10.41</td>
<td>3.46 ± 0.45</td>
</tr>
</tbody>
</table>

Values are means and S.E.M.

two successive periods were separated by a free interval of 90 and 120 min respectively. The first period commenced at 11.00. Starting after the first stimulation period, 200 ml of tepid water were given in 1 h intervals by gastric tube.

Four levels of hypothalamic thermal stimulation were employed in a randomized order. For cooling the thermodes were perfused with water whose temperature was kept constant throughout the stimulation period by means of a thermostatically controlled water bath at 33°C or 36°C. For warming the hypothalamus the water temperatures were 41°C and 43°C respectively. The spinal cord was cooled with water whose temperature was 33°C or 36°C.

c) Recordings. The intensity of the thermal stimuli applied to the hypothalamus or to the spinal cord was determined from the temperature of the perfusing water measured at the inlet of the thermodes by thermocouples ($\pm 0.1^\circ$ C). Rectal temperature was measured by a Quartz thermometer ($\pm 0.02^\circ$ C). All temperatures were recorded continuously. - An open circuit respiratory system, which has been described in detail elsewhere (Jessen and Clough, 1973a), was used to continuously measure heat production.

To determine plasma osmolality blood samples were drawn every 10 min and immediately centrifugated. Urine samples were continuously collected for 10 min periods. Total solute concentration (milliosmol/kg plasma or urine water) was measured cryoscopically with a Knauer osmometer, thus allowing calculation of osmolal clearance ($C_{osmol}$) and free water clearance ($C_{H_2O}$) (Pitts, 1963).

RESULTS

a) Control Periods. Thermal stimulation of hypothalamus or spinal cord induced thermoregulatory responses and altered urine formation. In the following sections these effects of thermal stimulation are presented as differences relative to the control values. To compare these changes with absolute levels, mean values and standard errors of the means for heat production, rectal temperature, urine volume, urine osmolality, osmolal clearance and free water clearance for all control periods in all animals are shown in Table 1.

b) Thermal Stimulation of the Hypothalamus at Neutral Air Temperature. Figure 1 displays the thermo-regulatory and diuretic responses which occurred during and after cooling or warming the hypothalamus in 3 animals. Each value represents the mean of 9 perfusion periods. The left column of data refers to hypothalamic cooling with water temperature of 33°C lasting from the 30th to the 60th min. The strong cooling induced shivering with a marked increase in heat