

THERMOSENSITIVITY OF DIFFERENT PARTS OF THE SPINAL CORD OF THE PIGEON (*COLUMBA LIVIA*)

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Summary

In the present study we compared the metabolic responses to selective cooling of the cervical (C₉–Th₁) and the thoracic (Th₁–Th₅) parts of the spinal cord of pigeons. To obtain selective cooling of the two parts, two thermodes (4.5 cm) were inserted into the vertebral canal through an aperture in the first thoracic vertebra. During the experiments, one of the two thermodes was perfused with water at a constant temperature for periods of 15 min. The thermosensitivity was defined as the relationship between the amount of extra heat produced and the amount of heat extracted from the stimulated area. Cooling of the thoracic part resulted in a substantially higher increase in metabolic heat production and body temperature (T_b) than did cooling of the cervical part. It is concluded that the thoracic part of the spinal cord has a greater thermosensitivity than the cervical part. In addition, it was found that the difference in elevation of T_b during cooling of the two parts was not simply a result of differences in the amount of heat produced. When the changes in T_b were related to the difference between the extra heat produced and the amount of heat extracted, the increase in T_b during thoracic cooling was greater than that recorded during cervical cooling. This indicates that cooling of the two different parts of the spinal cord also had different effects on the thermoregulatory effector mechanisms that influence thermal conductance.

The study seems to provide evidence in favour of afferent transmission of cold signals in the spinal cord.

Introduction

The control of the internal body temperature of homeothermic animals depends upon thermal inputs from thermosensitive neurones located throughout the body (Simon *et al.* 1986). These neurones are located both inside and outside the central nervous system (CNS). Birds and mammals differ somewhat as to the importance of the thermosensitive neurones situated inside the CNS. In mammals, hypothalamic thermosensitivity is very important for normal operation of the thermoregulatory system, whereas it is of only minor importance in birds (Mercer and Simon,

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1984; Simon *et al.* 1986). However, these differences may be more quantitative than qualitative (Mercer and Simon, 1987). In birds, the spinal cord seems to be an important thermosensitive structure, and several studies have shown that appropriate thermoregulatory effector responses occur during selective thermal stimulation of the spinal cord (Rautenberg, 1969a; Rautenberg *et al.* 1972; Hammel *et al.* 1976; Helfmann *et al.* 1981; Inomoto and Simon, 1981; Bech *et al.* 1982).

Both warm- and cold-sensitive neurones have been demonstrated in the spinal cord of pigeons (*Columba livia*; Necker, 1975), and appropriate effector mechanisms can be elicited by stimulating the spinal cord, even after spinal deafferentation (Necker and Rautenberg, 1975). This clearly indicates that the spinal cord contains thermosensitive elements. Similar results have been reported for the dog (*Canis familiaris*; Meurer *et al.* 1967; Jessen and Simon-Oppermann, 1976).

While some evidence exists that thermosensory information can originate from the spinal cord, information concerning the spatial distribution of such sensory elements is limited. In the marmot (*Marmota flaviventris*; Miller and South, 1978) and the guinea pig (*Cavia sp.*; Brück and Wünnenberg, 1970), the thoracic part of the spinal cord shows greater thermosensitivity than the lumbosacral part. In addition, antagonistic cardiovascular responses have been demonstrated in the rat (*Rattus norvegicus*) by selective cooling of the thoracic and the lumbosacral parts of the spinal cord (Tsuchiya *et al.* 1984). Cooling of the thoracic part produced tachycardia, while cooling of the lumbosacral part resulted in bradycardia. Thus, at least in mammals, the responses induced by thermal stimulation of different regions of the spinal cord can be both qualitatively and quantitatively different.

Since no corresponding studies exist for birds, the aim of the present study was to investigate whether, in pigeons, the different areas of the spinal cord differ in their sensitivity to cold. To study this, we compared the metabolic responses to selective cooling of the thoracic (Th₁–Th₅) and the cervical (C₉–Th₁) parts of the spinal cord.

Materials and methods

Animals

The experiments were carried out using five domestic pigeons (*Columba livia* Gmelin) with a mean body mass of 477 g (s.d. 31 g, range 412–508 g). Prior to the experiments the pigeons were housed indoors at room temperature and under a constant photoperiod of 12h:12 h L:D. Food and water were available *ad libitum*.

Spinal cord thermodes and implantation

Under halothane anaesthesia, two spinal thermodes were inserted into the vertebral canal dorsal to the spinal cord, through an aperture in the first thoracic vertebra. The thermodes were constructed from nylon tubing (i.d. 0.50 mm, o.d. 0.63 mm, Portex Ltd, UK) bent into a hairpin shape (Rautenberg, 1969a). One of the thermodes was pushed 4.5 cm in the caudal direction, extending from Th₁ to Th₅ (thoracic part), while the second one was pushed 4.5 cm in the cranial

direction, to extend from C₉ to Th₁ (cervical part). In addition, a tube of polypropylene (PP 30, Portex), closed at one end, was inserted 5 cm into the abdominal cavity by making an incision in the skin adjacent to the cloacal opening. This tube acted as a guide for a thermocouple used to measure the internal body temperature (T_b). The pigeons were used in the experiments 14 days after recovery from surgery. After the experiments, the positions of the spinal cord thermodes were verified by dissection.

Experimental procedure

During the experiments, the pigeons were confined to a 7-l metabolic chamber, in which the ambient temperature (T_a) was controlled at $26 \pm 1^\circ\text{C}$. To exclude biorhythmical factors, the experiments were always performed at a time of the day when the birds would normally be experiencing daylight. Within the metabolic chamber, however, the pigeons were in total darkness. During the experiments, one of the thermodes was perfused with water from a thermostatically controlled waterbath, at a rate of $2.5\text{--}3.4\text{ ml min}^{-1}$, for periods of 15 min. The total amount of water that passed through the thermode during the stimulation period was collected and weighed to the nearest 0.01 g. The connection between the thermode and the waterbath was equipped with Y-connectors through which thermocouples were inserted into the thermodes. The temperatures of the inlet and outlet water were measured where the thermode entered the body. The inlet water temperature during spinal cooling was kept between 27 and 35°C . The various stimulation periods were separated by at least a 30 min interval, during which no perfusion occurred.

Oxygen consumption (\dot{V}_{O_2}) was measured by open-flow respirometry (Withers, 1977). Air was sucked through the metabolic chamber by an air pump (Miniport, type N73.KN18) at a rate of approximately 2.11 min^{-1} . Actual airflow was measured with a calibrated flowmeter (Cole Parmer, type 034-39ST). After drying over silica gel, a fraction of the air was directed into an oxygen analyzer (Servomex, type 1100A), and the O₂ content of the excurrent air was continuously recorded on a pen recorder. The oxygen content could be read to an accuracy of 0.01 %. Oxygen consumption was calculated from the STDP airflow rate and the O₂ content of the excurrent air, using the appropriate formulae (Withers, 1977). Oxygen consumption values were converted into metabolic heat production values by using 20.3 kJ l^{-1} as the caloric equivalent for oxygen, assuming a respiratory quotient (RQ) of 0.85.

All temperature measurements were made with calibrated Co–Cu thermocouples (Finewire, California, type 0.005), continuously recorded on a five-channel recorder (type W+W).

Calculations and statistics

The amount of heat extracted (ΔH , in kJ kg^{-1}) during spinal thermode perfusion was calculated according to the formula:

$$\Delta H = g_w \times (T_{\text{in}} - T_{\text{out}}) \times \bar{C}/\text{BM},$$

where g_w is the amount of water (in grams) perfusing the thermode during the stimulation period, T_{in} and T_{out} are the respective temperatures of the inlet and outlet water, \bar{C} is the specific heat capacity of water ($4.187 \text{ J g}^{-1} \text{ }^\circ\text{C}^{-1}$, Weast, 1989), and BM is the body mass (in grams).

The amount of extra heat produced (ΔM , in kJ kg^{-1}) as a consequence of spinal cooling was calculated as the energetic equivalent of the oxygen consumption exceeding the pre-stimulation level. In practice, we integrated the oxygen consumption from the start of stimulation until the pre-stimulation level had again been reached.

Regression lines were calculated using the least-squares method. All the data were compared using the Student's t -test according to Zar (1984). Differences were considered to be statistically significant for values of $P < 0.05$.

Results

The mean values of \dot{V}_{O_2} and T_b prior to thermal stimulation of the spinal cord were $0.85 \pm 0.15 \text{ ml g}^{-1} \text{ h}^{-1}$ (s.d., $N=197$) and $41.2 \pm 0.21 \text{ }^\circ\text{C}$ (s.d., $N=152$), respectively. Values of these variables prior to cervical cooling and those prior to thoracic cooling were not significantly different. Selective cooling of both the cervical and thoracic parts of the spinal cord was accompanied by a sharp rise in metabolic heat production, typically reaching its peak shortly after the onset of cooling. Heat production thereafter dropped to a somewhat lower level, which was maintained until cooling was stopped. As a result of the elevated heat production, T_b showed an increase during stimulation, often reaching a constant level at the end of the stimulation period. This clearly indicated that the induced increase in heat production was higher than the amount of heat extracted.

In all the pigeons, ΔM was correlated positively with ΔH when either the cervical or the thoracic part of the spinal cord was cooled (Fig. 1). Linear regression analysis showed that the relationship between ΔM and ΔH was significant for all five pigeons (Table 1). The results are presented individually because of the individual differences existing in the relationship between ΔM and ΔH .

There were no significant differences between the slopes of the regression lines relating ΔM to ΔH for the cervical and the thoracic parts of the spinal cord for any of the pigeons (t -test; the two slopes compared). The mean slopes for the cervical and the thoracic parts were not significantly different (2.97 and 2.93, Table 1). However, in all the pigeons the mean relationship between ΔM and ΔH was higher when the thoracic part was cooled than when the cervical part was cooled. Consequently, the intercepts of the regression lines were significantly different (t -test, $P < 0.05$ for pigeon D, $P < 0.001$ for the other pigeons; the two elevations compared). The average y -intercept for cervical cooling was $-0.352 \text{ kJ kg}^{-1}$ compared to 1.061 kJ kg^{-1} for thoracic cooling (Table 1).

The increase in body temperature (ΔT_b) during cooling of the thoracic part was significantly higher than that found when the cervical part was cooled (Fig. 2,

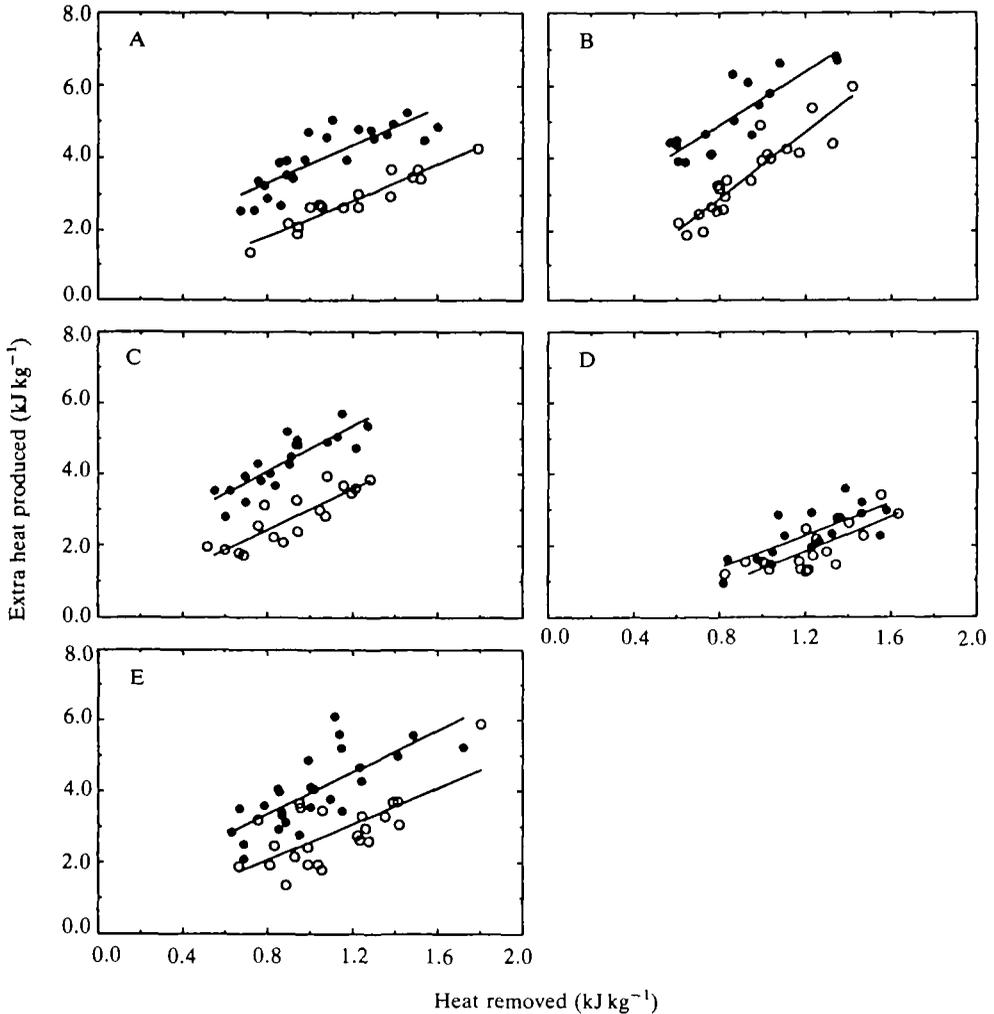


Fig. 1. Relationship between the extra heat produced and the amount of heat removed during selective cooling of the cervical (○) and thoracic (●) parts of the spinal cord in five pigeons (A–E).

unpaired *t*-test, $P < 0.001$ for all pigeons, two-tailed, T_b was not measured in pigeon E). This difference is not only a result of the greater production of metabolic heat that occurred during thoracic cooling. When the increase in T_b was related to the potential increase in heat content of the body ($\Delta E = \Delta M - \Delta H$), the body temperature itself showed a greater rise during thoracic cooling than during cervical cooling (Fig. 3). This difference was statistically significant (*t*-test, $P < 0.001$; the two elevations compared). The regression lines describing the relationships were $\Delta T_b = -0.053 + 0.211\Delta E$ ($r = 0.92$, $N = 73$, $P < 0.001$) and $\Delta T_b = 0.047 + 0.243\Delta E$ ($r = 0.92$, $N = 78$, $P < 0.001$) for the cervical and the thoracic parts, respectively.

Table 1. *Linear regressions relating the extra heat produced to the amount of heat removed during selective cooling of the cervical and thoracic parts of the spinal cord in five pigeons (A-E)*

Pigeon	<i>N</i>	<i>a</i>	<i>b</i>	<i>r</i>	<i>P</i>
Cervical part					
A	16	-0.152	2.48	0.95	<0.001
B	21	-0.744	4.56	0.92	<0.001
C	17	0.142	2.88	0.86	<0.001
D	19	-1.080	2.43	0.77	<0.001
E	23	0.073	2.50	0.69	<0.001
Mean		-0.352	2.97		
s.d.		0.54	0.91		
Thoracic part					
A	24	1.282	2.56	0.83	<0.001
B	17	1.980	3.67	0.86	<0.001
C	20	1.519	3.19	0.85	<0.001
D	17	-0.491	2.31	0.75	<0.001
E	26	1.015	2.93	0.73	<0.001
Mean		1.061	2.93		
s.d.		0.94	0.53		

Number of stimulations, *N*; *y*-intercept, *a*; slope, *b*; and correlation coefficients, *r* for the regression lines.

Mean values and s.d. are calculated for the slopes and *y*-intercepts.

Discussion

Experimental conditions

Since a weighted mean body temperature would appear to represent the controlled variable in homeothermic thermoregulation (Simon *et al.* 1986), it is important to ensure that birds are not thermally stressed by the experimental conditions. All the experiments in this study were carried out at an ambient temperature of 26°C, a value that is assumed to be within the thermoneutral zone for the pigeon (Rautenberg, 1969*b*; Saarela and Vakkuri, 1982). The mean \dot{V}_{O_2} measured before spinal cooling (0.85 ml O₂ g⁻¹ h⁻¹) falls within the range found in previous measurements of the basal metabolic rate of pigeons (0.83 ml O₂ g⁻¹ h⁻¹, Benedict and Riddle, 1929; 0.99 ml O₂ g⁻¹ h⁻¹, Calder and Schmidt-Nielsen, 1967). Our pigeons were, therefore, assumed to have been in a relatively non-stressed condition prior to spinal cooling. The effects of spinal cooling can consequently be used to obtain a quantitative estimate of the thermosensitivity of the spinal cord.

Experimental method

The local thermosensitivity of a thermosensory area has usually been determined by relating the maximal response of a thermoregulatory effector mechanism

(usually as metabolic heat production or as evaporative heat loss) to the experimentally induced temperature displacement, according to the concept of proportional control in temperature regulation (Hammel, 1968; Simon *et al.* 1986).

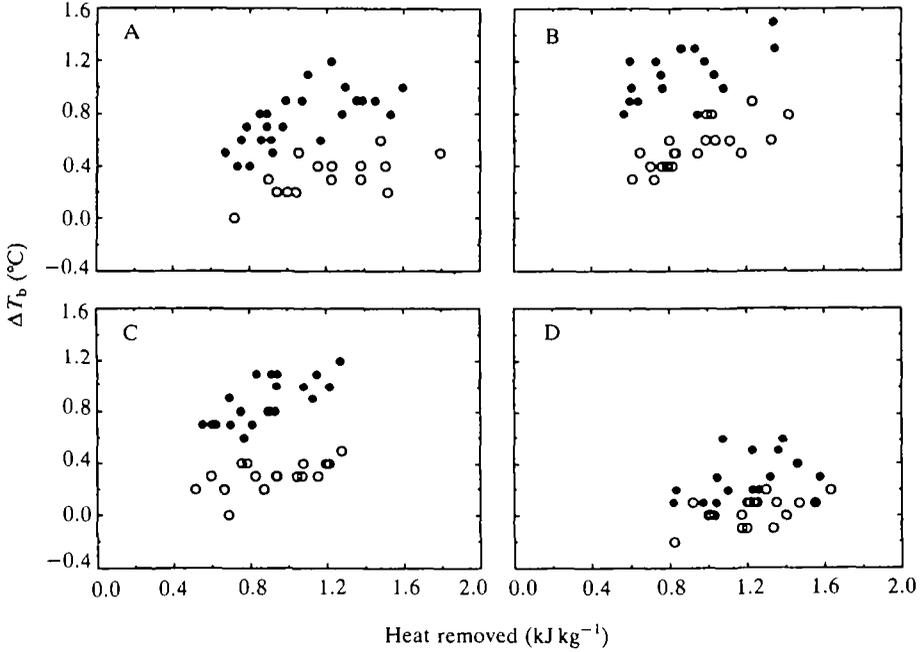


Fig. 2. Changes in body temperature (ΔT_b) in relation to the amount of heat removed during selective cooling of the cervical (○) and thoracic (●) parts of the spinal cord in four pigeons (A–D).

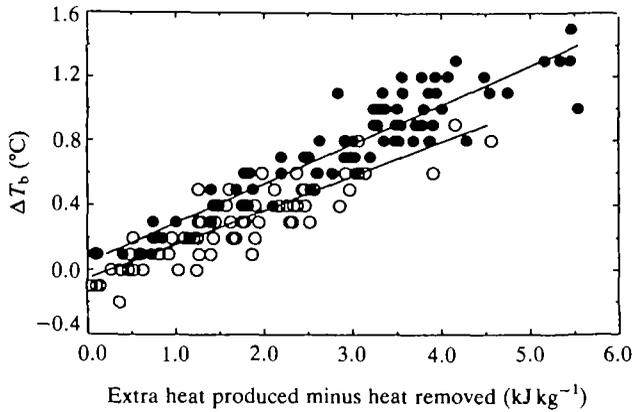


Fig. 3. Changes in body temperature (ΔT_b) in relation to the potential increase in heat content (i.e. the extra heat produced minus the amount of heat removed) during selective cooling of the cervical (○) and thoracic (●) parts of the spinal cord. Data are from four pigeons.

A general problem in assessing effector sensitivity to thermal stimulation of the spinal cord, using this method, has been the difficulty in defining the stimulation temperature. The exact location of the thermosensitive elements within and/or close to the spinal cord are not known and, consequently, their actual temperatures cannot be determined precisely (Mercer and Simon, 1984). In addition, thermal stimulation of the spinal cord using the thermode technique will give rise to appreciable temperature gradients within the vertebral canal (Reinertsen and Bech, 1989). Values varying between -0.9 and $-2.05 \text{ W kg}^{-1} \text{ } ^\circ\text{C}^{-1}$ have been reported for the spinal cord thermosensitivity of pigeons (Graf, 1980; Rautenberg, 1969a). Such a wide range of values can in part be explained by differences in the positioning of the thermocouple used to measure the stimulation temperature (Reinertsen and Bech, 1989). The difficulty in defining the stimulation temperature can lead to a miscalculation of the thermosensitivity of the spinal cord. In this study, therefore, we used the ratio between the amount of extra heat produced (ΔM), as a consequence of spinal cooling, and the amount of heat extracted (ΔH), as a measure of spinal cord thermosensitivity. This method was first introduced by Jessen (1974), who suggested that the ratio $\Delta M/\Delta H$ provides a quantitative estimate of the density of thermosensitive elements. Using this method, calculation of thermosensitivity will be independent of temperature measurements made within the stimulated area. This is significant when the thermosensitivity of different parts of the spinal cord are being compared. However, in our experiments, cooling of the spinal cord also caused a rise in body temperature. This will have had an inhibitory effect on heat production. Hence, the thermosensitivities of the two stimulated parts could have been underestimated. However, the effect of the increase in T_b was the same during cooling of either the cervical or the thoracic parts. As a consequence, any differences found between the sensitivities of the two parts can be considered as genuine.

Interpretation of results

Since selective cooling of either the cervical or the thoracic part of the spinal cord resulted in an increase in metabolic heat production and a rise in body temperature, one can conclude that thermosensitive elements exist in both these areas. Early on during the study, the assumption was made that the slope of the regression lines obtained for the relationship between the extra heat produced and the amount of heat extracted (Fig. 1) would provide a measure of the thermosensitivities of the two areas stimulated. The results of the present study showed that this estimate may not be correct. Based on the above procedure, the cervical and thoracic parts of the spinal cord should have equal thermosensitivities (Table 1). However, cooling of the thoracic part resulted in a substantially greater increase in metabolic heat production (Fig. 1) and in T_b (Fig. 2) and, consequently, the thoracic part must be presumed to possess a higher degree of thermosensitivity (Jessen, 1974). Hence, the actual ratio $\Delta M/\Delta H$ should provide a better estimate of the respective thermosensitivities of the two stimulated parts.

However, a specific quantitative value for the ratio $\Delta M/\Delta H$ cannot be calculated, as such a value will usually depend on the actual strength of stimulation. In addition to the differences in their sensitivity to cooling, the results of our study also revealed that cooling of one or other part of the spinal cord caused different effects on the thermoregulatory effector mechanisms (vasoconstriction and/or ptiloerection) that influence thermal conductance (Fig. 3). The results of the present study thus accord with those of similar studies made on mammals, for which quantitative differences in the thermosensitivity of different parts of the spinal cord have also been demonstrated (Miller and South, 1978; Brück and Wünnenberg, 1966, 1970).

During thermal stimulation of the spinal cord, both the afferent and the efferent parts of the thermoregulatory system may be affected (Necker, 1981). When discussing the responses of the central neurones to heat changes one must further discriminate between specific and non-specific responses. In addition to the well-known generation of specific spinal temperature signals (Simon, 1974), another factor has also been proposed to explain the responses of the neurones in the CNS to heat changes, namely the temperature dependence of signal transmission across the synapses (Simon, 1981). Synaptic transmission may be temperature-dependent, as a result of temperature-related changes in postsynaptic excitability and/or presynaptic transmitter release (Simon, 1989). Transmission of signals along the axons would not be affected (Paintal, 1965). The temperature dependence of hypothalamic signal transmission has been shown to be the dominant factor in birds (Simon *et al.* 1976; Simon-Oppermann *et al.* 1978). It thus appears likely that signal transmission up and down the spinal cord will also be sensitive to temperature changes (Simon *et al.* 1986). However, a recent study has failed to show that the temperature dependence of afferent signal transmission has any influence on the relationship between body temperature and thermoregulatory effector response, at least in the goat (Jessen *et al.* 1990).

Three different explanations can be put forward to explain why the thermosensitivity of the thoracic part is greater than that of the cervical part of the spinal cord in pigeons. (1) Cooling of the spinal cord affects the transmission of signals from peripheral temperature receptors to neurones in the dorsal horns and this effect is greater during cooling of the thoracic part. (2) Cooling of the spinal cord has a direct effect on the activity of motoneurones and this effect is greater during cooling of the thoracic part. (3) The density of thermosensitive elements is greater in the thoracic part than in the cervical part of the spinal cord.

The first explanation makes the assumption that cooling of the spinal cord affects the transmission of signals from cutaneous receptors to second-order neurones in the dorsal horns. Theoretically, both the presynaptic activity of the afferent fibres and the postsynaptic activity of the dorsal horn neurones could be affected. However, Necker (1983) has shown that cooling of the spinal cord of pigeons had only a small effect on both of these. This observation is also supported by the demonstration of appropriate effector responses during thermal stimulation of the spinal cord after spinal deafferentation (Necker and Rautenberg, 1975).

Thus, a direct temperature effect on the transmission of signals from peripheral temperature receptors to the neurones in the dorsal horns does not seem to explain the difference in the thermosensitivities of the two parts.

The second explanation requires a direct influence of spinal cooling on the activity of the motoneurones and that this effect should be greater during cooling of the thoracic part. Investigations on the thermosensitivity of motoneurones that are part of the efferent thermoregulatory system have shown that, in cats (Pierau *et al.* 1976) and in pigeons (Görke, 1980), motoneurones are temperature-sensitive and probably contribute to the shivering response. The large breast muscle and the leg muscles are the main heat producers in birds (Brück, 1973). The motoneurones that control shivering in the breast muscle of the pigeon are localized in the area from C₁₂ to C₁₄, whilst the motoneurones that control shivering in the leg muscles are localized in the lumbosacral cord (Nomoto, 1989). The area from C₁₂ to C₁₄ is included in the cervical part, while the lumbosacral cord was not stimulated in the present study. Hence, the motoneurones that control shivering in the breast muscle were probably affected during cooling of the cervical part. Cooling of the thoracic part, in contrast, cannot have had any direct influence on the motoneurones that control shivering by the muscles that are important in heat production. Because a greater thermosensitivity was demonstrated in the thoracic than in the cervical part, the difference in the thermosensitivity of these two stimulated areas could not have been due to a direct effect of temperature on the motoneurones. If this had been the case, the metabolic response should have been greatest during cooling of the cervical part.

Based on the above, it would seem that a difference in the density of the thermosensitive elements in these two parts of the spinal cord provides the best explanation for the observed differences in their thermosensitivity. Whether such thermosensitive elements are interneurones or primary afferents is not known (Boulant *et al.* 1989; Simon, 1989). However, the thermosensitivity of the neurones involved in thermoregulation seems to be coordinated in such a manner that the appropriate responses will be made. From the pigeon's point of view, it may not be very important whether the thermosensitive elements are true primary afferents or thermosensitive interneurones.

One can only speculate about the possible physiological significance of this greater thermosensitivity of the thoracic than of the cervical part of the spinal cord. If the spinal cord of birds is a reference area for the internal body temperature, then the present results would indicate that the temperature of the thoracic part is more representative of the core temperature than is the temperature of the cervical part. The cervical part lies close to the trachea and is more likely to undergo temperature fluctuations. Temperature changes in the cervical part of the spinal cord of pigeons paralleling changes in the inspired air temperature have been demonstrated (Bech *et al.* 1988). Simultaneous temperature measurements made in the cervical and the thoracic parts of the spinal cord at different ambient temperatures should indicate whether the temperature of the thoracic part is more stable than that of the cervical part.

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References

- BECH, C., RAUTENBERG, W., MAY, B. AND JOHANSEN, K. (1982). Regional blood flow changes in response to thermal stimulation of the brain and spinal cord in the Pekin duck. *J. comp. Physiol.* **147**, 71–77.
- BECH, C., RAUTENBERG, W. AND MAY-RAUTENBERG, B. (1988). Thermoregulatory responses of the pigeon (*Columba livia*) to selective changes of the inspired air temperature. *J. comp. Physiol.* **157**, 747–752.
- BENEDICT, F. G. AND RIDDLE, O. (1929). Measurement of the basal heat production of pigeons. II. Physiological technique. *J. Nutr.* **1**, 497–538.
- BOULANT, J. A., CURRAS, M. C. AND DEAN, J. B. (1989). Neurophysiological aspects of thermoregulation. In *Advances in Comparative and Environmental Physiology. Animal Adaption to Cold* (ed. L. C. H. Wang), pp. 117–160. Berlin: Springer-Verlag.
- BRÜCK, K. (1973). The modes and sites of extra heat production. In *Temperature and Life* (ed. H. Precht, J. Christophersen, H. Hensel and W. Larcher), pp. 536–539. Berlin: Springer-Verlag.
- BRÜCK, K. AND WÜNNENBERG, W. (1966). Beziehung zwischen Thermogenese im 'braunen' Fettgewebe, Temperatur im cervicalen Anteil des Vertebralkanals und Kältezittern. *Pflügers Arch.* **290**, 167–183.
- BRÜCK, K. AND WÜNNENBERG, W. (1970). 'Meshed' control of two effector systems: Nonshivering and shivering thermogenesis. In *Physiological and Behavioral Temperature Regulation* (ed. J. D. Hardy, A. P. Gagge and J. A. J. Stolwijk), pp. 562–580. Springfield: Charles C. Thomas.
- CALDER, W. A. AND SCHMIDT-NIELSEN, K. (1967). Temperature regulation and evaporation in the pigeon and the roadrunner. *Am. J. Physiol.* **213**, 883–889.
- GRAF, R. (1980). Diurnal changes of thermoregulatory functions in pigeons. II. Spinal thermosensitivity. *Pflügers Arch.* **386**, 181–185.
- GÖRKE, K. (1980). Influences of spinal cord temperature changes on reflex discharge and spontaneous activity of spinal motoneurons in pigeons and leguans. *J. comp. Physiol.* **139**, 251–259.
- HAMMEL, H. T. (1968). Regulation of internal body temperature. *A. Rev. Physiol.* **30**, 641–710.
- HAMMEL, H. T., MAGGERT, J., KAUL, R., SIMON, E. AND SIMON-OPPERMANN, C. (1976). Effects of altering spinal cord temperature on temperature regulation in the Adelle penguin, (*Pygoscelis adeliae*). *Pflügers Arch.* **362**, 1–6.
- HELFMANN, W., JANNES, P. AND JESSEN, C. (1981). Total body thermosensitivity and its spinal and supraspinal fractions in the conscious goose. *Pflügers Arch.* **391**, 60–67.
- INOMOTO, T. AND SIMON, E. (1981). Extracerebral deep-body cold sensitivity in the Pekin duck. *Am. J. Physiol.* **241**, R136–R145.
- JESSEN, C. (1974). Density of temperature sensing elements at various sites of the body core. In *Selected Topics in Environmental Physiology* (ed. B. Bhatia, G. S. Chhina and B. Singh), pp. 19–24. New Delhi: Interprint.
- JESSEN, C., FELDE, D., VOLK, P. AND KUHNEN, G. (1990). Effects of spinal cord temperature on the generation and transmission of temperature signals in the goat. *Pflügers Arch.* **416**, 428–433.
- JESSEN, C. AND SIMON-OPPERMANN, C. (1976). Production of temperature signals in the peripherally denervated spinal cord of the dog. *Experientia* **32**, 484–485.
- MERCER, J. B. AND SIMON, E. (1984). A comparison between total body thermosensitivity and local thermosensitivity in mammals and birds. *Pflügers Arch.* **400**, 228–234.
- MERCER, J. B. AND SIMON, E. (1987). Appropriate and inappropriate hypothalamic cold thermosensitivity in Willow Ptarmigan. *Acta physiol. scand.* **131**, 73–80.
- MEURER, K.-A., JESSEN, C. AND IRIKI (1967). Kältezittern während isolierter Kühlung des Rückenmarks nach Durchschneidung der Hinterwurzeln. *Pflügers Arch.* **293**, 236–255.

- MILLER, V. M. AND SOUTH, F. E. (1978). Thermoregulatory responses to temperature manipulation of the spinal cord in the marmot. *Cryobiology* **15**, 433–440.
- NECKER, R. (1975). Temperature-sensitive ascending neurons in the spinal cord of pigeons. *Pflügers Arch.* **353**, 275–286.
- NECKER, R. (1981). Thermoreception and temperature regulation in homeothermic vertebrates. In *Progress in Sensory Physiology 2* (ed. H. Autrum, D. Ottoson, E. Perl and R. F. Schmidt), pp. 1–47. Berlin: Springer-Verlag.
- NECKER, R. (1983). Effects of temperature on afferent synaptic transmission in the dorsal horn of the spinal cord of pigeons. *J. therm. Biol.* **8**, 15–18.
- NECKER, R. AND RAUTENBERG, W. (1975). Effect of spinal deafferentation on temperature regulation and spinal thermosensitivity in pigeons. *Pflügers Arch.* **360**, 287–299.
- NOMOTO, S. (1989). An anatomical study of neural circuits that mediate the inhibitory effects of treadmill exercise on shivering in pigeons. In *Thermal Physiology 1989* (ed. J. B. Mercer), pp. 703–705. Amsterdam: Elsevier Science Publishers B.V.
- PAINTAL, A. S. (1965). Effects of temperature on conduction in single vagal and saphenous myelinated nerve fibres of the cat. *J. Physiol., Lond.* **180**, 20–49.
- PIERAU, F.-K., KLEE, M. R. AND KLUSSMANN, F. W. (1976). Effect of temperature on postsynaptic potentials of cat spinal motoneurons. *Brain Res.* **114**, 21–34.
- RAUTENBERG, W. (1969a). Die Bedeutung der zentralnervösen Thermosensitivität für die Temperaturregulation der Taube. *Z. vergl. Physiol.* **62**, 235–266.
- RAUTENBERG, W. (1969b). Untersuchungen zur Temperatur-regulation wärme- und kälte-akklimatisierter Tauben. *Z. vergl. Physiol.* **62**, 221–234.
- RAUTENBERG, W., NECKER, R. AND MAY, B. (1972). Thermoregulatory responses of the pigeon to changes of the brain and the spinal cord temperatures. *Pflügers Arch.* **338**, 31–42.
- REINERTSEN, R. E. AND BECH, C. (1989). On the thermosensitivity of the spinal cord in pigeons. In *Physiology of Cold Adaptation in Birds* (ed. C. Bech and R. E. Reinertsen), pp. 27–36. New York: Plenum Press.
- SAARELA, S. AND VAKKURI, O. (1982). Photoperiod-induced changes in temperature-metabolism curve, shivering threshold and body temperature in the pigeon. *Experientia* **38**, 373–375.
- SIMON, E. (1974). Temperature regulation: The spinal cord as a site of extrahypothalamic thermoregulatory functions. *Rev. Physiol. Biochem. Pharmac.* **71**, 1–76.
- SIMON, E. (1981). Effects of CNS temperature on generation and transmission of temperature signals in homeotherms: A common concept for mammalian and avian thermoregulation. *Pflügers Arch.* **392**, 79–88.
- SIMON, E. (1989). Nervous control of cold defence in birds. In *Physiology of Cold Adaptation in Birds* (ed. C. Bech and R. E. Reinertsen), pp. 1–15. New York: Plenum Press.
- SIMON, E., PIERAU, F.-K. AND TAYLOR, D. C. M. (1986). Central and peripheral thermal control of effectors in homeothermic temperature regulation. *Physiol. Rev.* **66**, 235–300.
- SIMON, E., SIMON-OPPERMANN, C., HAMMEL, H. T., KAUL, R. AND MAGGERT, J. (1976). Effects of altering rostral brain stem temperature on temperature regulation in the Adelie penguin, (*Pygoscelis adeliae*). *Pflügers Arch.* **362**, 7–13.
- SIMON-OPPERMANN, C., SIMON, E., JESSEN, C. AND HAMMEL, H. T. (1978). Hypothalamic thermosensitivity in conscious Iriki ducks. *Am. J. Physiol.* **235**, R130–R140.
- TSUCHIYA, K., KOSAKA, M. AND IRIKI, M. (1984). Effects of selective thermal stimulation of the thoracic and lumbosacral cords on cardiovascular functions in urethane-anaesthetized rats. *J. therm. Biol.* **9**, 57–60.
- WEAST, R. C. (1989). *CRC Handbook of Chemistry and Physics*. Boca Raton, Florida: CRC.
- WITHERS, P. C. (1977). Measurement of \dot{V}_{O_2} , \dot{V}_{CO_2} , and evaporative water loss with a flow-through mask. *J. appl. Physiol.* **42**, 120–123.
- ZAR, J. H. (1984). *Biostatistical Analysis*. Englewood Cliffs, New Jersey: Prentice-Hall.