J Comp Physiol B (1997) 167: 241–248

ORIGINAL PAPER

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Ontogeny of deep-body cold sensitivity in Pekin ducklings *Anas platyrhynchos*

Accepted: 7 January 1997

Abstract The ontogeny of deep-body cold sensitivity was studied in 1 to 12 days old Pekin ducklings *Anas platyrhynchos*. Deep-body cold sensitivity was determined by means of thermodes implanted in the abdominal cavity. The thermodes were perfused with cold water for 15-min periods to lower the core temperature. Cooling of the body core elicited increases in metabolic rate and vasoconstrictions in the legs of all the ducklings. From the changes induced in metabolic rate and core temperature, deep-body cold sensitivity values of between -5.17 and $-6.36\ W \cdot kg^{-1} \cdot °C^{-1}$, were estimated. These values, which are in the range of those reported previously for adult Pekin ducks, did not change with age, and it is concluded that deep-body cold sensitivity is fully developed at hatching. Our next aim was to investigate whether the autonomic responses elicited by exposure of ducklings to cold ambient conditions could be explained by temperature changes within the body core. During cold exposure, the increase in metabolic rate was not accompanied by a concomitant decrease in core temperature. On the contrary, deep-body temperature increased slightly during the initial phase of cold exposure. The ducklings attained a metabolic rate amounting to 85–90% of their peak metabolic rate before the core temperature fell below the regulated level measured at thermoneutrality. Thus, despite the findings that Pekin ducklings have a highly-developed deep-body cold sensitivity, their metabolic cold defence under natural conditions seems to be mediated primarily by peripheral thermoreceptors.

Key words Temperature regulation · Thermosensitivity · Homeothermy · Metabolic rate · Chick

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Abbreviations *BM* body mass · *MR* metabolic rate(s) · *PMR* peak metabolic rate · *RMR* resting metabolic rate · T_a ambient temperature(s) · T_b deep-body temperature · T_{leg} leg skin temperature · T_{back} back skin temperature

Introduction

Birds inhabit most parts of the globe and are thus exposed to a wide range of ambient temperatures (T_a). To be able to cope with diverse T_a they have developed a finely tuned thermoregulatory system, intended to maintain a stable deep-body temperature (T_b). Models developed to explain the homeothermic regulation of T_b are based on a negative feedback mechanism, in which the hypothalamus has a primary control function (Hammel 1968; Simon et al. 1986). During the last few decades, several studies have shown that thermosensitive neurons, that provide afferent thermal information to the hypothalamus, are located throughout the body. A weighted mean body temperature would thus appear to represent the controlled variable in homeothermic thermoregulation (Simon et al. 1986).

Selective thermal stimulation of various parts of the body in mammals and birds, has provided important information concerning the existence and relative distribution of thermosensitive neurons in different parts of the body. In the few avian species studied so far, the overall body cold sensitivity has been estimated to range from -5 to $-12\ W \cdot kg^{-1} \cdot °C^{-1}$ (Mercer and Simon 1984). These studies have shown that peak metabolic rate (PMR) is elicited when the core temperature is lowered 2–3 °C below the resting level (Inomoto and Simon 1981; Mercer and Simon 1984). In birds, in contrast to mammals, the hypothalamus seems to be of only minor importance as a thermosensory area (Rautenberg et al. 1972; Simon et al. 1976; Simon-Oppermann et al. 1978; Mercer and Simon 1987). As in mammals, however, selective thermal stimulation of the spinal cord elicits appropriate thermoregulatory effector

responses (Rautenberg et al. 1972; Hammel et al. 1976; Inomoto and Simon 1981; Østnes and Bech 1992). However, the central nervous system in birds seems to play only a minor role in the overall body cold sensitivity (Inomoto and Simon 1981; Mercer and Simon 1984; Simon et al. 1986). In Pekin ducks *Anas platyrhynchos*, for example, the various parts of the central nervous system account for less than 10% of the overall body cold sensitivity (Inomoto and Simon 1981). Afferent signals from thermosensitive neurons in deep-body tissue external to the central nervous system would therefore appear to play the major role in the control of body temperature in birds (Inomoto and Simon 1981; Mercer and Simon 1984; Simon et al. 1986).

The ability of neonate birds to cope with cold surroundings range from an altricial development pattern, in which the chicks are poikilothermic at hatching, to a precocial pattern in which the newly-hatched chicks have a high thermogenic capacity (Ricklefs 1983; Starck 1993). While the development of heat producing mechanisms has been the subject of many studies, there are surprisingly few reports about the ability of neonate birds to sense cold. In consequence, information about the existence and relative distribution of thermosensitive neurons in different parts of the body of chicks is scarce. The results of two studies, however, have suggested that chicks may be more sensitive to cooling of the skin than to cooling of the central body core (Randall 1943; Klaassen et al. 1989).

The aim of the present study was to investigate the ontogeny of deep-body cold sensitivity in Pekin ducklings. Pekin ducklings are well suited for such an investigation for two reasons: firstly, neonate ducklings in general have a high thermogenic capacity (Koskimies and Lahti 1964; Steen et al. 1989) and, secondly, the adult Pekin duck is the most thoroughly investigated species of birds in regard to the relative distribution of thermosensitive neurons in different parts of the body (Simon-Oppermann et al. 1978; Inomoto and Simon 1981; Martin et al. 1981; Simon et al. 1981). The results obtained from the present study will therefore be comparable with the knowledge established for adult ducks.

Materials and methods

Experimental animals

Pekin duck eggs were received from a local farmer and hatched in the laboratory. After hatching, the ducklings were kept for about 12 h in the incubator at a T_a of 37 °C. Thereafter, they were moved to a wooden box (110 × 60 × 45 cm), where T_a was controlled at 28 °C. When the ducklings were 7 days old, they were moved to a larger room with free access to a water pool. In this room T_a was kept at 20 °C. After transfer from the incubator, food and water were available *ad libitum*. Groups of ducklings were used in the experiments when they were 1, 3, 6 or 12 days old. The day of hatching is defined as day 0.

Surgery

To be able to cool the central body core, the ducklings were equipped with a thermode (heat exchanger) placed in the abdominal cavity. The thermodes were constructed from silicone tubing wound into a double loop. The diameter of the tubes used were as follows: i.d. 1.1 mm, o.d. 2.0 mm (1 day and 3 days old ducklings), i.d. 1.8 mm, o.d. 3.1 mm (6 day old) and i.d. 2.4 mm, o.d. 4.0 mm (12 days old). Under a general anaesthesia using halothane, and locally applied lidocaine anaesthesia, the thermodes were inserted into the abdominal cavity through an incision made close to the cloacal opening. They were positioned in parallel with the intestines, just behind the liver. The entire surgical procedure lasted about 20 min. The ducklings recovered quickly after surgery and were soon transferred back to their room, where they immediately began to eat. Newly-hatched ducklings, however, in which the thermode was implanted only 2–4 h after hatching, were returned to the incubator. The exact position of the implanted thermodes were verified by post-mortem examinations.

Central body cooling

The experiments were performed about 24 h after insertion of the thermodes. At each age, six to eight individuals were used. The ducklings were weighed, to the nearest 0.1 g, before and after each experiment. In the subsequent calculations the decreases in BM were assumed to be linear during the course of an experiment. Prior to the experiments, a Cu-Co thermocouple (California fine wire, type 0.005) surrounded by a polypropylene tubing (PP 50, Portex Ltd, UK), was inserted into the cloaca, to measure T_b. Depending on their age, the thermocouple was inserted 1.8–4.5 cm into the duckling's cloaca. In addition, thermocouples were placed on the back and on the lower part of the tarsus, to measure back skin (T_{back}) and leg skin (T_{leg}) temperatures. Before placement of the thermocouple on the back, downy feathers were removed from a small area between the wings, and the thermocouple fixed by tape to the naked skin. The thermocouples were connected to a data logger (Squirrel series 1200, Grant Instruments, UK) and temperature measurements (accuracy ±0.1 °C) stored at 30-s intervals.

During the experiments, the ducklings were confined in metabolic chambers, made of Plexiglass. The volume of these chambers ranged from 1.3 l to 2.2 l. The chambers was placed inside a climatic chamber (7 l), made from a brass jacket, through which water, at a thermostatically controlled temperature, was circulated. The circulating water kept the T_a inside the chamber at thermoneutral conditions. Ambient temperatures of 31–33 °C for the smallest, and 27–29 °C for the largest ducklings had previously been estimated to lie within the thermoneutral zone (J.E. Østnes and C. Bech, unpubl. obs.).

Central body cooling was achieved by perfusing the thermode, for 15-min periods, with water from a thermostatically controlled waterbath (Heto, type CB 7). The flow rates of the water perfusing the thermode were varied depending on the ages of the ducklings as follows: 20 $ml \cdot min^{-1}$ (1 day and 3 days old ducklings), 50 $ml \cdot min^{-1}$ (6 days old) and 90 $ml \cdot min^{-1}$ (12 days old). The temperature of the water perfusing the thermode was varied between 28 °C and 39 °C for ducklings 1 day and 3 days old, and between 21 °C and 39 °C for ducklings 6 days and 12 days old. By use of these temperature ranges, it was possible to lower the temperature of the body core 0.2–3.0 °C below the regulated level. Consecutive periods of perfusion of the thermode were separated by at least a 30-min interval, during which no perfusion occurred. The total number of cooling periods varied from four to eight during any single experiment.

Oxygen consumption rates were measured by open-flow respirometry (Withers 1977). Dry atmospheric air was sucked through the metabolic chamber by an air pump (Miniport) at rates of 0.6–2.0 $l \cdot min^{-1}$. After drying over silica gel, the actual airflow rates were measured with a mass flow controller (Bronkhorst High-Tech, type 201C-FA), before a fraction of the air was directed into an O_2 analyzer (Servomex, type 1100A). Before each experiment, the O_2

analyzer was calibrated, using dry atmospheric air (20.95% O_2) and pure N_2. At the end of each experiment, the analyzer was again calibrated, and any changes in the readings were corrected for by assuming a linear drift. Measurements of the O_2 content of the excurrent air (accuracy 0.01%) were stored, along with the temperature measurements, on a Squirrel data logger, at 30-s intervals.

Oxygen consumption rates were calculated from the STPD air flow rates and the O_2 content of excurrent air, using the appropriate formula (Withers 1977), and corrected for wash-out delays by using the equation given by Niimi (1978). Each experiment lasted for about 8–10 h and the ducklings were not postabsorptive at the time they were placed in the metabolic chamber. Values of metabolic rate (MR) were calculated from the O_2, consumption rates using 5.5824 $W \cdot kg^{-1}$ as the caloric equivalent for O_2 assuming a constant RQ of 0.79. After each experiment, the data obtained were transferred to a computer for further analysis.

Deep-body cold sensitivity was calculated as the slope of the regression line describing the relationship between ΔT_b and ΔMR induced by central body cooling. For this purpose the average T_b and MR values recorded during the last 5 min prior to the beginning of each cooling period and the last 5 min of each cooling period were used.

Cold exposure

A second set of experiments were designed to measure RMR at thermoneutrality (T_a between 27 and 32 °C) and PMR during exposure to cold conditions. At each age, six to eight ducklings were used in the experiments. During the experiments, the metabolic chamber was placed inside a climatic chamber (Heraeus Vötsch, type VEM 03/500). Oxygen consumption rates and the various temperatures were recorded as described above. After 4–6 h exposure to thermoneutrality, the T_a inside the metabolic chamber was lowered at a constant rate of about 0.6 °C · min^{-1}. When the ducklings were exposed to T_a below thermoneutrality, their MR increased. Each experiment was terminated when the ducklings could no longer cope with the cold conditions, i.e. when MR began to decrease and T_b decreased sharply. An experimental run was normally terminated when T_b had dropped 3 °C below the regulated level at thermoneutrality. Each duckling was used only once in the experiments. RMR was defined as the lowest 5-min average MR measured at thermoneutrality, while PMR was defined as the highest 5-min average MR measured during the period of cold exposure.

Statistics

The relationship between ΔT_b and ΔMR was evaluated by linear regression analysis using the least squares method. Significant differences were determined using either analysis of covariance (ANCOVA) or analysis of variance (ANOVA). Where F indicated a significant difference, the Tukey test was used for pairwise multiple comparisons. Overall significance was set at $P < 0.05$. Results are expressed as means ± SD.

Results

Central body cooling

Mean values of MR and T_b recorded prior to cooling of the central body core are given in Table 1. Cooling of the body core, at thermoneutral ambient conditions, elicited an increase in MR in all the ducklings investigated. The time-course of a single experiment, in which T_b was lowered by repeated periods of water perfusion of the thermode, is shown in Fig. 1. Water perfusion induced an abrupt decrease in T_b, which was followed shortly by a sharp rise in MR. Shortly after the onset of cooling, MR reached a plateau which usually was maintained during the remaining cooling period. As shown, the increases in MR were generally related to the degree of cooling.

Table 1 Metabolic rate (MR) and deep-body temperature (T_b) measured prior to cooling of the central body core in Pekin ducklings of different ages. Values are given as means ± SD; N, number of individuals examined (BM body mass)

Age (days)	N	BM (g)	MR ($W \cdot kg^{-1}$)	T_b (°C)
1	8	52.2 ± 4.1	7.68 ± 0.85	39.9 ± 0.35
3	8	64.6 ± 6.3	9.54 ± 1.01	40.0 ± 0.55
6	6	107.9 ± 5.0	11.81 ± 0.64	40.7 ± 0.24
12	7	220.0 ± 19.4	12.85 ± 0.87	41.4 ± 0.33

Compared to the experimentally induced changes in T_b, only minor changes were observed in T_{back}. However, periods of central body cooling were accompanied by a considerable drop in T_{leg}, showing that in addition to the metabolic response, cooling of the body core also induced vasoconstriction in the legs. Such vasoconstrictions were most pronounced in the oldest ducklings,

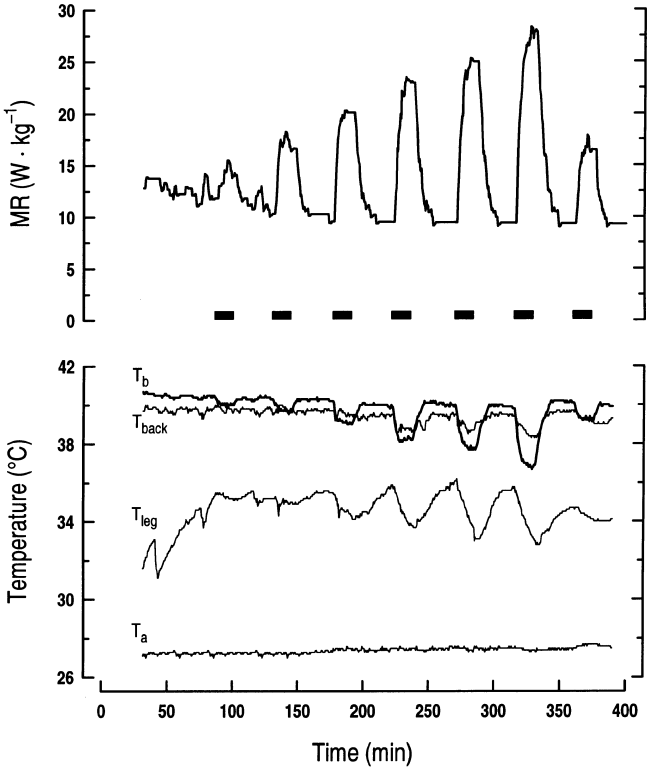

Fig. 1 Time-course of metabolic rate (MR), deep-body temperature (T_b), back skin temperature (T_{back}) and leg skin temperature (T_{leg}) before, during and after 15-min periods of central body cooling (*black bars*) in a 6 days old Pekin duckling. The experiment was performed at a thermoneutral ambient temperature (T_a). The temperature of the water perfusing the abdominal thermode was successively lowered for each of the first six cooling periods

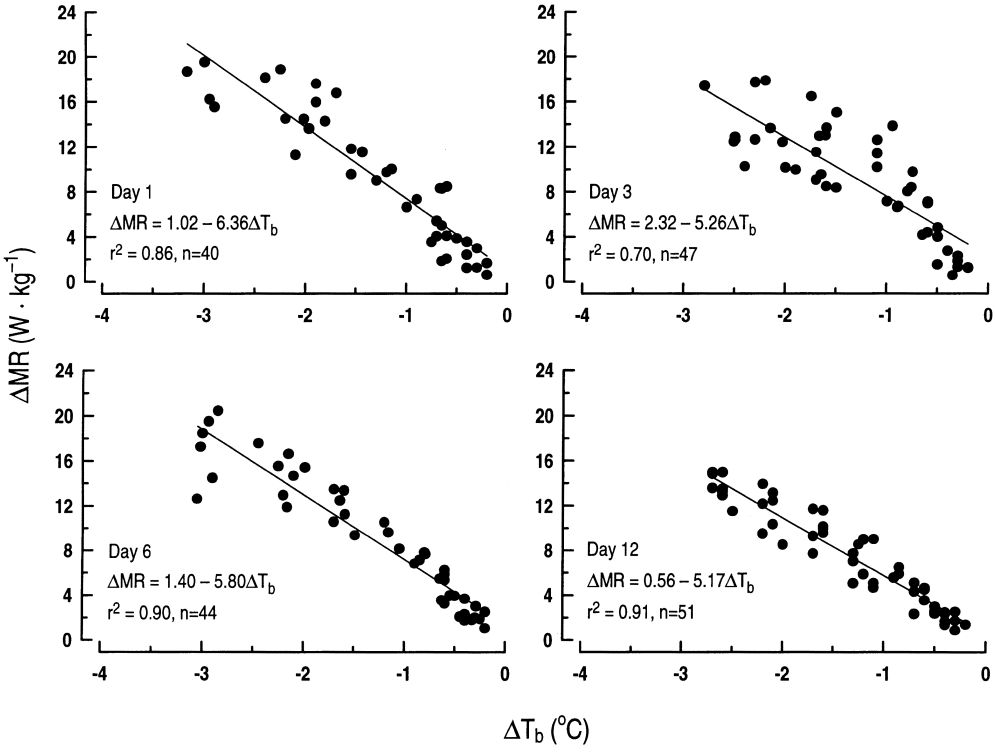

Fig. 2 Relationship between changes in deep-body temperature (ΔT_b) and changes in metabolic rate (ΔMR) induced by cooling of the central body core in Pekin ducklings of different ages. The slopes of the regression lines provide an estimate of deep-body cold sensitivity

probably because they maintained a higher gradient between T_{leg} and T_a at thermoneutrality. In ducklings 12 days old, declines in T_{leg} of up to 8 °C were observed when T_b was lowered 2–3 °C below the pre-cooling level.

An experimentally induced lowering of T_b of only 0.2 °C generally elicited an increase in MR (Fig. 2). The maximum MR induced by central body cooling (including the MR recorded prior to cooling, Table 1) amounted to 27–30 $W \cdot kg^{-1}$, with only slight differences between the different age groups. These responses were attained when T_b was decreased about 3 °C below the pre-cooling level. In each of the four age groups, ΔMR was negatively correlated with ΔT_b (Fig. 2). The coefficients of determination indicated a high degree of linearity in the relationship between ΔMR and ΔT_b. The slopes obtained for the different age groups ranged from −5.17 to −6.36 $W \cdot kg^{-1} \cdot °C^{-1}$. An analysis of covariance indicated that a significant difference existed between the slopes of the regression lines ($F = 9.04$, $P < 0.001$). However, a pairwise multiple comparison only revealed a significant difference between the slopes for the ducklings 1 day and 12 days old. The slopes *per se* did not suggest the existence of either an increase or a decrease in deep-body cold sensitivity with age.

Cold exposure

The RMR, measured at thermoneutral ambient conditions, increased significantly with age (Table 2; ANOVA, $F = 43.59$, $P < 0.001$). However, there were no significant differences between the values for ducklings 1 day and 3 days old, nor between ducklings 6 days and 12 days old. The ducklings responded to cold exposure with

Table 2 Resting (RMR) and peak (PMR) metabolic rates measured when Pekin ducklings were exposed to thermoneutral and to cold ambient temperatures, together with the temperatures of different body parts recorded at the times that the RMR and PMR were attained. Values are given as means ± SD; *N*, number of individuals examined (*BM* body mass, *MR* metabolic rate, T_a ambient temperature, T_b deep-body temperature, T_{back} back skin temperature, T_{leg} leg skin temperature)

Age (days)	*N*	*BM* (g)		*MR* ($W \cdot kg^{-1}$)	T_a (°C)	T_b (°C)	T_{back} (°C)	T_{leg} (°C)
1	8	56.8 ± 5.2	RMR	6.81 ± 0.88	31.0 ± 0.76	40.0 ± 0.50	39.3 ± 0.47	34.6 ± 1.21
			PMR	31.15 ± 3.30	−5.1 ± 5.74	38.7 ± 1.02	36.0 ± 2.30	8.4 ± 5.02
3	7	63.3 ± 7.5	RMR	7.66 ± 0.93	30.8 ± 0.54	40.1 ± 0.56	39.4 ± 0.68	34.7 ± 1.50
			PMR	28.58 ± 2.58	−5.5 ± 5.29	38.9 ± 0.75	36.6 ± 1.67	9.9 ± 5.83
6	6	99.0 ± 12.1	RMR	11.41 ± 1.17	28.2 ± 0.46	40.7 ± 0.17	40.1 ± 0.22	33.6 ± 2.12
			PMR	30.97 ± 2.50	−6.7 ± 4.04	39.5 ± 1.06	38.4 ± 0.94	10.6 ± 3.67
12	6	225.6 ± 13.8	RMR	12.10 ± 0.86	27.2 ± 0.33	41.2 ± 0.29	40.6 ± 0.39	38.6 ± 0.78
			PMR	32.34 ± 2.23	−19.0 ± 3.41	40.0 ± 0.53	38.9 ± 0.89	2.4 ± 0.93

an immediate increase in MR, which paralleled the decrease in T_a (Fig. 3). The rise in MR, however, was generally accompanied by an increase in T_b during the initial phase of the cold exposure period. This transient increase in T_b was normally in the order of 0.5–1.0 °C, independent of age. Usually, T_{back} was maintained at a relatively stable level during the first part of the cold exposure period, while T_{leg} decreased steadily along with T_a. At more intense cold exposure both T_b and T_{back} decreased below the levels measured at thermoneutrality. During this time, MR reached a plateau level when PMR was approached. During the further course of cold exposure, T_b decreased quickly and was accompanied also by a decrease in MR. Despite considerable individual variation, the ducklings of different ages reached PMR after almost the same average declines in T_b of 1.2–1.3 °C (Table 2). The average decline in T_{back} at which PMR was attained was about 2.8–3.3 °C in ducklings 1 day and 3 days old and was about 1.7 °C in ducklings 6 days and 12 days old. PMR values recorded during cold exposure did not differ with age (Table 2; ANOVA, $F = 2.05$, $P > 0.2$). Ducklings 1–6 days old attained PMR at nearly the same T_a, whereas PMR values in ducklings 12 days old was attained at a significantly lower T_a. The metabolic scope (PMR/RMR) corresponded to 4.57 times RMR in ducklings 1 day old, and to about 2.67 times RMR in ducklings 12 days old (Table 2).

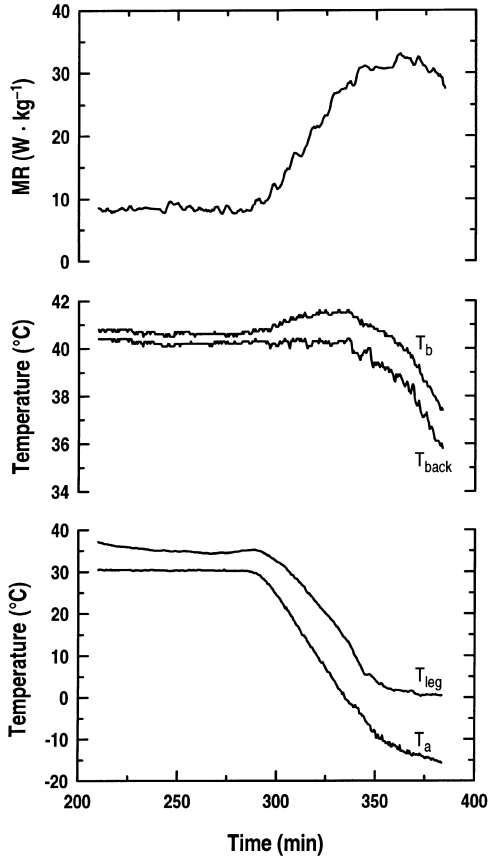

Fig. 3 Time-course of metabolic rate (MR), deep-body temperature (T_b), back skin temperature (T_{back}) and leg skin temperature (T_{leg}) in a 6 days old Pekin duckling recorded during the transition from thermoneutral to cold ambient temperatures (T_a)

To evaluate the importance of peripheral thermoreceptors in stimulating the thermogenic response, the increase in MR attained by the ducklings before T_b fell below the resting level, was calculated as a percentage of PMR (Table 3). The results of these calculations showed that ducklings were able to increase their MR by 85–92% of the PMR values before T_b decreased below the regulated level measured at thermoneutrality.

Discussion

The primary aim of the present study was to investigate the ontogeny of deep-body cold sensitivity in Pekin ducklings. As shown in Fig. 1, cooling of the central body core elicited both an increase in MR and vasoconstriction in the legs. At all ages, the increase in MR was related to the degree of cooling, according to the concept of proportional control in thermoregulation (Hammel 1968; Simon et al. 1986). The results clearly show that, in Pekin ducklings, cooling of the body core elicits appropriate thermoregulatory effector responses, thereby providing evidence for the existence of thermosensitive neurons in the central body core.

The local thermosensitivity of a specific part of the body is usually determined by relating the maximal response of a thermoregulatory effector mechanism to the experimentally induced temperature displacement (Simon et al. 1986). From the changes in T_b and MR induced by cooling the body core of ducklings of different ages, estimated values indicating a deep-body cold sensitivity of between -5.17 and $-6.36\ W \cdot kg^{-1} \cdot °C^{-1}$ were obtained. A significant difference was revealed between ducklings 1 day and 12 days old. In reality, this indicates a lower deep-body cold sensitivity of the oldest ducklings. However, the difference is probably more related to the precision of the method used to evaluate the thermosensitivity, than to genuine differences between the various age groups in deep-body cold sensitivity. As previously pointed out, a general problem in assessing the thermosensitivity of a specific part of the

Table 3 Metabolic rates (*MR*), expressed as a percentage of the peak metabolic rate (PMR), attained by Pekin ducklings of different ages before the deep-body temperature fell below the regulated level measured at thermoneutrality, together with the ambient temperatures (T_a) measured at that time. Values are given as mean ± SD; *N*, number of individuals examined

Age (days)	*N*	T_a (°C)	*MR* (% of PMR)
1	8	0.8 ± 6.4	87.8 ± 13.1
3	7	3.3 ± 7.4	84.6 ± 8.9
6	6	1.4 ± 5.0	85.8 ± 8.0
12	6	−13.9 ± 5.6	91.9 ± 6.2

body, using the thermode technique, is the difficulty in defining the precise stimulation temperature (Mercer and Simon 1984; Reinertsen and Bech 1989). The use of heat-exchangers to extract heat from the body will inevitably give rise to thermal gradients within the stimulated area, i.e. the tissues closest to the thermode will be cooler than more distal tissues. As the exact locations of the thermosensitive neurons are not known, their actual temperature cannot be determined with a high degree of precision. Small differences in the position of the thermocouple, in relation to the heat exchanger, could therefore be responsible for the apparent differences found in deep-body cold sensitivity. Another factor which also could have affected the results is the marked differences in BM of the different age groups. Although we attempted to solve this problem by using larger thermodes for the older ducklings to cool their body core, it is possible that a relatively smaller proportion of the total body core of the oldest ducklings was cooled.

Based on the above argumentation, we suggest that the relatively small differences found between the different age groups are more likely to be a result of the degree of precision of the experimental method, rather than to genuine differences in deep-body cold sensitivity. Furthermore, the range of values obtained by cooling the body core of the ducklings is of the same magnitude as the values reported for adult Pekin ducks, about -5 to -6 $W \cdot kg^{-1} \cdot °C^{-1}$ (Inomoto and Simon 1981). The conformity of the values obtained for the ducklings and those previously reported for adult Pekin ducks suggests that deep-body cold sensitivity is already fully developed at hatching.

To our knowledge, no previous study has investigated the ontogeny of deep-body cold sensitivity in birds. The results of the present study have shown that Pekin ducklings have a highly developed deep-body cold sensitivity which does not seem to differ from that of the adults. These findings contrast with some earlier suggestions, that indicated that bird chicks are less sensitive to changes in their body core temperature than are adult birds (Randall 1943; Klaassen et al. 1989). Based on the absence of a compensatory effect of heat increment of feeding of arctic tern chicks *Sterna paradisaea*, Klaassen et al. (1989) suggested that the thermosensitivity is more peripherally located in chicks as compared to adult birds. Randall (1943) showed that cloacal cooling of 1 week old chickens *Gallus domesticus* did not elicited shivering before T_b was lowered by 1.2 °C. Based on that result, he suggested that shivering was stimulated mainly by cutaneous cold receptors. The experimental method used by Randall (1943) is not particularly well described, wherefore it is impossible to evaluate whether the chickens really experienced central body cooling, or only cooling of more peripheral parts of the cloaca. However, in contrast to young Pekin ducklings, which are able to maintain a stable T_b at T_a close to 0 °C, both chickens and arctic tern chicks showed a marked decline in T_b when exposed to cold during the first week after hatching (Randall 1943; Klaassen et al. 1989). Thus, it is possible that the latter two species are less sensitive to changes in their body core temperature. Whether the contradictory results mentioned above are due to species differences in the development of deep-body cold sensitivity, or could be ascribed to the various experimental techniques used to evaluate the thermosensitivity, requires further investigation.

Due to an apparent lack of error signals in various homeostatic negative feedback system, Somjen (1992) proposed that the performance of autonomic responses is guided by past experience, i.e. autonomic responses are learned at an early age. With respect to the thermoregulatory system, the findings of the present study contradict with that view. Ducklings 1–6 days old had never experienced T_a of above 38 °C or below 28 °C. Despite their obvious lack of experience of cold conditions, they responded to central body cooling with an increase in MR which was related to the intensity of the cooling. Furthermore, as the estimated deep-body cold sensitivity values of ducklings could not be distinguished from the values reported for adult Pekin ducks (Inomoto and Simon 1981), our results indicate that neonate ducklings have a highly developed thermoregulatory system which seems to work in a proper manner without past experience. Clearly, such a system is most likely to be innate.

The RMR measured at thermoneutral conditions increased significantly with age (Table 2). A rapid increase in RMR during the first days after hatching is typical for species with a precocial mode of development (Ricklefs 1974). The RMR values measured for 1 day old Pekin ducklings (6.81 $W \cdot kg^{-1}$) is very close to the value previously reported for newly-hatched, undomesticated, mallard ducklings *Anas platyrhynchos,* 6.75 $W \cdot kg^{-1}$ (Koskimies and Lahti 1964). Numerous studies have suggested that RMR and working capacity are closely related both for adult birds (Kersten and Piersma 1987; Daan et al. 1990; but see Ricklefs et al. 1996) and for chicks (Drent and Klaassen 1989; Klaassen and Drent 1991), i.e. an increase in RMR should be accompanied by an increase in PMR. The results of the present study showed that the PMR of ducklings, in contrast to RMR, did not change with age. Thus, PMR does not seem to be coupled to RMR during the initial period of development. In consequence, the thermogenic capacity decreased from 4.6 to 2.7 in ducklings 1–12 days old. Similar results have also been reported for arctic tern chicks (Klaassen and Bech 1992). The thermogenic capacity determined for 1 day old ducklings (4.6 × RMR) is of the same magnitude as the values reported for adult pekin ducks [4–5 × RMR; Inomoto and Simon (1981)]. It has previously been shown that newly-hatched ducklings have a well-developed thermoregulatory ability, which mainly depends upon a very efficient metabolic cold defence (Koskimies and Lahti 1964; Steen and Gabrielsen 1986; Steen et al. 1989). The findings of the present study are in agreement with that view.

The multiple-input concept for homeothermic thermoregulation has developed from the fact that appro-

priate thermoregulatory effector responses can be elicited by thermal stimulation of nearly all parts of the body (Simon et al. 1986). However, thermoreceptors are not evenly distributed. In Pekin ducks, Inomoto and Simon (1981) found that the body core was six to ten times more sensitive to cooling compared to the skin. They concluded that the overall cold sensitivity depends mainly on thermal signals from deep-body thermoreceptors external to the central nervous system. Since we found that ducklings were also highly sensitive to cooling of the body core, our next aim was to investigate whether the autonomic effector responses elicited by exposing ducklings to cold, could be explained by temperature changes within the body core. As shown in Fig. 3, the ducklings responded to cold exposure by an immediate increase in MR, but the increase in heat production was not paralleled by a concomitant decrease in T_b. In fact, the transition from thermoneutral to cold conditions was associated with a transient increase in T_b. Such an increase in T_b during cold exposure is not unique for ducklings alone, but has also been described in adult pigeons *Columba livia* (Bech and Østnes 1996) and in several mammalian species (Johansen 1961; Timbal et al. 1976; Mercer and Hammel 1989; Székely et al. 1994). According to the concept of proportional control in thermoregulation, an increase in T_b should only have tended to lessen, instead of promote, the thermogenic response. Furthermore, the ducklings attained a MR amounting to 85–92% of PMR before T_b fell below the regulated level at thermoneutrality (Table 3). These results show that the MR increased despite the lack of any apparent error signals from thermoreceptors in deep-body tissue. Hence, deep-body thermoreceptors do not seem to have been important in mediating the metabolic responses observed during cold exposure. Except under extreme conditions, therefore, cold induced changes in MR would seem to be mediated primarily by peripheral thermoreceptors. Whether the transient increase in T_b observed during cold exposure reflects a sustained error signal, used to counteract the thermal input from peripheral thermoreceptors, or an actual increase in the 'preferred' T_b ('set-point') needs to be clarified.

The suggestion that metabolic cold defence is mediated mainly by peripheral thermoreceptors prompts the following question: where are these receptors located? The quantitative importance of error signals from different areas of the skin in birds has not been particularly well studied. The thermal input from cutaneous thermoreceptors is also difficult to quantify, not only because cold exposure results in wide local temperature differences, but also because of possible dynamic signal components (Kuhnen and Jessen 1988). Necker (1977) showed that selective cooling of feathered skin areas in pigeons was effective in eliciting shivering, whereas similar cooling of naked skin areas was ineffective. In Pekin ducks, Inomoto and Simon (1981) estimated the cutaneous cold sensitivity to be about $-0.6\ W \cdot kg^{-1} \cdot °C^{-1}$. This estimate was based on mean skin temperatures, weighted according to their presumed significance. In the present study, we found that ducklings exposed to cold increased their MR by roughly $18\ W \cdot kg^{-1}$ before T_b fell below the regulated level at thermoneutrality. At that time T_{back} had only fallen by 1–2 °C. If feathered skin areas have a cold sensitivity of only $-0.6\ W \cdot kg^{-1} \cdot °C^{-1}$, those areas could only account for a minor proportion (about 3–7%) of the increase in MR observed during the transition from thermoneutral to cold conditions. Thus, if shivering is mainly mediated by thermoreceptors in feathered skin areas, as indicated by the results of Necker (1977), those areas must have a much higher thermosensitivity than has been suggested above. Otherwise, the main contribution to the combined error signal which control metabolic cold defence must be provided by thermoreceptors located in other, still unknown, parts of the body. Naked skin areas does not seem to be a likely candidate (Necker 1977; Schmidt 1982).

To summarise, neonate Pekin ducklings have a highly developed deep-body cold sensitivity, which does not seem to differ from that of the adults. During exposure to cold conditions, however, peripheral thermoreceptors appear to provide the predominant cold signal inputs to the controller. This view accords with the primary aim of homeothermic thermoregulation, namely to maintain a stable internal body temperature.

Acknowledgements We are grateful to Philip A. Tallantire who kindly improved the language.

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Communicated by G. Heldmaier