Ontogeny of avian thermoregulation from a neural point of view

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The ontogeny of thermoregulation differs among (avian) species, but in all species both neural and endocrinological processes are involved. In this review the neural processes in ontogeny of thermoregulation during the prenatal and early postnatal phase are discussed. Only in a few avian species (chicken, ducklings) the ontogeny of some important neural structures are described. In the early post hatching phase, peripheral and deep-body thermoreceptors are present and functional, even in altricial species, in which the thermoregulation is still immature at hatch. It is suggested that the development of peripheral and deep-body thermoreceptors is not responsible for the inability to maintain a stable body temperature at cold ambient temperatures during early postnatal phase, although studies examined the ontogeny of thermoreception only in an indirect manner. Thus, other factors, such as volume to surface ratio and rate of insulation are important. Studies regarding the ontogeny of hypothalamic cold- and warm-sensitivity neurons in precocial species demonstrate that maturation of the hypothalamic temperature sensitivity takes place during the late prenatal and early postnatal period, with a relatively high cold sensitivity of the hypothalamus during the transition from poikilotherm to homeotherm. In addition, incubation temperatures are demonstrated to influence postnatal hypothalamic thermosensitivity. Brain temperature regulation is found to mature during avian ontogeny as well and is demonstrated to coincide with the ontogenic pattern of general thermoregulation in several avian species. Relevant information of the ontogeny of the spinal cord and effector pathways related to the development of avian thermoregulation is lacking. We concluded that both prenatal and early postnatal temperature affects hypothalamic thermosensitivity and consequently condition thermoregulation in later life.

Introduction

Already in 1943, Randall demonstrated that a chicken embryo acts as a poikilotherm and during incubation changes towards a homeotherm, which thermoregulatory development ends up in full-blown homeothermy shortly after hatching (Tazawa *et al.*, 1988; Nichelmann and Tzschentke, 2002). However, not all avian species show the same degree of thermoregulatory maturity at hatch. The ability of neonate birds to cope with variable environmental temperatures ranges from an altricial development pattern, in which the birds are poikilotherm at hatch, to a precocial pattern in which the newly hatched birds have a high thermogenic capacity (Starck and Ricklefs, 1998). Until now the physiological mechanisms behind the thermoregulatory transition during incubation and early life are unknown, although some suggestions have been made. Freeman (1964) and Bernstein (1973) suggested that the development of the thermoregulatory system probably is induced by developmental processes in neural and endocrine regulation. In addition, Marsh and Wickler (1982) and Tazawa *et al.* (1988) suggested that this transition starts with the development of the embryo nervous system and subsequently the embryo develops thermogenic and thermolytic mechanisms (including endocrinological) that enable the neural "controllers" to operate. The second step in this ontogeny starts before the first step is fully completed. Finally, in the post hatch phase, the alteration in surface to volume ratio in the first 10 days of life, determines the maturation and response of the thermoregulatory system (Visser, 1991; Dietz, 1995).

The lack of knowledge concerning the development of thermoregulation during incubation and early life becomes of more interest, since recent studies clearly have shown that perinatal thermoregulatory responses can have a conditioning effect on thermoregulation and performance in later life (Yahav and Hurwitz, 1996; Yahav and Plavnik, 1999; Nichelmann and Tzschentke, 2002; Tzschentke and Basta, 2002; Nichelmann, 2004a, b, c; Yahav *et al.*, 2004a, b; Baarendse *et al.*, 2006). Because this epigenetic adaptation seems to have large effects on later development and performance, it is important to have knowledge about the ontogeny of the thermoregulatory system during the perinatal phase. When this knowledge about ontogeny of thermoregulation (including time and duration) is available, ways to affect this development can be established. The aim of this review is to describe the current state of the art about the ontogeny of thermoregulation in birds. As the ontogeny of thermoregulation includes several processes and is a broad topic, this review will focus on the neural ontogeny of thermoregulation in avian species.

Developmental phases in thermoregulation

In general, the magnitude of thermoregulatory responses and stability of body temperature as a function of perinatal thermal exposure is used to describe the ontogeny of thermoregulation of avian species. For precocial birds, Nichelmann and Tzschentke (2002) distinguished three phases, characterized by different efficiencies of thermoregulatory responses: prenatal phase, early postnatal phase and full blown homeothermy phase. The first, prenatal phase refers to the late incubation period when the efficiency of endothermic reactions is low and the avian embryo is not able to stabilize its body temperature when exposed to thermal exposure. During the second, early postnatal phase, ending at approximately day 10, the young chick is more and more able to stabilize its body temperature when exposed to cold environmental temperatures. The third phase is the one of full-blown homeothermy, starting at approximately day 10 of life. This period is characterized by a more or less constant body temperature, which is to a large extent

independent on ambient temperature, as a result of the activation of thermoregulatory control elements.

According to Tazawa *et al.* (1988, 2001) the transition from a poikilotherm to a homeotherm takes place in four stages, which for a great part correspond with the phases mentioned by Nichelmann and Tzschentke (2002). In the first phase, called the Arrhenius-limited stage, the metabolic rate is directly related to the temperature. In the second phase, the O2-conductance-limited stage, the oxygen consumption, and thus heat production is limited by the rate of oxygen diffusion through the shell and the chorioallantoic membrane. Both these stages correspond with the first phase, described by Nichelmann and Tzschentke (2002). In the third, power limited stage, the embryo has a limited capacity to generate heat in response to cooling, depending on the maturity of the tissues and developmental state of thyroid activity. The final stage is the stage of full-blown homeothermy.

Avian species show variation in the development of thermoregulatory abilities and in the time needed to reach full-blown homeothermy. In several precocial species, the full blown homeothermy is suggested to start at approximately day 10 to 13 after hatching (Spiers *et al.*, 1974; Tzschentke and Nichelmann, 1999; Nichelmann and Tzschentke, 2002), whereas the Mallard duck showed a well-developed ability to regulate body temperature at hatching (Arad *et al.*, 1984).

A completely developed thermoregulatory system is a complex combination of insulative, thermogenic, neural and endocrine control systems. The neural mechanisms involved in the regulation of the body temperature of birds are to a large extent comparable to those in mammals. The differences in the neural organization of thermoregulatory control between both vertebrates appear to be more quantitative than qualitative (Dawson and Whittow, 2000). In general, the neural organization of thermoregulation can be divided into (1) thermoreception and afferent neural pathways, (2) integration of thermal inputs in the central nervous system, and (3) effector pathways for autonomic and behavioural regulation.

Thermoreception

THERMORECEPTORS

The thermosensory function of peripheral areas has been documented by neural recording and confirmation of appropriate thermoeffector responses to local heating and cooling. These studies have verified the involvement of peripheral thermoreceptors in the initiation of thermoregulatory effector mechanisms and thereby their interference in the control of internal body temperature in adult birds. The peripheral thermoreceptor is a transducer of neural origin, which activity changes with a change in its temperature (Hammel, 1968). Detailed investigation has revealed a differentiation of 'warm' and 'cold' spots, which are local areas responding in a dynamic fashion only to warm or cold sensations (Necker, 1972; Hensel, 1981). Irrespective of the initial temperature, a warm receptor will always respond with an overshoot of its discharge on sudden warming and a transient inhibition on cooling, whereas a cold receptor will respond in the opposite way with an inhibition on warming and an overshoot on cooling (Hensel, 1981). Birds appear well provided with peripheral thermoreceptors in the skin, tongue and beak (Dawson and Whittow, 2000).

Selective thermal stimulation of various parts of the body established that adult birds possess thermosensitive neurons located in the deep-body tissue as well (Hammel, 1968; Hensel, 1981; Simon *et al.*, 1986; Dawson and Whittow, 2000). These deep-body thermoreceptors are situated throughout different parts of the body, external to the central

nervous system and provide afferent thermal information to the hypothalamus (Dawson and Whittow, 2000).

ONTOGENY OF THERMORECEPTION

In general and from a teleological point of view, highly efficient autonomic thermoregulation in embryos of precocial birds is not essential for survival, because the embryos are kept warm by the incubating parents (Nichelmann and Tzschentke, 2002). In addition, the high thermal tolerance of the embryos protects them to some extent from disturbances caused by overheating and cooling (Whittow and Tazawa, 1991). Nevertheless, endothermic reactions occur very early during embryonic development, as Lourens *et al.* (2006) recently demonstrated in chicken embryos. From day 8 of incubation, chicken embryos reacted with a short term (<16 min) increase in heat production after decreasing the incubator temperature with 0.3ºC. Additionally, a short term decrease in heat production was found after increasing the incubator temperature with 0.3ºC.

During early embryogenesis of the domestic chicken the peripheral nervous system begins to differentiate (Freeman and Vince, 1974). At day 2-3 of incubation the sensory fibres from facial ganglions begin to enter the brain. Additionally, at approximately the 11th day of the embryonic period the myelinisation of the peripheral nerves is initiated (Freeman and Vince, 1974). Further direct knowledge about the ontogeny of peripheral and deep-body thermoreceptors in avian species is missing. However, several studies determined the ontogeny of peripheral and deep-body thermoreceptors in an indirect way (using local cooling or warming), although these studies only dealt with the presence of thermoreceptors during perinatal (Nichelmann and Tzschentke, 1997) and postnatal life (Randall, 1943; Østnes and Bech, 1997).

In one-week-old precocial chickens, cloacal cooling induced shivering and thereby indicated that the juvenile chicken could sense alteration in body temperature although an immediate metabolic response was not shown (Randall, 1943). A more indirect approach that suggests that thermoreceptors in avian embryos are developed comes from vocalization studies. After internal pipping of the Muscovy duck (*Cairina moschata*) embryo, *i.e.* 3-4 days before hatching, acoustic communication occurs between the embryos of the same clutch and between embryos and the incubating mother. One of the three most important calls in embryos of Muscovy duckling is the distress call (Nichelmann and Tzschentke, 1997). This call is produced by the embryo in uncomfortable situations and seems to give a signal for the incubating mother to help. Immediately after immersing an egg in cold water (20-22ºC), the distress call rate of the embryo increased because of the cold stimulus. After rewarming, this rate decreases again (Nichelmann and Tzschentke, 1997). Østnes and Bech (1997) investigated the cold reception in Shag nestlings (*Phalacrocorax aristotelis*), a large seabird with an altricial mode of development. Thermocouples were implanted in the cloaca, breast and back and the nestlings were exposed to thermoneutral and cold surroundings. Due to lack of a metabolic response to cold surroundings during the first week after hatching, vocalizations were used to provide evidence that the nestlings can detect cold by body cooling. After a significant fall in skin and body temperature the Shag nestlings responded by vocalization at all tested ages (day 1, 3, 6 and 9 post hatching). Based on these finding, it can be concluded that Shag nestlings can sense alterations in body temperature and that the peripheral and deep-body thermoreceptors are well developed at hatching in the altricial Shag nestlings, before the ability of facultative thermogenesis is functional.

All these studies indicate that peripheral and deep-body thermoreceptors are present and functional during the early post hatching phase, even in altricial species where the thermoregulation is still immature. If these results are applicable for other avian species, it

can be concluded that the development of peripheral and deep-body thermoreceptors is not responsible for the inability to maintain a stable body temperature at cold ambient temperature during the early postnatal phase. Thus other factors, such as surface to volume ratio and rate of insulation are involved. These finding imply that the theory of Marsh and Wickler (1982) and Tazawa *et al.* (1988), which stated that the transition from poikilothermy to homeothermy is a two-part process, is plausible.

Integration of thermal inputs

The controller functions in temperature regulation are accomplished by central nervous structures (Hammel, 1968; Hensel, 1981; Simon *et al.*, 1986). These structures form the integrative network by which coupling between certain inputs and different effectors is established. They transform the afferent thermal inputs detected by peripheral and deep-body thermoreceptors into efferent signals that direct the thermoregulatory effectors and provide the set value of the controlled variable. In addition to the integration of signals of peripheral thermoreceptors, thermosensory inputs originating in the spinal cord, the midbrain and the lower brainstem form the basis for the multiple-input concept of thermoregulation (Simon *et al.*, 1986) and interact either in a synergistic or in a antagonistic way (Hensel, 1981).

THERMOREGULATORY CONTROL BY THE BRAIN

About 40 years ago, the preoptic anterior hypothalamic (PO/AH)-area has been identified as a region of the brain, which is sensitive to changes in its local tissue temperature (Hensel, 1981; Stitt, 1983). With microelectrode recordings from the PO/AH-region, various types of units have been identified that respond to local thermal changes (Hensel, 1981). These units are often called 'thermoresponsive neurons' or 'thermodetectors' and are divided into insensitive, warm-sensitive and cold-sensitive units (Pierau *et al.*, 1998; Boulant, 2000). The latter two units are thermally insensitive over part of the temperature range and show either warm-sensitive or cold-sensitive responses only above or below a certain threshold level (Hensel, 1981), although more recent studies demonstrated that sensitive neurons are sensitive over all temperatures, but only react above or below a certain threshold (Boulant, 1996, 2000). Increased activity of hypothalamic warm-sensitive neurons induces an increase in the activity of heat loss mechanisms followed by a decrease in body temperature (Simon *et al.*, 1986). Stimulation of cold-sensitive neurons results in the opposite effect.

Besides the cold- and warm-sensitive neurons, a small number of what are referred to as 'temperature guardian neurons' have been identified in the PO/AH-area of 10-day-old Muscovy ducks (Basta *et al.*, 1997). These neurons are found to be exclusively sensitive to brain temperatures of approximately 36.1°C or 42.3°C. Basta *et al.* (1997) mentioned that these findings support the theory of the existence of two distinct levels of thermal control (Bligh, 1966): (1) the fine narrow control, which operates to keep body temperature within its normal variation and (2) a wide band control, which is normally inactive and is activated only when body temperature deviates markedly from a normal range. The 'temperature guardian neurons' help to maintain brain temperature within the temperature range of 36°C to 42°C.

In general, the hypothalamic area can be considered as the integrator of inputs from the spinal cord, brain, and peripheral plus deep-body thermoreceptors, rather than the sole and local controller of the thermoregulatory response, and plays a dominant role in regulation of the internal body temperature (Hammel, 1968; de Witte and Sessler, 2002). It appears that the entire brainstem from the septal-preoptic region through the caudal posterior

hypothalamus participates both in the sensing of temperature, the integration of afferent pathways from sites of peripheral thermal stimulation, and the organisation of the efferent pathways (Hensel, 1981). It can be concluded that several regions of the brain, especially the hypothalamic area, are important in the control of thermoregulation.

ONTOGENY OF BRAIN STRUCTURES INVOLVED IN AVIAN THERMOREGULATION

Studies with regard to the embryogenesis (Freeman and Vince, 1974; Rogers, 1995; Starck and Ricklefs, 1998) showed that the brain of the domestic fowl begins to differentiate as early as the second day of incubation. The development of the brain continues throughout the prenatal phase as well as during the first three weeks post hatching (Rogers, 1995). A remarkable observation is the considerable difference in the relative brain size of the hatchlings between altricial and precocial birds. Altricial chicks hatch with relatively small brains that exhibit considerable postnatal size increase, whereas precocial chicks hatch with relatively large brains that show less growth during the postnatal period (Starck and Ricklefs, 1998). This could imply that the brain of precocial avian species matures mainly during the embryonic period, whereas the brain of altricial species still develops for a larger proportion during the post hatching period. This difference in relative brain development could be one of the causes of the differences in thermoregulatory abilities between altricial and precocial species at hatching.

During early embryogenesis the primitive forebrain divides into two subdivisions; the telencephalon (endbrain) and the diencephalon. From a thermoregulatory point of view the diencephalon is of the main interest, because the hypothalamus develops from this part of the brain. In chicken embryos, the diencephalon starts to differentiate on the third day of incubation. At the 9th day of incubation, the diencephalon is anatomically similar to the diencephalon of a just hatched chicken (Rol'nik, 1970). These findings indicate that the basic brain structures for thermoregulation are formed during the early embryonic period in the domestic chicken, although a direct indication of their functionality in thermoregulation is not verified.

Tzschentke and Basta (2000, 2002) suggested that the increase in thermoregulatory abilities of the young bird during ontogeny is due to the 'maturation' of brain centres for thermoregulation, although an explicit explanation of this statement is not mentioned. The authors reported that the percentage of warm-sensitive and cold-sensitive PO/AH-neurons changed during the early ontogeny of the Muscovy duck, in other words, there seems to be a change in the thermosensitivity of the hypothalamus. Tzschentke and Basta (2000) divided the perinatal (from day 28 of incubation until day 10 post hatching; Muscovy ducklings) development of hypothalamic thermosensitivity into two stages. The first stage between day 28 of incubation and day 5 post hatching is characterized by a high neuronal cold-sensitivity (30% of the PO/AH-neurons) in combination with a low neuronal warm-sensitivity (5% of the-PO/AH neurons) of the PO/AH-region. During the second stage, between day 5 and 10 of age, a qualitative change occurs in the development of hypothalamic thermosensitivity. During this period a significant decrease in cold-sensitivity to 14% (of the PO/AH neurons) was reported in combination with a significant increase in warm-sensitivity to 15% (of the PO/AH-neurons) by the 10th day post hatching. In adult Pekin ducks, the neuronal thermoresponsiveness in the PO/AH-region is characterized by a low cold-sensitivity (6.2% of the PO/AH-neurons) and a high warm-sensitivity (58.3% of the PO/AH-neurons) (Nakashima *et al.*, 1987). It seems, in general, that the higher percentage of cold-sensitive neurons during the prenatal and early postnatal period compared with adult levels and the lower percentage of warm-sensitive neurons indicate a relatively high cold sensitivity of the hypothalamus during the transition from poikilotherm to homeotherm. These results indicate that the cold-sensitive neurons of the

PO/AH-area are developed before the bird is completely homeotherm. At the other hand, for e.g. ducklings, which are already homeotherm at hatch, it can also be assumed that the high cold sensitivity of the hypothalamus in early life is the result of the bad surface to volume ratio.

In addition, Tzschentke and Basta (2002) observed that exposure of Muscovy ducklings to temperatures of 35°C and 38.5°C during the last week of incubation changed the postnatal thermosensitivity of the PO/AH-neurons in all investigated 1-, 5-, and 10-day-old ducklings compared with the ducklings incubated at the control temperature (37.5°C). In 1- and 5- day-old ducklings, the alteration in hypothalamic thermosensitivity was non-specific and was independent of the incubation temperature (high or low). Both high and low incubation temperatures resulted in a significantly higher proportion of cold-sensitive hypothalamic neurons and an increase of warm-sensitive neurons (not significant) compared with the normally incubated ducklings. The proportion of temperature insensitive neurons was decreased. In 10-day-old ducklings, the alterations in hypothalamic thermosensitivity were related to the temperature during incubation. The ducklings exposed to the low incubation temperature had an increased proportion of warm-sensitive neurons and a reduced proportion of cold-sensitive neurons in comparison with the control group incubated at 37.5°C. Prenatal exposure to the high temperature induced the opposite effect. The changes in the thermosensitivity of hypothalamic neurons are suggested to be a result of epigenetic adaptation. Tzschentke and Basta (2002) assumed that the change in neuronal activity may be caused by a down- or upward shift in the range of temperatures over which the respective neurons are temperature sensitive due to exposure to various temperatures during a prenatal period.

In a preceding study, Tzschentke *et al.* (2000) observed a similar non-specific reaction of the PO/AH-neurons to bombesin application during early stage of ontogeny in Muscovy duck. Bombesin is known as a neuropeptide that influences thermoregulation in ectothermic and endothermic vertebrates. In birds, a high density of neurons, immunoreactive to bombesin or bombesin-like peptides, is found in the PO/AH-region (Nicolardi *et al.*, 1988). In adult mammals, bombesin changes the temperature sensitivity of warm-sensitive hypothalamic neurons and causes a transformation of the majority of temperature insensitive neurons into warm-sensitive neurons (Schmid *et al.*, 1993). Thereby, bombesin application simulates the effect of hot climate conditions in the brain. In both 5- and 10-day-old ducklings, bombesin had a significant modulatory effect on neural hypothalamic thermosensitivity, on the firing rate and on the temperature coefficient of the PO/AH-neurons (Tzschentke *et al.*, 2000). The ducklings were able to react to bombesin perinatally (day 28 of incubation and day 1 post hatching), so it seems that bombesin receptors are developed prenatally in Muscovy ducks (unpublished results, cited by Tzschentke *et al.*, 2000).

Arad and co-workers (Arad *et al.*, 1984; Arad, 1989, 1991) investigated the development of central control mechanisms by the examination of the development of brain temperature regulation, a major thermoregulatory characteristic of adult birds, in relation to the development of homeothermy in the precocial mallard duck (*Anas platyrhynchos*), altricial pigeon (*Columba livia*) and precocial chicken hatchlings. Both body and brain temperatures were measured the first week post hatching, while the hatchlings were exposed to thermoneutral temperatures or heat. A large variation in brain temperature regulation within the investigated avian species was reported. The hatchlings of the altricial pigeon were completely poikilotherm, reflected by a brain and body temperature closely following ambient temperature (Arad, 1989). During the post hatching period brain and body temperature of the altricial pigeon hatchling increased exponentially with age and the brain temperature regulation improved rapidly after hatching. In domestic chicken hatchlings, the brain and body temperature increased as a

power function with age and approached adult levels around day 10 (Arad, 1991).

The authors (Arad *et al.*, 1984; Arad, 1989, 1991) suggested that the ontogenic development of the rete ophthalmicum – the avian extracranial heat exchanger – is responsible for the increasing capacity of brain temperature regulation during the post hatching period. Arad *et al.* (1987) demonstrated a power function increase in the available heat exchange area of the rete ophthalmicum with post hatching growth. The number of blood vessels in the retial network, on the other hand, was fixed at the time of hatching. However, evidence for the direct role of the rete ophthalmicum in the development of avian thermoregulation is missing. Moreover, one cannot exclude the possibility that different rates of maturation of peripheral responsiveness and/or some hormonal control systems contribute to an improved brain temperature regulation as well.

THE SPINAL CORD AND AVIAN THERMOREGULATION

In adult birds, the cervical and thoracic levels of the spinal cord appear to be involved in thermoreception (Dawson and Whittow, 2000). Ascending neural activity has indicated the existence of both warm-sensitive and cold-sensitive neurons in the spinal cord of pigeons (Necker, 1975). Besides local thermosensitivity, the spinal cord seems to be the central pathway of peripheral and deep-body thermoreception and thereby plays an important role in the signal transmission of thermal inputs (Hammel, 1968). Studies in spinalized animals have shown that some integration of thermal afferents may already occur at spinal levels (Hensel, 1981).

In the domestic fowl, the spinal cord begins to differentiate the first week of incubation (Rogers, 1995). On day 5 of incubation, the first synapses can be detected and recordings from the spinal cord have revealed the presence of electrical activity beginning on day 4-5 of incubation. By embryonic day 7, the spinal tract is well developed (Freeman and Vince, 1974; Rogers, 1995). Although the basic structures of the spinal cord seem to be developed during embryogenesis, it is unknown whether the spinal cord is fully functional regarding signal transmission and integration of thermal signals during the avian perinatal period.

Effector pathways

After thermosensation by peripheral and deep-body thermoreceptors and the integration of these thermal signals by spinal cord, hypothalamus and some other parts of the brain, an appropriate thermoregulatory response has to be elicited. This thermoregulatory response requires completely developed effector pathways. The effector pathways interact with the sympathetic and parasympathetic nervous system resulting in the stimulation of the endocrine system, *i.e.* thyroid and adrenal gland. Studies regarding embryogenesis showed that on the sixth day of incubation most of the motor neuron cell formation has been completed. The first local proprioceptive muscle reflexes are detected on the 10th day of incubation (Freeman and Vince, 1974; Rogers, 1995). However, further knowledge of the ontogeny of effector pathways involved in avian thermoregulation is largely lacking.

Conclusion

It can be concluded that the knowledge about the ontogeny of neural structures involved in the development of avian thermoregulation is limited. The ontogeny of only some of the important neural structures is described in a few avian species. Studies regarding the

ontogeny of hypothalamic cold- and warm sensitivity neurons in precocial species demonstrate that maturation of the hypothalamic temperature sensitivity takes place during the late prenatal and early postnatal period. In addition, incubation temperatures are demonstrated to influence postnatal hypothalamic thermosensitivity. The findings, discussed in this review indicate that both prenatal and early postnatal temperature can condition thermoregulation of birds in later life.

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