

Heat thermosensitivity of the brain and spinal cord in Greenfinches

Elena V. Sedunova

*Sedunova, E. V., Sechenov Institute of Evolutionary Physiology and Biochemistry of the Russian Academy of Sciences, St. Petersburg, Russia**

Received 14 August 1998, accepted 10 August 1999 (revised by editors)

Heat thermosensitivity of 13 brain areas and of the thoracic and lumbar parts of the spinal cord was studied in freely-moving Greenfinches at different ambient temperatures. Of the brain areas studied, clear vasomotor responses were observed only during local heating of the anterior hypothalamus (POA/POM) and dorsal medulla. The thresholds were $40.9 \pm 0.1^\circ\text{C}$ (POA/POM) and $41.8 \pm 0.4^\circ\text{C}$ (medulla). No respiratory responses could be elicited by local brain heating. By contrast, spinal heating elicited both vasodilation and panting. During thoracic stimulation the vasomotor threshold was $41.7 \pm 0.2^\circ\text{C}$, and the panting threshold was $44.3 \pm 0.1^\circ\text{C}$. During lumbar stimulation the reaction thresholds were higher by 1.2 to 1.5°C and the reactions were weaker. However, lumbar heating retained the ability to activate vasomotor reactions even in moderate hyperthermia. The data suggest that, as in other birds, the spinal cord of passerine birds plays a pivotal role in central thermosensitivity. The mammalian-like hypothalamic thermosensors of birds, on the other hand, may have a role in specific control of brain temperature.



1. Introduction

The thermoregulatory system in all homeotherms has a number of similar traits. Part of them (shivering, pilo- and ptiloerection) results from the parallel development and seem to have arisen independently. However, most of the similar features of homeotherms were inherited from their poikilothermic ancestors. In particular, this is true for thermodetectors in the central nervous system (CNS).

Neurophysiological studies carried out in slices and neurons *in situ* have shown a wide similarity in thermosensitive unit characteristics in mammals and birds (Necker 1975, Simon et al. 1977, Nakashima et al. 1987). Thermosensor localization in CNS regions, the ratio of cold and

warm units, mean values of thermosensitivity and the response to ion balance shifts were found to be similar. Actually, the only difference is the absolute threshold needed for a change in firing rate, which is fully explained by the difference in average body temperature in the two groups of homeotherms.

However, experimental studies of whole organism thermoregulation have indicated that differences exist. In contrast to mammals, the main source of information on core temperature in birds seems to be the spinal cord rather than hypothalamus. In all bird species, local heating or cooling of the spinal cord induces adequate thermoregulatory responses: decrease or increase of metabolism, skin vasomotion, panting, activation or suppression of shivering and changes in thermoregu-

* For reprints, please contact: Esa Hohtola, Dept. of Biol., Univ. of Oulu, P.O. Box 3000, 90401 Oulu, Finland. E-mail: Esa.Hohtola@oulu.fi

latory behavior (Rautenberg 1969, Rautenberg et al. 1972, Hammel et al. 1976, Helfmann et al. 1981, Inomoto & Simon 1981, Bech et al. 1982). In the spinal cord of pigeons, warm- and cold sensitive units have been described (Necker 1981), but their distribution along the spinal cord has not been studied in detail. According to Østnes and Bech (1992), however, the thoracic part of the spinal cord in the pigeon is the most sensitive area, at least with respect to the cold sensors.

On the other hand, local cooling of the avian hypothalamus either does not produce any effector response (Rautenberg et al. 1972, Simon et al. 1976, Avery & Richards 1983) or, when the cooling is excessive, results in paradoxical reactions (Martin et al. 1981). Local heating of the hypothalamus leads mostly to appropriate thermoregulatory responses. However, it should be noted that these reactions are usually observed only when the ambient temperature is higher than thermoneutral and when the degree of heating is considerable (Mills & Heath 1972, Rautenberg et al. 1972, Simon et al. 1976, Snapp et al. 1977, Simon-Oppermann et al. 1978, Avery & Richards 1983, Graf et al. 1983, Mercer & Simon 1987). Even in one of the most "mammalian-like" (according to thermosensitivity) species — the emu — it was necessary to increase the hypothalamic temperature by 1.6–2.6°C to obtain an effector response (Jessen et al. 1982). The analogous value for mammals is 0.2–0.4°C (Dymnikova 1979).

It is theoretically possible that when the hypothalamic thermosensors are turned off from participating in organismal thermoregulation the role of main brain afferents is taken over by the neurons of the other brain areas. In fact, experiments in ducks have shown quite adequate though rather small effector reactions produced by changes in midbrain temperature (Martin et al. 1981, Bech et al. 1982).

Next to nothing is known about the CNS thermosensitivity in passerine birds, the youngest and the evolutionarily most advanced group of birds. Yet the passerines are especially interesting from the point of view of thermoregulation as their small body size means low thermal inertia but requires intensive metabolism to maintain the high body temperature. This poses an important challenge for heat balance regulation. Nevertheless, the experimental data indicate that these birds maintain

temperature homeostasis more precisely than mammals of similar mass (Sedunova 1992, 1994). Besides, it is of no small importance that despite their small size passerines are characterized by the same or even greater brain-to-body temperature difference than the larger birds (Sedunova 1992, 1993b). Mills and Heath (1972) have shown appropriate responses to abrupt changes in hypothalamic temperature in sparrows. However, the authors studied only metabolic reactions and locomotor activity of birds and the absence of data on spinal thermosensitivity gives no possibility for comparison.

Therefore the goals of the present work were threefold:

1. To determine the heat thermosensitivity value of different parts of the brain (giving particular attention to hypothalamus and midbrain) as well as thoracic and lumbar sites of spinal cord in small passerine bird, the Greenfinch;
2. To analyze the time course of heat loss responses during simultaneous hypothalamic and spinal stimulation;
3. To study the time course of thermoregulatory reactions during local heating to different degrees, in the thermoneutral zone and at higher and lower ambient temperatures.

2. Materials and methods

The experiments were carried out in 34 freely-moving Greenfinches (*Chloris chloris* L., *Fringillidae*). The mean body mass was 31 ± 1.1 g. Before experiments the birds were kept in individual spacious cages at an ambient temperature of (T_a) 25°C and at 12h:12h LD photoperiod. Water and food were given *ad libitum*.

To induce local changes in spinal temperature, a well isolated flat, oval spiral made of constantan wire (diameter 0.05 mm) was used as an electrical thermode. To heat brain structures, a needle-shaped electrical thermode consisting of two copper wires soldered to a U-shaped, 1.5–2 mm long constantan tip was used. In such thermodes the heating of the constantan tip is 5–6 times higher than that of copper part. Therefore the zone of brain tissue that was in the distance of no more than 1 mm from the constantan part of the ther-

mode was considered a stimulated part. After having been carefully insulated the thermode varnish was used to glue it together with a copper-constantan thermocouple. The heater diameter after the isolation was 0.15–0.17 mm, the total thermode and thermocouple diameter was 0.3 mm.

Body temperature (T_b) was measured with a thermocouple inserted in the colon at the depth of 1.8–2.0 cm; for measuring leg skin temperature (T_{leg}) an analogous thermocouple was fixed with an adhesive tape on the distal part of tarsometatarsus. All changes in temperatures of air, body, leg, and heater were continuously recorded on a multichannel tape recorder. Respiratory frequency (RF) was estimated by recording the time the bird required to make 5 breathing movements.

Thermode and thermocouple implantation was made under pentobarbital (Nembotal) anesthesia (3.6 mg/100 g body mass). In the first series of experiments the back skin and muscles were dissected and the heater was laid on the spinal column and sewed to the muscles. To avoid skin temperature changes during spinal stimulation a gauze pillow filled with eider down was fixed over the heater. The upper part of the pillow was sewed to the skin and the heater was fixed over the lower cervical and three upper thoracic segments of the spinal cord (hereafter the “thoracic part”) or over the last thoracic – three lumbar segments (hereafter the “lumbar part”). In the course of the experiment the heater temperature was measured. During a separate acute test in an anaesthetized bird, whose body temperature corresponded to the level that was characteristic of the activity period, the correlation between the temperature of heater and of the spinal cord inside the spinal channel at different heating temperatures and T_a was estimated. The data presented here reflect the spinal cord temperature estimated with reference to this correlation function.

For studying brain temperature sensitivity a thermode was inserted unilaterally and fixed to the skull with dental cement. The skin on the head was sutured and down feathers were glued on incision site to maximally restore the brain thermal insulation disturbed by the surgery.

The experiments began 7–10 days after the surgery. Local temperature stimulation of the spinal cord (Experiment 1), brain (Experiment 2) or simultaneous heating of the hypothalamus and

spinal cord (Experiment 3) were carried out at $T_a = 25^\circ\text{C}$ (thermoneutral zone) 14–17°C, and 34–37°C. The recordings were made in unrestrained (freely-moving) birds at the first half of the light phase of day. Usually, the recording session lasted 4–5 hours; the birds had *ad libitum* food and water except during measurements. At the end of each experiment with thermal stimulation of the brain structures, the exact thermode location was determined histologically.

3. Results

3.1. Experiment 1. The spinal cord.

At $T_a = 25^\circ\text{C}$ (thermoneutral zone) the mean T_b in Greenfinches was $41.5 \pm 0.2^\circ\text{C}$, spinal temperature (T_{sp}) was $41.2 \pm 0.1^\circ\text{C}$, and T_{leg} was $26.6 \pm 0.3^\circ\text{C}$.

Local temperature increase in the thoracic part of the spinal cord up to $41.7 \pm 0.2^\circ\text{C}$ led to a rapid increase in T_{leg} by 0.9–2.2°C (Fig. 1a). In some cases, an increase of spinal cord temperature by 0.3–0.4°C was enough to induce the response. The effector response depended not only on the heating but also on the initial temperatures of spinal cord and leg skin. Maximal reactions were observed when T_{sp} before the beginning of stimulation was 41.2–42.2°C and the initial T_{leg} was 21–27°C (Figs. 2 and 3). At lower and, especially, higher initial temperatures the effector response was drastically reduced.

Lumbar heating by 0.3–0.5°C could also produce an increase in T_{leg} . However, this was observed only when T_{sp} exceeded $42.9 \pm 0.1^\circ\text{C}$ (Figs. 1b and 4). An additional heating led to an increase in T_{leg} but the effect was smaller than during the thoracic stimulation (Fig. 1). The dependence of effector response on initial T_{sp} and T_{leg} also appeared to be quite different: the maximal reaction was observed when the initial temperature were notably higher (Fig. 2 and 3).

Under thermoneutral conditions, a local increase in T_{sp} induced activation of respiratory heat loss. A rapid increase in RF from 86 ± 1 to 279 ± 12 breaths/min (panting) was seen in birds as the thoracic temperature reached 44–44.5°C or as the lumbar temperature reached 46–47°C (Fig. 4). The resulting sharp increase in heat loss led to a re-

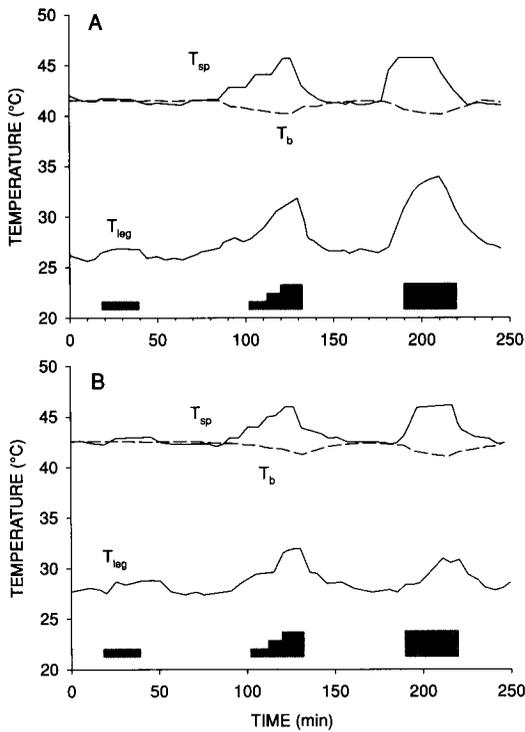


Fig. 1. Time course of body temperature (T_b), spinal temperature (T_{sp}) and leg temperature (T_{leg}) in Greenfinches during a typical experiment with thoracic (A) and lumbar (B) heating. $T_a = 25^\circ\text{C}$. The dark bars denote heating with the thermode.

duction of T_b by $0.3\text{--}1.0^\circ\text{C}$, local heating of the thoracic and lumbar parts having a similar influence on T_b (Fig. 1).

Changes in T_a led to shifts of thresholds for panting and vasodilation (Fig. 4). At low T_a ($14\text{--}17^\circ\text{C}$) the strengths of vasomotor reaction was similar to the thermoneutral values; when T_a exceeded thermoneutrality, thoracic heating resulted in an increase of T_{leg} only by $0.6\text{--}1.2^\circ\text{C}$, while the lumbar heating increased it by $2.7\text{--}3^\circ\text{C}$.

3.2. Experiment 2. The brain.

Heat sensitivity was tested in the following parts of the brain, at thermoneutral temperatures: lobus paraolfactorius, paleostriatum augmentatum, hyperstriatum accessorium, hyperstriatum ventrale, neostriatum intermedium, neostriatum caudale,

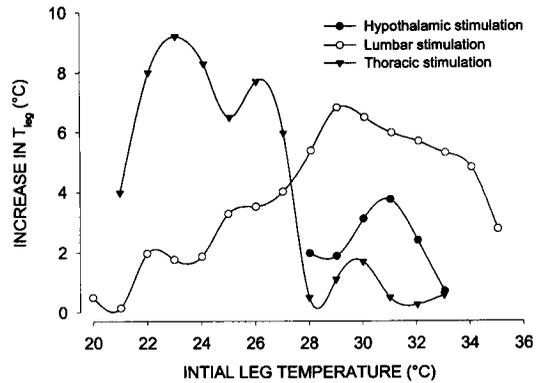


Fig. 2. Mean increase in leg temperature (T_{leg}) of Greenfinches in response to the standard heating of the hypothalamus, thoracic and lumbar parts of the spinal cord by 2°C plotted as a function of initial temperature of the stimulated area. $T_a = 25^\circ\text{C}$.

hippocampus, preoptic area of hypothalamus (nn. preopticus anterior, medialis et paraventricularis), area hypothalami posterioris, nn. lateralis hypothalami et posterioris, thalamus, area of the mid-brain close to n. ruber, medulla dorsale (nn. vestibularis, medialis, solitarius, intermedium, nervi X–IX); cerebellum.

While no panting was observed during the local heating of the brain structures studied, the thermal stimulation of two brain areas — preoptic area and dorsal medulla — led to an increase in T_{leg} .

Under thermoneutral conditions the average preoptic hypothalamic temperature (T_{hyp}) was $40.1 \pm 0.1^\circ\text{C}$. Its local elevation up to $40.9 \pm 0.1^\circ\text{C}$ induced a rapid increase in T_{leg} by $3\text{--}4^\circ\text{C}$ (Fig. 5a). As a rule, the minimal temperature increase necessary to activate the effector reaction was $0.7\text{--}1.0^\circ\text{C}$. Further elevation of T_{hyp} induced a corresponding increase in T_{leg} , but the maximum was attained after a considerable delay. T_b decreased by $0.2\text{--}0.4^\circ\text{C}$ during the stimulation (Fig. 5a). As in the case of the spinal stimulation, the strength of the effector response depended on initial temperatures: the maximal response was observed when T_{hyp} before heating was $39.8\text{--}40.2^\circ\text{C}$ and T_{leg} $27.6\text{--}31^\circ\text{C}$ (Figs. 2 and 3). As in case of spinal stimulation, changes in T_a shifted the reaction thresholds (Fig. 4).

The influence of the local heating of dorsal

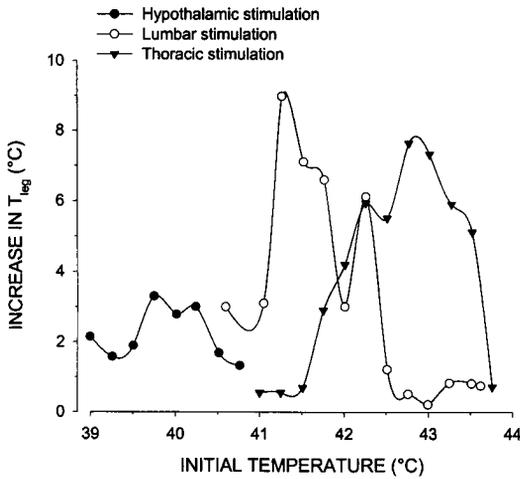


Fig. 3. Mean increase in leg temperature (T_{leg}) of Greenfinches in response to the standard heating of the hypothalamus, thoracic and lumbar parts of spinal cord by 2°C plotted as a function of initial T_{leg} . $T_a = 25^{\circ}\text{C}$.

medulla on T_{leg} was weaker. At $T_a = 25^{\circ}\text{C}$ when the initial temperature of medulla (T_{med}) was $39.9\text{--}40.2^{\circ}\text{C}$ the vasomotor reaction threshold was $41.8 \pm 0.4^{\circ}\text{C}$, the minimal value of heating necessary to activate the response was $1.8\text{--}2.1^{\circ}\text{C}$. The reaction was rather small; as a rule, even when T_{med} reached 44°C , T_{leg} increased only by $2\text{--}3^{\circ}\text{C}$. T_b remained stable (Fig. 5b).

3.3. Experiment 3. Simultaneous stimulation of the preoptic area of hypothalamus and the thoracic part of spinal cord

A separate experimental series was performed to evaluate the influence of simultaneous stimulation of the most thermosensitive brain and spinal areas in Greenfinches on the time course of panting under thermoneutral conditions. The experiments showed that during subthreshold heating of spinal cord to 43.5°C additional elevation to T_{hyp} by $1.5\text{--}2.0^{\circ}\text{C}$ (on average to $41.7 \pm 0.1^{\circ}\text{C}$) resulted in a sharp increase in RF (Fig. 6). Similarly, artificial maintenance of T_{hyp} at the level $41.7\text{--}42.2^{\circ}\text{C}$ and an increase in T_{sp} to 43.5°C elicited panting. No significant drop in T_b was observed (Fig. 6).

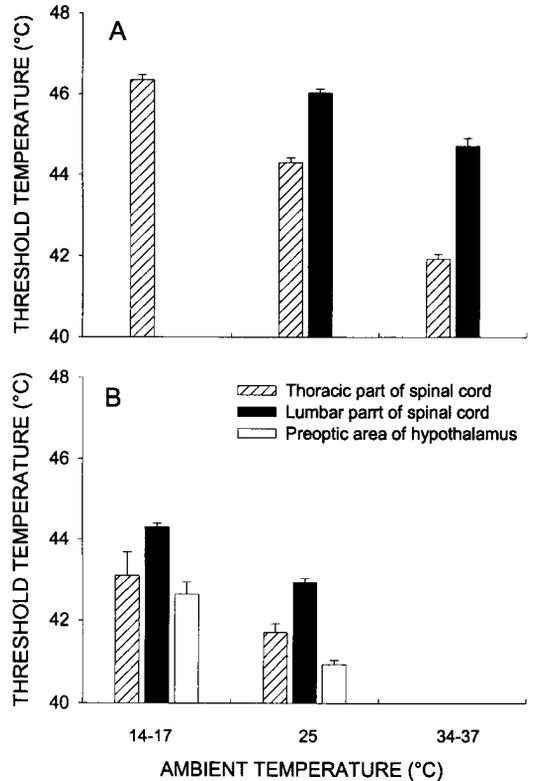


Fig. 4. Mean (\pm SD) panting (A) and vasodilatation (B) thresholds in Greenfinches during hypothalamic, thoracic and lumbar heating at $T_a = 14\text{--}17^{\circ}\text{C}$, 25°C and $34\text{--}37^{\circ}\text{C}$.

4. Discussion

These experiments have shown that spinal thermosensitivity in Greenfinches is similar to that in other birds and mammals (Rautenberg 1969, Simon 1974, Bech et al. 1982, Avery & Richards 1983).

It should be noted that the minimum heating necessary to activate the reactions ($0.3\text{--}0.5^{\circ}\text{C}$) lies inside the limits of the natural core temperature fluctuations characteristic for small animals. However, the strength of effector reaction, i.e. the degree of the leg temperature increase in response to thermal stimulation, is much lower than under natural conditions. In small passerine birds even a short-term spontaneous terrestrial activity or flight can produce the increase in T_{leg} by $10\text{--}13^{\circ}\text{C}$ reached with a rate of $8.5^{\circ}\text{C}/\text{min}$ (Sedunova

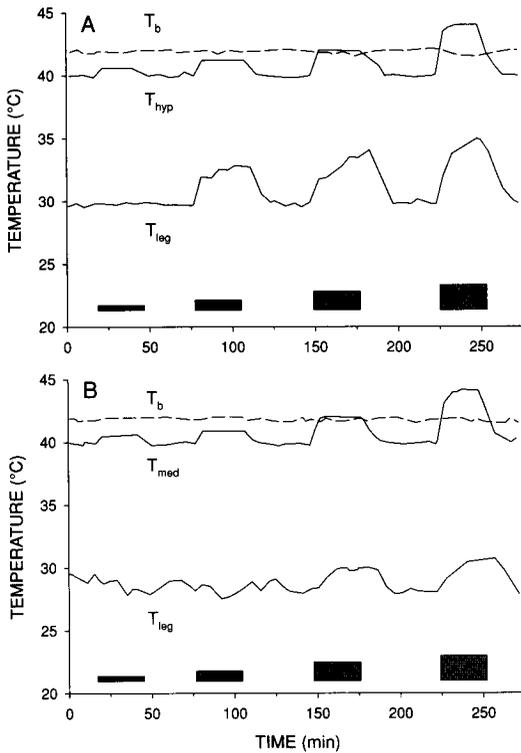


Fig. 5. Time course of body temperature (T_b), brain temperature (T_{hyp} , T_{med}) and leg temperature (T_{leg}) in the Greenfinch during a typical experiment with preoptic (A) and medullar (B) heating. $T_a = 25^\circ\text{C}$. The dark bars denote heating with the thermode.

1993a). The present data show that in Greenfinches the relationships between the increase in T_{sp} and T_{leg} during artificial local heating and during spontaneous temperature fluctuations are quite different (Fig. 7).

Thermosensitivity is inherent both in the thoracic and the lumbar part of the spinal cord in Greenfinches. But its parameters are quite different. The mean threshold for vasomotor activation and panting during thoracic stimulation is much lower than during lumbar stimulation (Fig. 4). Moreover, while a small temperature increase in thoracic and lumbar parts produces nearly the same vasomotor reaction, a further increase of the thoracic zone temperature results in a stronger effector response (Fig. 1). However, the difference in spinal sensitivity is not only concerned with thresholds and strength of the effector reactions. One and the same value of temperature stimula-

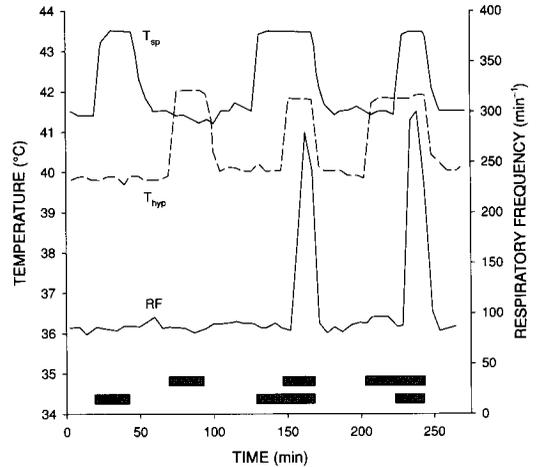


Fig. 6. Time course of spinal temperature (T_{sp}) and hypothalamic temperature (T_{hyp}) as well as respiratory frequency (RF) in the Greenfinch during simultaneous hypothalamic and thoracic heating. $T_a = 25^\circ\text{C}$. The dark bars denote heating with the thermode.

tion leads to the peak response if the initial thoracic temperature is $41.2\text{--}42.2^\circ\text{C}$ or if the initial lumbar one is $42\text{--}43.5^\circ\text{C}$. Similarly, during thoracic heating the most "favourable" initial T_{leg} is $21\text{--}27^\circ\text{C}$, but during lumbar heating it is $25\text{--}34^\circ\text{C}$ (Figs. 2 and 3). Besides, a significantly greater vasomotor response is obtained when the lumbar part is being stimulated at elevated T_a . Thus, if a relatively low T_b signalling from the thoracic part exerts the greatest influence on the temperature homeostasis, then under an increased heat load the lumbar part of spinal cord acquires an important role. It is difficult to say whether this is connected with a lower density of thermosensitive elements in the lumbar zone or with some peculiarities of thermodetector characteristics of this part. In any case, it is important that when heat stimulation of the thoracic part produces only a weak effector response, further rise in T_b may lead to activation of the lumbar thermodetectors and, consequently, to additional heat loss removing the hazard of hyperthermia.

In comparison with other bird species, hypothalamic thermosensitivity in Greenfinches is rather high. The vasomotor threshold and minimum heating necessary to activate the vasodilation are almost the lowest among all avian species studied (Rautenberg 1969, Snapp et al. 1977,

Simon-Oppermann et al. 1978, Jessen et al. 1982). Despite the fact that in contrast to hens, ducks and willow ptarmigans, no panting can be induced in Greenfinches with local hypothalamic heating even at elevated T_a when T_{sp} is rather high (but subthreshold), an additional increase in T_{hyp} may induce panting (Fig. 6). Apparently, as is known for pigeons (Rautenberg et al. 1972), the hypothalamic temperature can influence the respiratory heat loss activation also in Greenfinches.

Judging, however, from the time course of effector reactions it is clear that in Greenfinches preoptic thermosensitivity is noticeably lower than spinal thermosensitivity. Even taking into account that unilateral stimulation of brain structures was used, the difference is substantial. Thermosensitivity in other brain areas was also found to be low. No effector responses could be induced by midbrain stimulation. Heating of the medulla can produce a vasomotor response, but the threshold is still higher than that of hypothalamic stimulation. Thus, in passerines, as in other birds, the hypothalamus seems to occupy a subordinate place in the afferent system. Possibly, the thermosensors of the avian hypothalamus play another role.

One of the most pronounced peculiarities of avian thermoregulation is the constant maintenance of the brain-to-body temperature difference due to the counter current heat exchange in *rete mirabile ophthalmicum* (RMO). In most of the birds studied, T_{hyp} is lower than T_b by 0.7–1.3°C even in thermoneutral zone. In Greenfinches the difference reaches 1.2°C (Sedunova 1993b). A similar phenomenon is observed in some mammals (particularly goats) in hyperthermia or during flight in bats. Characteristically, in these mammals the participation of hypothalamic thermoreceptors in the regulation of the organism's heat balance is drastically reduced (Kluger & Heath 1971, Kuhnen & Jessen 1994).

Mitchell et al. (1987) have suggested that apart from total thermoregulatory system the brain temperature can – at least in some species – be additionally regulated along the feedback circuit between T_{hyp} and arterial blood influx to the base of the brain. In a number of recent works Kuhnen and Jessen (Kuhnen & Jessen 1991, 1994, Kuhnen 1995) clearly demonstrated the participation of the hypothalamus in the control of brain tempera-

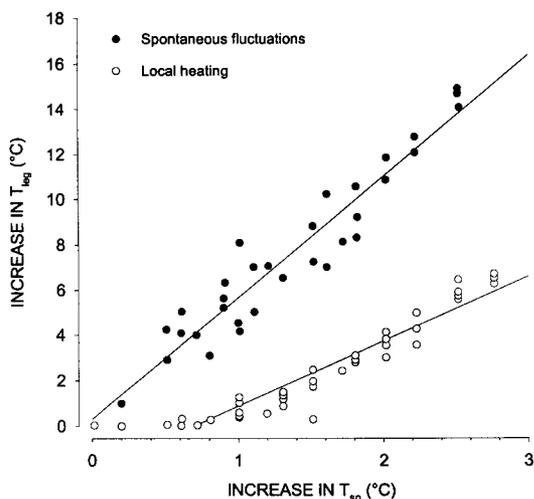


Fig. 7. The increase in leg temperature (T_{leg}) in the Greenfinch plotted as a function of spinal temperature (T_{sp}) shifts during local heating of the spinal cord and during spontaneous core temperature fluctuations. Each point is an individual measurements. $T_a = 25^\circ\text{C}$.

ture. These authors independently changed or maintained the temperatures of hypothalamus, other parts of the brain, body and arterial blood in goats. The results showed that local heating of hypothalamus induced a marked decrease in extra-hypothalamic temperature and, consequently, establishment of the brain-to-body temperature difference due to vasodilatation in the carotid network that is not homologous but analogous to the RMO in birds. Possibly, the highly sensitive "mammalian-like" hypothalamic thermoreceptors of birds discovered by electrophysiological experiments also take part in specific control of brain temperature rather than in thermoregulation of the whole organism.

Selostus: Viherteipon aivojen ja selkätimen lämpöaisti

Tasalämpöisten eläinten lämmönsäätelyjärjestelmässä on useita samankaltaisuuksia. Osa niistä (esim. lihasvärinä, höyhenten ja karvojen pörhistely) on analogisen kehityksen tulosta. Useimmat samankaltaisuudet ovat kuitenkin homologisia ja siten perua niiden vaihtolämpöisiltä esimuodoilta. Erityisesti keskushermoston lämpöaisti on evolu-

tiivisesti hyvin vanha.

Tässä työssä tutkittiin 13 aivoalueen ja selkäytimen rinta- ja lannealueen lämpöherkkyyttä viherpeipolla. Lämpöstimulaatiot tehtiin ultraohuella (0.3 mm) metallitermodilla. Stimulaation vasteiden indikaattorina käytettiin jalan ihon lämpötilaa, joka kuvaa ääreisverenkierron avulla tapahtuvaa lämmönpoistoa, hengitysnopeutta, joka kuvaa haihtumisen avulla tapahtuvaa lämmönpoistoa, sekä ruumiinlämpötilaa.

Tutkituista aivoalueista vain väliaivojen pohjan (hypotalamus) ja aivorungon (medulla) kattoosien lämpöstimulaatio sai aikaan lämmönsäätelyvasteita: molemmissa tapauksissa havaittiin jalan lämpötilan nousu, mutta ei muutoksia hengitystehdessä. Hypotalamuksessa vasteen kynnyslämpötila oli alempi. Selkäytimen lämmitys sitä vastoin aiheutti sekä jalan lämpötilan nousun että hengitystaajuuden kasvun (läähäytys). Rintanikamien alueella lämpötilakynnys verenkierron muutokselle oli 41.7 ± 0.2 ja läähäytykselle 44.3 ± 0.1 °C. Lannealueen vastaavat kynnysarvot olivat runsaan asteen korkeampia ja vastheet heikompia. Lannealueen lämmitys aiheutti vasteen kuitenkin myös silloin, kun lintu oli lievästi ylikämpöinen. Tulokset osoittavat, että myös varpuslinnuilla selkäytimen lämpöherkkyys on keskeinen osa koko elimistön lämmönsäätelyjärjestelmää. Väliaivojen pohjan lämpöherkkyys liittyy erityisesti aivojen oman lämpötilan säätelyyn.

References

- Avery, P. & Richards, S. 1983: Thermosensitivity of the hypothalamus and spinal cord in the domestic fowl. — *J. Thermal Biol.* 8: 237–239.
- Bech, C., Rautenberg, W., May, B. & Johanssen, 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.
- Dymnikova, L. P. 1979: The thermosensitive neurons of the posterior hypothalamus and the thermoregulation. — *Fiziol. Zh.* 65: 1592–1597. (In Russian with English summary).
- Graf, R., Heller, H. G. & Sakagushi, S. 1983: Slight warming of the spinal cord and the hypothalamus in the pigeon: effects on thermoregulation and sleep during the night. — *J. Thermal Biol.* 8: 159–161.
- Hammel, H., Maggert, J., Kaul, R., Simon, E. & Simon-Opperman, C. 1976: Effects of altering spinal cord temperature on temperature regulation in the Adelie penguin (*Pygoscelis adeliae*). — *Pflügers Arch.* 362: 1–6.
- Helfmann, W., Jannes, P. & Jessen, C. 1981: Total body thermosensitivity and its spinal and supraspinal fractions in the conscious goose. — *Pflügers Arch.* 391: 60–67.
- Inomoto, T. & Simon, E. 1981: Extracerebral deep-body cold sensitivity in the Pekin duck. — *Am. J. Physiol.* 241: R136–R145.
- Jessen, C., Hales, J. & Molyneux, G. 1982: Hypothalamic thermosensitivity in an emu (*Dromiceius novaehollandiae*). — *Pflügers Arch.* 393: 278–280.
- Kluger, M. & Heath, J. 1971: Fluctuation in the preoptic-anterior hypothalamic temperature in the bat, *Eptesicus fuscus*. — *Comp. Biochem. Physiol.* 40A: 809–813.
- Kuhnen, G. 1995: Unilateral selective brain cooling. — *Pflügers Arch.* 430: 1018–1020.
- Kuhnen, G. & Jessen, C. 1991: Threshold and slope of selective brain cooling. — *Pflügers Arch.* 418: 176–183.
- Kuhnen, G. & Jessen, C. 1994: Thermal signals in control of selective brain cooling. — *Am. J. Physiol.* 267: R355–R359.
- Martin, R., Simon, E. & Simon-Opperman, C. 1981: Brain stem sites mediating specific and non-specific effects on thermoregulation in the Pekin duck. — *J. Physiol. (Lond.)* 314: 161–174.
- Mercer, J. & Simon, E. 1987: Appropriate and inappropriate hypothalamic cold thermosensitivity in willow ptarmigan. — *Acta Physiol. Scand.* 131: 73–80.
- Mills, S. & Heath, J. 1972: Responses to thermal stimulation of the preoptic area in the house sparrow. — *Am. J. Physiol.* 222: 914–919.
- Mitchell, D., Laburn, H. P., Nijland, M., Zurovsky, Y. & Mitchell, G. 1987: Selective brain cooling and survival. — *S. Afr. J. Sci.* 83: 598–604.
- Nakashima, T., Pierau, F.-K., Simon, E. & Hori, T. 1987: Comparison between hypothalamic thermoresponsive neurons from duck and rat slices. — *Pflügers Arch.* 409: 236–243.
- 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. — *Progr. Sensory Physiol.* 2: 1–47.
- Østnes, J. & Bech, C. 1992: Thermosensitivity of different parts of the spinal cord of the pigeon (*Columba livia*). — *J. Exp. Biol.* 162: 185–196.
- Rautenberg, W. 1969: Die Bedeutung der zentralnervösen Thermosensitivität für die Temperaturregulation der Taube. — *Z. Vergl. Physiol.* 62: 235–266.
- Rautenberg, W., Necker, R. & May, B. 1972: Thermoregulatory responses of the pigeon to changes of the brain and spinal cord temperatures. — *Pflügers Arch.* 38: 253–260.
- Sedunova, E. V. 1992: The effect of ambient temperature and locomotor activity on the brain temperature in the bullfinch. — *Fiziol. Zh.* 78: 56–62. (In Russian with English Summary).

- Sedunova, E. V. 1993a: Leg temperature in the bullfinch during locomotor activity. — *Zh. Evol. Fiziol. Biochim.* 29: 186–191. (In Russian with English Summary).
- Sedunova, E. V. 1993b: Physiological thermoregulation in the Greenfinch, *Chloris chloris*. — *Zh. Evol. Fiziol. Biochim.* 29: 256–264. (In Russian with English Summary).
- Sedunova, E. V. 1994: Brain temperature in laboratory mice at different ambient temperatures. — *Fiziol. Zh.* 80: 81–88. (In Russian with English Summary).
- Simon, E. 1974: Temperature regulation: The spinal cord as a site of extrahypothalamic thermoregulatory functions. — *Rev. Physiol. Biochem. Pharmacol.* 71: 1–76.
- Simon, E., Hammel, H. & Oksche, A. 1977: Thermosensitivity of single units in the hypothalamus of the conscious Pekin duck. — *J. Neurobiol.* 8: 523–535.
- Simon, E., Simon-Opperman, C., Hammel, H., Kaul, R. & 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-Opperman, C., Simon, E., Jessen, C. & Hammel, H. 1978: Hypothalamic thermosensitivity in conscious Pekin ducks. — *Am. J. Physiol.* 235: R130–R140.
- Snapp, B., Heller, G. & Gospe, J. 1977: Hypothalamic thermosensitivity in the California quail (*Lophortyx californicus*). — *J. Comp. Physiol.* 117: 245–352.