

The Postnatal Development of Homoiothermy in the Norwegian Lemming (*Lemmus lemmus*)

Although many studies concerning the ecology and ethology of the Norwegian lemming (*Lemmus lemmus* L.) have been published¹, little attention has been paid to the physiology of this species. The purpose of this study is to describe the postnatal development of homoiothermy of the lemming. Earlier the development of homoiothermy in the albino mouse and in the golden hamster have been investigated in this laboratory².

Lemmings used in the experiments were obtained from Prof. O. KALELA (Department of Zoology, University of Helsinki), at the beginning of 1963. The animals were kept one pair, or two females and one male, to a cage in the cold room at 11–14°C. The rearing conditions and food were the same as used in the University of Helsinki and described in detail elsewhere¹.

The development of homoiothermy was studied by subjecting young lemmings at different age levels to ambient temperatures (T_A) of 33, 24, 12 and 0°C, and subsequently measuring their body temperature (T_B) at intervals until it was stabilized. The details of the method have been described earlier². Three to five animals were used of each age group. The mean skin temperature was used in all age groups as the measure of T_B .

Oxygen consumption was measured by using the Pauling oxygen analyser (Beckman E 2) with an open circuit system. Measurements were performed at T_A 's of 33, 24 and 12°C. The oxygen consumption was measured after the T_B was stabilized at the T_A used. Thereafter the readings were taken for about 30 min at intervals of 2 min. T_B was measured at the beginning of the measurement and after it.

Muscle shivering was measured using a Grass P-5 A.C. preamplifier and Mingograph 24B jet recorder. Three small safety pin electrodes were attached under the skin on the thigh muscles and on the back³. Muscle activity was measured at T_A 's of 30 and 10–12°C. Recordings were taken at intervals of 5 to 10 min until no further change in T_B occurred. The animals were not restrained during the recordings and were under continuous visual control in small glass containers. The muscle activity was measured, beginning from the age of 6 days. There were two test animals in each age group. The maximum peak-to-peak amplitudes were measured and 10 to 20 measurements averaged.

In Figure 1 an attempt is made to describe the development of homoiothermy. The mean stabilized T_B 's have been plotted against T_A at each age level. The straight diagonal line represents complete poikilothermy. Complete poikilothermy has been observed in the golden hamster up to the age level of 10 days. The curves for the lemming, however, indicate that the metabolic response to cold exists as early as the first postnatal day. From this age level the metabolic response rapidly increases. The increasing insulation and metabolism leads to the regulation at first at higher T_A 's. The normal T_B (35.6°C) at the age level of 3 to 4 days is maintained at T_A of 33°C. At T_A 's of 24 and 12°C, T_B does not decline at the age level of 6–8 days. At the lowest T_A studied, the temperature constancy is achieved at the age of 11 days. When compared with the golden hamster and the mouse, the lemming achieved the homoiothermy 8–12 days earlier. It has been observed that in the collared lemming (*Dicrostonyx rubricatus rubricatus*) the development of thermoregulation is achieved at the age of 11 days at an ambient temperature of 2–4°C⁴.

One of the primary factors of the development of the homoiothermy is the increase of the metabolic rate. The

maximal metabolic rate at each T_A is achieved approximately simultaneously with the homoiothermy at that T_A . No increase in the metabolism during the first ten days was observed in the golden hamster. In comparison with the golden hamster of about the same size, the values for the lemming are definitely higher.

Figure 2 shows the mean maximum muscle shivering potentials at T_A 's of 30 and 10–12°C plotted against T_B .

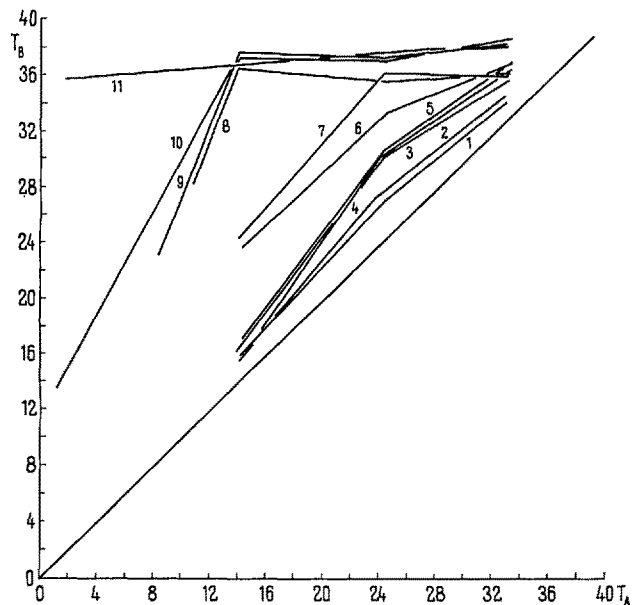


Fig. 1. The mean stabilized T_B of lemmings at different ages as a function of T_A . Age in days.

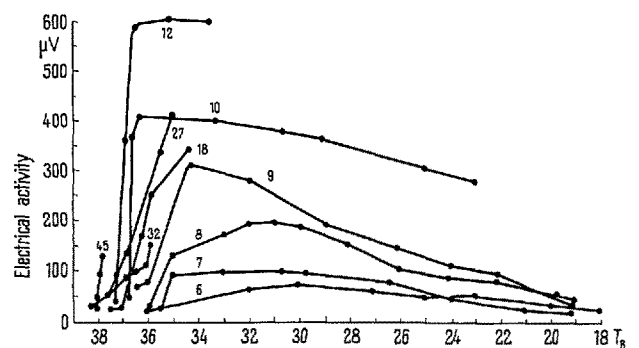


Fig. 2. Mean maximal muscle shivering potentials at different age levels as a function of T_B . Age in days.

¹ T. KOPONEN, A. KOKKONEN, and O. KALELA, Ann. Acad. Sci. fenn. Ser. A IV, 52, 1 (1961). – O. KALELA, Ann. Acad. Sci. fenn. Ser. A IV, 55, 1 (1961). – A. MYLLYMÄKI, J. AHO, E. A. LIND, and J. TAST, Ann. Zool. Soc. 'Vanamo' 24, 1 (1962). – K. ASP, E. BRANDER, and T. KOPONEN, Acta tub. pneumol. scand. 43, 216 (1963). – T. KOPONEN, unpublished.

² K. LAGERSPETZ, Exper. 18, 282 (1962). – R. HISSA and K. LAGERSPETZ, Ann. med. exp. fenn. 42, 43 (1964).

³ K. A. SELLERS, J. W. SCOTT, and N. THOMAS, Am. J. Physiol. 177, 372 (1954). – K. LAGERSPETZ, Ann. med. exp. fenn. 41, 202 (1963).

⁴ P. R. MORRISON, F. A. RYSER, and R. L. STRECKER, J. Mammal. 35, 376 (1954).

The general trend seen is the increase of the shivering potentials and the shift of the maximum to higher T_B 's during the ontogeny. At the age of 6 days, there is only a slight increase in the tonus with cooling and no visible shivering. Visible shivering can also be seen at the age of 7 to 8 days, first on the neck. In comparison with the golden hamster, the shivering appeared 3 to 4 days earlier. The shivering does not reach the intensity observed in the golden hamster and it is perhaps less important in the thermogenesis in the lemming than in the golden hamster.

It appears that the so-called chemical thermogenesis is well developed already on the first postnatal days in the lemming. It can be concluded that the first metabolic response is not correlated with the first signs of the shivering. The metabolic increase without shivering has been shown in the adult rats⁵. Although the effector muscles are present at birth and are capable of activation by their motor neurons, they nevertheless fail to respond to cooling. This is perhaps in connection with the immaturity of the integrating system⁶. On the first postnatal days, the threshold of the integrating centre is so high that only the decline of T_B and now longer-lasting impulse volleys from the receptors can evoke a response of motor neurons⁷. It has been proposed that the improvement in temperature regulation is correlated with the process of myelination of nerve fibres⁸.

The first signs of curling and emotional reactions at the age of 6 days shows that they are also connected with the development of the central nervous system.

As the present results are descriptive in character, further studies should be planned to give information on the following points: (1) The effect of various nest temperatures⁹. (2) The development of the enzyme activities in various tissues. (3) The maturation of the central

nervous system and the endocrines participating in the thermoregulation¹⁰.

Zusammenfassung. Die Entwicklung der Homoiothermie des Feldlemmings (*Lemmus lemmus* L.), wurde durch die Messung der stabilisierten Körpertemperatur, des Sauerstoffverbrauchs und des Kältezitterns in verschiedenen Umgebungstemperaturen studiert. Diese Homoiothermie-Entwicklung ist beim Lemming schneller als bei Maus und Goldhamster.

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⁵ P. HAHN, J. KŘEČEK, and J. KŘEČKOVÁ, *Physiol. Bohemosl.* 5, 283 (1956). – O. HÉROUX, *Am. J. Physiol.* 181, 75 (1955). – J. S. HART, O. HEROUX, and F. DEPOCAS, *J. appl. Physiol.* 9, 404 (1956). – A. C. L. HSIEH and L. D. CARLSON, *Fed. Proc.* 16, 62 (1957).

⁶ P. MORRISON and J. H. PETAJAN, *Physiol. Zool.* 35, 52 (1962).

⁷ K. KOIZUMI, J. L. MALCOLM, and C. McC. BROOKS, *Am. J. Physiol.* 179, 507 (1954). – I. SUDA, K. KOIZUMI, and C. McC. BROOKS, *Am. J. Physiol.* 189, 373 (1957).

⁸ A. R. BUCHANAN and R. M. HILL, *Proc. Soc. exp. Biol. Med.* 66, 602 (1947).

⁹ S. GELINEO and A. GELINEO, *Bull. Acad. Serbe Sci. méd.* 3, 149 (1951).

¹⁰ This study forms Part VI of the series *Contributions to the Biology of the Norwegian Lemming* (for the previous parts see ASP et al.¹). The author wishes to express his gratitude to Prof. O. KALELA and Dr. K. LAGERSPETZ for their advice, and to Miss H. KURPPA and Miss S. TALONEN for their assistance in experiments. This study has been aided by grant from the Finnish Cultural Foundation.

Untersuchungen über das Verhalten von Tumorgewebe in Diffusionskammern gegenüber eindringenden Wirtszellen bei tumorresistenten Ratten

In Vorversuchen wurden Membranfilter (MF) der Gruppen 1–4 und Aerosolfilter AF 250, eingebaut in Diffusionskammern¹, nach 5 Wochen langer i.p. Implantation in Wistar-Ratten auf ihre Durchlässigkeit für Wirtszellen geprüft. Wie zu erwarten war, enthielten die Kammern mit AF 250, die normalerweise nicht für Gewebeimplantationen verwendet werden, massenhaft von aussen eingewanderte Einzelzellen, in der Hauptsache Lymphocyten. Bei MF 1 waren in den Kammern ebenfalls Einzelzellen, aber in weitaus geringerer Anzahl festzustellen und in deutlicher Abstufung auch bei MF 2 und 3 und ganz vereinzelt bei 6 von 10 Kammern mit MF 4. Weiterhin konnte gezeigt werden, dass unter Verwendung von MF 1–6 in Kammern i.p. implantierte Rattennormalgewebe wie Milz, Lymphknoten, Thymus², Lunge und Leber³, von den eindringenden Zellen innerhalb von 10–30 Tagen kaum oder nicht beeinflusst werden. Jensen-Sarcom (JSa)- und Walker-Carcinom (WCa)-Gewebe überlebten in den Kammern mit MF 1–9 in normalen Ratten ebenfalls⁴; bei Kombination von Rattenleber- oder -Lungengewebe mit JSa oder WCa gingen die Normalgewebe nach einer gewissen Überlebenszeit zugrunde. Die Tumor-

gewebe blieben virulent erhalten, wie durch Erzeugung identischer Tumoren nach Transplantation dieser Kammerinhalte auf normale Ratten bewiesen wurde⁴.

Porengrößen der verwendeten Membranfilter
(nach Angaben der Membranfilter-Gesellschaft GmbH, Göttingen)

Bezeichnung		Porendurchmesser in μ m	
		maximal	minimal
Membranfilter	grob	1	1000
	grob	2	800
	grob	3	500
	mittel	4	450
Aerosolfilter	AF 250	mittlerer Durchmesser 1000–3000 μ m	

¹ B. TEICHMANN und G. WITTIG, *Acta biol. med. germ.* 10, 429 (1963); *Z. Naturforsch.* 18b, 526 (1963).

² B. TEICHMANN, unveröffentlicht.

³ B. TEICHMANN und G. WITTIG, *Naturwissenschaften* 50, 673 (1963).

⁴ B. TEICHMANN und G. WITTIG, *Z. Naturforsch.* 19b, 54, 58 (1964).