Correlation between torpor frequency and capacity for non-shivering thermogenesis in the Siberian hamster (*Phodopus sungorus*)

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Abstract

We investigated the correlation between torpor frequency and capacity for non-shivering thermogenesis (NST) in Siberian hamsters (*Phodopus sungorus*) during 25 weeks of acclimation to cold and short days. We hypothesized that torpor use is conditioned on the development of brown adipose tissue (BAT) capacity for NST. We found that (1) the degree of noradrenaline (NA)-induced hyperthermia was positively correlated with torpor frequency and its length and depth, and (2) the maximum response to NA occurred at the time of day when hamsters naturally arouse from torpor. The present study quantifies the correlation between torpor frequency and NST capacity and we suggest that a well-developed NST capacity is a prerequisite for the occurrence of torpor.
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1. Introduction

The Siberian hamster, *Phodopus sungorus*, is a highly photosensitive species that, to a great extent, relies on changes in the photoperiod to cue seasonal acclimatization (Heldmaier and Steinlechner, 1981a, b). When day length shortens, Siberian hamsters switch to their "winter status" characterized by the occurrence of a daily torpor, a decrease in body mass, gonadal regression and molting to a white pelage (Hoffmann, 1973; Heldmaier and Steinlechner, 1981b; Bartness et al., 1989; Ruf et al., 1993). Acclimation to winter conditions also involves improvement of the capacity for non-shivering thermogenesis [NST, (Heldmaier et al., 1982; Heldmaier and Buchberger, 1985; Heldmaier et al., 1985)]. A high capacity for NST is necessary not only because of the low environmental temperature experienced by animals in winter but also because of its role during everyday arousals from torpor and subsequent activity (Smalley and Dryer, 1963; Hayward and Lyman, 1967; Smalley and Dryer, 1967; Janský, 1973). Under laboratory conditions, administration of noradrenaline (NA) activates NST and induces hyperthermia (Janský, 1973).

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The aim of the present set of experiments was to examine the correlation between torpor use and thermogenic efficiency of NST in the Siberian hamster, during 25 weeks of acclimation to cold and short photoperiod (SP). Because both torpor frequency and thermogenic capacity of NST increase with the time of exposure to short and cold days, we hypothesized that torpor use is conditioned on the development of brown adipose tissue (BAT) capacity for non-shivering thermogenesis. To verify our hypothesis, we tested the following predictions: first, that a high frequency of torpor, and thus frequent arousals and return to everyday normothermy, would be correlated with a high capacity for NST, and second that the time of the highest capacity for NST would be correlated with the time of arousal from torpor. Support of our hypothesis will allow us to evaluate the significance of NST for the occurrence of torpor.

2. Materials and methods

2.1. Animals and surgery

Experiments described in this study were done in the Department of Biology of Nara Women's University in Japan. We used 12 adult (3-month old) male Siberian hamsters *Phodopus sungorus* weighing 34.0 ± 1.5 g. Animals originated from our own breeding colony. Hamsters were housed individually in standard laboratory cages ($30 \times 18 \times 17$ cm) where food and water were available ad libitum. Animals were implanted intra-abdominally with wax-coated, pre-calibrated, temperature-sensitive transmitters (MiniMitter, XM-FH; mass: 1.5–1.7 g with wax) under Nembutal anesthesia. After surgery, animals were allowed to recover for 1 week and then were transferred to a climatic chamber (ambient temperature $= 10\,^{\circ}$C; relative humidity $= 60 \pm 5\%$; light regime: 8L: 16D, lights on at 09:00) for 25 weeks. About every 8 weeks, transmitters' batteries were replaced, and after each bout of surgery, animals were allowed to recover for 3 days at T_a of $22\,^{\circ}$C, but with a short photoperiod (SP, 8 h of light). To assess seasonal changes in body mass (m_b), hamsters were weighted every 4 weeks with an accuracy of 0.1 g.

2.2. Experimental design

Every 4 weeks, starting from the first day of acclimation to cold and SP (indicated as "0 week"), we conducted experiments with noradrenaline (NA). Each experiment lasted for 48 h. On the first day of the experiment, half of the hamsters (first group) were injected subcutaneously (s.c.) with 0.6 mg $\cdot$ kg^{-1} of NA ($\pm$Arterenol, Sigma) and the other half were injected with saline in the same volume as NA. On the next day,

the first group was injected with saline while the second group was injected with NA. Injections were administered every 4 h, starting at 09:00, and nighttime injections were administred under dim red light. Experiments after 4 ("4 weeks") and 12 ("12 weeks") of acclimation were done on 12 hamsters and the others ("0 weeks", "8 weeks", "16 weeks", and "20 weeks") on six animals. During all experiments, body temperature (T_b) was recorded at 1 min intervals.

T_b below or equal to $32\,^{\circ}$C was regarded as indicative of torpor (Ruf and Heldmaier, 1992), thus torpor bout duration means the time spent at body temperatures below or equal to $32\,^{\circ}$C. During subsequent weeks of acclimation, all torpor bouts were counted for 12 individuals. Additionally, the number of torpor bouts recorded 1 week before and 1 week after each experiment with NA were counted separately, in order to obtain the most accurate correlation of torpor frequency and the response to NA. Data are presented as mean $\pm$ SE, unless otherwise indicated.

2.3. Data analysis

The results were tested for normality and analyzed with analysis of variance (ANOVA), or the Kruskal–Wallis H test, as appropriate. Because the baseline level of T_b declines with the time of acclimation to cold and SP, an increase in T_b induced by NA injections is presented as the difference between mean T_b recorded within 30 min after- and 30 min before the injection (ΔT_b). A maximum increase in T_b after each NA injection (10–20 min after injection; ΔT_bmax) was also calculated. If an animal was found torpid on the day of the experiment with NA or saline, data were not used for analysis. Three-way ANOVA followed by post-hoc Tukey's HSD test were used to investigate the influence of time of acclimation, time of day and type of injection on ΔT_b. The frequency of torpor was analyzed using the Kruskal–Wallis H test. Spearman rank correlation coefficient (R_S) was used to test for correlation between torpor frequency and ΔT_bmax, and between torpor bout duration and minimum T_b during torpor. Differences were considered statistically significant at $P < 0.05$.

Experiments were performed according to Japanese law (Act No. 105) and the guidelines of the Animal Care (Proclamation No. 6 by Prime Minister's Office).

3. Results

3.1. Body mass (m_b)

Time of acclimation significantly influenced the body mass of hamsters ($F_{6,77} = 5.51$; $P < 0.0001$). The initial m_b, 34.0 ± 1.5 g, was gradually decreasing as time of acclimation increased. After 4 weeks of acclimation m_b

was significantly lower (29.0 ± 1.0 g, $P < 0.05$). After 16 weeks m_b was at its lowest, reaching 26.8 ± 0.6 g ($P < 0.001$). Four weeks later m_b was slightly higher and increased continuously but at the end of the experiment, m_b was still lower than before acclimation (29.4 ± 0.6 g).

3.2. Torpor pattern

The frequency of torpor was clearly correlated with the time of acclimation (Kruskal–Wallis test: $H_{25,312} = 164.43$; $P < 0.001$, Fig. 1). The first torpor bouts were recorded after 6 weeks of exposure while the highest number of torpor bouts was recorded between the 13th and 19th week of acclimation. From week 13 to week 16, all hamsters entered torpor, although its frequency was different among individuals (Kruskal–Wallis test: $H_{9,420} = 42.00$; $P < 0.001$). From week 13 to week 19, the highest number of torpor episodes (40–41) was recorded in two hamsters, while in two others it was the lowest (6–8 bouts). The number of torpor bouts at that time in remaining hamsters ranged from 13 to 33.

The duration of the torpor bouts ranged from 48 min to 13 h 57 min (mean 7 h 28 min $\pm$ 14.8 min) and depended on the time of acclimation (one-way ANOVA: $F_{19,227} = 2.54$; $P < 0.001$, Fig. 1). The duration of torpor bouts lengthened gradually, reached its maximum during the 16th week of acclimation, and then decreased again.

Minimum body temperature (T_b) during torpor was inversely correlated with the duration of torpor ($R_S = 0.80$; $P < 0.0001$). During torpor bouts shorter than 1 h the average minimum T_b was 29.2 ± 0.7 °C, while during bouts lasting for 6–9 h the average minimum T_b was 16.9 ± 0.2 °C. The lowest T_b

(14.6 ± 0.3 °C) was recorded during torpor bouts longer than 12 h.

On average, hamsters entered torpor between 08:00 and 12:00 h (Fig. 2). With the time of acclimation, entrance into torpor occurred earlier. During the period between 8th and 12th weeks of acclimation torpor was initiated between 09:00 and 10:00 h, while during the period of maximum torpor frequency (16th week), hamsters entered into torpor by as much as 2 h earlier. Most often, hamsters returned to normothermia with the beginning of the dark phase of the day, i.e. at about 17:00 h (16:45–18:30 h, Fig. 2). The longest torpor bouts lasting for 10–12 h were terminated late at night (21:00–23:00 h).

3.3. Influence of time of acclimation and time of day on the response to NA

Time of acclimation and type of injection significantly affected changes in T_b within 30 min after injection (three-way ANOVA: $F_{5,461} = 2.29$, $P < 0.05$). While response to saline did not change with the time of acclimation, the response to NA gradually increased until the 16th week, and then decreased (Fig. 3). However, there were no significant differences between saline and NA-injected hamsters.

Time of day influenced an increase in T_b only in NA-injected hamsters (three-way ANOVA: $F_{5,461} = 2.30$, $P < 0.05$, Fig. 4), and the pattern of these variations was similar in all experiments, i.e. it was independent of the time of acclimation. The maximum effect of NA was recorded during the day, i.e. after the injection at 13:00 and 17:00 h. In saline-injected hamsters time of day had no effect.

3.4. Torpor frequency and NA-induced changes in T_b

Time of acclimation influenced the number of torpor bouts recorded 1 week before and 1 week after each NA experiment (Kruskal–Wallis test: $H_{6,498} = 293.29$;
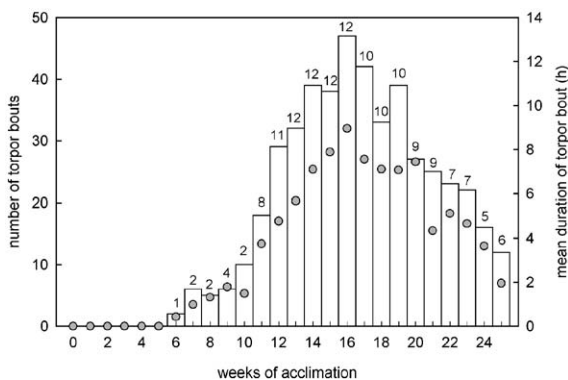

Fig. 1. Total number of torpor bouts (bars), mean duration of torpor bouts (circles, error bars are not presented for clarity) and number of Siberian hamsters found in torpor (numbers above bars) during succeeding weeks of acclimation to cold and short photoperiod.
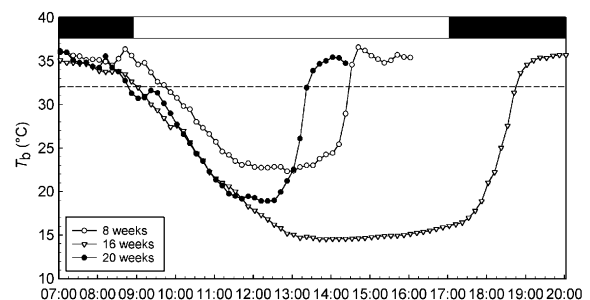

Fig. 2. The examples of torpor bouts recorded in one Siberian hamster during the 8th, 16th and 20th week of acclimation to cold and short days. The white bar at the top of the figure indicates the light phase of the day.
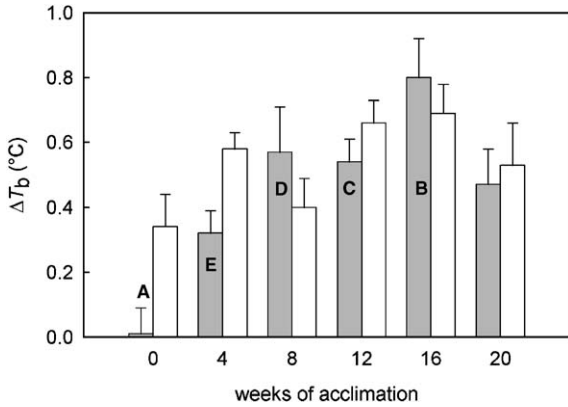
Fig. 3. Influence of time of acclimation on the mean increase (mean for all six injections within one experiment) in body temperature (T_b) of Siberian hamsters after noradrenaline (NA; grey bars) and saline (open bars) injections. Significantly different values within groups are indicated by the superscripts: A – B, A – C: $P < 0.001$, A – D, B – E: $P < 0.01$.
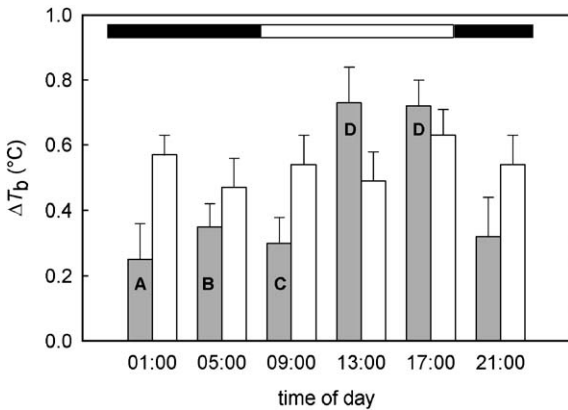

Fig. 4. Influence of time of day on the mean increase (mean for all injections from 0 to 20th week) in body temperature (T_b) of Siberian hamsters after noradrenaline (NA; grey bars) and saline (open bars) injections. Significantly different values within groups are indicated by the superscripts: A – D: $P < 0.001$, C – D: $P < 0.01$, B – D: $P < 0.05$. The white bar at the top of the figure indicates the light phase of the day.

$P < 0.001$). The number of torpor episodes increased gradually from the 8th to 16th week of acclimation and then decreased. The time course of NA-induced hyperthermia followed a similar pattern. After 16 weeks of acclimation, i.e. during the highest torpor frequency, the increase in T_b after NA was the largest ($1.2 \pm 0.13\,°C$). There was a significant correlation between torpor frequency and a maximum NA-induced increase in T_b ($R_S = 0.32$; $P < 0.0001$; Fig. 5). However, when hamsters were analyzed individually, significant correlation was found in six individuals (R_s: 0.45 to 0.80,
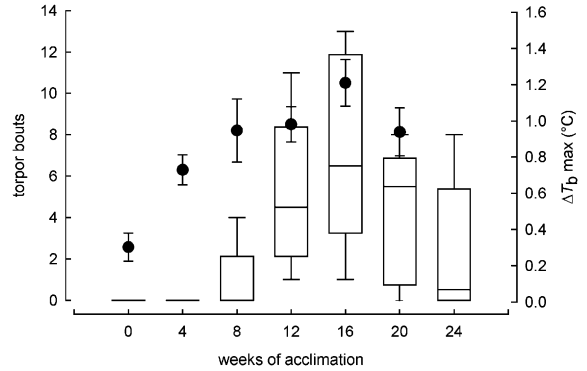

Fig. 5. The correlation between torpor frequency (bars) and maximum increase in body temperature (T_b; circles, mean $\pm$ SE) of Siberian hamsters after noradrenaline (NA) injections. Boxes indicate the lower quartile, median and upper quartile, whiskers indicate minimum and maximum number of torpor bouts.

$P < 0.05$), which showed the most regular torpor pattern, i.e. a gradual increase followed by a gradual decrease of torpor frequency. In the remaining six hamsters, the correlation was either weak or non-existent.

4. Discussion

In the present experiments, all hamsters responded to short photoperiod (SP) and cold with daily torpor, lowered body mass (m_b) and increased capacity for non-shivering thermogenesis (NST).

4.1. Torpor pattern

The frequency and duration of torpor bouts increased gradually, reached its maximum during the 16th week of acclimation, and then shortened again (Fig. 1). In Siberian hamsters, a gradual increase of the frequency and the lengthening of torpor bouts until a maximum in the middle of the winter season followed by a gradual shortening was reported previously (Elliott et al., 1987; Bartness et al., 1989; Kirsch et al., 1991). A similar pattern of gradual lengthening of torpor bouts (with concurrent reduction in the duration of inter-bout normothermy) and then its gradual shortening is commonly observed in hibernating animals during the winter season (French, 1985; Geiser et al., 1990; Barnes and Ritter, 1993). In the present study, torpor bouts were usually limited to the photophase but we also recorded two short bouts, lasting about 1 h (data excluded from analysis), during darkness. Such a restriction to the light phase of the day has been previously reported by Kirsch et al. (1991) and Ruf et al. (1993).

4.2. Body mass

In the present experiments, changes in hamsters' body mass (m_b) followed the typical pattern observed during acclimation to cold and SP. Body mass decreased towards the 16th week of exposure to cold, short days and then began to increase slowly, indicating the period of refractoriness. One might suggest that the gradual decrease in m_b is a result of a compensatory loss of body tissue mass due to transmitters' implantation (Adams et al., 2001). However, similar changes of m_b in the course of acclimation to cold and SP were previously described in Siberian hamsters that were not implanted with transmitters (Elliott et al., 1987; Masuda and Oishi, 1988, also personal observations).

4.3. NST capacity and torpor frequency

In Siberian hamsters, NST is a primary source of heat when they are exposed to cold (Heldmaier and Buchberger, 1985). In the present experiments, noradrenaline (NA) was injected on a daily basis, every 4 weeks. Such an experimental design allowed us to estimate the influence of the time of acclimation and the time of day on NST capacity. The mean increase in body temperature (T_b) after NA reached a maximum after 16 weeks and then decreased again (Fig. 3) reflecting the intra-seasonal changes in the capacity for NST. This pattern of the response to NA also indicates the phenomenon of refractoriness after 20 weeks of acclimation. Heldmaier et al. (1982) reported similar seasonal changes in NST capacity in hamsters living under natural photoperiod. The maximum capacity for NST was recorded during autumn and winter, i.e. from September to February. At the end of the winter NST capacity was reduced (returned) to the summer level.

Although we did not record significant differences between the hyperthermic effects of saline and NA, the dose of NA used in this study induced maximum physiological stimulation of NST (Böckler et al., 1982). A higher dose of NA could induce long-lasting effects and mask the daily rhythmicity of NST. An increase in T_b after saline, reflecting stress of handling and injection, results from activation of the endogenous sympathetic system and stress-induced thermogenesis.

Maximum increase in T_b of NA-injected hamsters was correlated with the time of acclimation and thus with the frequency of torpor (Fig. 5). This correlation may suggest that the ability to enter torpor as well as temporal characteristics of torpor bouts (depth and length), are strongly related to the thermogenic capacity of NST. High capacity for NST is undoubtedly very important during arousal from torpor. We recorded the maximum effect of NA in hamsters acclimated to cold and SP for 16 weeks, when the torpor was used most frequently. Sixteen weeks of acclimation may corre-

spond to the middle of the winter season under natural conditions (probably the most unfavorable period of the year), when animals enter the longest and the deepest episodes of torpor. Thus, a high daily torpor frequency and a high efficiency of NST may ensure winter survival. However, we did not record a correlation between torpor frequency and NA-induced increase in T_b in all hamsters. Most probably it results from inter-individual differences in the use of torpor. In all hamsters, intra-seasonal changes in magnitude of NA-induced hyperthermia were recorded, while some of the hamsters did not show a regular torpor pattern during acclimation. Although we did not perform experiments with NA after 24 weeks of acclimation, when the frequency of torpor decreased, we can predict that the thermogenic effect of NA would be lower.

4.4. The effect of the time of day

The effect of NA depended not only on the time of acclimation but also on the time of day (Fig. 4). The maximum increase in T_b was recorded after daytime injections at 13:00 and 17:00 h, i.e. during the resting phase of the day, when T_b was kept at a low level. This pattern of daily variations might result from the daily rhythm of T_b, and it might also reflect the need for increased heat production at the time of arousal from torpor. The first possibility is supported by the fact that an inverse correlation between baseline T_b and NA-induced increase in T_b was also recorded in the golden hamster *Mesocricetus auratus* (Jefimow et al., 2004). The latter suggestion arises from results of the present study: the largest NA-induced increase in T_b was recorded after the injections at 13:00 and 17:00 h (17:00 h corresponds to the beginning of the dark phase of the day) when torpor was usually terminated. Thus, the significant amounts of heat necessary during reversion to normothermy could be gained by means of NST.

The daily rhythm of the response to NA was also recorded in golden spiny mice (*Acomys russatus*; Kronfeld et al., 1994) and common spiny mice (*A. cahirinus*; Haim and Zisapel, 1999). The maximum response to NA was recorded at the time when T_b and oxygen consumption of control animals were the lowest. As suggested by authors, the daily rhythm of the response to NA could be a result of changes in the level of endogenous NA occupying adrenergic receptors and we also cannot exclude this possibility. In addition, sensitivity of adrenergic receptors could also contribute to observed rhythmicity of NA-induced hyperthermia. In wood mice (*Apodemus sylvaticus*), the daily pattern of the response to NA is opposite, namely, the minimal response was recorded when T_b was low (Haim et al., 1995). Such variations were explained by changes in GDP-binding. (Redlin et al. (1992) found that GDP-binding to BAT mitochondria (which reflects the

thermogenic activity of BAT) in juvenile rats was lower during the low phase of T_b rhythm than during its high phase (Redlin et al., 1992). Thus, the effectiveness of exogenous noradrenaline might be lower when body temperature is maintained at the low level.

One might suggest that repeated injections in the same animals could induce a cumulative effect. However, repeated injections of NA in 4-h intervals do not induce the effect of addition. Before subsequent injection, T_b always returned to the initial level. Adaptation of adrenergic receptors can also be excluded since there was no linear, gradual augmentation of the response to NA. Dicker et al. (1996) found that repeated injections of NA in intervals of 1 h do not induce a phenomenon of refractoriness. In rats, oxygen consumption after NA injection returns to the baseline level within 2 h (Scarpace et al., 1992). Thus, 4-h intervals are long enough to observe an effect of each injection.

5. Summary

If we consider the temporal sequence of the physiological changes that occur during the acclimation to short, cold days, we can see that after the first 4 weeks of acclimation only a significant change in body mass is recorded. After 8 weeks, a significant increase in NA-induced thermogenesis and use of torpor can be seen, while after 16 weeks a maximum level of changes is achieved: the torpor frequency and NST capacity are at their highest, and body mass is at its lowest. Heldmaier and Lynch (1986) summarized seasonal changes in morphological and physiological parameters that occur in Peromyscus leucopus and Phodopus sungorus. They found similar temporal patterns: beginning with a decrease in body mass, and ending with the appearance of daily torpor. However, correlation between NST capacity and torpor frequency was not described in their study.

To the best of our knowledge, the results of the present experiments provide the first evidence of temporal correlation between torpor frequency and NST capacity. A gradual increase in NA-induced hyperthermia confirms the improvement of the capacity for NST during seasonal acclimation. A positive correlation between torpor frequency and maximum increase in T_b induced by exogenous NA reflect the importance of NST for the occurrence of daily torpor. In natural environments, maximum torpor frequency occurs in the middle of the winter season, when ambient temperature is at its lowest. The largest increase in T_b after NA injection during light-to-dark transitions coincides with the usual time of arousal from torpor, at the end of the light phase of the day. A high capacity for NST enables a return to normothermy after daily torpor, and also allows hamsters the option of being active during cold nights.

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