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Effects of Exercise and Intermittent Cold Exposure on Shivering and Nonshivering Thermogenesis in Rats

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Abstract The effects of both exercise training and intermittent cold acclimation on heat production (shivering and nonshivering thermogenesis (NST)) in rats were studied. Warm-acclimated rats (housed at 24°C, WA) and intermittently cold-acclimated rats (exposed daily to −5°C for 2 h, CA) were forced to run (25 m·min^{-1} for 1 h) every day (WA-T and CA-T). WA and CA left sedentary (WA-S and CA-S) served as controls. Norepinephrine (NE)-induced thermogenic capacity assessed from the increment of oxygen consumption ($\dot{V}_{O_2}$) and colonic temperature (T_c) were measured 4 weeks after commencing acclimation and exercise training. The thermogenic capacity was greater in CA than in WA. However, in WA, WA-T responded to NE less than WA-S, whereas the response of CA-T and CA-S did not differ. Wet weight of interscapular brown adipose tissue (IBAT) and its protein (and dry matter——regarded to be highly representative of protein) content were larger in CA than in WA. Respective sedentary and exercised groups of rats had similar IBAT protein (and dry matter) content although tissue weight was lighter in WA-T than in WA-S. Lipid content of IBAT was also larger in CA than in WA. IBAT of WA-T had less lipid compared to that of WA-S while no difference was seen between CA-S and CA-T. Shivering activity during acute cold (4°C) exposure was less in CA compared to WA and there was no difference between respective groups of exercised and sedentary rats. Propranolol, a blocker of NE-dependent NST, eliminated the difference in shivering among these four groups. When exposed to severe cold (−10 or −20°C), the fall in T_c of rats fasted for 18 h was greater in WA than in CA. CA-T showed a greater decrease in T_c than CA-S during −20°C exposure while it did not differ during −10°C exposure. On the other hand, T_c of WA-T and WA-S did not differ significantly during either cold exposure period. These results suggest that exercise training in rats housed at 24°C suppresses NE-dependent NST whereas another nonshivering thermogenic mechanism (NE-independent) may compensate this suppression. However, NE-dependent NST of WA-S and WA-T did not

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parallel protein (dry matter) content of IBAT; no difference existed in IBAT protein between these two groups. Our results also show that exercise training: i) does not suppress NE-dependent NST in CA and ii) does not affect maximal shivering activity of WA and CA.

Key words: exercise training, intermittent cold acclimation, shivering activity, norepinephrine response, brown adipose tissue.

Exercise training has been reported to improve cold tolerance of mammals (CHIN *et al.*, 1973; ÖSTMAN-SMITH, 1979; ASTRUP, 1986) and to retard the loss of cold adaptability of animals that were exercised during the process of cold deacclimation (MORIYA, 1986). The latter study suggests that the greater degree of norepinephrine (NE)-stimulated nonshivering thermogenesis (NST) retained in the exercised, cold-deacclimating animals would exclude the participation of brown adipose tissue (BAT). BAT is thought to be the dominant site of NST in cold-acclimated rats (FOSTER and FRYDMAN, 1978, 1979). In addition, exercise training performed concomitantly with intermittent cold exposure was observed to prevent the increased growth of BAT and the change in energy balance that occurred in sedentary, intermittently cold-exposed rats (ARNOLD and RICHARD, 1987). In other words, exercise performed during intermittent cold exposure appeared to eliminate the cold acclimation observed to occur in sedentary cold-exposed rats. The results of Arnold and Richard (1987) also suggest that if exercise-induced improvement in cold tolerance occurs (CHIN *et al.*, 1973; ÖSTMAN-SMITH, 1979; ASTRUP, 1986), it would not seem to be directly related to BAT thermogenic capacity. However, the mechanism and tissues involved in the interaction between exercise training and cold acclimation (including improved cold tolerance) remain unidentified.

Thus the present study was conducted to examine the effects of intermittent exposure to severe cold followed by exercise training at room temperature on NST and BAT properties in rats. In other words, would intermittent cold exposure and exercise training prove to have an additive effect in terms of improvement in thermoregulatory thermogenesis in rats? Moreover, it was postulated that endurance exercise training, by modifying muscle characteristics (BANCHERO *et al.*, 1979; HURLEY *et al.*, 1986; MÜLLER, 1976) might also alter shivering thermogenesis, which is known to occur via contractions in skeletal muscle. Therefore shivering activity and nonshivering thermogenic capacity were simultaneously evaluated in exercise-trained and intermittently cold-acclimated rats.

MATERIALS AND METHODS

Animals and treatments. Male Wistar rats with a mean initial body weight of 147 g were divided into two groups. One group was housed at 24 ± 1°C for 6 weeks (warm-acclimated rats, WA) and the second group was exposed to -5°C for 2 h

every morning (7 days/week) but lived the remainder of the time at 24 ± 1°C for 6 weeks (intermittently cold-acclimated rats, CA). These WA and CA groups were each further subdivided into two groups, sedentary (WA-S, CA-S) and exercise-trained (WA-T, CA-T) groups. WA-T and CA-T were forced to run daily (7 day/week) at a speed of 25 m·min^{-1} for 1 h on a motor-driven treadmill (mdl 2A, Quinton Instruments, Washington, U.S.A.). Exercise training of WA-T was performed in the morning while CA-T was exercised in the afternoon approximately 2 h after their daily cold exposure. Animals were caged individually and provided standard commercial laboratory chow (Rodent Laboratory Chow No. 5001, Ralston Purina Co., Indiana, U.S.A.) and tap water ad libitum. The animal room was illuminated from 0600 to 1800 H. Food intake and body weight were measured twice a week with spilled food collected, weighed and subtracted from the intake values. These measurements were made for a 4-week period in the experiments, between weeks 2 and 5.

The measurement of oxygen consumption ($\dot{V}_{O_2}$) and colonic temperature (T_c) responses to NE (NE tests) were made 4 weeks into the experiment. Shivering activity was measured in the 5th week, 4 days after completing NE tests. Change in T_c during acute severe cold (−10 or −20°C) exposure (cold tolerance tests) was examined in rats fasted for 18 h during the 6th week of the experiment, approximately 6 days after the measurement of shivering. Six days thereafter, rats were sacrificed by decapitation for analysis of BAT.

NE tests. The calorigenic response to NE administration was assessed by measuring changes in $\dot{V}_{O_2}$ and T_c. Four weeks into the experiment, NE (*l*-arterenol bitartrate, Sigma Chem. Co., St. Louis, U.S.A.) was intramuscularly administered at a free base dose of 200 μg (in 100 μl of 0.9% NaCl)·kg body weight^{-1} in rats anesthetized with pentobarbital (Somnotol, M.T.C. Pharmaceuticals, Mississauga, Canada; 50 mg·kg body weight^{-1}, i.p.; 20 mg·kg body weight^{-1}, s.c. added 45 min later).

$\dot{V}_{O_2}$ was measured by an open circuit system with animals contained in small plastic cages (volume 2,000 ml) in an experimental room at 27 ± 1°C. Air was drawn through the cages at a flow rate of 500 ml·min^{-1} and pumped into an oxygen analyzer (mdl S-3AI, Thermox Instruments Division, Pittsburgh, U.S.A.). $\dot{V}_{O_2}$ was calculated by multiplying the air flow through the cages by the difference in oxygen concentration between room air and air from within the cages. A stable resting $\dot{V}_{O_2}$ of each rat was measured over 45 min, and thereafter $\dot{V}_{O_2}$ response to NE was measured for 60 min following the injection. The first $\dot{V}_{O_2}$ measurements obtained in the resting and in NE response conditions were excluded due to the 15 min equilibration time of this $\dot{V}_{O_2}$ analyzing system.

T_c was measured at rest and 60 min after NE administration using a thermocouple inserted 5 cm beyond the anus.

BAT analysis. Interscapular BAT (IBAT) was dissected and cleaned of adhering muscle, white fat and connective tissue before being weighed. A sample of IBAT (100–200 mg) was put in a lipid-extraction mixture (chloroform : methanol,

2:1 (v/v)) (FOLCH *et al.*, 1951) and thereafter gently shaken for 6 h. Lipid, lipid-free dry matter (essentially protein and carbohydrate), and water content of IBAT were thereafter assayed and calculated as described previously (KUROSHIMA and YAHATA, 1985). The remaining IBAT was homogenized in ice-cold sucrose buffer solution (pH 7.2) and a sample was used for the determination of the total protein content (SCHACTERLE and POLLACK, 1973).

Shivering measurements. Prior to the measurement of shivering, animals were adapted to rest quietly in wire cages custom-constructed to their body sizes. Thus rats did not turn or move excessively once placed in these cages. Shivering activity was measured at 24°C for 5 min in all rats and then at 4°C for 2 min every 15 min for 150 min. Sixty min after commencing cold exposure, propranolol (5 mg·kg body weight^{-1}, s.c.) was injected in order to induce maximal shivering. Shivering activity was assessed from the electromyographic activity of the gastrocnemius muscle, using needle electrodes and a dynograph (mdl R 411, Beckman Instruments Inc., Illinois, U.S.A.). The mean shivering activity of each measurement was quantified from the amplitude of approximately 300 consecutive spikes. T_c was simultaneously measured immediately prior to propranolol injection and 90 min after the injection, as described above.

Cold tolerance tests. After 18 h of fasting, half of the rats from all groups, in their individual wire cages, were exposed to -10°C for 6 h while the remaining rats were exposed to -20°C for 3 to 4 h. During cold exposure, T_c was measured as described above.

Statistics. Data were analyzed using 2×2 analysis of variance to evaluate the significance of intermittent cold exposure, exercise load, and any interaction between these factors. Individual mean comparisons were performed using one-way analysis of variance (ANOVA) and Student's *t*-tests. Data were considered statistically significant if $p < 0.05$. The results are expressed as mean values $\pm$ S.E.

RESULTS

Food intake and body weight gain

As presented in Table 1, food intake (g) for WA-S, CA-S, and CA-T was comparable and significantly larger than that of WA-T. Both exercise training and intermittent cold exposure tended to retard body weight gain (Table 1) although the differences were not significant.

NE tests

Table 2 shows $\dot{V}_{O_2}$ and T_c responses to intramuscularly injected NE in rats from the four groups. Resting $\dot{V}_{O_2}$ of the four groups did not differ. Maximal $\dot{V}_{O_2}$ response to NE was observed to occur consistently with the third air sample (48 to 52 min after NE injection) and for that reason this value was used as representative of NE response. The $\dot{V}_{O_2}$ response to NE, expressed as the difference between resting and maximal response values, was significantly greater in CA compared to

Table 1. Food intake and body weight gain in cold-exposed and exercise-trained rats.

	WA-S ($n=10$)	WA-T ($n=10$)	CA-S ($n=9$)	CA-T ($n=10$)
(1) Food intake (g)	741 ± 10^{a}	701 ± 11^{b}	$734\pm13^{a,b}$	747 ± 15^{a}
(2) Initial body weight (g)	198 ± 4^{a}	191 ± 3^{a}	189 ± 3^{a}	186 ± 4^{a}
(3) Final body weight (g)	342 ± 8^{a}	$325\pm6^{a,b}$	320 ± 6^{b}	313 ± 7^{b}
(4) Body weight gain (g)	144 ± 7^{a}	135 ± 5^{a}	131 ± 7^{a}	127 ± 5^{a}
(5) Food intake × body weight gain^{-1} ((1) · (4)$^{-1}$)	$5.3\pm0.3^{a,b}$	5.3 ± 0.2^{a}	$5.7\pm0.3^{a,b}$	6.0 ± 0.3^{b}

Values are mean ± S.E. WA-S, sedentary warm-acclimated rats (24°C); WA-T, exercise-trained, warm-acclimated rats; CA-S, sedentary cold-acclimated rats (exposed to 4°C for 2 h daily); CA-T, exercise-trained, cold-acclimated rats. Within each row, values not sharing same superscripts are significantly different at $p<0.05$ (e.g. $734\pm13^{a,b}$ is not different from 741 ± 10^{a} or 701 ± 11^{b} but 741 ± 10^{a} is different from 701 ± 11^{b}). These measurements were made over a 4-week period between 2 and 5 weeks. See MATERIALS AND METHODS for further details.

Table 2. Changes in oxygen consumption ($\dot{V}_{O_2}$) and colonic temperature (T_c) induced by norepinephrine (NE) injection in pentobarbital-anesthetized rats following 4 weeks of acclimation and exercise training.

	WA-S ($n=10$)	WA-T ($n=10$)	CA-S ($n=8$)	CA-T ($n=10$)
$\dot{V}_{O_2}$ (ml · kg body weight$^{-0.67}$)				
(1) Resting	16.3 ± 1.09^{a}	$15.7\pm0.67^{a,b}$	$16.4\pm1.38^{a,b}$	16.4 ± 0.67^{b}
(2) 48–52 min after NE injection	30.2 ± 1.50^{a}	24.7 ± 1.12^{b}	36.5 ± 2.59^{c}	$33.1\pm1.19^{a,c}$
(3) Difference ((2)−(1))	$+13.9\pm1.29^{a}$	$+9.0\pm0.90^{b}$	$+20.1\pm1.96^{c}$	$+16.9\pm1.26^{c}$
T_c (°C)				
(1) Resting	37.9 ± 0.19^{a}	37.7 ± 0.14^{a}	37.7 ± 0.12^{a}	37.0 ± 0.26^{a}
(2) 60 min after NE injection	$40.2\pm0.32^{a,b}$	39.2 ± 0.22^{b}	$41.5\pm0.27^{c,d}$	40.4 ± 0.31^{d}
(3) Difference ((2)−(1))	$+2.3\pm0.22^{a}$	$+1.4\pm0.17^{b}$	$+3.8\pm0.29^{c}$	$+3.4\pm0.20^{c}$

Values are mean ± S.E. Abbreviations are the same as those used in Table 1. Within each row, values not sharing same superscripts are significantly different at $p<0.05$. Details of NE tests are given in MATERIALS AND METHODS.

WA. In WA, WA-S showed a greater response to NE than WA-T while no difference was observed between CA-S and CA-T.

Resting T_c of the four groups was also not different among these four groups. T_c response to NE, the difference between resting T_c and T_c measured 60 min after

Table 3. Compositions of interscapular brown adipose tissue (IBAT).

	WA-S ($n=10$)	WA-T ($n=10$)	CA-S ($n=9$)	CA-T ($n=10$)
IBAT				
(1) Wet weight (mg)	366 ± 26^a	277 ± 18^b	757 ± 35^c	662 ± 60^c
(2) Relative weight (mg·100 g body weight^{-1})	102 ± 6^a	87 ± 5^a	218 ± 8^b	199 ± 17^b
(3) Protein (mg)	25.5 ± 1.4^a	28.1 ± 2.1^a	55.1 ± 1.9^b	57.7 ± 2.4^b
(4) Relative protein (mg·100 g body weight^{-1})	7.2 ± 0.46^a	8.9 ± 0.75^a	16.0 ± 0.79^b	17.5 ± 1.0^b
(5) Lipid (mg)	182 ± 21^a	116 ± 6^b	410 ± 18^c	321 ± 33^c
(6) Lipid-free dry matter (mg)	39 ± 3^a	33 ± 2^a	79 ± 6^b	80 ± 7^b
(7) Water (mg)	147 ± 12^a	127 ± 13^a	266 ± 17^b	262 ± 24^b

Values are mean±S.E. Lipid-free dry matter=protein+carbohydrate. Abbreviations are the same as those used in Table 1. Within each row, values that not sharing same superscripts are significantly different at $p<0.05$. See MATERIALS AND METHODS for further details.

NE injection, was greater in CA than in WA while WA-T responded less than WA-S. T_c response in CA-S and CA-T did not differ.

BAT analysis

IBAT weight and its protein (lipid-free dry matter), lipid and water content were greater in CA compared to WA (Table 3). In WA, exercise training decreased IBAT weight and its lipid content, but not its protein (dry matter) content. However, the relative weight of IBAT (relative to body weight) was not different between WA-T and WA-S. Weight and protein content of IBAT was similar in CA-S and CA-T.

Shivering measurements

As can be seen in Table 4, shivering activity assessed from electromyographic recordings (Fig. 1) did not differ at 24°C among the four groups. During 15 to 60 min of cold (4°C) exposure, shivering increased strikingly in WA and moderately in CA. The increment in shivering induced by acute cold exposure was greater in WA than in CA. On the other hand, propranolol injection eliminated the difference in shivering activity between both CA and WA by enhancing shivering in CA more than in WA. No significant difference was observed in shivering between respective sedentary and exercised groups of rats.

T_c measured simultaneously with shivering activity are reported in Table 4. Propranolol injection caused a similar significant fall in T_c in the four groups.

Table 4. Changes in shivering activity and colonic temperature (T_c) during cold exposure for 150 min.

	WA-S ($n=10$)	WA-T ($n=10$)	CA-S ($n=8$)	CA-T ($n=10$)
Shivering activity (μV)				
(1) Resting	19 ± 3^a	26 ± 3^a	23 ± 5^a	36 ± 8^a
(2) Mean of cold exposure before propranolol injection	104 ± 7^a	103 ± 5^a	80 ± 7^b	72 ± 6^b
(3) Difference ((2)−(1))	$+85\pm 7^a$	$+77\pm 6^{a,b}$	$+58\pm 9^{b,c}$	$+34\pm 7^c$
p*	<0.01	<0.01	<0.01	<0.01
(4) 90 min after propranolol injection	136 ± 21^a	156 ± 13^a	141 ± 12^a	126 ± 14^a
(5) Difference ((4)−(2))	$+23\pm 10^a$	$+50\pm 8^{a,b}$	$+59\pm 16^{a,b}$	$+52\pm 8^b$
p*	<0.05	<0.01	<0.01	<0.01
T_c (°C)				
(1) In cold immediately prior to propranolol injection	38.1 ± 0.17^a	38.3 ± 0.11^a	38.1 ± 0.13^a	38.1 ± 0.17^a
(2) 90 min after propranolol injection	35.7 ± 0.82^a	36.0 ± 0.79^a	37.1 ± 0.29^a	37.4 ± 0.28^a
(3) Difference ((2)−(1))	-2.3 ± 0.88^a	-2.3 ± 0.76^a	-1.1 ± 0.37^a	-0.7 ± 0.32^a
p*	<0.05	<0.05	<0.05	<0.05

Values are mean±S.E. p* for difference. Abbreviations are the same as those used in Table 1. Within each row, values not sharing same superscripts are significantly different at $p<0.05$. Details of shivering measurements are given in MATERIALS AND METHODS.

Cold tolerance tests

Change in T_c in rats fasted for 18 h was determined during acute exposure to −10°C (Fig. 2) and −20°C (Fig. 3). Resting T_c was not different between groups. As illustrated in Fig. 2, T_c of CA was higher than their resting T_c 3 to 6 h after commencing exposure at −10°C. On the other hand, T_c of WA-T increased 3 h after commencing −10°C exposure but decreased thereafter. T_c of WA-S did not increase at any time in the experiment. T_c of WA-S was lower than that of CA-S and CA-T during −10°C exposure. WA-T showed lower T_c than CA-S after 3 h of −10°C exposure although no significant difference was observed between WA-S and WA-T or between CA-S and CA-T. T_c of rats decreased faster during exposure at −20 than −10°C, except for CA-S. A few rats of WA had T_c lower than 30°C after 3 h of exposure; cold tolerance test at −20°C was thus terminated for WA after 3 h of exposure. During −20°C exposure, T_c of WA decreased strikingly, T_c of CA-T decreased slightly and T_c of CA-S increased (Fig. 3). CA-T had lower T_c than CA-S while the T_c of WA-T did not differ from those of WA-S during −20°C exposure.

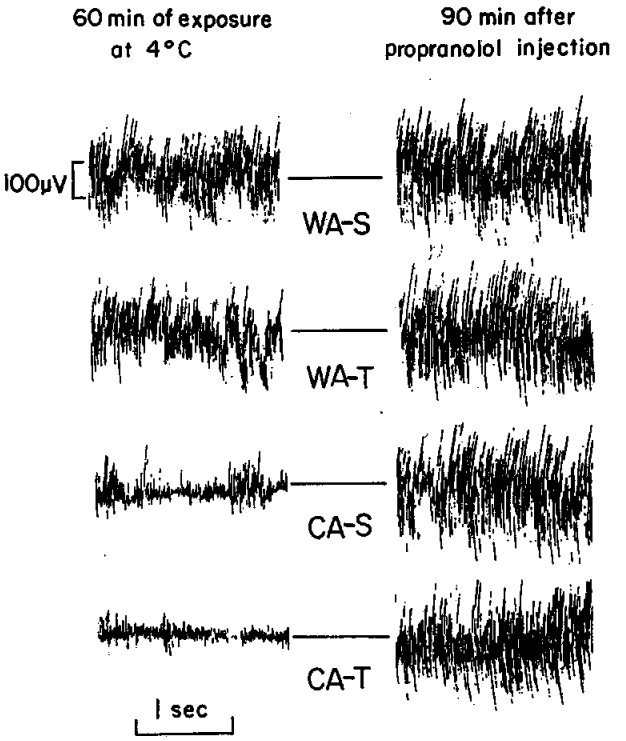

Fig. 1. Examples of typical experimental electromyographs measured in all groups of rats at 4°C before and after propranolol administration (directly photographed from recording sheets). Details of shivering measurements are described under MATERIALS AND METHODS. Abbreviations are the same as those used in Table 1.

DISCUSSION

When compared to WA (WA-S and WA-T), CA (CA-S and CA-T) showed hypertrophy and increased protein content of IBAT (Table 3), greater calorigenic response to NE (Table 2), less shivering activity upon cold exposure (Table 4), and a greater cold tolerance (smaller fall of T_c) in severe cold (Figs. 2, 3). These findings observed in intermittently cold-acclimated rats have been partially reported by other investigators (LEBLANC 1967; LEBLANC *et al.*, 1967; BARNARD and SKALA, 1970; ARNOLD and RICHARD, 1987) and are among the common adaptations detected in chronically cold-acclimated animals (ALEXANDER, 1979). However, food intake of intermittently CA in the present study was not augmented (Table 1) as observed in other studies (HARRI *et al.*, 1984; ARNOLD and RICHARD, 1987). In chronically cold-exposed animals energy intake is generally increased compensatory to increased energy expenditure (HARRI *et al.*, 1984; RICHARD *et al.*, 1986).

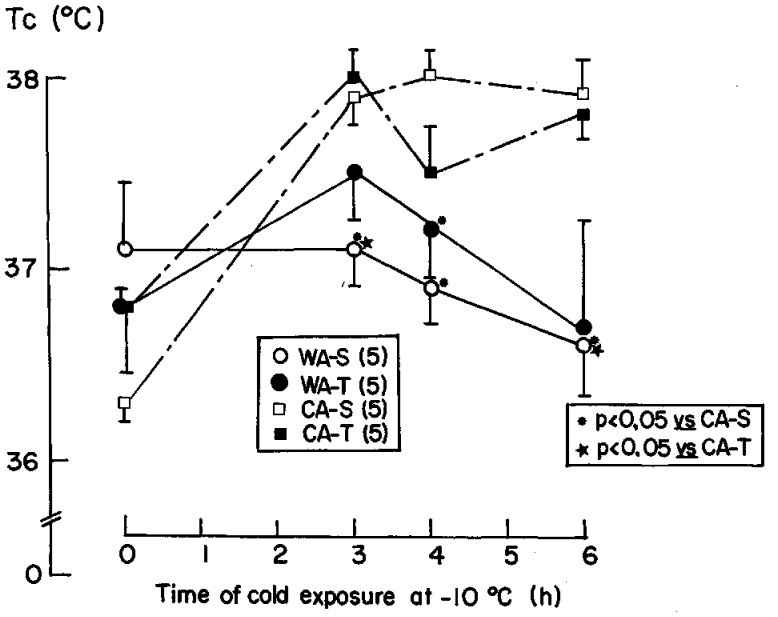

Fig. 2. Time-course change in colonic temperature (T_c) of all groups of rats exposed to −10°C for 6 h. Details of T_c measurements of rats exposed to severe cold (cold tolerance tests) are described under MATERIALS AND METHODS. Abbreviations are the same as those used in Table 1.

After 4 weeks of exercise training, WA-T had less thermogenic response to NE compared to WA-S (Table 2). However, IBAT protein (and lipid-free dry matter regarded to be essentially representative of protein) content, determined 6 weeks after commencing exercise training, did not differ between WA-S and WA-T (Table 3). It is well known in rodents that BAT is the dominant site of NST (FOSTER and FRYDMAN, 1978, 1979) which is mainly mediated by NE (see review of LANDSBERG and YOUNG, 1983). Since overall IBAT protein content is reported to correspond with the mitochondrial uncoupling protein content (directly proportional to BAT thermogenic capacity) of this tissue (DESAUTELS, 1985), diminished NE-induced heat production in our WA-T does not appear related to depressed BAT function. Indeed, contribution of total BAT to NE-induced heat production is approximately 40% in anesthetized warm-acclimated rats (FOSTER, 1984). Thus in WA-T, the response to NE in tissues other than BAT might be decreased, but further studies are necessary to detect the depressed tissue sites of exercise training-induced suppression of NE-stimulated thermogenesis. Although endogenously produced free fatty acids, apart from being the major substrate molecule in oxidative heat production in BAT, also regulate the uncoupling protein in the inner mitochondrial membrane (directly related to heat production) (BUKOWIECKI, 1984; NICHOLLS and LOCKE, 1984), it can not be stated with certainty that the lower fat content in IBAT

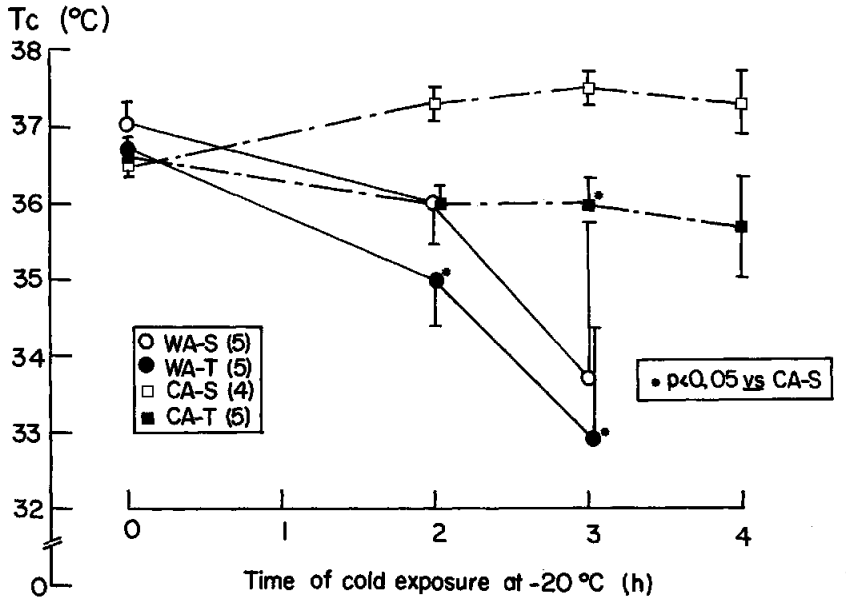

Fig. 3. Time-course change in colonic temperature (T_c) of all groups of rats exposed to −20°C for 3 to 4 h. Details of T_c measurements of rats exposed to severe cold (cold tolerance tests) are described under MATERIALS AND METHODS. Abbreviations are the same as those used in Table 1.

of WA-T (Table 3) causes their diminished calorigenic response to NE. Small amounts of free fatty acids compared to endogenous glycerides can induce heat production in BAT (BUKOWIECKI, 1984; NICHOLLS and LOCKE, 1984) and our lipid measures include both free fatty acids and glycerides. This result has to be interpreted cautiously.

However, WA-T shivered with similar magnitude compared to WA-S when they were exposed to 4°C (Table 4). Since shivering and NST are two heat production systems activated in a cold environment (ALEXANDER, 1979) and T_c of both WA-S and WA-T did not differ during the period of cold exposure for shivering measurement (Table 4), overall NST capacity is inferred not to be different between both groups, even though greater NE-dependent NST exists in WA-S than in WA-T (Table 2). Between both WA-S and WA-T, maximal shivering (following propranolol administration) was also similar (Table 4). Shivering activity after propranolol administration, known to block main NST in rodents (ALEXANDER, 1979), appeared to be close to maximal values since body temperature progressively dropped during the period of cold exposure (Table 4). Shivering in the gastrocnemius muscle was used to predict changes in total shivering capacity of animals. Since shivering in various skeletal muscle was highly synchronous (HEROUX *et al.*, 1956; HOHTOLA, 1982), the values of shivering in the gastrocnemius

muscle are deduced to be representative of total shivering activity of our animals. The results of the cold tolerance tests (Figs. 2, 3) also suggest that WA-T have similar nonshivering thermogenic capacity compared to WA-S. In addition to identical maximal shivering activity (Table 4), decrease in T_c during exposure at $-10°C$ and $-20°C$ was also not different between these two groups. In warm-acclimated rats BAT, as well as heart, respiratory muscles, splanchnic organs, and skeletal muscle, has been shown to respond to infused NE (FOSTER, 1984). Further, other hormones that have been shown to influence BAT NST, such as glucagon (KUROSHIMA *et al.*, 1978; BILLINGTON *et al.*, 1987) and corticosteroids (WÜNNENBERG *et al.*, 1974) might play a significant role in heat production in other tissues of WA-T.

CA-T and CA-S showed comparable thermogenic response to NE (Table 2), similar hypertrophy, and protein content of IBAT (Table 3), similar submaximal (4°C) and maximal (propranolol) shivering activity (Table 4), comparable food intake and body weight gain (Table 1), and similar increase in T_c when exposed to $-10°C$ (Fig. 2). These observations indicate that our moderate-intensity exercise training program performed with daily, short-term cold exposure did not modify any of the adaptations that were observed to occur in our sedentary, intermittently cold-acclimated rats. Exercise (running) performed simultaneously with intermittent cold exposure has been previously shown to suppress cold acclimation (ARNOLD and RICHARD, 1987). However, in CA-T, T_c decrease measured at $-20°C$ was greater than that in CA-S (Fig. 3). In the severe cold environment, fasted CA-T were unable to maintain their body temperature to the same extent as fasted CA-S. The difference might be explained by the finding that fasting depresses overall metabolism, especially in gut and skeletal muscle (MA and FOSTER, 1986) and our trained rats may have had a greater skeletal muscle mass, due to the exercise program. Thus, fasting would have caused a larger depression of metabolism in skeletal muscle of our exercised rats and diminished their ability to augment thermogenesis in the cold. However, CA-T would have had a similar degree of NE-induced nonshivering thermogenic capacity in the fed state compared with CA-S. Thus the overall metabolic response to NE (measured in the normally fed state) appeared similar between sedentary and exercise-trained CA rats despite thermogenic differences between different tissues. However, further studies, possibly involving blood flow and oxygen uptake measurements in individual tissues, are required to test this hypothesis in exercise-trained rats.

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