6. HUMAN ADAPTATIONS TO COLD STRESS

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Abstract

This paper reviews the experimental findings describing human physiological adaptations induced by chronic or repeated cold exposure. The adaptations are classified as acclimatization when they occur naturally as a result of climatic or seasonal changes in temperature, or as acclimation when they occur in response to artificial or experimental manipulations of the ambient thermal environment. Three different patterns of cold adaptation can be identified. Habituation, the most common pattern observed in both acclimatization and acclimation studies, is characterized by a blunted shivering and vasoconstrictor response to cold exposure. Habituation appears to require only brief, intermittent cold exposures to be induced, and can develop when only small body regions are exposed unprotected to cold. It allows extremity skin temperatures to be maintained higher during cold exposure. The higher skin temperatures coupled with the absence of shivering are advantageous in that manual dexterity and comfort are enhanced. In one acclimation study in which subjects were exposed to moderate cold conditions for a prolonged period, a metabolic form of cold acclimation appeared to develop. This adaptation was characterized by an enhanced shivering thermogenesis during cold exposure. When individuals acclimatize or acclimate to cold conditions severe enough to repeatedly cause a significantly body temperature fall, an insulative pattern of adaptation develops, characterized by enhanced mechanisms for body heat conservation. The mechanisms determining the pattern of adaptation to chronic cold exposure appear related to type of cold exposure conditions, the amount of body heat lost and the degree to which shivering thermogenesis compensates for heat loss and defends body temperature.

Introduction

Human thermoregulatory adaptations to chronic cold exposure are less understood than adaptations to chronic heat. Whereas chronic heat induces a fairly uniform pattern of thermoregulatory adjustment among different people, chronic cold produces three different patterns of adaptation. In cold habituation, sometimes referred to as hypothermic habituation, physiological responses to cold are blunted. Metabolic cold adaptations are characterized by enhanced thermogenic response to cold. Insulative cold adaptations are characterized by enhanced body heat conservation.

Physiological adjustments to chronic cold are classified acclimatization or acclimation. Cold acclimatization results naturally from living and working in cold environments, whereas cold acclimation is induced by experimental alterations in environmental conditions (*e.g.* chamber experiments). The distinction is not just semantic, since acclimatization reflects stimuli besides temperature. For example, circumpolar residents not only live in colder climates,

but their diet and day length differs from that of tropical residents. With cold acclimation, nonthermal factors are controlled, so adaptations are directly attributed to temperature. Comparing responses of persons naturally acclimatized to cold and those of persons experimentally cold acclimated, provides a basis to explain the determinants of different adaptation patterns.

Habituation

Habituation, the most common cold adaptation, is characterized by a blunted shivering, blunted cutaneous vasoconstrictor response, or both. Circumpolar residents such as the Inuits (Andersen *et al.*, 1963; Hildes, 1963; Hart *et al.*, 1962), other Native North Americans from the Arctic (Elsner *et al.*, 1960a; Irving *et al.*, 1960a) and Norwegian Lapps (Andersen *et al.*, 1960) respond to whole-body cold exposure in the same general manner as persons from temperate climates. That is, metabolic heat production increases due to shivering, and convective heat loss decreases due to vasoconstriction of peripheral blood vessels. However, these responses may be less pronounced in circumpolar residents, as demonstrated in studies of Norwegian Lapps shown in Figure 1 (Andersen *et al.*, 1960). The Lapps exhibited a smaller increase in oxygen consumption, indicative of less shivering, compared to control subjects. Lapps also maintained warmer skin during cold exposure than unacclimatized persons. Other circumpolar residents also exhibited blunted shivering (Andersen *et al.*, 1963) and blunted vasoconstrictor responses to cold (Rennie *et al.*, 1962; Hildes, 1963) compared to control subjects.

The warmer skin in cold-exposed circumpolar residents than control subjects results from altered vasomotor responses. Inuits maintained higher hand blood flow than unacclimatized subjects during two-hour water immersions at temperatures ranging from 45 °C down to 5 °C, and the difference was greatest at the colder temperatures (Brown and Page, 1952). Elsner *et al.* (1960b) observed that during immersion of the hand in cold water Native Americans from the Arctic exhibited greater hand heat loss than unadapted control subjects. Forearm blood flow during arm immersion in cold water was greater in Inuits than control subjects (Brown *et al.*, 1953). Collectively, these observations indicate that cold-induced vasoconstriction is less pronounced in circumpolar residents than in unacclimatized persons.

The blunted shivering and vasonconstrictor responses that develop with habituation, might lead to a greater fall in core temperature during cold exposure. This is evident in the studies of the Lapps depicted in Figure 1. However, not all cold habituated circumpolar residents manifest hypothermic habituation. Americans native to Arctic regions and unacclimatized subjects do not differ in core temperature response to cold exposure (Rennie *et al.*, 1962; Hart *et al.*, 1962; Andersen *et al.*, 1963; Hildes, 1963; Irving *et al.*, 1960b).

The blunted response to cold is less apparent in young circumpolar residents suggesting that the adaptation is developed over time rather than inherited (Miller and Irving, 1962). Also, other ethnic groups from temperate climates whose occupations necessitate frequent cold exposure of the hands, and people who sojourn in circumpolar regions experience cold habituation (Nelms and Soper, 1962; LeBlanc *et al.*, 1960; Bittel *et al.*, 1989; Carlson *et al.*,
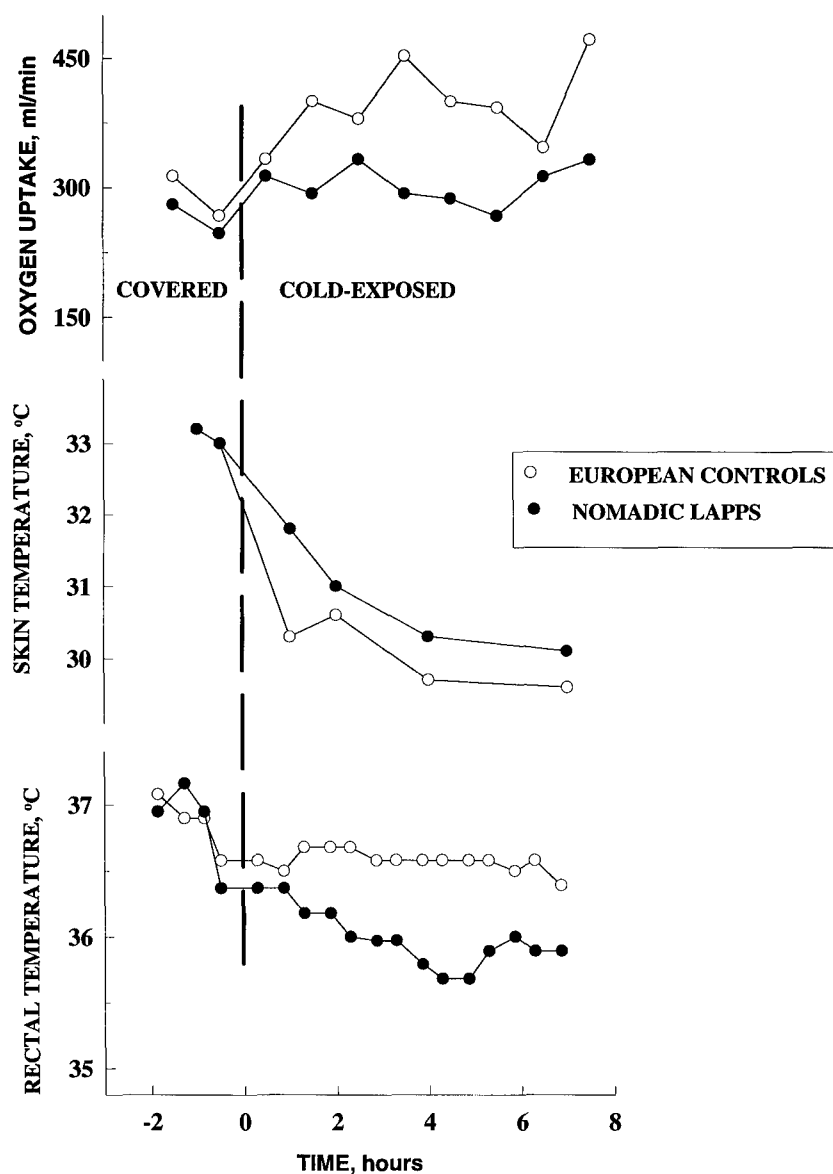
Fig. 1. Physiological responses during overnight cold exposure measured in 9 nomadic Norwegian Lapps and 5 European control subjects. The subjects began the night covered in blankets and lying on a wire mesh bed in a chamber with an air temperature of 0 °C; after 2 hours, the blankets were removed leaving the subjects covered only in a thin windproof cover. Drawn from data of Andersen *et al.* (1960).

Table 1. Acclimation programs employing cold air exposure.

STUDY	COMMENT	Tair	EXPOSURE DURATION	ACCLIMATION CONDITIONS USED ACCLIMATION PERIOD	EFFECTS
Hesslink *et al.* (1992)	chamber; shorts & T-shirts; 16 men	4.4 °C	30 min; twice daily	5 days/week for 8 weeks	shivering habituation
Armstrong and Thomas (1991)	chamber; shorts & T-shirts; 4 women	4 °C	45 min/day	5 days/week for 2 weeks	shivering habituation
Silami-Garcia (1989)	chamber shorts; 5 women	10 °C	1 hr/day	10 of 14 days	shivering habituation
Mathew *et al.* (1981)	chamber; shorts 15 men	10 °C	4 hr/day	21 days	shivering habituation; vasomotor acclimation
Keatinge (1961)	chamber; shorts 5 men	6 °C	7.5 hr/day	17 days	hypothermic habituation
Davis (1961)	chamber; shorts; 6 men in summer; 10 men in winter				
Kreider *et al.* (1959)	chamber; shorts; 5 men	12-14 °C 15 °C	8 hr/day 24 hr/day	31 days 14 days	hypothermic habituation hypothermic habituation (metabolism not measured)
Scholander *et al.* (1958a)	living outdoors in Autumn; light summer clothes and sleeping bags	nighttime temperatu res ~ 5 °C	24 hr/day	6 wks	metabolic acclimation

1953; Milan *et al.*, 1961; Bodey, 1978), even when those cold exposures are rare and brief (Milan *et al.*, 1961; Bodey, 1978). Thus, habituation can occur even when cold exposures are too mild or brief to cause increased body heat loss or a fall in body temperature. Cold acclimation studies confirm this suggestion.

Attempts to induce cold acclimation by repeated cold-air exposure have employed a wide range of temperatures and exposure durations, and Table 1 summarizes findings reported by different investigators. Brief (< 1-hr) cold air exposures, repeated over a two-week period, resulted in blunted shivering but had no effect on body temperature during cold exposure (Hesslink *et al.*, 1992; Armstrong and Thomas, 1991; Silami-Garcia, 1989). In studies employing longer exposure durations and a longer acclimation period, reduced shivering was accompanied by blunted vasoconstriction (Mathew *et al.*, 1981). Habituation of both shivering and vasoconstrictor responses can lead to more pronounced declines in body temperature during cold exposure than occur in unadapted persons exposed to the same conditions (Keatinge, 1961; Davis, 1961; Kreider *et al.*, 1959). Hence, this is termed hypothermic habituation.

On the surface, habituation may not seem beneficial since the thermoregulatory adjustments do not help maintain normal body temperature during cold exposure. However, people living in regions experiencing the most extreme cold weather on earth generally have adequate clothing and shelter to protect them from the cold, so they probably do not experience significant whole-body cooling, thus, explaining the lack of more dramatic thermoregulatory adjustments. On the other hand, periodic short-term exposure of small portions of the body would be common, such as when gloves are removed to complete a task requiring dexterity or when individuals moved through unheated corridors of a polar base. Indeed, when whole body cooling is unlikely, warmer skin and reduced shivering would help conserve energy, improve comfort and prevent peripheral cold-injuries.

Metabolic cold adaptations

Thermoregulatory responses to cold in the Alacaluf people have been cited as evidence for a metabolic cold adaptation (Hammel, *et al.*, 1961; Hammel, 1964). These nomadic Native Americans lived on coastal islands off the southern tip of South America, where the climate was rainy and cool (lows from 0 to 8 °C and highs from 5 to 15 °C). Overall, when they were studied for signs of cold acclimatization, the Alacaluf's way of life was similar to Inuits of the North American Arctic. While the environment was less severe, the Alacaluf's clothing (loin cloth and cloak) and shelter (lean-tos built from scrap lumber) were less protective than that of the Inuits.

During a standardized overnight cold exposure, Hammel *et al.* (1961) observed that metabolic heat production was higher in Alacaluf than unacclimatized subjects. Some researchers consider this evidence of enhanced thermogenesis, or metabolic acclimatization, induced by chronic cold. However, in contrast to the progressive rise in metabolic heat production exhibited by unacclimatized subjects during the overnight cold exposure, Alacaluf

subjects exhibited a progressive fall in heat production, so that the Alacaluf and non-adapted subjects reached similar metabolic rates by the end of the cold exposure (Hammel *et al.*, 1961). Therefore, these people may, in fact, have been exhibiting effects of cold habituation (*i.e.* blunted shivering) rather than an enhanced thermogenic response.

Only one other study reported suggests that an enhanced metabolic response to cold can develop due to repeated cold exposure. Scholander *et al.* (1958a) studied eight students who camped six weeks in the Norwegian mountains during autumn when it was moderately cold, and rain, sleet and snow were frequent. To increase cold stress, the students had only light-weight summer clothing and minimal shelter. As shown in Figure 2, after completing this acclimation period, the campers exhibited a greater increment in metabolism upon cold exposure than unadapted subjects. However, Scholander *et al.* (1958a) failed to measure the responses before the campers underwent the acclimation. It is unclear whether control and acclimation groups were matched for confounding factors such as body composition, physical fitness or age. Therefore, the possibility that repeated cold exposure humans can induce enhanced thermogenic response remains open to question.

Insulative cold adaptations

Studies of the Aborigines living in the central Australian desert suggested an insulative pattern of cold acclimatization (Hicks, 1964; Scholander *et al.*, 1958b; Hammel *et al.*, 1959). Night-time lows in the central Australian desert reach 0 °C in winter and 20 °C in summer; low humidity and clear atmosphere facilitated evaporative and radiative cooling. When these studies were being completed, the central Australian Aborigines were nomadic people who lived out of doors and wore no clothing. They slept on bare ground and their only protection from the cold was a small fire at their feet and wind-break made from light brush.

Whereas metabolic rate of unadapted European subjects sleeping in the cold increased, the Aborigine's metabolic rate remained unchanged as ambient temperature fell at night (Hicks, 1964; Scholander *et al.*, 1958b; Hammel *et al.*, 1959). In contrast to habituated circumpolar residents, the Aborigines exhibited a greater fall in skin temperature than did Europeans which was attributed due to a more pronounced cutaneous vasoconstrictor response to cold (Hicks, 1964; Scholander *et al.*, 1958b). Additionally, the Aborigine's rectal temperature also fell more than in control subjects (Hammel *et al.*, 1959). However, thermal conductance (metabolic heat production divided by the core to skin temperature gradient) was less in the Aborigine than unacclimatized Europeans suggesting that the lower thermal conductance of the Aborigine reflected an enhanced vasoconstrictor response to cold. Alternatively, the Aborigines may have exhibited a lower thermal conductance simply because their shivering had become habituated, but unlike the Inuits and Lapps, vasoconstrictor responses had not.

Long-distance swimmers, surfers and scuba divers all reportedly show a blunted or delayed shivering during cold-water immersion (Dressendorfer *et*

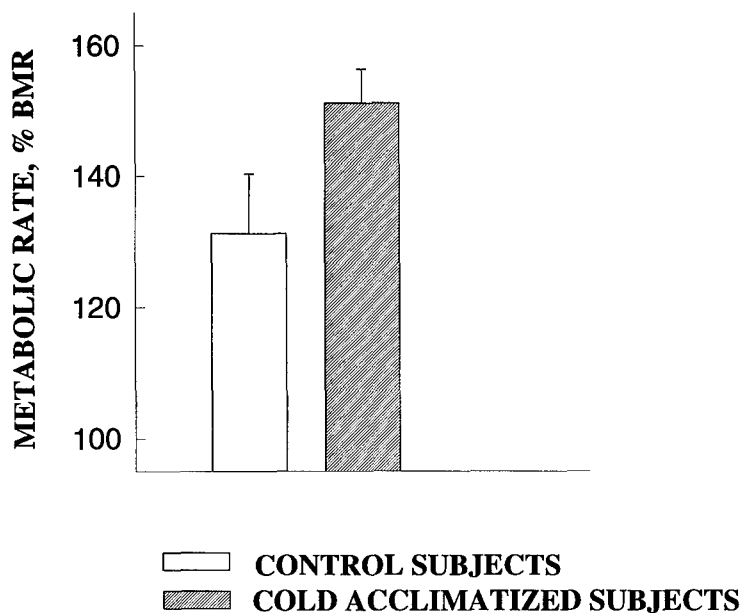## INCREMENT IN RESTING METABOLIC RATE
DURING COLD-AIR EXPOSURE

Fig. 2. Increment in resting metabolic rate exhibited by cold-acclimated and non acclimated subjects during exposure to 20 °C, expressed as a % of basal metabolic rate (BMR) measured in thermoneutral condition. Drawn from data reported by Scholander *et al.* (1958a).

al., 1977; Skreslet and Aarefjord, 1968) suggesting that they have become cold habituated. However, studies of professional breath-hold divers of Korea, the Ama, and their counterparts in Japan, suggest development of a more complex adaptation to repeated cold-water immersion. Traditionally, the divers wore only a light-weight cotton bathing suit which offered little insulation, and they dove year round in water as cold as 10 °C in the winter and 25 °C in the summer (Hong *et al.*, 1987; Hong *et al.*, 1986). During these dives, they experienced marked whole-body cooling. The divers continued working in the water until their core temperature fell about 2 °C (Kang *et al.*, 1965; Kang *et al.*, 1983). These people's willingness to repeatedly subject themselves to such stressful conditions alone seems evidence for their acclimatization to cold. However, thermoregulatory responses of these divers, studied extensively over the last three decades by. S.K. Hong, Y.S. Park, K. Shiraki and colleagues, provide more physiological proof of cold acclimatization.

Kang *et al.* (1963) observed that the Korean diving women exhibited a seasonal variation in basal metabolic rate (BMR) consistent with a metabolic acclimatization. In the summer, when water temperatures were warmest, the
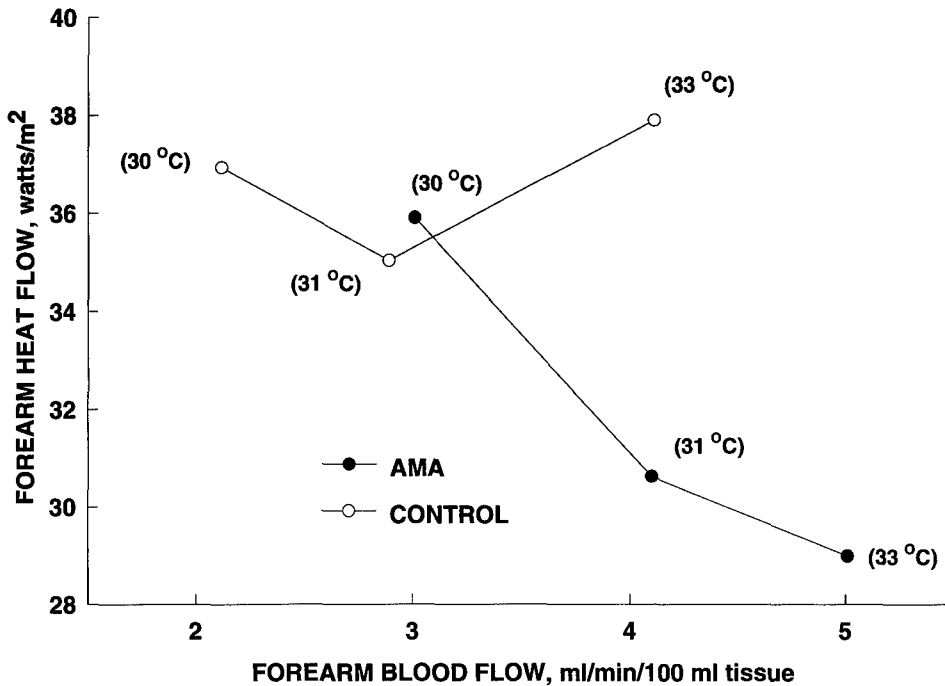
Fig. 3. Forearm skin heat loss expressed as a function of forearm blood flow measured in six Ama diving women and six non-diving women from the same Korean community while they were immersed in water at three different temperatures (water temperature shown in parenthesis). Redrawn from the data of Hong *et al.* (1969).

Ama's BMR was lowest. Throughout the fall, the Ama's BMR increased, becoming highest in the winter when water temperatures were coldest. Non-diving control subjects from the same community exhibited no seasonal fluctuation in BMR. While the elevated BMR during winter appeared related to increased cold stress, the practical value of an increased BMR was negligible (Hong *et al.*, 1986; Kang *et al.*, 1963). Other observations are consistent with the development of cold habituation in the diving women. The Korean diving women tolerated much colder water without shivering than non-divers of comparable fat thickness (Hong, 1963; Hong, 1973). Although the Ama's shivering responses indicate that they had become cold-habituated, their vasomotor responses and skin heat flow during cold exposure suggest that a more complex acclimatization.

The Ama diving women appeared to have developed an insulative form of cold acclimatization; that is, mechanisms for body heat conservation were enhanced. Maximal tissue insulation was greater in divers than in non-divers with comparable subcutaneous fat thickness (Hong, 1973). The mechanisms for the insulative acclimatization remain unidentified. However, assuming that skin thickness contributes negligibly to insulation, the increased insulation in divers must derive from their control of circulation to the peripheral shell. Figure 3 shows that while they rested in 30, 31 and 33 °C water, diving

women reduced peripheral heat loss with a smaller reduction in peripheral blood flow than unacclimatized women (Hong *et al.*, 1969). It is tempting to speculate that improved countercurrent heat exchange allowed higher muscle blood flow despite maximal cutaneous vasoconstriction, but the blood flow measurements do not distinguish between cutaneous and skeletal muscle flows.

Unfortunately, follow-up studies are no longer possible. Since 1977, the divers have used wet suits, and modern divers have substantially more subcutaneous fat than the first diving women studied (Park *et al.*, 1983). Thus, modern divers experience less body cooling than traditional divers and insulative acclimatization is no longer apparent (Park *et al.*, 1983). This suggests that the stimulus for the different pattern of cold acclimatization exhibited by the traditional divers as opposed to circumpolar residents or Aborigines was the more substantial whole-body cooling experienced by the traditional divers. Acclimation studies tend to support this thesis.

As shown in Table 2, repeated cold-water immersion induces different acclimation patterns, depending on cold intensity, exposure duration and length of acclimation period. Brief immersions induce habituation, even when only a few immersions are completed (Lapp and Gee, 1967; Leftheriotis *et al.*, 1990; Radomski and Boutelier, 1982). For example, Radomski and Boutelier (1982) had subjects immerse themselves in 15 °C water 20-60 minutes a day for 9 days, and observed shivering and vasoconstrictor responses to cold became blunted, allowing a greater fall in rectal temperature. This hypothermic habituation also diminished the sympathetic response to cold (Radomski and Boutelier, 1982). When the immersion durations are increased and the immersions repeated over a longer acclimation period, acclimation patterns besides habituation are induced.

Young *et al.* (1986; 1987) studied the effects of an acclimation program consisting of 90 minutes of immersion in 18 °C water, repeated five days per week for eight weeks. During each immersion, subjects experienced about a 1 °C decrease in rectal temperature. Before and after acclimation, physiological responses were measured while the subjects were exposed to cold (5 °C) air. Some acclimation effects appeared consistent with hypothermic habituation. Metabolic heat production increased more slowly during cold-air exposure following acclimation, and the fall in rectal temperature during cold-air exposure was greater and more rapid. However, other adaptations suggested the development of an insulative type of cold acclimation.

As shown in Figure 4, following repeated cold-water immersion, cold-air exposure caused skin temperature to fall about 4 °C lower than before acclimation (Young *et al.*, 1986). The greater fall in skin temperature during cold exposure suggests that a more pronounced cutaneous vasoconstrictor response to cold had developed. The increment in plasma norepinephrine concentration elicited by cold air exposure was more than two-fold greater following acclimation suggesting that acclimation increased sympathetic nervous responsiveness to cold (Young *et al.*, 1986). In addition, a smaller increment in blood pressure during cold exposure was observed after acclimation, while cardiac output responses to cold were unaffected (Muza *et al.*, 1988). The blunting of the systemic pressure response to cold indicated that subcu-

Table2. Acclimation programs employing cold-water exposure.

| STUDY	COMMENT	Twater	EXPOSURE DURATION	ACCLIMATION PERIOD (ACCLIMATION CONDITIONS USED)	EFFECTS
Eagan (1963)	immersion of one finger; cross-sectional study; 6 acclimated; 6 unacclimated men	"ice water"	10 min; 6 times/day	126 consecutive days	habituation of vasoconstrictor response to cold (observed in nonimmersed as well as immersed hand)
Leftheriotis *et al.* (1990)	hand & forearm immersion; longitudinal study; 5 men	5 °C	20 min/day	30 consecutive days	habituation of vasoconstrictor response to cold
Lapp and Gee (1977)	whole-body immersion; longitudinal study 3 men; 5 women	reduced progressively from 32 to 21 °C	1 hr/day	2 days/week for 8 weeks	shivering habituation
Radomski and Boutelier (1982)	whole-body immersion; cross-sectional study; 3 acclimated; 8 unacclimated men	15 °C	20 to 60 min/day depending on individual tolerance	9 out of 14 days	hypothermic habituation
Young *et al.* (1986)	whole-body immersion; longitudinal design; 7 men	18 °C	90 min/day	5 days/week for 5 weeks	insulative acclimation
Bittel (1987)	whole-body immersion; longitudinal design; 10 men	10-15 °C; wet suits worn	1-3 hr/day depending on individual tolerance	4 or 5 days/week for 8 weeks	metabolic insulative and mixed metabolic-insulative depending on individual subject anthropometric characteristics
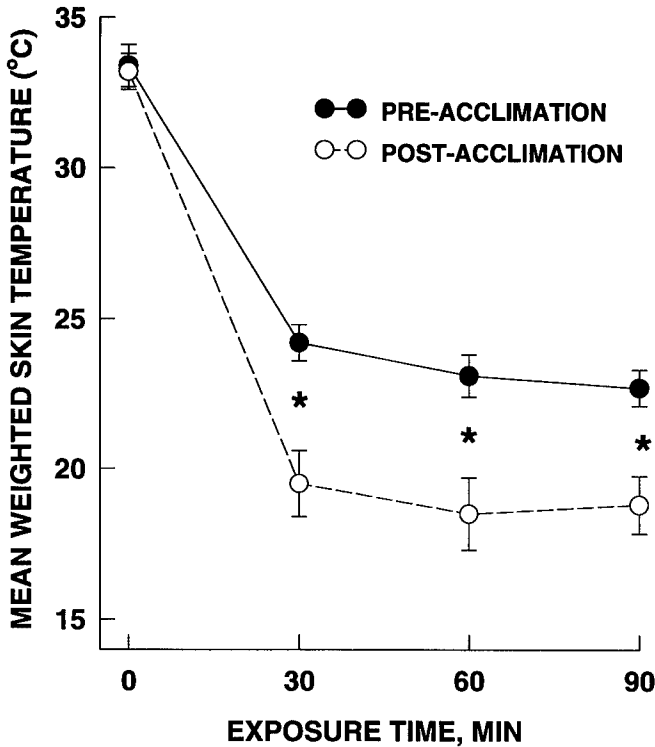
Fig. 4. Effect of acclimation by repeated cold-water immersion on mean weighted skin temperature before and during a 90-minute resting cold-air exposure. From Young *et al.* (1986).

taneous vascular beds are better perfused following acclimation. Thus, as was suggested to have occurred in the Korean diving women, acclimation by repeated cold-water immersion may enable better heat conservation by improved insulation at the shell surface, while perfusion of the subcutaneous shell is more optimally maintained than before acclimation.

The lower skin temperatures during cold air exposure following acclimation (Young *et al.*, 1986; Bittel, 1987) have two implications. First, at a given air temperature, lower skin temperatures reduce the thermal gradient for heat transfer between skin and air, which improves insulation. Secondly, the magnitude of the acclimation effect on skin temperature maintained during cold exposure exceeds the magnitude of the acclimation effect on core temperature maintained during cold air exposure (Bittel, 1987; Young *et al.*, 1986). Therefore, the core-to-skin thermal gradient is enlarged. A larger thermal gradient between core and skin would favor redistribution of body heat from the core to the subcutaneous muscle shell, while lower skin temperature due to enhanced cutaneous vasoconstriction in cold air would limit heat loss from the body's shell.
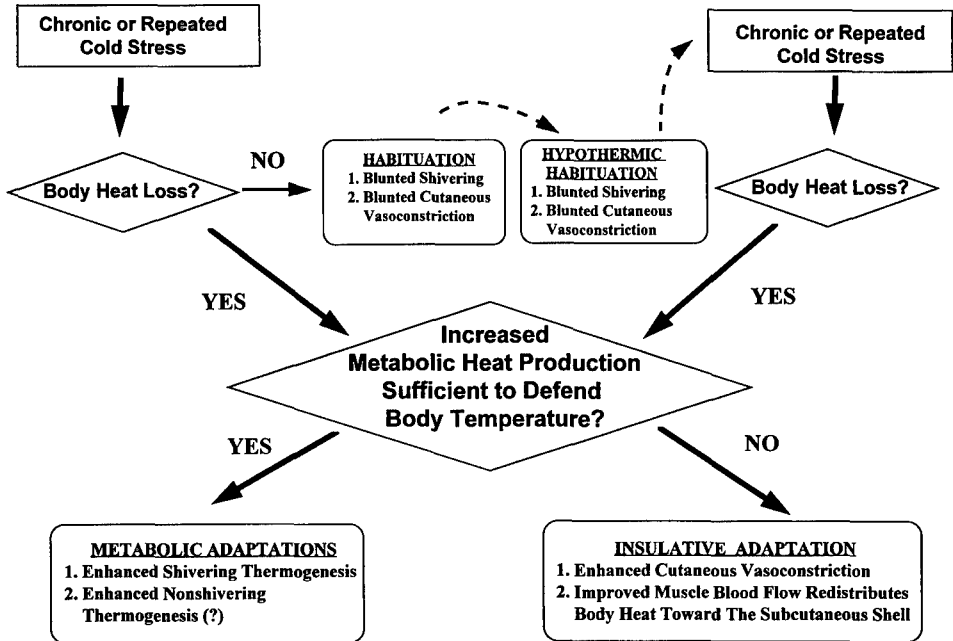
Fig. 5. Flowchart illustrating a theoretical scheme to explain the development of different patterns of cold acclimatization/acclimation which are observed in humans.

Determinants of the pattern of adjustments

A theoretical schematic depicting the development of different patterns of cold adjustments is shown in Figure 5. Brief, intermittent cold exposures appear sufficient to induce habituation of shivering and vasoconstrictor responses to cold, even when only very limited areas of the body surface are exposed and whole body heat losses are probably negligible. More pronounced physiological adjustments are observed only when the repeated cold-exposure causes significant body heat loss. Insulative adjustments appear to develop when repeated cold exposures are too severe for body heat loss to be offset by increased metabolic heat production; that is, when cold causes deep body temperature to decline significantly. The possibility that an enhanced thermogenic capability can develop in humans in response to chronic cold cannot be dismissed. It is tempting to speculate that the stimulus for this metabolic pattern of cold adaptation is prolonged periods in which significant body heat loss was experienced, but under conditions in which body heat production increased sufficiently to prevent a significant decline in deep body temperature. This speculation is not unjustified, since the metabolic pattern of cold adjustments has only been reported in studies in which acclimatization or acclimation was induced by exposure to such conditions, *i.e.* prolonged exposure to moderately cold air.

Alternative explanations for the different patterns of cold adaptations have

been proposed. Bittel (1987) speculated that body composition and physical fitness determined the acclimation type. His data suggested that lean, fit individuals develop metabolic adjustments and fat, less fit individuals develop insulative adjustments. However, he studied too few subjects to statistically substantiate this hypothesis (Bittel, 1987). Skreslet and Aarefjord (1968) studied three scuba divers during a standardized cold-water immersion test before and at two week intervals throughout a 45 day period of daily diving in 2-4 °C sea-water. Initially, all subjects responded to cold with an increase in metabolic heat production, which in two out of three was sufficient to prevent rectal temperature from falling. After two weeks of diving, all three divers exhibited shivering habituation and the two divers who tolerated the first immersion without a decline in rectal temperature now experienced a decline. After 45 days of diving, the subjects tended to maintain higher rectal temperatures and lower torso and thigh skin temperatures during immersion than during the initial test. They hypothesized that different cold adjustment patterns did not represent development of mutually exclusive physiological states, but rather, different stages in the progressive development of complete cold acclimatization. Thus, their divers initially responded to whole-body cold exposure by shivering; eventually, however, this response disappeared and insulative adaptations developed to help limit body heat loss.

Summary

Humans adaptations to chronic cold exposure have been demonstrated in both cross-sectional and longitudinal studies. Three basic patterns of cold adjustments are observed. The most common is cold habituation in which shivering and cutaneous vasoconstriction are blunted; body temperature may decline more in the acclimatized than unacclimatized state. A metabolic pattern may develop in which cold exposure elicits a more pronounced increment in shivering or nonshivering thermogenesis than in the unacclimatized state. When individuals are repeatedly exposed to cold conditions severe enough to induce a significant decline in deep body temperature an insulative type of acclimatization appears to take place. The exact determinant of which pattern will be induced by chronic cold exposure is unclear, but the magnitude and extent of body cooling, frequency and duration of exposure, and individual factors all may influence the adaptive process.

Disclaimer

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