6. HUMAN ADAPTATIONS TO COLD STRESS

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Keywords: Habituation, acclimatization, shivering, acclimation, body heat, shivering thermogenesis, metabolic cold adaptation, insulative cold adaptation

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 significant 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 vasoconstrictor 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).
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<td>Hesslink et al. (1992)</td>
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<td>Armstrong and Thomas (1991)</td>
<td>5 days/week</td>
<td>indoor chamber, shorts &amp; T-shirts;</td>
<td>shivering habituation, shivering habituation, vasomotor acclimation</td>
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<td>Silani-Garcia (1989)</td>
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<td>Mathew et al. (1981)</td>
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<td>indoor chamber, shorts &amp; T-shirts;</td>
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<td>7 days</td>
<td>indoor chamber, shorts &amp; T-shirts;</td>
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<td>Davis (1991)</td>
<td>7 days</td>
<td>indoor chamber, shorts &amp; T-shirts;</td>
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<td>Kreider et al. (1959)</td>
<td>14 days</td>
<td>indoor chamber, shorts &amp; T-shirts;</td>
<td>shivering habituation, shivering habituation, vasomotor acclimation</td>
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<td>Scholander et al. (1958a)</td>
<td>6 weeks</td>
<td>sleeping bags, outdoor</td>
<td>metabolic acclimation</td>
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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 re-
sponse 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 incre-
ment 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 ques-
tion.

**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 atmos-
phere 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 ambi-
ent temperature fell at night (Hicks, 1964; Scholander et al., 1958b; Hammel et
al., 1959). In contrast to habituated circumpolar residents, the Aborigines ex-
hibited a greater fall in skin temperature than did Europeans which was at-
tributed due to a more pronounced cutaneous vasoconstrictor response to
cold (Hicks, 1964; Scholander et al., 1958b). Additionally, the Aborigine's rec-
tal 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 unaccli-
matized Europeans suggesting that the lower thermal conductance of the
Aborigine reflected an enhanced vasoconstrictor response to cold. Alterna-
tively, the Aborigines may have exhibited a lower thermal conductance sim-
ply 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
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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
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-
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<th>EXPOSURE DURATION</th>
<th>ACCLIMATION CONDITIONS USED</th>
<th>EFFECTS</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eagan (1963)</td>
<td>immersion of one finger; cross-sectional study; 6 acclimated; 6 unacclimated men</td>
<td>“ice water”</td>
<td>10 min; 6 times/day</td>
<td>126 consecutive days</td>
<td>habituation of vasoconstrictor response to cold (observed in nonimmersed as well as immersed hand)</td>
</tr>
<tr>
<td>Leftheriotis et al.</td>
<td>hand &amp; forearm immersion; longitudinal study; 5 men</td>
<td>5 °C</td>
<td>20 min/day</td>
<td>30 consecutive days</td>
<td>habituation of vasoconstrictor response to cold</td>
</tr>
<tr>
<td>(1990)</td>
<td>whole-body immersion; longitudinal study 3 men; 5 women</td>
<td>reduced progressively from 32 to 21 °C</td>
<td>1 hr/day</td>
<td>2 days/week for 8 weeks</td>
<td>shivering habituation</td>
</tr>
<tr>
<td>Lapp and Gee (1977)</td>
<td>whole-body immersion; cross-sectional study; 3 acclimated; 8 unacclimated men</td>
<td>15 °C</td>
<td>20 to 60 min/day depending on individual tolerance</td>
<td>9 out of 14 days</td>
<td>hypothermic habituation</td>
</tr>
<tr>
<td>Radomski and Boutelier (1982)</td>
<td>whole-body immersion; longitudinal design; 7 men</td>
<td>18 °C</td>
<td>90 min/day</td>
<td>5 days/week for 5 weeks</td>
<td>insulative acclimation</td>
</tr>
<tr>
<td>Young et al. (1986)</td>
<td>whole-body immersion; longitudinal design; 10 men</td>
<td>10-15 °C; wet suits worn</td>
<td>1-3 hr/day depending on individual tolerance</td>
<td>4 or 5 days/week for 8 weeks</td>
<td>metabolic insulative and mixed metabolic-insulative depending on individual subject anthropometric characteristics</td>
</tr>
<tr>
<td>Bittel (1987)</td>
<td>whole-body immersion; longitudinal design; 10 men</td>
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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
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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.

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