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Different types of cold adaptation in humans

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1. ABSTRACT

Human adaptation to cold may occur through acclimatization or acclimation and includes genetic, physiologic, morphological or behavioural responses. It has been studied in indigenous populations, during polar or ski expeditions, sporting activities, military training, in urban people, or under controlled conditions involving exposures to cold air or water. Although divergent results exist between the studies, the main cold adaptation responses are either insulative (circulatory adjustments, increase of fat layer) or metabolic (shivering or nonshivering thermogenesis) and may be positive (enhanced) or negative (blunted). The pattern of cold adaptation is dependent on the type (air, water) and intensity (continuous, intermittent) of the cold exposure. In addition, several individual factors like age, sex, body composition, exercise, diet, fitness and health modify the responses to cold. Habituation of thermal sensations to cold develops first, followed by cardiovascular, metabolic and endocrinological responses. If the repeated cold stimulus is discontinued, adaptation will gradually disappear. The functional significance of physiological cold adaptation is unclear, and some of the responses can even be harmful and predispose to cold injuries. The article summarises recent research information concerning with the thermoregulatory responses related to repeated exposures to cold (air or water), and also discusses the determinants of cold adaptation, as well as its functional significance.

2. INTRODUCTION

People have colonized the planet efficiently, even the most extreme environments. In these areas the habitual cold

Table 1. Different forms of cold adaptation and associated physiological responses

Parameter	Metabolic	Insulative	Hypothermic	Insulative-hypothermic	Metabolic-insulative
Rectal temperature	Normal (no change)	Normal (no change)	Decreases	Decreases	Normal
Skin temperature	Increases (vasodilation)	Decrease (vasoconstriction)	Normal (remains warm)	Decreases	Decreases (vasoconstriction)
Metabolic heat production	Increases	Normal (no change)	Decreases	Increases	Increases

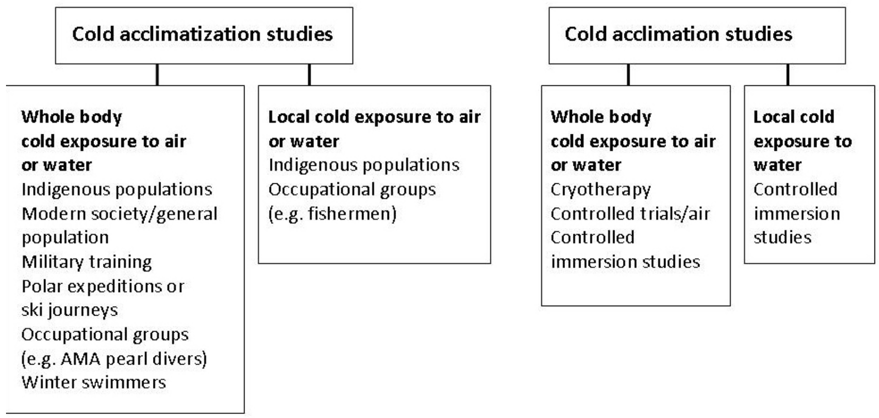

Figure 1. Cold adaptation studies.

exposure during work and leisure times is significant and has required adaptation to mitigate adverse performance and health effects. A part of this adaptation as included genetic influences, but also morphological, physiological and behavioural responses.

This article summarizes research in the area of cold adaptation with its main focus on the more recent findings following the detailed overview by Young (1). The emphasis of the present summary is on the observed thermoregulatory responses related to repeated exposures to cold (air or water), and also briefly discuss the factors related to cold adaptation, as well as its functional significance. The information concerning with cold adaptation is diverse and originates from field and controlled laboratory trials of various study populations Figure 1.

3. DEFINITIONS OF COLD ADAPTATION

Adaptation of cold can be either inherited or acquired and both types can result in morphological and/or physiological changes. The definitions of the IUPS Thermal Glossary (2) are presented in Figure 2.

Thermal acclimation reflects a transition from one steady state to another (3). Active organisms are thermodynamically open and an open system in steady state is relatively stable and the energetic costs are kept minimal. Hence, cold adaptation results in a greater homeostatic economy (preservation of heat), but often at a cost of lower mean body temperature (4).

Werner (5) indicates that adaptation is a higher control level, where persistent stressors, either the heat transfer process or the controller properties are adjusted (or both). Hence, cold adaptation involves both "process" (passive heat transfer processes) and "controller" (thermosensors, integrative centers, thermoeffectors) adaptation. Both of these forms may consist of morphological and physiological modifications. Autonomic cold adaptation aims primarily at an enhanced preservation of heat (often at the cost of a lower mean body temperature in cold). Furthermore, behavioural alterations bring about a higher efficiency of control, at the cost of higher energy expenditure. In summary, cold adaptation involves different outcomes where variations in the proportional contributions of process and controller (processor) adaptations (and morphological and functional adaptations) within a person affect the observed responses (5).

4. TYPES OF COLD ADAPTATION

4.1. Physiological and morphological adaptation

Physiological responses to cold exposure are either insulative (decreased mean skin temperature, T_{sk}) or metabolic (shivering or non-shivering thermogenesis, NST) (6). Physiological responses to repeated exposures to cold have been summarised by several authors (1, 4, 7, 8). In conclusion, either positive or negative responses (potentiated or blunted) to repeated cold stimuli are observed.

The different forms of cold adaptation have been traditionally distinguished by the observed responses as 1) hypothermic, 2) insulative or 3) metabolic (9). Sometimes also mixed responses (insulative-hypothermic, metabolic-insulative) are observed (Table 1). In hypothermic cold adaptation, the core temperature is allowed to decrease more pronouncedly compared with non-acclimatized people before heat production responses are initiated. At the same time, thermal conductance is less compared with

Adaptation denotes the changes that reduce physiological strain produced by stressful components of the total environment. This may occur within the lifetime of an organism (phenotypic) or be the result of genetic selection in a species or subspecies (genotypic). Phenotypic adaptation occurs when an organism modifies either its morphological configuration (e.g. amount of subcutaneous fat, fur thickness) or its physiological responses.

Acclimatisation means the physiological or behavioural changes occurring within the lifetime of an organism that reduce the strain caused by stressful changes in the natural climate (e.g. seasonal or geographical).

Acclimation means the physiological or behavioural changes occurring within an organism that reduce the strain caused by experimentally induced stressful changes in particular climatic factors.

Habituation denotes the reduction of responses to, or perception of a repeated stimulation.

Figure 2. Definitions of thermal adaptation (Reproduced with permission from 2).

non-acclimatized subjects. This is due to enhanced vasoconstriction and more considerable decrease in skin temperature, which preserves heat. It can also reflect lower metabolic heat production (M). The metabolic type of cold acclimatization is characterised by increased M while exposed to cold. This is primarily achieved through shivering thermogenesis. However, also non-shivering thermogenesis (NST) could play a role in people chronically exposed to cold (10). A recent study showed that brown adipose tissue (BAT) is found in high proportions in young men, but the metabolic action of BAT is reduced in overweight and obese subjects (11). Furthermore, Cypess *et al.* (12) reported defined regions of functionally active BAT in adult humans, are more frequent in women than in men. The same study reported that the amount of brown adipose tissue was inversely correlated with BMI, especially in older people. The insulative type of cold acclimatization is associated with an enhanced vasoconstriction and consequent insulation which prevents cooling (1).

It has been postulated that the type of adaptation responses are related to energy intake which effect would have been emphasized especially among the different indigenous populations. For example, metabolic adaptation occurs with severe cold exposure associated with high energy intake (e.g. Eskimos), whereas insulative adaptation develops with light cold exposure and a low energy intake (e.g. Australian Aborigines of the north coast), hypothermic adaptation with moderate cold stress and very low energy intake (Bushmen of the Kalahari desert) and isolative adaptation for moderated cold stress with low energy intake (Aborigines of central Australia (8). In addition to energy intake Bittel (13) further suggests that the type of cold adaptation is dependent on body composition. Hence lean persons develop metabolic adaptation and less fit individuals insulative adjustments.

Young (1) postulates that the type of cold adaptation response is dependent on the amount of cooling of the body (Figure 3). Habituation is the most common form of cold adaptation and develops in response to repeated cold exposures where whole-body cooling is not substantial. When being habituated to cold, thermal cold sensations are less intense and shivering and the vasoconstrictor response is blunted. At the same time stress responses are reduced, meaning a lesser rise in blood pressure (BP) and reduced release of stress hormones in the circulation. More pronounced physiological adjustments occur when repeated exposures to cold cause significant heat loss. Insulative adaptation to cold is believed to develop when M is insufficient to prevent cooling of the core. On the other hand, the metabolic type of adaptation is suggested to prevail when core cooling can be compensated by increased heat production (1).

There is a marked variation between the observed responses in the various cold adaptation studies. Tipton *et al.* (4) indicate that partially these apparent differences could be due to the interchangeable or incorrect use of terms describing cold adaptation (acclimation, acclimatization and habituation) (4). Furthermore, it is difficult to determine when the post adaptive state occurs, and whether the differences between the studies refer to different phases of the adaptation process (4). Moreover, varying observations could also be due to individual differences where the proportion of morphological and functional adjustments could vary between persons and studies (5).

4.2. Genetic adaptation to cold

Genetic adaptation (e.g. several generations) to a specific climate results in morphological (e.g. size, shape, skin colour) and functional alterations (14, 15). Genetic aspects and ethnic differences cannot be ruled out in human cold adaptation, although no conclusive evidence has been presented (14). The difficulties of distinguishing genotypic differences in thermal adaptation are due to the fact that studies would need to control for environmental and lifestyle factors which themselves affect morphological and physiological changes (14, 15).

Cold exposure affects the expression of 20 mammalian genes (16). A study by Piazza and others (17) demonstrated that 60 % of the 39 independent alleles of different loci from various indigenous populations around

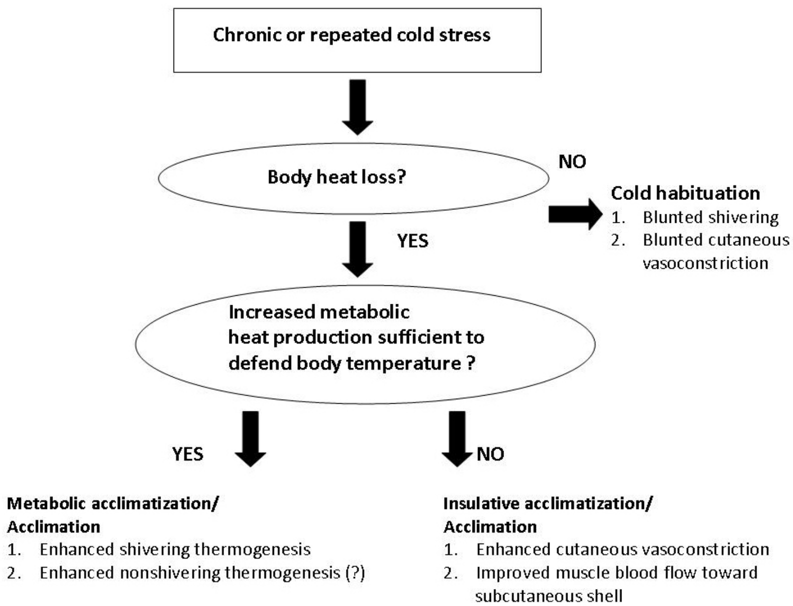

Figure 3. Flowchart illustrating a theoretical scheme for the different forms of cold adaptation (Reproduced with permission from the Oxford University Press).

the world showed significant associations with climate. Furthermore, latitude, more particularly distance from the equator, suggested selective pressures for certain genes (17).

Maintaining homeostasis and a high body temperature are energetically expensive and may have been conflicting selection pressures influencing the variability of thermogenesis in humans (18). Cold adaptation as a life style strategy could be energetically beneficial, and the increased prevalence of metabolic disorders related to Western diet and lack of exercise, could also be partially related to the eroded cold adaptation (19). In fact, human adaptive thermogenesis is closely linked to long term energy expenditure and regulation of body weight (20).

Anthropological studies have demonstrated a higher BMR in northern indigenous populations which suggest that the genetics of thyroid functions could be partially related to the adaptation to these environments (21). The role of thyroid hormone metabolism in adult human cold adaptation has not been fully clarified, and the enhanced T_3 production could for example be related to deiodination of T_4 in skeletal muscle or to the recruitment of brown adipocytes from white adipose tissue (22). Although there is no direct evidence, also polymorphism of the uncoupling proteins (UCPs) could be associated with cold-induced metabolism (6).

4.3. Behavioural adaptation to cold

It is probable that much of the modern cold acclimatization is behavioural. Support for this hypothesis is found from a study where inhabitants of Northern Europe protected their extremities (e.g. use of hats, gloves and scarves) more efficiently compared with residents from Southern Europe with a given fall in temperature and reducing winter mortality (23). Overall, mortality has been shown to increase to a greater extent with a given fall in temperatures in regions with warm winters, in households with low indoor heating, and among people wearing fewer clothes and being less active outdoors (24). This observation could support behavioural adaptation to life in northern climates.

5. ACCLIMATIZATION TO COLD

5.1. Cold acclimatization among indigenous people

Biological differences between ethnic groups offered scientists a way to study the effects of cold acclimatization on human thermal responses as early as in the 1950s (1, 4, 14, 25). This laid a foundation for the current understanding of how humans can adapt to severely cold climates. Indigenous populations tend to have both shelter and clothing of poor protective value, with the exception of for example Arctic indigenous populations. In many cases the cold exposure was intermittent and periodic, such as nocturnal cold temperatures. In summary, depending on the climate and lifestyle either hypothermic, insulative or metabolic responses have been reported (1, 4, 14, 25).

One of the first native groups investigated were Australian aborigines who live in a semi-desert environment with average night temperatures of 4°C. They slept semi-nude and without shelter. Compared with non-acclimatised people, the metabolic and thermal responses of the aborigines showed no increase (but a slight decrease) in M and a greater drop in T_{rect}, T_{sk} and body temperatures. These responses suggest hypothermic insulative acclimatization (26). The hypothermic response is beneficial in these climatic conditions since it saves energy when compared to the situation where core temperature is maintained.

Similar to the Aborigines, the Kalahari Bushmen wore little or no clothing, and were exposed to nocturnal temperatures as low as 0°C. When exposed to cold, the Bushmen did not shiver, showed only a small increase in M, and allowed their body temperature to drop (but not as low as the Aborigines). These responses suggest insulative acclimatization to cold (27).

In contrast to the Aborigines and Bushmen, the Alacuf Indians of Tierra del Fuego were exposed to cold for 24-h being semi-nude. This population had a resting metabolic rate that was 160% higher than that of non-cold-acclimatised people. Otherwise, no major differences in rectal, body and skin temperatures were observed. This pattern of thermal responses suggests metabolic acclimatization (28).

A specific occupational group whose acclimatization to cold has been studied are the pearl divers (AMA) from Korea. In their occupation, these women are immersed in cold water for several hours per day. It has been shown that repeated exposures to these conditions resulted in metabolic (higher BMR), insulative-hypothermic (lowered lower critical temperature) and local cold acclimatization (vascular adaptation, lowered heat flux in limbs) (29). It is noteworthy that the more recent use of wet suits abolishes the cold acclimatization responses (30, 31).

The Arctic Indians of the Yukon and Arctic Inuit were intermittently exposed to cold while travelling, hunting and trapping. and often well protected with Arctic clothing. Adaptation to cold was largely restricted to the extremities (e.g. hands) where higher skin temperatures were recorded (32-35). M was also higher compared with non-acclimatised people. The pattern of adaptation of the Inuit resembles metabolic acclimatization. In contrast to the Inuit, the nomadic Lapps showed no increase in M but a pronounced drop in T_{rect}. This pattern resembles the responses of the Aborigines (36).

Some recent reports concerning with indigenous adaptation to cold come from anthropologic studies examining the BMR of indigenous, northern circumpolar populations compared with non-indigenous people (37-39). A meta-analysis combining data from several circumpolar populations from North America and Siberia implicate that indigenous populations have a higher BMR, which is suggested to be due to both functional and genetic factors and is suspected to be partially related to climatic influences (i.e. cold stress) (37).

5.2. Polar expeditions

The physiological responses and health outcomes to the environmental conditions and residence in Antarctica include light-related changes in circadian rhythms, altitude-related cardiopulmonary symptoms; and cold-related changes in peripheral circulation, hypothermia and frostbite, suppression of the immune system and hormonal changes (40). Due to these concurrent stressors it is difficult to distinguish the separate effects of cold on the physiological responses. Cold acclimatization responses of the personnel residing in Antarctica for defined periods have been examined in several studies (41-46). Compared with their regular daytime work, overwintering personnel of the Antarctic expeditions are often confronted with increased amounts of outdoor exposure to cold temperatures associated with field research. Ambient temperatures in Antarctica may be very low, even -70°C in the winter. The results of the different studies concerning thermal responses and cold acclimatization have provided divergent results and can be attributed to differences in the length and severity of the exposures, individual characteristics, physical activity and the clothing used.

Residents staying in Antarctica for 29 weeks and infused with NE after the expedition demonstrated a lesser rise in BP, enhanced vasoconstriction and calorigenic response (41). On the other hand, four men working in Antarctica for 24 weeks showed an improved ability to maintain their T_{rect}, but showed no changes in shivering, skin temperatures or BP in response to cooling (42). Obviously, individual characteristics also play an important role in what type of thermal responses are observed. Wyndham & Loots (43) found that thin men developed thermal responses resembling those in men with more subcutaneous fat after the year in Antarctica (weight gain, reduced metabolic response, decreased skin temperature and increased T_{rect}). Consistent with this observation, a reduction in sympathetic activity and stress hormones has been observed (47-49). This would support cold habituation responses due to repeated cold exposures. Naidu & Sachdeva (45) measured 64 tropical men after an 8- week stay in Antarctica and detected increased finger blood flow, but also a more pronounced vasoconstrictor response towards cooling. Similarly, enhanced vasoconstriction was observed in fingers of the personnel of an Australian research expedition after one year in Antarctica (50). In the study of Rintamäki *et al.* (46) personnel residing in Antarctica for 53 days demonstrated a delayed onset of shivering, as well as higher forearm and finger temperatures in response to cooling In summary, the divergent results from the Antarctic expeditions are explainable by the variation in the type and amount of cold exposure resulting in different thermal responses.

5.3. Ski journeys

Acclimatization responses during ski expeditions/journeys have also been recorded where the environmental conditions have varied considerably. A 63-day ski journey to the North Pole lowered T_{rect} and M, but increased local skin temperatures (51). Morevover, a ski journey across Greenland for 21 days resulted in hypothermic (lowered T_{rect}), insulative (decreased T_{sk}) and isometabolic (unaltered M) acclimatization. At the same time also local cold acclimatization (warmer foot temperatures) was observed (52). Livingstone (53) did not observe any peripheral acclimatization among military personnel after a 2-wk stay in the Arctic where ambient temperatures ranged between -10 and -40°C. Also a depressed, rather than enhanced CIVD response was observed after a 2-wk journey (54). .O'Brien & Frykman (55) detected lowered temperatures in fingers of explorers after an Arctic ski journey (105 days), and suggested that the heavy load carrying could have impaired cold acclimatization responses. In summary, no consistent acclimatization patterns have been demonstrated, but rather the differences between the studies reflect the variations in the length and severity of the exposures, the physical activity and the clothing used.

5.4. Sojourn in tropical climates

It has been shown that a 4-weeks stay in tropical climate not only modifies thermal responses to heat, but also affects cold responses. The stay in a hot environment resulted in increased sensitivity of the thermoregulatory system to cold and responses like a higher T_{sk} and decreased onset of shivering (but unaltered core temperature and M) (56).

5.5. Cold acclimatization in modern societies

5.5.1. General population

Seasonal differences in thermal responses in modern populations have been reported in only a few recent studies (Table 2). A study conducted in the Netherlands, with a moderate oceanic climate (outdoor temperatures in winter above 0°C), observed an increased response in M in winter compared with summer when subjects were exposed to moderate (15°C) cold suggesting acclimatization to cold (57). On the other hand, another study comparing thermal responses in urban young people in winter and summer in Finland, an Arctic country, did not detect cold habituation responses in winter. Instead, the responses in winter resemble aggravated reactions of non-cold acclimatized subjects (58). This finding was postulated to be due to the fact that urban residents are exposed concurrently to cold only for brief periods (59) which is insufficient to cause cold habituation. Seasonal thermal responses have also been assessed in Japanese subjects during mild cold exposure (10 to 15°C) (60-62). These studies revealed some seasonal changes in M, T_{rect} and skin temperatures, but could not demonstrate a consistent pattern of wintertime cold acclimatization. A study on Japanese schoolchildren who did not wear socks during wintertime showed adaptive responses by keeping their skin temperatures higher even in the cold and enhancing the metabolic rate (63).

A study examining the pituitary-thyroid axis of high latitude outdoor working residents (Finland) showed gradually lowered serum free trijodothyronine (T(3) concentrations with decreasing temperatures suggesting that the output of thyroid hormones is accelerated in winter, leading to low serum free T(3) levels and a high urinary free T(3) excretion (64-66). Based on the abovementioned studies, seasonal physiological responses occur. The lack of consistency with regards to the type of adaptive responses is masked due to differences in living environments, study populations and designs.

4.4.2. Winter swimmers

Winter swimmers are repeatedly exposed to cold water for several months during the year with water temperatures of ca. 0-13°C and exposure times ranging from a few seconds to even 60 min (67-71) (Table 3). Winter swimming results in a suppressed M and heart rate in response to cold, which is mediated through altered β-adrenoceptor activity (71). Regular winter swimming also attenuates the catecholamine response to cold water (69). A follow-up study of winter swimmers over the swimming season observed a decreased BP and catecholamine responses in the end of the winter (70). However, the response was similar in controls, suggesting either habituation to the research situation itself or seasonal adaptation.

Longer periods of winter swimming (1 h at 13°C water) elicit a hypothermic response (lowered threshold) and delayed onset of shivering (68). In the study of Vybiral *et al.* (68) winter swimmers also exhibited a greater bradycardia and a more considerable reduction in plasma volume compared with controls.

Winter swimming is often combined with sauna bathing. Both exposures involve significant thermal stress and challenge the neuroendocrine and immune systems. However, habitual winter swimmers show adaptive responses in their immune defence (leukocytes, monocytes, IL-6), but also an impaired release of some interleukins from mononuclear cells (72). With regards to health effects, regular winter swimming does not seem to be harmful, as judged by the unaltered total peroxyl radical-trapping antioxidant capacity of plasma (TRAP) in response to repeated cold exposure (73). In fact, winter swimmers may have an improved antioxidant protection compared with non-cold acclimatized subjects as judged by lower baseline concentration of glutathione (GSH) and the activities of erythrocytic superoxide dismutase (SOD) and catalase (Cat) (67). In summary, sudden immersion in cold water in unaccustomed persons may lead to detrimental consequences, while, in regular winter swimmers, adaptive physiologic mechanisms increase tolerance to cold (74).

5.4.3. Military training

Conscripts are repeatedly exposed to cold during their wintertime training in northern climates. Military training (15 mo) in a cold climate (northern Sweden) showed increased baseline finger temperatures and improved recovery from the hand cold recovery test (hand 10 min in 10°C) in trainees whose responses to warming had been moderate and slow (75). Individual differences in cold induced vasodilatation (CIVD) predicted the occurrence of cold injuries during extended military training in a cold climate (76). Marrao *et al.* (77) studied participants of military cold weather survival courses where cold exposure was extended for 5-9 days (-24- to 4°C) but did not detect any daily differences in T_{core}, but T_{fing} during the training period. This period was probably too short to elicit circulatory or metabolic changes. Based on the abovementioned studies extended military training in a cold climate elicits local cold acclimatization responses which could be beneficial with regards to manual performance and recovery from cooling.

6. ACCLIMATION TO COLD

6.1. Repeated exposures to cold air

6.1.1. Short exposures to extreme cold

Cold therapy is used to relieve pain and inflammatory symptoms and for treating rheumatoid

Table 2. Human cold acclimatization studies during exposure to cold air

Study	Temperature	Duration	Repetitions	Area of exposure	Area of interest	Thermal response	Outcomes/conclusion
Lee and Tokura (60)	10°C (cold stress test)	2 h	Measurements in summer and winter	Whole body with two different sets of clothing varying the thermal insulation of the upper and lower body	Thermoregulatory responses at ambient temperatures of 20 and 10 degrees C in six male subjects wearing two different kinds of clothing were compared between summer and winter	T_{rect} lowered more in cold in summer than winter, lower T_{sk} in summer, M was higher in summer	Seasonal thermal responses were observed and were to some degree affected by clothing. Reduced M in winter.
Li et al. (61)	4-26°C	3 mo	Daily exposures to the climate	Daily worn clothing with legs either covered or uncovered	To investigate effects of two types of clothing, leaving the legs covered or uncovered, on seasonal cold acclimation	T_{rect} and HR in the subjects wearing skirts were shifted to lower levels when the season became colder	Clothing type worn in daily life may affect seasonal cold acclimation of thermal physiological responses in man
Inoue et al. (62)	17°C (cold stress test)	1 h	Daily exposures to the climate (outdoor mean temp 5-28°C)	Whole body (swimming trunks)	To study seasonal changes in metabolic and thermal responses	Smaller decrease in T_{rect} in winter. T_{foot} decreased more in winter. T_{sk} did not change with season. Blunted M in winter.	Older men have a lowered thermoregulatory capacity throughout the year
Hassi et al. (64)	Varying	-	14 months follow-up on residents living in cold	Winter clothing	To evaluate the effects of climate on the secretion of thyroid hormones in a high latitude population	Not measured	Disposal of thyroid hormones is accelerated in winter, leading to low serum free T(3) levels and a high urinary free T(3) excretion
Launay etl. (56)	47°C or 1°C (heat and cold stress test)	2 h	4 weeks sojourn in a tropical climate	Whole body	To study anthropology and thermal responses to heat and cold after a sojourn to a tropical climate	Higher T_{sk} and a decreased onset for continuous shivering, no significant change in internal temperature or M	Increased sensitivity of the thermoregulatory system to cold after a stay in a tropical climate
Farrace et al. (48)	-11°C (mean of station)	40 d stay in Antarctica	Daily outdoor exposures of 6-8 h	Face (other parts winter clothing)	To examine autonomic nervous function and hormonal changes	Not measured	Reduction of sympathetic and increase in parasympathetic activity, reduction of the anterior pituitary and adrenal hormonal secretory patterns
Harinath et al. (49)	Varying	60 d stay in Antarctica	Daily outdoor exposures	Winter clothing	To evaluate the roles of the autonomic and adrenal systems in acclimatization to cold in tropical men during prolonged sojourns in Antarctica	An initial increase in HR, BP, E, NE and cortisol with decline to basal levels by the end of the expedition. The increased sympathetic activity decreased during the stay	Gradual attenuation of sympathetic tone and a shift of autonomic balance toward the parasympathetic side.
van Ooijen et al. (57)	15°C (cold test)	3 h	Measurements in summer and winter	Face, hands, ankles (other parts clothed, 0.71 clo)	To study seasonal changes in metabolic and thermal responses	M increased by 7% in summer and 11.5% in winter. No change in T_{rect} in winter and summer, Temperature gradient between T_{rect} and T_{sk} higher in winter	Metabolic response was higher in winter than summer. The relative contribution of metabolic and temperature response was subject specific and consistent throughout the seasons
Mäkinen et al. (58)	10°C (cold test)	24 h	Different subjects measured in winter and summer	Face, hands exposed (other parts clothed 0.7 clo)	To study seasonal changes in metabolic and thermal responses in urban residents	T_{sk} 28-29°C, T_{rect} 36.6-36.7°C, T_{fing} 16-17°C, VO_2 increased by 7% (summer) and 14% (winter)	Increased preservation of heat especially in the peripheral areas in winter. Blunted vasomotor and skin temperature responses were not observed in winter

The table includes studies performed since the overview provided. Reproduced with permission from (1).

Table 3. Whole body exposure to cold water during winter swimming

Study	Temperature	Duration	Repetitions	Area of exposure	Area of interest	Thermal response	Outcomes/conclusion
Siems *et al.* (67)	1-4°C water	5-10 min	1 x week for winter period (winter swimmers)	Whole body immersion	To examine whether the winter swimming improves antioxidative capacity	Not measured. The baseline concentration of GSH and the activities of erythrocytic SOD and Cat, were higher in winter swimmers	An adaptative response to repeated oxidative stress, increased tolerance to environmental stress
Vybiral *et al* (68)	13°C water	1 h	Winter swimming	Whole body immersion	To determine thermal responses of winter swimmer	The threshold for induction of cold thermogenesis was lowered (by 0.34 C).. Delayed onset of shivering in winter swimmers.	Winter swimmers exhibit metabolic, hypothermic and insulative types of cold adaptation
Huttunen *et al.* (69)	4-10°C water	-	Three months	Whole body immersion	To determine hormonal responses at the beginning and end of the winter swimming period	Not measured	Winter swimming attenuates catecholamine responses to cold water. Adrenaline responses are also affected prior to the immersion.
Hirvonen *et al.* (70)	Ice cold water	-	5-6 times per week followed for 8 months	Whole body immersion	To determine BP and hormonal changes during a season of winter swimming	Not measured	BP and plasma catecholamine levels decreased during winter swimming, but these changes were also observed in the control persons. Plasma serotonin was lower in the spring in both groups
Jansky *et al.* (71)	2-12°C	3-12 min	2 x per week for 6 months	Whole body	To specify the role of adrenoceptors in mediating adrenergic functions after adaptation of humans to cold	Lower T_{rect} of winter swimmer at thermoneutrality when infused with β1-agonist	Increase in metabolic rate, mediated by beta1 and beta2 adrenomimetics, was attenuated after cold adaptation, indicating downregulation of beta1 and beta2 adrenoceptors. The significance of beta2 adrenoceptors in mediating heart rate was depressed after cold adaptation.
Dugué *et al.* (72)	Ice-cold water and sauna	15 min (sauna), followed by 0.5 min swim in ice-water	-	Whole body exposure to sauna and immersion in cold water	To investigate cytokine response after thermal stress in habitual winter swimmers	In winter swimmers plasma IL-6, leukocytes, and monocytes at rest were higher than in inexperienced subjects. Cortisol changes were larger in habitual winter swimmers.	Sauna and winter swimming challenge both the neuro-endocrine and the immune systems and adaptive mechanisms occur in habitual winter swimmers
Duguet *et al.* (73)	-110°C air or 0-2°C water	20 s cold water, 2 min cold air	3 x per week for 12 weeks	Whole body (cold air or water)	To study the effects of severe cold stress on total peroxyl radical trapping antioxidant capacity of plasma	Not measured	Regular cryotherapy and winter swimming do not seem to be harmful as far as plasma antioxidative capacity is concerned.
Smolander *et al* (80)	0-2°C water or -110°C	20 s cold water, 2 min cold air	3 x week for three months (13 weeks), air temp ca. -4 to 14°C	Whole body (cold air or water)	To examine thermal sensation and thermal comfort during cryotherapy and winter swimming	Cryotherapy subjects reported colder sensations than winter swimmers, temperature responses not reported	Thermal sensations and comfort become habituated during the first exposure
Leppäluoto *et al.* (81)	0-2°C water or -110 °C air	20 s immersed in 0-2 °C, 2 min at -110 °C	3 x week for 12 weeks	Whole body (cold air or water)	To determine the influence of long-term regular exposure to acute cold temperature on humoral factors.	Plasma ACTH and cortisol were lowered at certain time points (habituation). Plasma NE increased 2-fold to 3-fold each time for both cold exposures. Plasma cytokines did not change	Sustained cold-induced stimulation of NE was similar between the exposures. The frequent increase in NE might have a role in pain alleviation in whole-body cryotherapy and winter swimming

Smolander *et al.* (82)	0-2°C water or -110 °C air	20 s immersed in 0-2 °C, 2 min at -110 °C	3 x week for 12 weeks	Whole body (cold air or water)	To examine the effects of winter swimming and whole body cryotherapy on the serum levels of the growth hormone, prolactin, thyrotropin and free fractions of thyroid hormones	Winter swimming increased thyrotropin and decreased prolactin at certain time points during the acclimation period, but did not change thyroid hormone concentrations. Cryotherapy did not affect hormonal secretion.	Winter swimming or cryotherapy repeated do not lead to disorders related to altered secretions of the growth hormone, prolactin, thyrotropin, or thyroid hormones

The table includes studies performed since the overview provided. Reproduced with permission from (1).

arthritis (78). This involves repeated short exposures (ca. 2 min) to extreme cold temperatures (-110°C). The exposure elicits a slight bronchoconstriction (79). Furthermore, habituation of thermal sensations occurs already after the second exposure to extreme cold (80). Leppäluoto *et al.* (81) compared repeated brief (2 min) whole body exposures at -110°C with short (20 s) cold water immersions (0-2°C) and examined humoral factors. Both exposures resulted in similar increases in NE and could, according to the authors, have a role in pain alleviation in whole-body cryotherapy and winter swimming. Furthermore, whole body cryotherapy does not lead to disorders in the hormonal secretion of growth hormone, prolactin,thyrotropin or thyroid hormones (82) (Table 4).

6.1.2. Acclimation to cold air

Different acclimation protocols have employed various air temperatures and exposure durations and resulted in different cold acclimation patterns.. In general, short exposures (30 min to 1 h) to cold air result in shivering habituation (delayed onset of shivering, reduced VO_2 response) (83-85), but in no marked changes in rectal or skin temperatures. A cold acclimation protocol of 1-h exposures to cold for 11 days did not change epinephrine (E), thyroid hormones of TSH or reduce norepinephrine (NE) responses to cold suggesting that the exposure was not sufficient for reducing the sympathetic response (86). Brief (2 h) exposures to cold air cause habituation of thermal sensations after only one or two repetitions (87). This type of cold acclimation is further accompanied by a higher T_{sk} and T_{fing}, and reduced M and NE responses (88). At the same time a lowered sympathetic activation and a shift toward increased parasympathetic activity was observed (89) (Table 4).

Repeated cold exposures of longer duration (3 h to 14 days with cold exposures ranging from 5 to 15°C) result in hypothermic habituation, which involves both a reduced metabolic response towards cold exposure and lowered temperatures (90-93). Chronic, long-term exposure (several weeks of camping in tents with inadequate clothing and other type of protection) caused an increased M suggesting metabolic acclimation (94). However, this is one of the very few studies where metabolic acclimation has been demonstrated.

Interestingly, the habituation response seems to be specific to the core temperature experienced during the repeated cold exposures (95). A more considerable drop in core temperature than experienced during the cold acclimation results in an enhanced metabolic response resembling the unacclimated state. At the same time habituation causes a threshold shift (delayed onset of shivering), but does not affect the sensitivity of the response (95).

6.2. Repeated exposures to cold water
6.2.1. Whole body immersions

As heat loss in water is more pronounced than in air, the exposure temperatures and durations to cause acclimation responses are different. A summary of recent cold water immersion studies is presented in Table 5.

The initial response to immersion to cold water involves a "cold chock" response associated with hyperventilation, tachycardia and a reduced breath holding time. Tipton *et al.* (96) showed that it is possible to produce habituation of the initial response to cold elicited from a specific region of the body surface without repeatedly exposing that region to a cold stimulus. Furthermore, habituation to cold (five immersions for 2.5 min in 12°C water) increases breath holding time, and was not augmented by psychological training (97). It has also been demonstrated that repeated immersions in cold water result in a long lasting (7-14 months) reduction in the magnitude of the cold shock response (98). The precise pathways and mechanisms behind habituation are not well understood, but could occur at the spinal cord or the higher centres of CNS. Eglin and Tipton (99) showed that repeated cold (but not warm) showers reduced the respiratory drive when subject were immersed head-out to cold water. The authors conclude that the level of habituation seems to be affected by a combination of the magnitude of change in T_{sk}, surface area and the magnitude of the initial response (99).

Very brief repeated whole body immersions (20 s) to cold water (0-2°C) causes habituation of thermal sensation and comfort already after the first exposure (80). Brief (10-90 min) repeated whole-body immersions into cold water (4-21°C) cause habituation responses (100-106), for example, blunted metabolism (delayed onset and decreased intensity of shivering) and vasoconstriction. Although Jansky *et al.* (104) observed less discomfort and delayed onset and reduced intensity of shivering, they also detected lowered T_{sk}, which would suggest insulative cold acclimation. At the same time they did not detect marked changes in autonomic nervous system reactivity (104). Even three brief (60 min) immersions into cold water, where the temperature was reduced from 29 to 23°C, caused a reduced metabolic response and lowered T_{rect} (107). Whole-body immersion of longer durations (90 min to 3 h) into cold water (10-18°C) causes insulative or metabolic insulative acclimation (13, 109). Young *et al.* (109) found lowered T_{rect} and T_{sk}, increased plasma NE

Table 4. Whole body cold acclimation in cold air

Study	Temperature	Duration	Repetitions	Area of exposure	Area of interest	Thermal response	Outcomes/conclusion
Smolander *et al.* (79)	-110°C	2 min	Three times per week for 12 weeks	Whole body	To examine the effects of cryotherapy on lung function in healthy humans after acute and repeated exposures	PEF values were slightly lower compared with values before whole body cryotherapy	Cryotherapy induced minor bronchoconstriction in healthy humans.
Korhonen *et al.* (86)	10°C	1 h	11 successive days	Whole body	To examine adrenal and thyroid hormones and TSH in serum before and after the cold acclimation	No change in E, thyroid hormones and TSH. NE increased by 2.2-2.5-fold and did not change during the acclimation.	Cold acclimation did not reduce the cold-induced sympathetic response.
Leppäluoto *et al.* (87)	10°C	2 h	10 days	Whole body	To study habituation processes	Increased local skin temperatures, decreased NE and systolic BP response	Repeated cold-air exposures lead to habituations of cold sensation and NE response and to attenuation of hemoconcentration
Mäkinen *et al.* (89)	10°C	2 h	10 successive days	Whole body	The study examined cardiovascular autonomic function at the sinus node level during whole-body cold exposure before and after cold acclimation	Cold acclimation resulted in higher T_{sk} (0.6 degrees C) and lower NE (24%) response in cold T_{sk} 26-27°C, T_{rect}: no changes	Cold habituation lowers sympathetic activation and causes a shift toward increased parasympathetic activity.
Launay *et al.* (129)	1°C (cold stress test)	2 h	Training at 21°C, or at 1°C, or sedentary at 1°C 5 days/week for 4 weeks	Whole body	To examine how physical training in cold would alter thermoregulation	Those who had trained in warm exhibited a higher T_{rect} than the other groups. Training in cold did not changes thermal responses. Cold exposed subjects showed a lower T_{rect} but no change in Tsk or M	Thermal responses in cold differed for the climatic conditions of the training. Training performed in the cold prevented the development of a general cold adaptation. Hypothermic response was observed in subjects exposed to cold, but who had not exercised

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concentrations and delayed onset of shivering after repeated immersion into cold water. Bittel (13) detected similar thermal responses, but also an enhanced M after the acclimation, suggesting metabolic acclimation.

Stocks *et al.* (110) studied whether cold acclimation in water would alter body fluid regulation. According to their observations fluid from extravascular cells is displaced into the interstitium during acute cold-water immersion, and acclimation does not affect body fluid regulation. A study examining the importance of skin vs. core temperature in the development of cold acclimation due to repeated cold-water immersions (60 min exposures daily for 5 wks to 20°C) suggested that a decrease in skin temperature is sufficient for the increased vasoconstrictor response (111). However, a reduction in core temperature by ca. 0.8°C may be needed to enhance sympathetic activation during cold exposure.

6.2.2. Local immersion in cold water

Previous studies reporting local cold acclimatization have shown that repeated exposure of hands and fingers to cold water results in blunted vasoconstriction, higher peripheral skin temperatures, less pain and an earlier onset of CIVD. Local adaptation of hands to cold has been observed among specific occupational groups like British fish filleters (112), Gaspé fishermen (113, 114) and North Norwegian fishermen (115). Similar responses were also observed during local cold-water acclimation trials (116, 117).

The more recent local cold immersion studies have shown divergent thermal responses (Table 6). Some have demonstrated that repeated local immersion of 5-30 min to 5-12°C water produces habituation responses (118, 119), while others have observed enhanced insulative responses (enhanced vasoconstriction, blunted CIVD response) at exposures of 8°C for 30 min (120-122).For example, Geurts *et al.* (120) detected an enhanced vasoconstriction and blunted CIVD response after cold acclimation, and the majority of acclimation responses occurred within a week of the exposures. These thermal responses were not only detected in the immersed but also in the contralateral hand (122). Furthermore, central factors (catecholamines, changes in temperature and cardiovascular response over time) did not differ between the exposed and non-exposed hand over time (121). The discrepancies in the results could partially be related to the duration of the cold exposure.

Table 5. Whole body cold acclimation in water

Study	Temperature	Duration	Repetitions	Area of exposure	Area of interest	Thermal response	Outcomes/conclusion
Leppäluoto *et al.* (81)	0-2°C water or -110 °C air	20 s immersed in 0-2 °C or 2 min at -110 °C	3 times/ week for 12 weeks	Whole body exposures to cold air or water	To determine the influence of long-term regular exposure (winter swimming, cryotherapy) to acute cold temperature.	Plasma ACTH and cortisol were lower at certain time points (habituation). NE increased (2-fold to 3-fold) each time for 12 weeks after both cold exposures. No changes in cytokines.	Sustained cold-induced stimulation of NE, was remarkably similar between exposures. The frequent increase in NE might have a role in pain alleviation in whole-body cryotherapy and winter swimming
Tipton *et al.* (96)	10°C	3 min	Two times in control and 8 times in habituation group	Head-out immersions	To examine the central and peripheral mechanisms involved in habituation to the initial response	Repeated immersions to cold water reduced HR, respiratory frequency and volume responses	Habituation of the initial responses are located more centrally than at the peripheral receptors
Barwood *et al.* (97)	12°C	2.5 min	7 times (5 times with no breath hold attempts)	Head-out immersion	To examine whether repeated cold water immersion and psychological training improved breath holding times	Not measured	Habituation to cold water increases breath hold time, but was not further increased by psychological training
Eglin and Tipton (99)	10°C	two 3-min head-out seated immersions	6 cold showers	3 min at 10°C on the back; or 3 min at 15°C on the back, or 30 s at 10°C on the back followed by 30 s on the front	To examine whether the initial responses to cold water could be attenuated by repeated cold showers	Decrease in skin temp of back on average by 0.4-0.5°C	Repeated showering in cold water (but not warm) reduced the respiratory drive during head-out immersion in water at the same temperature.
Jansky *et al.* (104)	14°C	1 h	3 x week for 4-6 weeks	Head-out immersions	To monitor changes in body and skin temperatures, heat production, shivering, cold sensation and body fat content	Central and peripheral body temperatures at rest and during cold immersion were lowered. The metabolic response to cold was delayed, subjective shivering attenuated and cold sensations dampened.	Development of hypothermic cold adaptation due to repeated cold water immersions
Castellani *et al.* (105)	20°C	2 h	Three repetitions during one day	Whole body	To examine shivering and vasoconstriction during serial cold water immersions within a short time period	Lower T_{rect} and higher heat debt, lowered M, habituation of thermal sensations	Repeated cold exposures may impair the ability to maintain normal body temperature because of a blunting of M
Stocks *et al.* (106)	18°C (Cold-water stress tests were performed on days 1, 8 and 15)	(60 min seated, followed by 30 min cycling (1 W.kg-1), and 90 min resting exposures during the intervening days	15 d of cold-water adaptation	Subjects immersed to the fourth intercostal space	To examine the effects of repeated, resting cold-water immersion on M and T_{core} defence during subsequent rest and exercising immersions	Blunted metabolic response, no changes in T_{es}. During exercise, this metabolic blunting was only apparent over the first 10-min period.	Repeated cold-water exposures produced a habituated-thermogenic response (blunted metabolism). For an equivalent drop in T_{es} during rest, neither this response, nor an elevated M, was apparent during subsequent cold-water exercise.

Marino *et al.* (107)	29°C (start)→23°C (end)	60 min	Three repetitions on three successive days	Whole body	To examine metabolic, thermoregulatory and sympathoadrenal responses due to repeated bouts of brief cold stress	Lowered T_{rect} and reduced metabolic response	Repeated brief bouts of cold exposure results in adaptive responses evidenced by the changing trends in body temperature, M and plasma NDR.
Jansky *et al.* (108)	14°C	1 h	Three times per week for 6 weeks	Head-out immersions	To determine whether repeated immersions induce a change in the activity of the sympathetic nervous system and cardiovascular functions	Peripheral vasoconstriction and an increase in systolic and diastolic blood BP occurred due to cold acclimation. No change in reactivity of the sympathetic nervous system.	The repeated cold stimuli were not sufficient to induce significant changes in sympathetic activity and hormone production.
Stocks *et al.* (110)	18°C (Cold-water stress tests were performed on days 1, 8 and 15)	60 min cold stress test and 90 min exposures during the intervening days	14 d	Subjects immersed to the fourth intercostal space	To investigate how cold acclimation affects intracellular and extracellular fluid compartments, plasma protein, electrolyte and hormone concentrations	T_{es} -0.6 °C, T_{sk} -7.4 °C, VO_2 +0.5 l/min^{-1}, acclimation did not change the distribution of total body water, or plasma osmolality, total protein, electrolyte, atrial natriuretic peptide or aldosterone concentrations	Fluid from extravascular cells is displaced into the interstitium during acute cold-water immersion, both before and after cold acclimation

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Many of the studies examining peripheral cold adaptation have used relatively brief immersion protocols (5-15 min) (112, 113, 118) and observed habituation responses. It is possible that cold exposures of longer duration results in insulative responses (120).

A few studies have examined the association between repeated local cooling responses with general cooling. Savourey *et al.* (118) detected that repeated local cooling of legs in water was associated with habituation responses (higher skin temperatures, decreased NE) of the lower limbs, but at the same time a hypothermic insulative general cold adaptation response during a cold stress test (decreased T_{sk} and T_{rect}). Also Jansky *et al.* (119) observed that repeated local exposures of legs to cold water produced habituation responses, such as a lesser vasoconstriction, HR and BP response which were observed during the initial cooling phase. However, when locally cold adapted subjects where exposed to whole body cold exposure they did not demonstrate hypothermic cold adaptation responses typical of systemic cold adaptation.

7. TIME COURSE OF COLD ADAPTATION

Due to the different regulatory systems (e.g. respiratory, cardiovascular) of humans which often involve the same effector organs, physiological adaptation to cold varies depending on the stimuli (e.g. cold air or water, continuous, intermittent) and produces similar, but not entirely identical adaptation responses. Furthermore, several individual factors effect the rates at which people respond to the same stimuli (4). The time course of adaptation is dependent on the threshold of the stimulus, a latency period, the physiologically and possible genetically determined maximum of an effector organ, the speed of tissue/organ/systemic adaptation. In addition, optimal adaptation occurs when the cumulative adaptation response in maximised and at the same time the physiological strain remains in the tolerance limit. Finally, if the cold stimulus is discontinued a gradual reversal of adaptation occurs (4) (Figure 4).

Habituation responses seem to develop first, only after a few exposures to cold air or water which can be either local or affect the whole-body (80, 87, 123). Circulatory changes (e.g. blunted vasoconstriction) can be observed after ca. 5-10 days of repeated exposures (87, 88, 120). For example hemoconcentration has been shown to develop within 11 days of repeated cold exposures (87). Many of the studies examining adaptation to cold and heat consider that acclimation regimes of ca. two weeks is sufficient to detect the major physiological changes (4,88).

8. DETERMINANTS OF COLD ADAPTATION

8.1. Individual factors

Several individual factors affect human physiological responses to cold (124-126) and, no doubt, the subsequent adaptation. Important determinants are body composition, fitness, sex, age, exercise, diet and health (7, 126). For example, cold elicits a blunted thermogenic responses in overweight compared with lean men (127). As mentioned previously, also body composition affects the observed thermal responses (13). Also advanced age impairs thermoreception, attenuates vasosconstriction and lowers heat production capacity (128). Health may also affect thermal balance. For example, cardiovascular,

Table 6. Local cold acclimation in water

Study	Temperature	Duration	Repetitions	Area of exposure	Area of interest	Thermal response	Outcomes/conclusion
Savourey *et al.* (118)	5°C (foot) and 1°C (whole body)	5 min	lower limbs 5 x week for 1 mo (5 min)	repeated immersion of lower limbs, foot and whole body cold tests	To study the association between local and general cold adaptation	Local cold acclimation: higher skin temperatures of the lower limbs and a hypothermic insulative general cold adaptation (T_{rect} and T_{sk}) without a change either in M or in lower limb skin temperature	Local cold habituation was observed (decreased NE). The hypothermic insulative general cold adaptation (increased NE) was unrelated either to local cold adaptation or to the habituation.
Jansky *et al.* (119)	12°C	30 min	20 times during 4 weeks	Leg immersed up to the knee	To examine whether repeated local cooling induces the same or different adaptation responses as repeated whole body cooling	Repeated cooling of the legs attenuated the initial increase in HR and BP and educed vasoconstriction. HR and systolic BP was generally lower due to cold acclimation	Repeated local cooling of legs induces different physiological changes than systemic cold adaptation
Geurts *et al.* (120)	8°C water	30 min	5 days/week for 3 weeks	Left hand	To investigate the effects of cold acclimation on the thermal response and neuromuscular function of the hand	$T_{fing\ min}$ decreased from 10.6 to 9.3 °C after 3 weeks. $T_{fing\ mean}$ dropped from 14.2 to 11.7°C following cold acclimation. Delayed onset and decreased amplitude of CIVD	Cold acclimation did not enhance hand temperature or function, but may put the hands at a greater risk of cold injury when exposed to the cold.
Geurts *et al.* (121)	8°C	30 min	5 days/week for 3 weeks	Left hand	To investigate the role of central and peripheral factors in repeated cold exposure and their effects on temperature response, neuromuscular function, and subjective thermal sensation	Minimum index finger temperature did not change significantly post-acclimation	Neuromuscular function was impaired, but did not differ between the hands nor over time. Central factors did not change and there were no differences in responses between the exposed and non-exposed hand over time (peripheral adaptation), nor were there any differences in local factors. Subjective thermal comfort was improved
Mekjavic *et al.* (122)	8°C	30 min	5 days/week for 3 weeks	Right hand, left hand immersed in the beginning and end of acclimation	To examine thermal response across the fingers with repeated local cold exposure of the hand, along with the transferability of acclimation to the contralateral hand	Seven distinct patterns of thermal responses were evident, including plateaus in finger temperature and superimposed waves. Amount of CIVD waves decreased in all digits of the right hand over the acclimation period	CIVD is not trainable and may lead to systemic attenuation of thermal responses to local cooling.

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endocrinological, muscular or neural disorders may significantly affect heat production and loss. Also, the use of certain medication and drugs may predispose subjects to cold sensitivity (88).

8.2. Exercise

Exercise attenuates or inhibits cold adaptation. Stocks *et al.* (106) found that the blunted thermogenic response related to repeated immersions in cold water applied only to resting conditions and was abolished during light exercise. Moreover, Golden & Tipton (123) reported that exercise prevented the development of an adaptive reduction in M to cold during a subsequent resting immersion. Interval training in a cold environment prevented the development of a general (hypothermic) cold adaptation that was observed in non exercising subjects exposed to cold (129). Interestingly, exercise in the cold compared with resting exposures to cold also accelerates

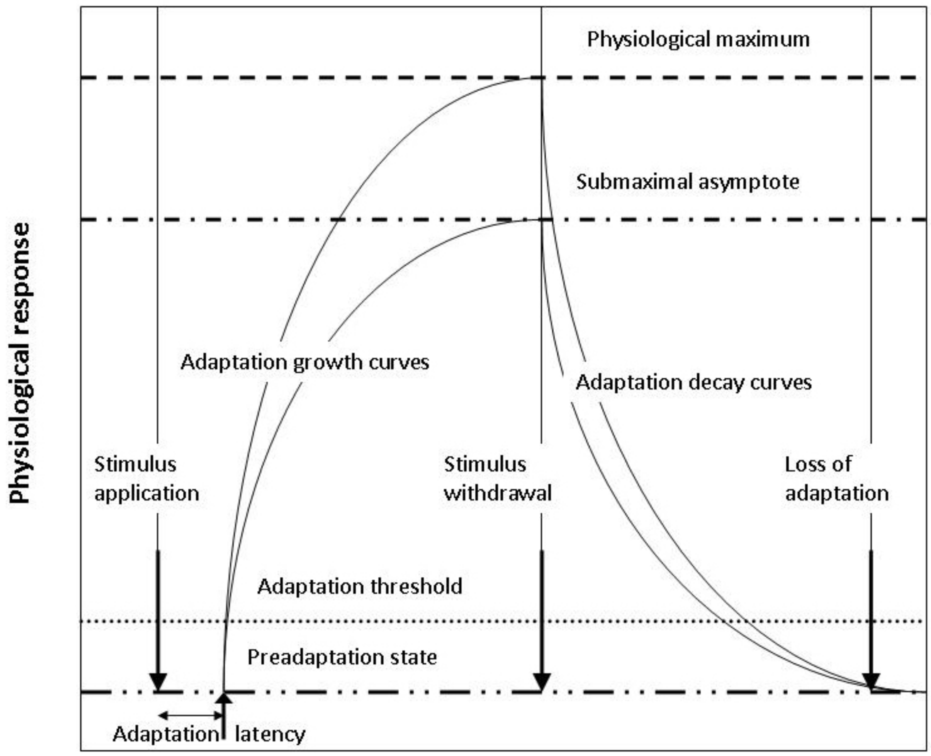

Figure 4. Physiological changes following the application and withdrawal of an adaptation stimulus. Adapated with permission from (Reproduced with permission from 143).

the deadaptation from heat (130). However, not all studies have found an association between exercise and cold adaptation responses. For example, Geurts *et al.* (131) did not detect that exercise (50% VO_{2max}) affected thermal responses in legs due to repeated local immersion to cold water, despite of an increase in T_{rect} and improved thermal ratings during the exposures.

8.3. Hypoxia

Exposure to chronic hypoxia induces marked elevations in the sympathetic reactivity (132) and affects many of the same effector systems as with thermal responses and cold adaptation. For example, hypoxia may alter the neural processing speeds and/or decreased nerve conduction velocity (133) or increase the thresholds for cold sensations (134). Residence at high altitude (2 wks >4000 m) modifies both general and local cold tolerance. Following the hypoxic conditions a decreased systolic BP and lowered skin temperatures of the upper limb were observed during a local cold stress test (135). In addition, during whole body exposure to cold M was slightly lowered, the onset time for shivering shortened and T_{sk} was higher suggesting an increase in the sensitivity of the thermoregulatory system. The study concluded that general and local cold tolerance were modified by a short-term residence at altitude and that the changes observed were not in accordance with general or (and) local cold adaptation (135). A study examining acclimation to intermittent hypoxia in comfortable ambient temperature detected normothermic-insulative-metabolic general cold adaptation (136).

9. SIGNIFICANCE OF COLD ADAPTATION

9.1. Performance and health

There are few studies attempting to evaluate the functional significance of cold adaptation. It could be assumed that cold habituation would enhance performance. For example, the improved thermal comfort due to cold habituation could be beneficial for reducing cold-induced distraction and improving concentration on a given task. However, there is no scientific evidence supporting this hypothesis. Moreover, the blunted thermal responses of hands could improve circulation, increase dexterity and enhance working ability in cold conditions. Experimental studies examining the association between cold habituation and performance showed no marked improvements on balance (137) or cognitive performance (138). With regards to health, the diminished stress response related to repeated cooling could be beneficial. However, to the best of my knowledge, there is no scientific evidence available for this assumption. Recent results on the use of cryotherapy has shown some beneficial effects, like adaptation to oxidative stress (67). Cold as a treatment method alleviates pain, and is suitable for treating rheuamatoid arthritis (78).

Overall, cold temperatures of arctic climates is associated with adverse health, like increased infant and perinatal, as well as age-standardized mortality rates from respiratory diseases (139). Furthermore, morbidity from cardiovascular and respiratory diseases increases with decreasing temperatures (140). For example, rates of coronary events increase during comparatively cold periods, and especially in warm climates (141). In addition, the seasonal fluctuation in blood pressure is greater in populations closer to the equator than in colder regions (142). Excess winter mortality has been recognized worldwide and displaying a U or V-shaped association with temperature and is due mainly to deaths due to cardiovascular diseases and to a lesser extent to respiratory diseases (24, 140). The differences in morbidity and mortality according to latitude could at least partially be associated with adaptation to cold, and particularly behavioural adaptation described earlier (see 3.3.).

Cold adaptation responses can be beneficial in one context but harmful in another. For example a blunted vasoconstriction response in hands due to repeated exposures to cold may improve manual dexterity, but at the same time put the hands at greater risk of adverse cooling. In fact, repeated experimental local cooling of hands has resulted in attenuated thermal responses which could predispose the extremities to cold injuries (120). Furthermore, the improved insulation due to cold adaptation could be harmful when humans are exposed to heat (5).

10. SUMMARY

In summary, behavioural acclimatization of humans to cold exceeds their capacity to preserve and produce heat by physiological means. However, when necessary (e.g. when clothing, exercise or housing is inadequate to prevent cooling), human adjust physiologically to chronic cold exposures. Habituation responses develop first, only after a few repeated exposures to cold and do not often involve marked whole body cooling. In the case of more substantial cooling of the body metabolic and/or insulative adjustments occur. The pattern of cold adaptation is dependent on the type and intensity of the cold exposure, as well as several individual factors. In addition, factors such as exercise and hypoxia affect cold adaptation responses. The increased tolerance to cold preserves energy, but often at the cost of a lower body temperature in the cold.

There are only a few studies attempting to evaluate the significance of cold adaptation, and those have not detected marked benefits from the physiological adaptation responses. Local adaptation can in some cases improve comfort and performance, but sometimes be even harmful, and predispose human to cold injuries. In summary, human physiological responses against the adverse effects of cold are rather limited. Therefore, even with general or local cold adaptation responses different behavioural and technical measures are needed to reduce or prevent the adverse effects of cold on human performance and health. Further studies related to human cold adaptation and its functional significance contributes to our understanding of human adaptation in general.

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Abbreviations: E: epinephrine, BAT: brown adipose tissue, BP : blood pressure, BMR: Basal metabolic rate, CIVD: cold induced vasodilatation, CNS: central nervous system, DBP : diastolic blood pressure, HR : heart rate, M: metabolic heat production, metabolic rate (Wom-2), NE: norepinephrine, NST: nonshivering thermogenesis, SBP : systolic blood pressure (mmHg), Ta : ambient temperature

(°C), Tb : mean body temperature (°C), Tf: finger temperature (°C), Trect : rectal temperature (°C), Tsk : mean skin temperature (°C), VO2 : oxygen consumption (absolute: l··min-1, relative: ml·min-1·kg-1)

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