NEUROMUSCULAR ACTIVITIES IN EXTREME TEMPERATURES

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Contents

Summary

The primary function of the motor system is motion, which includes postural activity, locomotion, and manipulation. However, the motor system also participates in some autonomic and sensory functions, such as respiration, swallowing, hearing, or vision through highly specialized muscles. The motor system also makes a unique contribution to temperature regulation by modifying heat production and heat loss of the organism by means of 1) shivering thermogenesis, and 2) behavioral thermoregulation. In its turn, environmental temperature exerts significant influence on the efficiency of neuromuscular performance and manual dexterity. This influence becomes vitally important at extreme hot or cold temperatures. Very often, the motor system has to perform both motion and thermoregulatory functions simultaneously, for example in circumpolar regions, highlands, in cold water, or in hot climates.

1. Thermoregulatory Activity of the Motor System

Humans are increasingly being exposed to climatic extremes, whether cold or hot, in development of polar or equatorial regions, military operations, space exploration, and broadening recreational activities. The reciprocal influence of motion and thermoregulation, and hence their competition, can impair both of these functions of the motor system. This article provides data on thermoregulatory function of the motor system, and on motor function in extreme temperatures (see also *Thermoregulation*).

1.1. Cold Shivering and Thermoregulatory Muscle Tonus

Traditionally, shivering thermogenesis is believed to comprise of two patterns: 1) thermoregulatory muscle tone (or preshivering tone) and 2) cold shivering itself. Shivering thermogenesis aims to prevent hypothermia by increasing heat production.

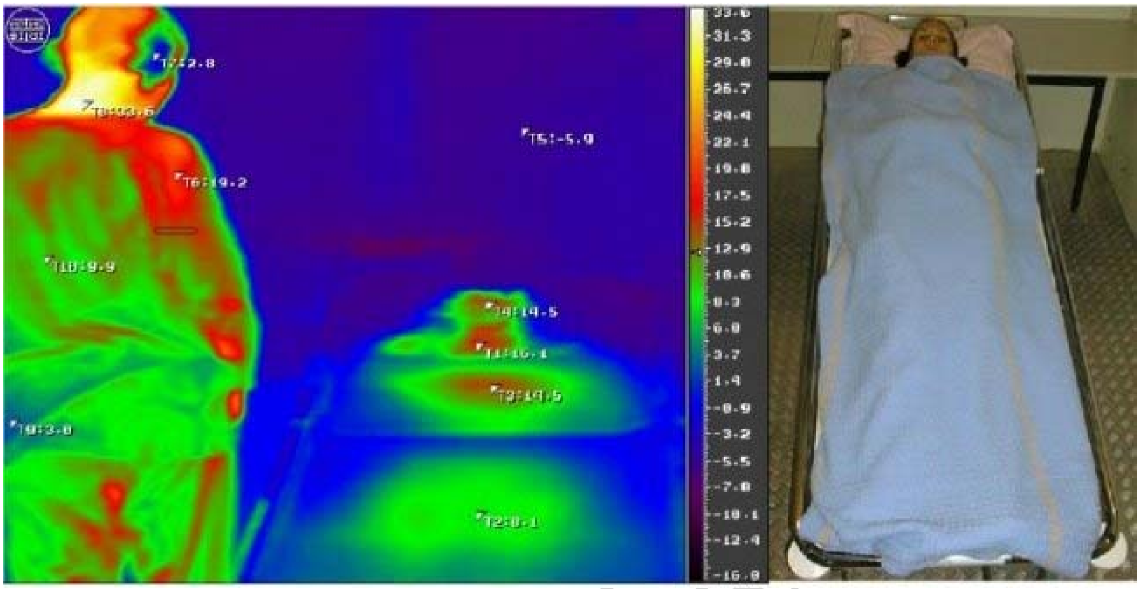

Figure 1. The loss of thermal energy from a subject lying on a stretcher under an emergency cover (right panel) used by rescue services. In the middle panel, the stretcher has been photographed with the aid of infrared camera (Dr. Nina Zaproudina) after the person stood up (left). Please note the low temperatures of the back site of the stretcher surface.

Thermoregulatory muscle tone is seen as a low-amplitude continuous stable pattern of electromyogram (EMG) and is defined as: “the increase in electrical activity of the skeletal musculature of a resting tachymetabolic regulator during moderate cooling.” All muscle activity provides heat (see *Muscle Energy Metabolism*). During more intensive cooling, thermoregulatory muscle tone is superimposed by microvibrations and eventually by shivering tremors.

Accordingly, cold shivering is defined as: “involuntary tremor of skeletal muscles as a thermoeffector activity for increasing metabolic heat production.” Cold shivering may be subdivided into a burst-like pattern and a pattern with clustering of EMG. Bursts of cold shivering occur 6–12 times per minute and are presented as slow amplitude modulations on EMG. The EMG clustering occurs in humans with a frequency of 4–8 Hz. The clustering of EMG coincides with the most intensive tremors (shuddering and shaking), and it probably corresponds to maximal development of shivering.

A rapid decrease of mean skin temperature is essential to start cold shivering. In near naked subjects exposed to moderate cold air at 10 ºC the shivering starts within 15–45 minutes, when the mean skin temperature has decreased to 27–28 ºC, but core temperature is not yet affected or has only slightly declined. During exposure to more severe cold at –3 ºC to 5 ºC shivering starts within 4–15 minutes.

The decrease of core temperature during body cooling is essential for the maximal development of shivering and, therefore, for maximal heat production. Cold shivering may be induced even in humans with thermoneutral skin temperature by cold saline infusion or breathing cold air. In hypothermic humans, when core temperature falls to 30 °C the shivering stops.

Thus, both peripheral and deep body temperature sensors are involved in the control of shivering thermogenesis and in different circumstances one or the other influence may be dominant.

During immersion to cold water or in cold-wet conditions (rain combined with cold and wind) shivering starts earlier than in the exposure to cold air because of a faster rate of body cooling, caused by water. The body cools faster in water because of conduction and intensive convection during swimming and faster heat loss from the skin. For example, in 20 ºC water, shivering starts within 15–20 minutes of immersion, while in 20 ºC air, shivering is rarely observed. In 10 ºC water, most subjects start to shiver immediately after being immersed.

Relative shivering intensity ranges from 5% to 16% of maximal voluntary contraction in central muscles (thigh, thorax, and abdomen). In the peripheral muscles, it ranges from 1% to 4% of MVC. Most (71%) of the heat production originates from the central trunk muscles and 21% from the thigh muscles, while peripheral muscles contribute the remaining 8%. However, shivering is a very individual reaction in respect of a set of muscles involved and skin or core temperature thresholds.

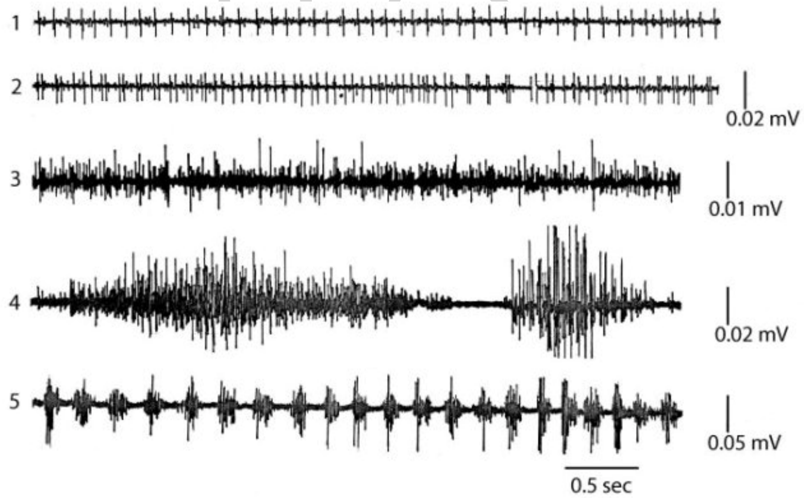

Figure 2. The cold shivering patterns recorded with the aid of EMG.
1. One motor unit firing when cooling has just started.
2. Two motor units while cooling continues. The core temperature is not yet affected.
3. Many motor units recruited, which form interference EMG that corresponds to thermoregulatory muscle tone (low-amplitude stable EMG).
4. Burst of cold shivering 1–2 s long, when core temperature just started to decline (T_c = 36.9 ºC).
5. Clustering of EMG, which coincides with vigorous tremor, and shuddering (or shaking). This happens during prominent decline of core temperature (T_c = 36.5 ºC).

The initiation of shivering might also be related to a change of muscle and tendon receptor sensitivity in the cold, because of either the elevated level of serum catecholamines or the activation of γ-motor neurones. Overt tremor, which is characteristic of cold shivering, may also result from the declined stabilizing effect of the stretch reflex when the firing rate of motor units fails to match with the speed of muscle contraction.

During shivering muscles do not produce external work, and therefore contractile activity aims to provide heat. Shivering can generate heat in humans at a rate of 10–15 kJ min^{-1}, thus causing a two- to threefold increase of oxygen consumption at ambient temperature of –3 ºC, twofold at 5 ºC, and 1.5-fold at 10 ºC. During cold-water immersion, the metabolic rate can increase 4.5-fold. Shivering thermogenesis is supported by an increase in the oxidation of free fatty acids.

1.2. Spinal and Supraspinal Mechanisms of Cold Shivering

On the supraspinal level, cold shivering is controlled by ventromedial and dorsomedial hypothalamus, *nucleus caudatus*, *putamen*, *globus pallidus*, *substantia nigra*, red nucleus, mesencephalic reticular formation, lateral portion of reticular formation of pons, and *medulla oblongata*, that is, by the structures responsible for the control of muscular tonus and rhythmical stereotyped movements. The shivering command descends to the spinal cord through rubro- and reticulospinal pathways.

In the spinal cord cold shivering is programmed in VII, VIII, and IX laminas of Rexed. Smaller γ-motor neurones are activated first during the local cooling of the spinal cord of the cat, but with further cooling α-motor neurones are driven into activity, while at such temperature γ-activity is depressed again. Within the group of α-motor neurones the smaller tonic α-motor neurones are activated earlier than the larger cells of the phasic type.

Thermoregulatory muscle tonus, seen at the initial stage of cooling, is generated by continuous asynchronous discharges of low-threshold MUs at rates of 4–16 impulses per second, with relatively high standard deviation of mean interspike interval. These motor units may correlate with slow, fatigue-resistant motor units, which are active during weak isometric contraction or posture.

Bursts of cold shivering coincide with the periods of activity of higher-threshold, probably fast motor units, which are usually recruited at lower rates. This is consistent with the fact that in bantam cocks aerobic (slower) muscles are involved in cold shivering prior to the anaerobic (faster) ones. Clustering of EMG discharges that coincide with fast decrease of core temperature appears to rely on the long-term synchronization of motor unit discharges.

Cold shivering is generally assumed to be a cold-induced form of enhanced physiological tremor and postural muscle tonus. The analogy between shivering and physiological tremor arises from similar amplitude and frequency characteristics of tremor and EMG, and similar characteristics of motor unit activity (see Table 1).

Patterns of thermoregulatory muscle activity	**Normal patterns of motor unit (MU) activity**	**Patterns of voluntary muscle activity**	**Patterns of spontaneous muscle activity**
Thermoregulatory muscle tone (preshivering tone)	Asyncronical (with a small portion of short-term synchronised MUs) activity of low-threshold MUs at firing rates 4-12 ips	Postural tonus, voluntary isometric contraction)	Muscular rigidity in akynetiko-rigid form of Parkinson's disease (PD)
Periods of cold shivering	Periods of burst-like activity of high-threshold MUs	Rhythmical movements	Hyperkinetic syndromes
Cold tremor (clonus-like shuddering)	Long-term synchronisation (grouping) of MU activity with clustering of electromyogram	Normal enhanced (activated) physiological tremor (fatigue, sympathetic hyperactivity etc.)	Tremor in shaking form of PD
Not evidenced	Doublets	Initiation of movement	Tremor in shaking form of PD

Source: adapted from Lupandin, Meigal, and Sorokina, 1995.

Table 1. Probable correlation between thermoregulatory and non-thermoregulatory patterns of motor system activity in humans

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Biographical Sketch

Alexander Meigal was born in Petrozavodsk (Rep. of Karelia, former Soviet Union, currently Russian Federation) in 1964. In 1987 he graduated from the Medical Faculty of Petrozavodsk State University (PSU), and started work as a researcher in the Laboratory for Neurophysiology of Thermoreception and Heat Exchange of the PSU. In 1990 he defended his Candidacy dissertation "Neurophysiological analysis of thermoregulatory muscle activity," and in 1997 his Doctoral dissertation "Neurophyiological basis of coordination between thermoregulatory and motor activity in humans." In 1998 he was elected as a professor of the Department of Human and Animal Physiology of PSU. Alexander Meigal has participated in joint scientific investigations at the University of Minnesota (Duluth, 1992), and in the University of Kuopio (since 1989), and in the Institute of Occupational Health (Oulu, since 1994). He was awarded the medal of Russian Academy of Sciences for the best scientific work in Physiology for the year 1999. He is an acting member of the NY Academy of Sciences (2000).

His major interests are: neurophysiology of the motor system in humans, motor unit activity, electromyography, cold shivering, tremor, normal and pathological muscular tonus, and muscular performance in cold and hot conditions.

Alexander Meigal is currently investigating the influence of extreme temperatures on the accuracy of precision motor tasks, on the intensity of muscular tonus in the Parkinson's disease patients, on muscle performance, fatigue, recovery and adaptation in cold and hot conditions.