

## GROSS AND FINE NEUROMUSCULAR PERFORMANCE AT COLD SHIVERING

*(Int J Circumpolar Health 2002; 61; 163-172)*

Cold exposure may decrease the efficiency of voluntary motor activity due to a decrease of muscular temperature, and to involvement of the motor system in thermoregulatory motor behaviour and shivering thermogenesis. Traditionally, shivering thermogenesis is believed to comprise two patterns – 1) thermoregulatory muscle tone (or preshivering tone) and 2) cold shivering itself (Burton, Bronk, 1937). Since it was observed in animal experiments, this classification has been proved to be practical in human measurements. Shivering thermogenesis is aimed to prevent hypothermia by increasing heat production. Shivering and voluntary movements compete for common neural circuits (Kleinebeckel, Klusmann, 1990), and this may affect fine and gross performance. Mechanical tremor and elevated muscle tone during shivering may also influence accuracy of movements. This review focuses on the mechanisms of interaction between shivering thermogenesis and exercise and on the mechanisms which may compensate for this interaction.

### *Patterns of cold-induced activity of the motor system*

According to the 2nd edition of "Glossary of terms for thermal physiology (Pflügers Archive, 1987) thermoregulatory muscle tone is "the increase in electrical activity of the skeletal musculature of a resting tachymetabolic regulator during moderate cooling". Thermoregulatory muscle tone is seen as a low-amplitude continuous stable pattern of electromyogram (EMG). During more intensive cooling, thermoregulatory muscle tone is superimposed by microvibrations and eventually by shivering tremor.

Cold shivering is defined as "involuntary tremor of skeletal muscles as a thermoeffector activity for increasing metabolic heat production" (Pflügers Archive, 1987). In human in-

*Alexander Meigal*

*Petrozavodsk State University,*

*Department of Physiology,*

*Petrozavodsk, Russia*

vestigations cold shivering may clearly be subdivided into a burst-like pattern and a pattern with clustering of EMG. Bursts of cold shivering occur 6-12 times/min and are presented as slow amplitude modulations on EMG (Israel, Pozos, 1989). EMG clustering occurs in humans with the frequency 4-8 Hz (Meigal et al., 1993). The clustering of EMG coincides with the most intensive tremor, and it probably corresponds with "shuddering" or "shaking", first described by Denny-Brown et al. (1935) as a "maximum development of shivering". These two different patterns of cold shivering (with burst-like EMG and grouping discharges on EMG) were also documented for animal species (Kleinebeckel, Klusmann, 1990).

*Thermal and non-thermal stimuli for thermoregulatory muscle tone and cold shivering*

The more rapidly the mean skin temperature decreases, the earlier is the onset of cold shivering. When near naked subjects were exposed to moderate cold ( $T_a=10^{\circ}\text{C}$ ) generalised continuous shivering started within 15-45 min (Tikuisis et al., 1999; Meigal et al., 1997; Hurley et al., 1963; Golenhofen, 1965; Spurr et al., 1957), when mean skin temperature decreased from  $32-33^{\circ}\text{C}$  to  $27-28^{\circ}\text{C}$ , but core temperature was still not affected or was only slightly decreased. During severe cold ( $T_a=-3$  to  $5^{\circ}\text{C}$ ) shivering started within 4-15 min after entering cold chamber, while core temperature was unchanged (Israel, Pozos, 1989; Bawa et al., 1987; Muza et al., 1986; Horvath et al., 1956).

However, there are data that decrease of core temperature during body cooling is necessary for maximum development of shivering or heat production (Meigal et al., 1993; Mittleman, Mekjavic, 1991). Cold shivering may be induced in man with thermoneutral skin temperature by cold saline infusion (Frank et al., 1997) or breathing cold air (Buguet et al., 1976). In high spinal patients shivering occurs when core temperature fall to approximately  $35.6^{\circ}\text{C}$  (Downey, 1984). At  $30^{\circ}\text{C}$  shivering stops (Pozos, Wittmers, 1981). Most likely, both peripheral and deep body temperature sensors are involved in the control of shivering thermogenesis, and in different circumstances the one or the other influence may be dominant (Bligh, 1973).

Several studies provide evidence that initiation of shivering might be related either to change of muscle and tendon receptor sensitivity during cooling (Schafer 1973; Lupandin,

1983), or to the activation of  $\gamma$ -motoneurons (Sato, 1981; Lupandin, 1979).

## RELATION OF COLD SHIVERING TO POSTURE AND MOVEMENT

There are several lines of evidence showing that exercise and cold shivering are analogous processes with regard to neural circuits, EMG and mechanical characteristics.

### *Cold shivering and physiological tremor*

Cold shivering (cold-induced tremor) is believed to be a manifestation of physiological tremor (Hemingway, 1963; Lupandin, 1981), namely of its enhanced ("activated") form (Freund, 1983). The "activated" physiological tremor, i.e. the essential tremor, is distinguished from the regular physiological tremor by higher amplitude, lower frequency, and distinct clustering of EMG, and it is based on the long-term synchronisation of discharges of motor units due to common excitatory input from proprioceptors (Freund, 1983; Findley, Koller, 1987). The analogy between shivering and physiological tremor is evidenced by similar characteristics of tremor and EMG (Pozos, Iazzo, 1991), by demonstration of long-term synchronisation of motor units during cold shivering in humans (Meigal et al., 1993), and by the fact that deafferentation of muscles destroys the rhythmicity and decreases the intensity of cold shivering (Stuart et al., 1966).

The alternative approach explains mechanical oscillations during physiological tremor as a result of unfused asynchronous activity of several motor units (Allum et al., 1978). However, this possibility has been demonstrated by Lupandin (1983, 1979), who documented asynchronous activity of motor units at firing rates 4-12 ips during cold tremor in cats.

### *Nervous control of shivering*

Microelectrode technique allowed to trace in animals the "efferent tract of shivering", which includes 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* (Morimoto, Murakami, 1988; Amini-Sereshki, 1977). It means that activity of the central nervous system related to cold shivering utilises the struc-

tures responsible for control of muscular tonus and rhythmical stereotyped movements. The command to start shivering descends to spinal cord through rubro- and reticulospinal pathways (Hemingway, 1963).

#### *Spinal mechanisms of shivering*

In spinal cord VII, VIII and IX laminae of Rexed are responsible for cold shivering (Klussmann, Kleinebeckel, 1990). In accordance with Hennemann's size principle  $\gamma$ -motoneurons are activated first during local cooling of the spinal cord of the cat, but with further cooling  $\alpha$ -motoneurons are driven into activity, while at such temperature  $\gamma$ -activity is depressed again (Lupandin, 1981; Sato, 1981; Klussmann et al., 1969). Within the group of  $\alpha$ -motoneurons the smaller tonic  $\alpha$ -motoneurons are activated earlier than the larger cells of the phasic type (Klussmann et al., 1969), which is consistent with earlier development of thermoregulatory muscle tone in comparison to shivering.

The behaviour of human motor units, which comprise of the  $\alpha$ -motoneurone, its axon and all muscle fibres it controls, during cold shivering has been reported in few studies (Meigal et al., 1993; Petajian, Williams, 1972). Thermoregulatory muscle tone, seen at the initial stage of cooling, was shown to be generated by continuous asynchronous discharges of low-threshold MU:s at rates of 4-16 s<sup>-1</sup>, 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 coincided with the periods of activity of higher-threshold, probably fast motor units, which were 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 (Aulie, Toien, 1988). Clustering of discharges on EMG, which coincided with fast decrease of core temperature, appeared to rely on mechanism of long-term synchronisation of motor unit discharges (Meigal et al., 1993).

#### *Cold shivering and muscular tonus*

Several reports provide evidence for a relationship between shivering and postural muscle tonus. Hohtola (1981) reported that shivering in birds may be temporarily suppressed by tonic immobility – a phenomenon which is related to regulation of postural muscle tonus. Meigal et al. (1996) found that aftercontraction tone in human m. biceps

brachii depends on ambient temperature: at  $T_a=5^\circ\text{C}$  after-contraction was doubled in its amplitude in comparison to  $T_a=22^\circ\text{C}$ , but it was two times less at  $T_a=70^\circ\text{C}$ . Similarly, the amplitude of pathological muscular tonus (rigidity) in Parkinson's disease patients was found to decrease in heating condition, but it increased in the cooling condition (Lupandin et al., 1996; Antonen et al., 2001). Similarly, Meigal et al. (1996) demonstrated that body and head position affect thermoregulatory muscle tone in deltoid muscles according to tonic neck and labyrinthine reflexes. Meigal and Kuzmina (1989) found that EMG activity during thermoregulatory muscle tone in *m. triceps brachii* was higher in standing position with arms freely positioned along the trunk, while in the sitting position with arms flexed at elbow and resting on the thighs *m. biceps brachii* was predominantly active. In the cat modulation of motor unit tonic activity by cold was evidenced for *m. sphincter ani externus*, *m. levator ani* (Gerasimova, Kuzmina, 1996), and respiratory muscles (Burachevskaya, 1981), which may in the cold affect defecation and breathing, respectively.

Lupandin (1979) has earlier shown in cats that pain and cold stimuli evoke identical motor responses, namely, activation of flexor musculature. It was proposed that thermoregulatory muscle tone is activated via the afferents of flexor reflex (AFR), represented by  $A\delta$  and C nerve fibres (Lupandin, 1983).

## SKILLED MOTOR PERFORMANCE DURING COLD SHIVERING

Shivering can generate heat in man at a rate of 10-15 kJ/min (Shepard, 1985), thus causing a 2-3-fold increase of oxygen consumption at  $T_a=-3^\circ\text{C}$  (Spurr et al., 1957; Horvath et al., 1956), a 2-fold increase at  $T_a=5^\circ\text{C}$  (Muza et al., 1986), and a 1.5-fold increase at  $T_a=10^\circ\text{C}$  (Golenhofen, 1965; Hurley et al., 1963). Shivering thermogenesis is supported by an increase in the oxidation of fat (Weller et al., 1998; Tipton et al., 1997), and it is generally believed to impair skilled performance and to hasten the onset of fatigue and mental confusion (Shepard, 1985).

It is known from several studies that cold shivering in man can "co-exist" with voluntary exercise (Meigal et al., 1998, 1997; Nadel et al., 1973; Stolwijk, Nadel, 1973). Nadel et al. (1973) demonstrated that shivering contrac-

REFERENCES

1. Allum JH, Dietz V, Freund H-J. Neuronal mechanisms underlying physiological tremor. *J Neurophysiol* 1978; 41: 557-571.
2. Amini-Sereshki L. Brainstem control of shivering in the cat. *Am J Physiol* 1977; 232: R190-202.
3. Antonen EG, Meigal AYu, Gerasimova LI, Lupandin Yu.V. Electromyographic parameters of muscular fatigue in the Parkinson's disease patients under the whole body cooling. *Fiziologia cheloveka. (Human Physiology, Moscow)*. 2001; 27: 115-123 (Russian).
4. Bawa P, Matthews PB, Mekjavic IB. Electromyographic activity during shivering of muscles acting at the human elbow. *J Therm Biol* 1987; 12: 1-4.
5. Bell DG, Tikuisis P, Jacobs I. Relative intensity of muscular contraction during shivering. *J Appl Physiol* 1992; 72: 2336-2342.
6. Blish J. Temperature regulation in mammals and other vertebrates. *Frontiers of Biology* 1973; 30: 436.
7. Buguet AGC, Livingstone SD, Reed LD, Limmer RE. Cold-induced shivering in men with thermoneutral skin temperatures. *J Appl Physiol* 1976; 41: 142-145.
8. Burachevskaia LE. Intercostal muscle motor unit activity during shivering. *Fiziol Zh SSSR Im I M Sechenova (Sechenov's Physiol J of the USSR)* 1981; 67: 306-312 (Russian, summary in English).
9. Burton AC, Bronk DW. The motor mechanism of shivering and thermal muscular tone. *Am J Physiol*. 1937; 119: 284.
10. Denny-Brown D, Gaylor JB, Uprus V. Note on the nature of motor discharge in shivering. *Brain* 1935; 58: 233-237.
11. Downey JA. The spinal patient and thermoregulation. *Thermal physiology*. Hales JRS (ed). NY: Raven Press, 1984; 225-228.
12. Findley LJ, Koller WC. Essential tremor. *Neurology*. 1987; 37: 1194-1197.
13. Frank SM, Higgins MS, Fleisher LA, Sitsmann JV, Raff H, Breslow MJ. Adrenergic, respiratory, and cardiovascular effects of core cooling in humans. *Am J Physiol* 1997; 272: R557-562.
14. Freund H-J. Motor unit and muscle activity in voluntary motor control. *Physiol Rev* 1983; 67: 387-436.
15. Gerasimova LI, Kuzmina GI. The thermoregulating function of the motor units in the muscles of pelvic floor of the cats. tions, evoked by 20 min swimming in 18°C water, are superimposed on top of shortening contractions during bicycle ergometer exercise (150-200 W, 15 min), even when heat production is considerably elevated. Similarly, Stolwijk and Nadel (1973) showed that during cold exposure at  $T_a=10^\circ\text{C}$  shivering has an additive effect on exercise metabolism. This shows that the thermoregulatory effect of shivering is sensitive to central temperature rather than to the level of heat production of exercise. Kung et al. (1980) have also reported the possibility of simultaneous occurrence of muscle performance and cold shivering with a special note that when muscle work exceeds 50W cold shivering ceased. Meigal et al. (1998) observed shivering in subjects when they kept isometric contraction in the upper limb joints at 10% of maximal voluntary contraction (MVC).

It seems that during cold shivering subjects do not lose the ability to perform accurate motor tasks precisely. Meigal et al. (1997) reported that the ability of subjects to recruit the assigned number of discharges (from 1 to 7) of single motor unit of *m. triceps brachii* using audio- and video-feedback was not impaired by generalised cold shivering, evoked by 1 hr exposure at  $T_a=10^\circ\text{C}$ . Correct recruitment of motor unit discharges in shivering condition was associated with the decrease of firing rate of motor units (Meigal et al. 1997).

Similarly, the accuracy of force output at 10 % of MVC during 15 sec hand grip and elbow flexion with help of bio-feedback aided control from the force was not altered either by thermoregulatory muscle tone or by cold shivering, when core temperature decreased to 36.5°C, and mean skin temperature declined to 26-27°C (Meigal et al., 1998). However, the accuracy of performance of shoulder flexion during cold shivering was adversely affected, which is consistent with the fact that proximal muscles are more active during shivering.

### *EMG of skilled performance during cold shivering*

The ability to perform a skilled motor task during shivering was found to correlate with an increase of amplitude of EMG and the decrease of mean power frequency (MPF) (Meigal et al., 1998). The increase of EMG amplitude during exercise in the cold may originate from the increase of the excitability of spinal motoneurons (Oksa et al., 2000), thus causing recruitment of more motor units than in the ther-

moneutral condition (Yona, 1997).

The increased activity of the antagonists makes joints more stiff by restricting the number of the degrees of freedom of a joint to a minimum, and consequently, making them less susceptible to mechanical tremor. For this reason, increased activity of antagonists (*mm. biceps vs. triceps brachii*, *mm. pectoralis major vs latissimus dorsi*, *mm. pectoralis major and latissimus dorsi vs m. deltoideus*) may serve as a stabilising mechanism for joint position.

The MPF of exercising muscles was found to shift to lower frequencies in the cold condition, eliciting shivering (Meigal et al., 1998; Oksa et al., 1997, 1996; Holewijn, Heus, 1992; Winkel, Jørgensen, 1991). The decrease of MPF is related to decreased conduction velocity along the muscle fibres and to increased synchronisation of motor unit discharges caused by declined muscle temperature (Mucke, Heuer, 1989).

#### *Interaction of shivering and skilled performance on the level of motor units*

The increase of EMG amplitude during the motor performance in the cold, regardless of the mechanisms which evoke it, should be considered as a positive shift in terms of thermoregulation. The increased EMG reflects the increased number of recruited motor units, which produce additional amounts of heat. The reduction of firing rate of MUs during motor control in the state of cold shivering (Meigal et al., 1997) is also substantial with regard to heat production, since it transforms fused tetanus to unfused contraction, which is less economical and thus more thermogenic (Gurfinkel et al., 1981).

Static voluntary contraction at 10% MVC recruits mostly slow low-threshold motor units (H.-J. Freund, 1983), therefore the "co-existence" of cold shivering with voluntary contraction at 10% of MVC may be based on the recruitment of different motor unit types for shivering and exercise (Lucas et al., 1980), or different motor units of the same type.

#### *Mechanisms of voluntary suppression of cold shivering*

Temporary voluntary inhibition of cold shivering is believed to be one the mechanisms which allow skilled performance in cooling conditions. It is known from several studies that voluntary muscle relaxation, holding of breath and mental

- Fiziol Zh Im I M Sechenova (Sechenov's Physiol J USSR) 1996; 82: 100-104.
16. Giesbrecht GG, Goheen MS, Johnston CE, Kenny GP, Bristow GK, Haywards JS. Inhibition of shivering increases core temperature afterdrop and attenuates rewarming in hypothermic humans. *J Appl Physiol* 1997; 83: 1630-1634.
  17. Giesbrecht GG, Bristow GK. Decrement in manual arm performance during whole body cooling. *Aviat Space Environ Med* 1992; 63: 1077-1081.
  18. Glickman N, Mitchell HH, Keeton RW, Lambert EH. Shivering and heat production in men exposed to intense cold. *J Appl Physiol* 1967; 22:1-8.
  19. Glossary of terms for thermal physiology. *Pflugers Arch* 1987; 410: 567-587.
  20. Golenhofen K. Das Reaktionsmuster der Menschlichen Muskulatur in Rahmen der Thermoregulation. *Pflügers Arch* 1965; 285: 124-146.
  21. Gurfinkel VS, Levik IuS, Poleshchuk NK, Korovin IuV. Heat production of the skeletal muscle at different regimes of contraction. *Fiziol Cheloveka (Human Physiol)* 1981; 7: 46-54. (Russian).
  22. Hemingway A. Shivering. *Physiol Rev* 1963; 43: 397-422.
  23. Hohtola E, Johansen K. Respiratory modulation of shivering intensity in the pigeon. *Acta Physiol Scand* 1987; 131: 215-220.
  24. Hohtola E. Tonic immobility and shivering in birds: evolutionary implications. *Physiology and Behavior* 1981; 27: 475-480.
  25. Holewijn M, Heus R. Effects of temperature on electromyogram and muscle function. *Eur J Appl Physiol* 1992; 65: 541-545.
  26. Horvath SM, Spurr GB, Hamilton IH. Metabolic cost of shivering. *J Appl Physiol* 1956; 8: 595-602.
  27. Israel DJ, Wittmers LE, Hoffman RG, Pozos RS. Suppression of shivering by breath holding, relaxation, mental arithmetic, and warm water digestion. *Aviat Space Environ Med* 1993; 64, 1108-1112.
  28. Israel DJ, Pozos RS. Synchronised slow-amplitude modulations in the electromyograms of shivering muscles. *J Appl Physiol* 1989; 66: 2358-2363.
  29. Johnston CE, Elias DA, Ready AE, Giesbrecht GG. Hypercapnia lowers the shivering threshold and increases core cooling rate in humans. *Aviat Space Environ Med* 1996; 67: 438-444.
  30. Kleinebeckel D, Klusmann FW. Shivering.

- In: Schönbaum E, Lomax P eds. Thermoregulation: Physiology and Biochemistry. NY: Pergamon Press 1990; 235-253.
31. Klussmann FW, Stelter WJ, Spaan G. Temperature sensitivity of spinal motoneurons of the cat. Fed Proc 1969; 28: 992-995.
  32. Kung M, Tachmes L, Birch SJ, Fernandez RJ, Abraham WM, Sachner MA. Hemodynamics at rest and during exercise in comfortable, hot and cold environments. Measurements with a rebreathing technique. Bull Eur Physiopathol Respir 1980; 16: 429-441.
  33. Lucas A, Therminarias A, Tanche M. Maximum oxygen consumption in dogs during muscular exercise and cold exposure Pflug Arch 1980; 388: 83-87.
  34. Lupandin IuV, Meigal Alu, Antonen EG. The effect of body cooling and warming on motor unit function in patients with different clinical forms of parkinsonism. Zh Nevrol Psikhiatr Im S S Korsakova (Korsakov's J Neurol Psychiatr) 1996; 96: 86-87 (Russian).
  35. Lupandin IuV. Regulation of the function of gamma- and alpha-motor neurons of antagonist muscles during cold tremor in the cat. Neurofiziologiya (Neurophysiology) 1983; 15: 242-248 (Russian, summary in English).
  36. Lupandin IuV. Role of the fusimotor system in regulating shivering. Fiziol Zh SSSR Im I M Sechenova (Sechenov's Physiol J of the USSR) 1979; 65: 1661-1670 (Russian, summary in English).
  37. Martin SM, Cooper KE. Factors which affect shivering in man during cold water immersion. Pflug Arch 1981; 391: 81-83.
  38. Meigal Alu, Oksa J, Hohtola E, Lupandin YuV, Rintamäki H. Influence of cold shivering on fine motor control in the upper limb. Acta Physiol Scand 1998; 163: 41-47.
  39. Meigal Alu, Gerasimova LI, Zolotova EV, Lupandin YuV. Voluntary recruiting of motor units under conditions of cold shivering. Human Physiol 1997; 23: 701-705.
  40. Meigal Alu, Lupandin IuV, Hänninen O. Head and body position affect thermoregulatory tonus in deltoid muscles. J Appl Physiol 1996; 80: 1397-1400.
  41. Meigal Alu, Lupandin IuV, Hänninen O. Influence of cold and hot conditions on postactivation in human skeletal muscles. Pflug Arch - Eur J Physiol 1996; 432: 121-125.
  42. Meigal Alu, Lupandin IuV, Kuzmina GI. Electromyographic patterns of thermoregu-

arithmetic suppress shivering (Martin, Cooper, 1979; Glickman et al., 1967). According to Israel et al. (1993) cold shivering induced by 2 hours' exposure to  $T_a=0^{\circ}\text{C}$  was most effectively suppressed for at least 60 sec by voluntary muscle relaxation (mean EMG reduction was 35%) and 30 sec breath-holding (24% reduction). Mental arithmetic evoked an 18% reduction of shivering, and drinking warm water ( $50^{\circ}\text{C}$ ) only a 5% reduction.

Suppression of cold shivering during voluntary muscle relaxation may result from direct cortical inhibitory projections on shivering centres in hypothalamus and brainstem reticular formation, or on spinal cord circuits. Reduction of shivering during breath-holding may be due to transient changes in blood pressure and central venous pressure, as well as blood gas content via baroreceptors and chemoreceptors (Mott, 1963). Hypercapnia, which takes place during breath-holding, may also delay shivering onset (Johnston et al., 1996). It is also known that in the pigeon the intensity of shivering is highest at end-expiration and lowest at end-inspiration (Hohtola, Johansen, 1987), whereas in man respiration and shivering burst coincided only in 33% cycles (Israel, Pozos, 1989). Respiration may stimulate the onset of shivering by stretching mechanically linked muscles. There is thus the possibility that holding breath deprives shivering generators of excitatory input from proprioceptors during expiration. Thus, the mechanism of shivering suppression may be integrated with reflex and voluntary motor mechanisms, and is essential for performance of movements and postural function.

Skilled performance during shivering may also be supported by increased vigilance during body cooling (Poulton, 1976), and, probably, by increased sensitivity of muscle receptors due to elevated tone of sympathetic nervous system and increased level of noradrenaline (Frank et al., 1997)

### *Skilled muscular performance and topography of cold shivering*

Topography of shivering thermogenesis is "distribution of thermoregulatory muscle tone, microvibrations, and cold shivering in skeletal muscles of tachimetabolic temperature regulators during cold exposure" (Pflügers Archive, 1987). Golenhofen (1965) has found in man that at the initial state of cooling thermoregulatory muscle tone was confined to the forearm, with lesser activity in the calf, and the least activity in the shoulder and thigh. With prolonged cooling EMG

(cold shivering) shifted to more centralised type of activity (thigh and abdomen muscles). Meigal et al. (1993, 1998) have reported that elevated muscle tone was observed in many functionally different muscles. In contrast, overt shivering was found in *m. pectoralis major* and *m. latissimus dorsi*, with lesser involvement of *m. deltoideus*, *m. biceps* and *triceps brachii*, and the minimum activity of forearm muscles.

Israel and Pozos (1989) have demonstrated that the peaks in EMG activity seen as slow-amplitude modulations occurred simultaneously 6-12 times/min in the majority of widely separated muscles. Bell et al. (1992) showed that shivering intensity was higher in the central muscles, ranging from 5% (*m. rectus femoris* and *m. biceps brachii*) to 16% (*m. pectoralis major*) of MVC, compared with that in the peripheral muscles, which ranged from 1 to 4% of MVC. They estimated that 71% of the heat production originated from the central muscles of the trunk and 21% from thigh muscles, while the remaining 8% were contributed by smaller peripheral muscles.

Topography of shivering thermogenesis in homeothermic animals is related to the flexor reflex (Lupandin, 1983, 1979). In man distribution of shivering thermogenesis in antagonists is not as evident as it is in animals. Bawa et al. (1987) reported that tonic EMG, which may relate to thermoregulatory muscle tone of flexor *m. biceps brachii*, was higher than that in extensor *m. triceps brachii*, while shivering was equally intensive in both antagonistic muscles. Petajian and Williams (1972) demonstrated that thermoregulatory muscle tone and cold shivering develop earlier in *m. triceps brachii* in comparison to *m. biceps brachii*, with a special note that sudden cold stimulation produced abrupt inhibition of tone or shivering in *m. biceps brachii* but activation of activity in *m. triceps brachii*. Similarly, Meigal et al. (1998) found that EMG activity during thermoregulatory tone was the same in the upper arm muscles, but during cold shivering EMG was significantly higher in *m. triceps brachii* in comparison to *m. biceps brachii*.

Thus, only the larger and centrally located muscles contribute to shivering and heat production, and thermoregulatory muscle tone is probably distributed in accordance with flexor reflex. This topography seems to be optimal, because it maximises heat production and minimises heat losses from the smaller muscle masses of the periphery due to the high surface-to-volume ratio of limbs (Bell et al., 1992). Specific distribution of cold shivering in massive, centrally located muscles appears to be one of the basic mechanisms preventing contest between shivering and motor performance.

- latory activity of motor units in the course of body cooling. *Fiziol Cheloveka* (Human Physiol) 1993; 19: 106-114 (Russian).
43. Meigal Alu, Kuzmina GI. The effect of posture on the thermoregulatory activity of the shoulder muscles. *Fiziol Cheloveka* (Human Physiol) 1989; 15: 147-149 (Russian).
  44. Mercer JB. The shivering response in animals and man. *Arct Med Res* 1991; 50; Suppl 6: 18-22.
  45. Mittelman KD, Mekjavic IB. Contribution of core cooling rate to shivering thermogenesis during cold water immersion. *Aviat Space Environ Med* 1991; 62: 842-848.
  46. Morimoto A, Murakami N. [C] deoxyglucose incorporation into rat brain regions during hypothalamic or peripheral thermal stimulation. *Am J Physiol* 1985; 248: R84-92.
  47. Mucke R, Heuer D. Behavior of EMG-parameters and conduction velocity in contractions with different muscle temperatures. *Biomed Biochem Acta* 1989; 48: 459-464.
  48. Muza SR, Young AJ, Sawka MN, Pandolf KB, Boghart JE. Power spectral analysis of surface electromyogram during shivering. *Aviat Space Environ Med* 1986; 57: 1150-1153.
  49. Nadel ER, Holmér I, Bergh U, Åstrand P-O, Stolwijk JAJ. Thermoregulatory shivering during exercise. *Life Sciences* 1973; 13: 983-989.
  50. Oksa J, Rintamäki H, Rissanen S, Rytty S, Tolonen U, Komi PV. Stretch- and H-reflexes of the lower leg during whole body cooling and local warming. *Aviat Space Environ Med* 2000; 71: 156-161.
  51. Oksa J, Rintamäki H, Rissanen S. Muscle performance and electromyogram activity of the lower leg muscles with different levels of cold exposure. *Eur J Appl Physiol* 1997; 75: 484-490.
  52. Oksa J, Rintamäki H, Mäkinen T, Martikkala V, Rusko H. EMG-activity and muscular performance of lower leg during stretch-shortening cycle. *Acta Physiol Scand* 1996; 157: 71-78
  53. Petajian JH, Williams DD. Behaviour of single motor units during preshivering tone and shivering tremor. *Am j Phys Med* 1972; 51: 16-23.
  54. Poulton EC. Arousing environmental stresses can improve performance, whatever people say. *Aviat Space Environ Med* 1976; 47: 1193-1204.
  55. Pozos RS, Iaizzo PA. Shivering and pathological and physiological clonic oscillations

- of the human ankle. *J Appl Physiol* 1991; 71: 1929-1932.
56. Pozos RS, Wittmers LE. The relationship between shiver and respiratory parameters in humans. In: Pozos RS, Wittmers LE, eds. *The nature and treatment of hypothermia*. Minneapolis: University of Minnesota Press 1983; 121-130.
57. Sato H. Fusimotor modulation by spinal and skin temperature changes and its significance in cold shivering. *Exp Neurol* 1981; 74: 21-32.
58. Schafer S, Schafer S. The role of the primary afferents in the generation of a cold shivering tremor. *Exp Brain Res* 1973; 17: 381-393.
59. Shephard RJ. Adaptation to exercise in the cold. *Sports Med* 1985; 2: 59-71.
60. Spurr GE, Hutt BK, Horvath SM. Shivering, oxygen consumption and body temperatures in acute exposure of men to two different cold environment. *J Appl Physiol* 1957; 11: 58-64.
61. Stuart D, Ott K, Ishikava K, Eldred E. The rhythm of shivering. *Am J Phys Med* 1966; 45: 61-104.
62. Tikuisis P, Bell DG, Jacobs I. Shivering onset, metabolic response, and convective heat transfer during cold air exposure. *J Appl Physiol* 1991; 70: 1996-2002.
63. Tipton MJ, Franks GM, Meneilly GS, Mekjavic IB. Substrate utilisation during exercise and shivering. *Eur J Appl Physiol* 1997; 76: 103-108.
64. Winkel J, Jørgensen K. Significance of skin temperature changes in surface electromyography. *Eur J Appl Physiol* 1991; 63: 345-348.
65. Yona M. Effects of cold stimulation of human skin on motor unit activity. *Jpn J Physiol* 1997; 47: 341-348.

*Professor*

*Alexander Meigal*

*Petrozavodsk State University*

*Department of Physiology*

*Lenin Str. 33*

*Petrozavodsk, Russia 185640*

*email: meigal@mainpgu.karelia.ru*

This leaves central muscles free to shiver, thus allowing distal muscles to contribute to fine control of hand joints and elbow joint during shivering.

## CONCLUSIONS AND RESEARCH NEEDS

1. Man is able to perform accurate movements and to keep posture at 10% of MVC under the condition of cold shivering for at least 15 s (near naked man at  $T_a=10^{\circ}\text{C}$  for 60-90 min, with cold drinking, when core temperature declines as much as  $36.5^{\circ}\text{C}$ , and mean skin temperature decreases to  $27^{\circ}\text{C}$ ). However, it is still not known how long beyond 15 sec man is able to perform accurate motor tasks, when fatigue may influence accuracy of performance. It would be also important to know how shivering and accurate performance interact during exercise at MVC higher than 10%.

2. Mechanisms which compensate for cold shivering during muscular performance may include voluntary and reflexory suppression of cold shivering, cold-induced growth of vigilance and attention, increased EMG amplitude, decreased rate of motor unit firing. It is not known how shivering influences human performance when core temperature decreases to  $35^{\circ}\text{C}$ , when shivering becomes maximally developed and is hardly suppressed. Suppression of shivering may improve performance, but it leads to hypothermia (Pozos, Wittmers, 1981). In this connection, investigation of the relationship between cold shivering, fine muscle performance and heat production is needed in order to shed light on the balance between hypothermia-prevention measures and muscular performance.

3. The neural mechanisms which allow cold shivering to co-exist with exercise in man are still poorly understood. With regard to motor unit activity cold shivering and various types of exercise may be assumed as analogous processes. However, substrate utilisation during exercise and shivering at the same oxygen consumption rate was reported to be strikingly different (Tipton et al., 1997). There is also still no direct evidence as to whether motor units of different types, or different motor units of the same type are involved to voluntary exercise and cold shivering. It makes sense to trace, using needle EMG electrode technique, behaviour of a single motor unit during shivering and to investigate its characteristics during voluntary exercise at the same intensity of EMG.