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Modulation of skin sensitivity by dynamic and isometric exercise in man

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Summary. The effect of dynamic cycle ergometer exercise and isometric leg exercise on skin sensitivity was studied in man. Exercise was performed at different loads. Cutaneous sensitivity to innocuous and noxious thermal stimuli was tested using a contact thermostimulator and sensitivity to tactile stimuli was tested using electrical stimuli. During isometric exercise a segmental (the exercising limb), but not a multisegmental, phasic decrease of cutaneous thermal sensitivity to innocuous stimuli was found. At the isometric forces used the effect on tactile and heat pain sensitivity was not significant. During dynamic exercise a multisegmental, load-dependent decrease of sensitivity in all tested sensory modalities was found and this attenuation disappeared gradually after the end of exercise. In contrast to isometric exercise, the decrease of sensitivity produced by dynamic exercise was most evident in tactile sensitivity. The size of the stimulus area (7.9 vs 11.8 cm^2) did not have a significant effect on the magnitude of the exercise-induced decrease of cutaneous thermal sensitivity to innocuous stimuli. It was concluded that underlying the modulation of skin sensitivity by dynamic and isometric exercise were mechanisms that were different, at least to a small extent. Isometric exercise produced a segmental modulation of skin sensitivity due to central neuronal mechanisms, independent of exercise-induced stress. Exercise-induced stress could have caused the modulation of skin sensitivity by dynamic exercise.

Key words: Exercise - Modulation - Somatosensory system

Introduction

Dynamic exercise at high exercise intensities (e.g. running or cycling) has been shown to produce a load-dependent multisegmental modulation of somatosensory sensitivity the effect of which disappears gradually after the end of the exercise (Janal et al. 1984; Kemppainen et al. 1985; Kemppainen et al. 1986; Kemppainen et al. 1990; Olausson et al. 1986; Pertovaara et al. 1984). Movement of the limb or finger unloaded is known to modulate skin sensitivity of the moving region without long-lasting aftereffects (e.g. Rushton et al. 1981). Isometric muscle work can also phasically modulate skin sensitivity of the exercising limb (Feine et al. 1990). These findings raise the question as to whether the exercise-induced effects on somatic sensitivity depend on the type of motor activity; i.e. whether under different exercise conditions the modulation is segmental or multisegmental and phasic or tonic. The possibility has not yet been excluded, with the exception of limited forces (Rushton et al. 1981), that with increasing force the sensory modulation produced by isometric force becomes multisegmental and tonic. Also, it is not known whether the exercise-induced effects differ depending on the somatic submodality.

Since it is difficult to compare results obtained using different methods, we wished to determine under the same experimental conditions whether the modulation of skin sensitivity produced by isometric exercise differs from that produced by dynamic exercise in respect to load-dependence, spread of effect, somatosensory submodality, and temporal parameters. It was expected that any similarities or differences found in the effects would reflect similarities or differences in the underlying modulatory mechanisms.

Methods

Subjects. The total number of human volunteers tested in the psychophysical experiments of this study was 11 (all males, age range 25–42 years). The subjects were healthy university graduates from whom informed consent was obtained before the experiments. Two of the subjects participated in every experiment.

Isometric exercise. Two different levels of isometric exercise (30% and 70% of the maximal force) were produced by pressing the right foot against a static load. The subject was in a sitting position and his ankle and knee joint were at an angle of 90°. The foot was fixed to a special device by which the load was produced and

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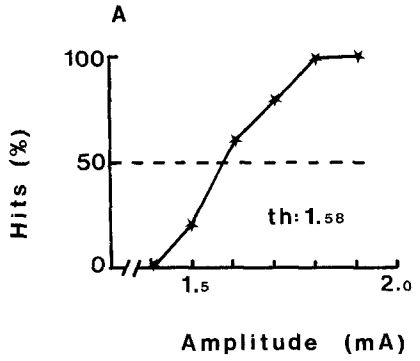

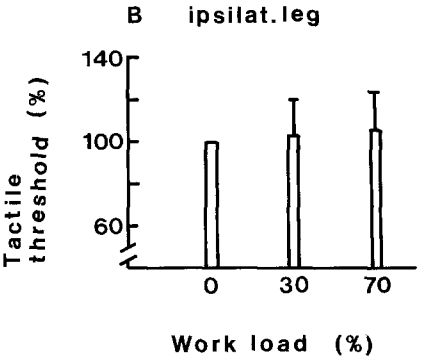

Fig. 1A. An example of a psychometric function curve relating the number of tactile sensations (hits) to the amplitude of the tactile stimulus under control conditions in 1 subject. Each point was derived from five stimulus deliveries of the electrotactile test stimulus. Detection threshold was taken as the test stimulus amplitude at which 50% hit level (*broken line*) was reached. The detection threshold (th) is also given in mA in the *lower right corner of the graph*. **B.** Average standardized detection thresholds for 6 subjects at different isometric work loads. The control threshold (100%) was derived from psychometric function curves without a work load. *Vertical lines* represent SEM

the isometric force was measured by strain gauges. At the beginning of each experiment the maximal force of the right foot was measured. The calibration of the device was checked by weights.

Dynamic exercise. A cycle ergometer (Tunturi, Turku, Finland) was used to produce different intensities (100, 150, 200, 250 W) exercise. The subjects pedalled in a sitting position with a pedal frequency of 50 rpm. The exercise intensity was increased stepwise without rest between the different levels. The maximal aerobic power of each subject was determined from linearized exercise intensity-heart rate response curves and adjustments for age were made according to Walthuis et al. (1971).

Tactile thresholds. Tactile threshold was determined by applying single electrical pulses (duration, 0.5 ms) from a constant current unit to the skin via two closely spaced Pb-Zn electrodes of 8-mm diameter. The skin was cleaned with alcohol and smeared with electrode paste. The subjects were instructed to say "yes" if they detected the test stimulus. A light was triggered to flash simultaneously with the test pulse and the subjects were requested to make their decision immediately following the light flash. The repetition rate of the stimuli was 0.2 Hz. The test stimulation was delivered at six different amplitudes in a random order. Psychometric function curves were constructed by plotting the number of "yes" responses from five stimulus deliveries at each amplitude of the stimulation. The stimulus amplitude at which the subject gave "yes" responses to 50% of the stimulus deliveries was arbitrarily defined as the threshold (Fig. 1A).

Cutaneous sensitivity to innocuous thermal stimuli. Cutaneous thermal sensitivity was tested by a thermostimulator composed of Peltier elements with a stimulation surface of 11.8 or 7.9 cm^2 (Fruhstorfer et al. 1976). A thermocouple was attached to the stimulating surface to record the stimulus temperature during the test. The stimulator could be either warmed or cooled depending on the direction of the current applied. The rate of temperature change was $2.2° C \cdot s^{-1}$. The calibration of the thermocouple was done before and after each session in water baths, the temperature of which was measured by a conventional mercury thermometer. The task of the subject was to respond by pressing a button immediately when the thermal stimulus produced a sensation which could be described as warm (ascending temperatures) or cool (descending temperatures). By pressing the button the subject also changed the direction of the temperature change. The thermal limen (thermoneutral zone) was determined by calculating the difference between the warm and cool thresholds. On each subject, the determination of thermal limen consisted of six single measurements of warm and cool thresholds. Previously, it has been shown that with an increase of skin temperature, both warm and cool thresholds are obtained at a higher stimulus temperature, whereas with a decrease of skin temperature, both warm and cool thresholds are obtained at a lower stimulus temperature (Kojo and Pertovaara 1987; Rozsa et al. 1985). These findings suggested that the change of skin temperature influences the thermal limen less than the warm and cool thresholds. This led us to use the thermal limen as a parameter of cutaneous thermal sensitivity in the current experiment.

Heat pain thresholds. Heat pain thresholds were determined with the same thermostimulator as described above. The task of the subject was to respond immediately by pressing a lever when the ascending thermal stimulus produced a sensation which could be described as heat pain. Individual heat pain thresholds consisted of six single measurements which were made at 2-min intervals on three closely spaced skin areas. Since the measurements were made in an identical way under the different control (pre and postexercise) and test conditions, a possible sensitization of cutaneous receptors as a cause of threshold changes was excluded. The critical temperature needed to produce a heat pain sensation is only minimally, if at all, influenced by a change in skin or body temperature (Croze et al. 1977; Kojo and Pertovaara 1987).

Experimental procedure

Sensory threshold determinations during isometric exercise. The subject dorsiflexed his right foot at the required force (30% or 70% of his maximal force) for about 2 min during which time the sensory measurements were made. Control thresholds were measured before and about 2 min after each exercise period (see Fig. 2A). The interval between each exercise period was 5 min.

Tactile thresholds were determined from the ipsilateral leg (exercising leg). Thermal limens were tested in three different skin areas: ipsilateral leg, contralateral leg and forearm. Heat pain thresholds were measured in the ipsilateral leg only. During both thermal limen and heat pain threshold determinations the stimulus area was 11.8 cm^2 and the adaptation skin temperature was recorded continuously by a thermo-electrode (Thermometer Olli 535, Kone Inc., Helsinki, Finland) which was located about 5 cm from the thermostimulator. The order of testing the different skin regions and work forces was counterbalanced among all the subjects tested. Only one sensory modality was tested each day.

Sensory threshold determinations during dynamic exercise. The subjects pedalled 6–8 min at each level of exercise intensity (100, 150, 200, 250 W). Heart rates and sensory thresholds were measured before exercise, at each exercise intensity and 30 min after the end of exercise.

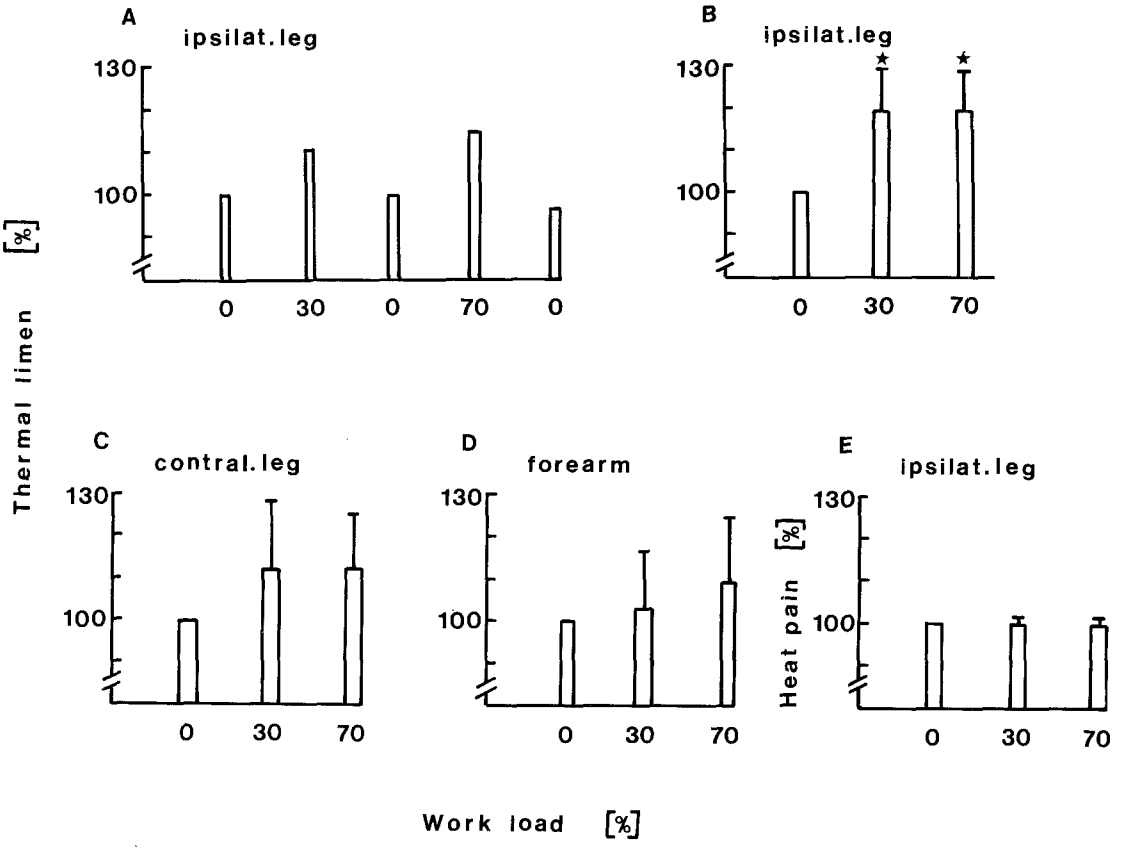

Fig. 2A. The standardized thermal limen (neutral zone between the warm and cool thresholds) of 1 subject at different isometric work loads. First pre-exercise control, 100%. **B, C** and **D.** The average standardized thermal limens for 6 subjects determined in three skin areas at different isometric work loads. The ipsilat. leg is the exercising leg. **E.** The average standardized heat pain threshold in the ipsilateral (exercising) leg for 6 subjects at different isometric work loads. *Vertical lines* represent SEM. * indicates a significant difference ($P<0.05$) from the pre-exercise control (100%)

Tactile thresholds were determined from the forearm and the stimulated skin area was kept free from sweat during the session by frequent drying. In addition, the resistance between the stimulus electrodes was recorded repeatedly throughout the session. Only results obtained with the same constant resistance have been included in this study. During tactile threshold determination the 250-W exercise intensity was not used and tactile thresholds were determined twice (15 and 30 min) after the end of exercise. Thermal limens were determined in the forearm with two stimulus areas of the contact thermostimulator (11.8 and 7.9 cm^2). The order of testing different stimulus areas was counterbalanced among all the subjects tested. The adaptation skin temperature and the room temperature were monitored during both thermal limen and heat pain determinations. Only one sensory modality was tested each day during the dynamic exercise experiments.

Statistical analysis. In each condition somatosensory thresholds (including every measurement), heart rates, adaptation skin temperature adjacent to the thermostimulator and room temperatures were calculated for all subjects. One-way analyses of variance (ANOVA) and Willcoxon's matched-pairs, signed-ranks tests were used in statistical comparisons. A value of $P<0.05$ was considered to indicate a significant difference. Unless specified, the significance values in the results are from the Willcoxon's test.

Results

Effect of isometric exercise

Tactile thresholds. In general, neither of the isometric forces used (30% or 70% of the maximal force) had any marked effect on tactile thresholds determined from the ipsilateral leg (Fig. 1B). Only 2 subjects had a tactile threshold elevation which was more than 10% at the higher force. In 1 subject isometric exercise induced a decrease in tactile thresholds. The average tactile threshold for 6 subjects was 1.33 mA in control conditions, and 1.37 mA and 1.41 mA during the isometric forces of 30% and 70% of the maximal force, respectively. These differences were not statistically significant.

Cutaneous sensitivity to innocuous thermal stimuli. Figure 2A shows the thermal limen of 1 subject at different isometric forces; the larger the thermal limen, the worse the thermal sensitivity. The increase of thermal limen was based on equal increases of warm and cool thresholds. Figure 2B–D gives the average thermal limens for 6 subjects in different experimental conditions. When the ipsilateral leg was tested (Fig. 2B) thermal limens had increased in 5 subjects and this increase was larger with higher isometric forces. The average limen in the

control condition was 7.3° C, SEM 0.7 and it was significantly elevated at both 30% and 70% isometric forces ($P<0.05$). Thermal limens determined from the contralateral leg (Fig. 2C) and forearm (Fig. 2D) were also slightly larger in 3 subjects during isometric exercise. However, the average increase in thermal limen in these skin areas was nonsignificant. There were no changes in the adaptation skin temperatures adjacent to the thermostimulator on any of the tested skin areas during isometric exercise.

Heat pain thresholds. Heat pain thresholds were determined only in the ipsilateral leg. Neither of the isometric forces used (30% or 70% of the maximal force) had any effect on heat pain thresholds determined from the ipsilateral leg (Fig. 2E). The average heat pain threshold for 6 subjects was 45.6° C, SEM 0.6 in control conditions, and 45.5° C, SEM 0.7 and 45.4° C, SEM 0.8 at isometric forces of 30% and 70% of the maximal force, respectively. The adaptation skin temperature surrounding the thermostimulator remained constant during heat pain threshold determinations.

Effect of dynamic exercise

Tactile thresholds. The maximal aerobic power of the subjects varied from 250 to 320 W. The mean was 275 W. The subjects used on average 36.5%, 54.5%, 73.3% and 91.3% of their maximal aerobic capacity at the exercise intensities of 100 W, 150 W, 200 W and 250 W, respectively. The exercise intensity of 250 W was not used during tactile threshold determination. In all subjects the heart rate increased as a function of increasing exercise intensity (Fig. 3A). The average heart rate for the 6 subjects tested was 72 beats·min^{-1}, SEM 16 before starting exercise, and it was significantly elevated ($P<0.05$) at the lowest exercise intensity of 100 W. Heart rates measured 15 and 30 min after exercise remained significantly higher than the pre-exercise values ($P<0.05$).

All 6 subjects had an elevation of tactile thresholds during dynamic exercise varying from 26% to 102%. The average pre-exercise tactile threshold was 1.83 mA, SEM 0.17. The effect of dynamic exercise on tactile thresholds was significant ($P<0.02$; ANOVA). Tactile thresholds were significantly elevated ($P<0.05$) at the lowest exercise intensity of 100 W (Fig. 3B). Tactile thresholds measured 15 and 30 min after exercise remained significantly higher than the pre-exercise control values ($P<0.05$). The repeated measures of resistance between the stimulus electrodes varied from 0.3 to 0.6 MΩ among the subjects. Only results obtained with similar resistances within a session were included in the analysis and the small changes in the resistances within the session did not explain the tactile threshold elevation for the following reason. In some cases there were about 10% increases or decreases in the resistances; but in both cases there were significant increases in tactile thresholds.

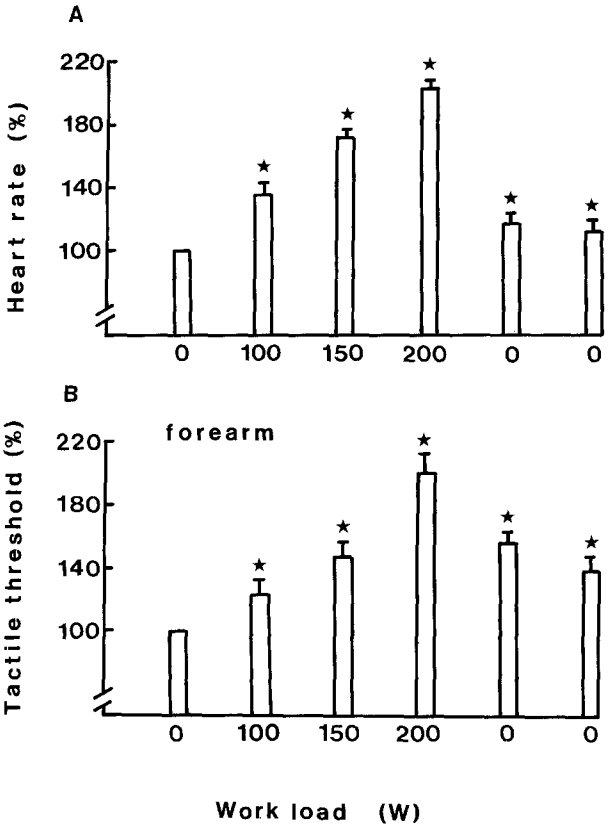

Fig. 3. The average standardized heart rates [beats·min^{-1}; (**A**)] and tactile thresholds (**B**) for 6 subjects at different dynamic work loads. 100%, pre-exercise control. The *vertical lines* represent SEM. The * indicates a significant difference ($P<0.05$) from the pre-exercise control

Cutaneous sensitivity to innocuous thermal stimuli. Figure 4A shows the average thermal limens for 6 subjects at different dynamic exercise intensities. In five subjects the thermal limen increased as a function of increasing exercise intensity and was based on equal increases in warm and cool thresholds. The effect of dynamic exercise on the thermal limen determined by the small or the large stimulus surface was significant ($P<0.01$ and $P<0.05$, respectively; ANOVA). The average thermal limen for all 6 subjects was significantly elevated ($P<0.05$) only at the two highest exercise intensities (200 and 250 W) when compared to pre-exercise control values. Thermal limens measured 30 min after exercise were at the same level as the pre-exercise controls. The stimulus area had a significant effect on thermal limens ($P<0.05$). The average pre-exercise limens were 8.6° C, SEM 1.3 and 11.3° C, SEM 1.4 determined for the stimulus areas of 11.8 and 7.9 cm^2, respectively. This difference in the limens determined with two stimulus areas remained at the same significance level ($P<0.05$) throughout the session. The exercise-induced increase of thermal limens was of equal magnitude with the larger and smaller stimulus surface of the contact thermode.

Before exercise, the adaptation skin temperature in the surrounding forearm was 31.8° C, SEM 0.5. In every subject after starting the dynamic exercise the adapta-

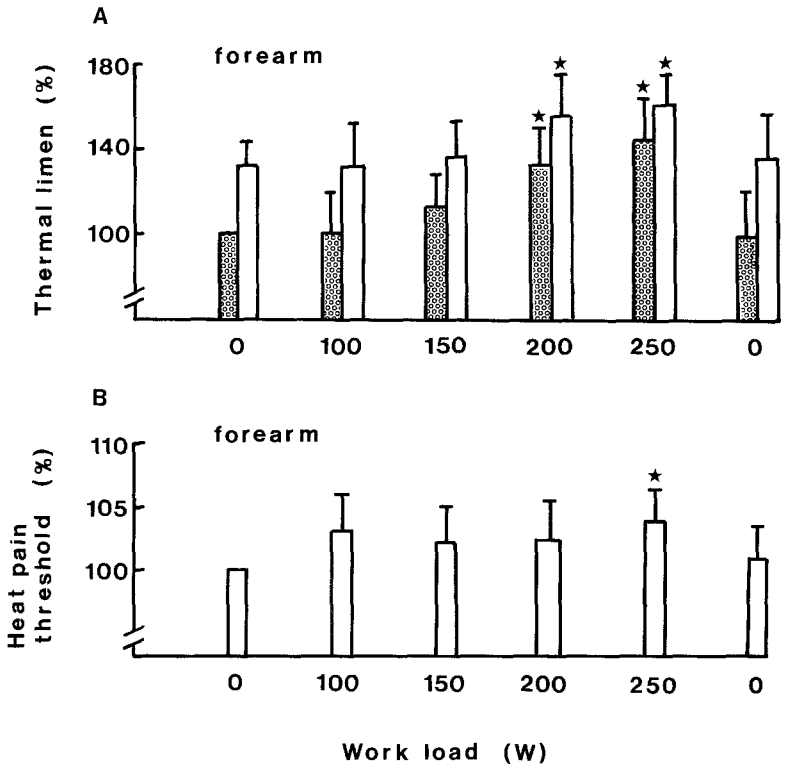

Fig. 4A. The average standardized thermal limens for 6 subjects at different dynamic work loads. The *dotted bars* indicate the results obtained with the smaller stimulus surface of the contact thermostimulator (7.9 cm^2) and the *empty bars* those with the larger stimulus surface (11.8 cm^2). 100%, pre-exercise control with the smaller stimulus surface. The *vertical lines* represent SEM. The * indicate a significant difference ($P<0.05$) from the pre-exercise control within each stimulus category. **B.** The average standardized heat pain thresholds for 6 subjects at different work loads. The *vertical lines* represent SEM. The * indicate a significant difference from the pre-exercise control (100%)

tion skin temperature, in contrast to thermal limens, decreased slightly, and only after the exercise intensity was increased further (200–250 W) did the adaptation skin temperature tend to increase, too. The changes in skin temperatures were slight (< 1° C) when compared with the changes in thermal limens which were as large as 9° C. The average room temperature before starting the exercise was 22.2° C, SEM 0.3 and it remained unchanged throughout the sessions.

Heat pain thresholds. Figure 4B shows the average heat pain thresholds for 6 subjects during dynamic exercise. In 5 subjects dynamic exercise induced an increase in threshold. The average threshold increased significantly ($P<0.05$) only at the highest exercise intensity (250 W) when compared with the pre-exercise values. Heat pain thresholds measured 30 min after exercise were at the same level as the pre-exercise thresholds, 44.8° C, SEM 0.3 and 44.3° C, SEM 0.4, respectively. Before starting exercise, the average adaptation skin temperature in the surrounding forearm was 31.8° C, SEM 0.1. The average pre-exercise room temperature was 21.9° C, SEM 0.2. Neither adaptation skin temperature nor the room temperature changed significantly during the dynamic exercise.

Discussion

The present findings indicated that both isometric and dynamic exercise can produce an attenuation of somatic sensitivity but this attenuation differs with respect to the spread of the effect, preference for somatic submodality and temporal parameters.

In the current study isometric leg exercise produced a phasic attenuation of cutaneous thermal sensitivity to innocuous stimuli. This attenuation was not multisegmental but restricted to the exercising limb also at high isometric forces. Isometric forces which were sufficient to produce an attenuation of cutaneous thermal sensitivity to innocuous stimuli did not have a significant effect on tactile or heat pain thresholds in this study. This finding, however, did not exclude the possibility that at still higher isometric forces or under other experimental conditions an attenuation of tactile and heat pain sensitivity may be seen. In fact, an increased threshold for heat pain and tactile stimuli has been reported during brief isometric contractions of the upper limb (Feine et al. 1990). Also preliminary unpublished experiments in our laboratory have indicated that, in contrast to the effect of isometric contractions of long duration (> 1 min in the current study), during brief isometric contractions of the forearm muscles a threshold elevation for electrically evoked tactile stimuli was found in the fingers of the exercising limb. With respect to the spread of modulation and temporal parameters, the effect of isometric exercise on somatic sensitivity resembles that of isotonic limb or unloaded finger movement (Angel et al. 1985; Chapman et al. 1987; Coquery 1978; Dyhre-Poulsen 1978; Milne et al. 1988).

In the current study dynamic cycle exercise produced an exercise intensity-dependent multisegmental attenuation of especially tactile sensitivity and this attenuation lasted at least 15–30 min after the end of exercise. Also, cutaneous thermal sensitivity to noxious and innocuous stimuli was attenuated by dynamic exercise but the attenuation was not as marked as for tactile sensitivity. This preferential effect was indicated by the

finding that the exercise intensities needed to produce a change in cutaneous sensitivity to noxious or innocious thermal stimuli were considerably higher than those needed to produce a change in tactile sensitivity. The tonic multisegmental attenuation of pain sensitivity by dynamic exercise at high exercise intensities has also been demonstrated in several previous studies in man (Janal et al. 1984; Kemppainen et al. 1985; Kemppainen et al. 1986; Kemppainen et al. 1990; Olausson et al. 1986; Pertovaara et al. 1984) and rodents (Shyu et al. 1982).

In our previous study, the decrease of cutaneous thermal sensitivity to innocuous stimuli by cycle exercise varied, depending on the skin region and being largest in skin areas with a small area of cortical representation (Kemppainen et al. 1985). However, in the current study the decrease of thermal sensitivity to innocuous stimuli was not greater when using a smaller stimulus area, a finding which does not fit the hypothesis that the magnitude of modulation depends on the size of the cortical representation of the skin area under study. On the other hand, the variation in the size of the stimulus area was possibly not large enough in this study and with respect to the cortical representation of cutaneous thermal sensitivity to innocuous stimuli only little is known (Hellon and Mitchell 1975).

Underlying neuronal mechanisms

Consistent with the psychophysical results, several previous investigations have demonstrated attenuated responses to somatic stimuli during movement of the limb, as revealed by electrophysiological recordings made at the dorsal column-medial lemniscus (Coquery 1978; Dyhre-Poulsen 1978; Ghez and Pisa 1972), thalamic (Chapman et al. 1988) and cortical levels (Chapin and Woodward 1981; Chapman et al. 1988; Coquery 1978; Rushton et al. 1981). Somatic responses have been shown to be attenuated during isometric exercise also (Jiang et al. 1987; Rushton et al. 1981). Electrophysiological evidence of the modulation of somatically evoked responses by high intensity dynamic exercise is still scarce.

At least two types of neuronal mechanism may underly the modulation of somatic responses by isometric and dynamic exercise. Firstly, afferent inhibition could be activated, especially during dynamic exercise via afferent barrage in proprioceptive, cutaneous and muscle afferents. There is some indirect evidence which suggests that afferent inhibition might indeed contribute significantly to movement-induced suppression of somatic sensitivity (e.g. passive movement has been shown to be enough to produce modulation of skin sensitivity; Milne et al. 1988). On the other hand, the lack of dependence of multisegmental modulation of somatic sensitivity on pedalling rate (Kemppainen et al. 1985) did not support a major role for afferent inhibition in the effect produced by high-intensity dynamic cycle exercise. Furthermore, the long-lasting (15–30 min) aftereffects produced by high intensity dynamic exercise are difficult to explain by afferent inhibitory mechanisms as are the effects produced by isometric exercise.

The other neuronal mechanism worth consideration here is the efferent motor barrage to somatosensory structures and its modulatory influences on somatic responsivity. Anatomical and electrophysiological studies have demonstrated efferent connections from cortical and subcortical motor areas to the somatosensory cortex and to subcortical somatic relay nuclei including the spinal dorsal horn (e.g. Gray and Dostrovsky 1984; Shin and Chapin 1989). Efferent motor barrage to somatic structures might well explain the suppression of skin sensitivity found briefly prior to active movement of the limb (Coquery 1978; Dyhre-Poulsen 1978) and during isometric exercise, and contribute to the suppression found during active movement and dynamic exercise. However, the long-lasting after effects obviously cannot be explained by efferent barrage from motor to somatic areas.

A change in attention has been shown to modulate skin sensitivity (Bushnell et al. 1985) and neuronal responses to somatic stimuli (Hayes et al. 1981). In the current study, the task of the subject was to focus his attention on the test stimulus. Under isometric conditions threshold changes were obtained only in one of the skin regions. Under dynamic conditions there was a considerable aftereffect. These findings suggested that a change in attention did not explain the present results.

A change in vigilance is also known to influence neuronal responses to somatic stimuli (Casey and Morrow 1985). In the present study, exercise may have produced an arousal but since under isometric conditions the threshold elevation was found only in one of the test regions, a change in arousal cannot explain the suppression of somatic sensitivity produced by isometric exercise. Lack of any significant modulation of thermal sensitivity at 100-W dynamic exercise intensity, which should be enough to produce changes in vigilance, does not support the contribution of vigilance-dependent modulatory mechanisms to the current threshold elevations by dynamic exercise.

Underlying stress-related mechanisms

Stress induced mechanisms have been shown to produce marked changes in pain sensitivity in animal studies (Lewis et al. 1984). High-intensity dynamic exercise also activates stress mechanisms in an intensity dependent way concomitantly with the multisegmental pain threshold elevation (Kemppainen et al. 1985). The time course of the effect of high intensity dynamic exercise on pain thresholds is similar to that on endocrine responses with a long-lasting after effect. Accordingly, it has been proposed that exercise-induced stress mechanisms might have a major role in the modulation of somatic, especially pain, sensitivity by dynamic high-intensity exercise (Janal et al. 1984; Kemppainen et al. 1985; Pertovaara et al. 1984). Since the effects of isometric exercise in this and previous studies have been restricted to the exercising limb and areas immediately adjacent to it and the time course has been of short du-

ration, it does not seem probable that exercise-induced stress mechanism contribute significantly to the modulation of somatic sensitivity by isometric exercise. Furthermore, growth hormone-dependent stress mechanisms have been excluded as a cause of exercise-induced analgesia (Kemppainen et al. 1986). From naloxone (an opioid-antagonist) studies it seems that endogenous opioids can explain the attenuation of experimental ischaemic pain, but not heat pain (Janal et al. 1984) or dental pain (Olausson et al. 1986), by dynamic high-intensity exercise. In a recent study, dexamethasone attenuated dental pain threshold elevations induced by cycle-ergometer exercise concomitantly with the attenuation of exercise-induced adrenocorticotropic hormone (ACTH) release (Kemppainen et al. 1990); this finding indicated that the corticotropin releasing factor-ACTH/beta-endorphin axis was involved in analgesia induced by dynamic high intensity exercise.

Conclusion

The present results indicated that isometric and dynamic muscle exercise modulated somatic sensitivity by mechanisms that were, at least in part, different. It is proposed that the modulation of somatic sensitivity by isometric exercise could have been due mainly to efferent barrage from motor to somatic areas and that the multisegmental modulation of sensitivity by high intensity dynamic exercise could be due mainly to stress-induced mechanisms. In future psychophysical studies on this subject, attention should be paid to the type of exercise, the intensity, the time course of the effects, the somatic submodality and the spread of effects.

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References

Angel RW, Weinrich M, Siegler D (1985) Gating of somatosensory perception following movement. Exp Neurol 90:395–400

Bushnell MC, Duncan GH, Dubner R, Jones RL, Maixner W (1985) Attentional influences on noxious and innocuous cutaneous heat detection in humans and monkeys. J Neurosci 5:1103–1110

Casey KL, Morrow TJ (1985) Arousal-related changes in the response of ventral posterior thalamic neurons to somatic and spinothalamic stimulation in the awake monkey. Adv Pain Res Ther 9:285–294

Chapin JK, Woodward DJ (1981) Modulation of sensory responsiveness of single somatosensory cortical cells during movement and arousal behaviors. Exp Neurol 72:164–178

Chapman CE, Bushnell MC, Miron D, Duncan GH, Lund JP (1987) Sensory perception during movement in man. Exp Brain Res 68:516–524

Chapman CE, Jiang W, Lamarre Y (1988) Modulation of lemniscal input during conditioned arm movements in the monkey. Exp Brain Res 72:316–334

Coquery JM (1978) Role of active movement in control of afferent input from skin in cat and man. In: Gordon G (ed) Active touch. Pergamon Press, Oxford, pp 161–169

Croze S, Duclaux R, Russek M (1977) Constancy of heat pain characteristics to changes in skin and body temperature. Brain Res 131:367–372

Dyhre-Poulsen P (1978) Perception of tactile stimuli before ballistic and during tracking movements. In: Gordon G (ed) Active Touch. Pergamon Press, Oxford, pp 171–176

Feine JS, Chapman CE, Lund JP, Duncan G, Bushnell MC (1990) The perception of painful and nonpainful stimuli during voluntary motor activity in man. Somatosens Mot Res 7:113–124

Fruhstorfer H, Lindblom U, Schmidt WG (1976) Method for quantitative estimation of thermal thresholds in patients. J Neurol Neurosurg Psychiatr 39:1071–1075

Ghez C, Pisa M (1972) Inhibition of afferent transmission in cuneate nucleus during voluntary movement in the cat. Brain Res 40:145–151

Gray BG, Dostrovsky JO (1984) Red nucleus modulation of somatosensory responses of cat spinal cord dorsal horn neurons. Brain Res 311:171–175

Hayes RL, Dubner R, Hoffman DS (1981) Neuronal activity in medullary dorsal horn of awake monkeys trained in a thermal discrimination task II. Behavioral modulation of responses to thermal and mechanical stimuli. J Neurophysiol 46:428–443

Hellon RF, Mitchell D (1975) Convergence in a thermal afferent pathway in the rat. J Physiol (Lond) 248:359–376

Janal MN, Colt EW, Clark WC, Glusman M (1984) Pain sensitivity, mood and plasma endocrine levels in man following long-distance running: effects of naloxone. Pain 19:13–25

Jiang W, Lamarre Y, Parent MT, Marchand S, Chapman CE (1987) Modulation of somatosensory input to sensory cortex during isotonic and isometric limb movements in the monkey (Abstr). Soc Neurosci 13:673

Kemppainen P, Pertovaara A, Huopaniemi T, Johansson G, Karonen SL (1985) Modification of dental pain and cutaneous thermal sensitivity by physical exercise in man. Brain Res 360:33–40

Kemppainen P, Pertovaara A, Huopaniemi T, Johansson G (1986) Elevation of dental pain threshold induced in man by physical exercise is not reversed by cyproheptadine-mediated suppression of growth hormone release. Neurosci Lett 70:388–392

Kemppainen P, Paalasmaa P, Pertovaara A, Alila A, Johansson G (1990) Dexamethasone attenuates exercise-induced dental analgesia in man. Brain Res 519:329–332

Kojo I, Pertovaara A (1987) The effects of stimulus area and adaptation temperature on human heat pain and warm thresholds. Int J Neurosci 32:875–880

Lewis JW, Terman GW, Shavit Y, Nelson LR, Liebeskind JC (1984) Neural, neurochemical, and hormonal bases of stress-induced analgesia. Adv Pain Res Ther 6:277–288

Milne RJ, Aniss AM, Kay NE, Gandevia SC (1988) Reduction in perceived intensity of cutaneous stimuli during movement: a quantitative study. Exp Brain Res 70:569–576

Olausson B, Eriksson E, Ellmarker L, Rydenhag B, Shyu BC, Andersson SA (1986) Effects of naloxone on dental pain threshold following muscle exercise and low frequency transcutaneous nerve stimulation: a comparative study in man. Acta Physiol Scand 126:299–305

Pertovaara A, Huopaniemi T, Virtanen A, Johansson G (1984) The influence of exercise on dental pain thresholds and the release of stress hormones. Physiol Behav 33:923–926

Rozsa AJ, Molinari HH, Greenspan JD, Kenshalo DR (1985) The primate as a model for the human temperature-sensing system. 1. Adapting temperature and intensity of thermal stimuli. Somatosens Res 2:303–314

Rushton DN, Rothwell JC, Craggs MD (1981) Gating of somatosensory evoked potentials during different kinds of movement in man. Brain 104:465–491

Shin HC, Chapin JK (1989) Mapping the effects of motor cortex stimulation on single neurons in the rat: direct responses and afferent modulation. Brain Res Bull 22:245–252

Shyu BC, Andersson SA, Thoren P (1982) Endorphin mediated increase in pain threshold induced by long-lasting exercise in rats. Life Sci 30:833–840

Walthuis RA, Froehlicher VF, Fischer J, Triclermasser JH (1971) The response of healthy men to treadmill exercise. Circulation 55:153–163