Effects of exercise intensity, posture, pressure on the back and ambient temperature on palmar sweating responses due to handgrip exercises in humans

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Key words: human, palmar sweating, handgrip exercise, ipsi-lateral response, contra-lateral response, hemihidrotic reflex, ambient temperature

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Abstract

We have, by using newly developed ratemeters, attempted to examine the effects of exercise intensity, posture, pressure on the skin of the back, and ambient hyperthermic conditions (~30 °C) on the 5-s handgrip exercise-mediated responses of active palmar sweating in humans. Thirty-five right-handed male (n=5) and female (n=30) volunteer students (20.2 ± 1.3 yr. old) participated in the present study. Oral explanation of only the isometric handgrip exercise (IHG) caused a rapid and oscillatory response (pre-operational) of active palmar sweating in almost all subjects (10 of 14 subjects). Performing the IHG for 5-s caused a significant increase in active sweating rate (operation-mediated response) in both ipsi- and contra-lateral palmar surfaces of the thumbs of all subjects. The operation-mediated responses of active palmar sweating to the IHG were reproducible, resulting in no habituation. The increase of operation-mediated responses to the IHG was dependent upon exercise intensity (100-25% maximal voluntary contractions). The IHG-mediated ipsi- and contra-lateral responses of active palmar sweating were significantly decreased by changing the body posture from a seated to a supine position or by pressing the skin of the back. Ambient hyperthermic conditions (~ 30 °C) for 60 min also resulted in a significant decrease in the back-pressure-dependent reduction of the operation-mediated

responses of active palmar sweating to the IHG. In conclusion, in order to optimize the precision and reproducibility of clinical tests involving palmar sweating responses, it is important that subjects maintain a constant handgrip force and posture and that ambient temperature be kept under normothermic conditions.

Introduction

Recently we designed and constructed a new ratemeter for directly and quantitatively measuring human perspiration, especially active palmar sweating responses in humans [Sakaguchi et al., 1990; Ohhashi et al., 1998]. By using the newly developed ratemeter, Homma et al. (1998, 2001) demonstrated that mental calculations or recall questions activated the medial part of the amygdala 5-s prior to the onset of active palmar sweating responses in humans. In addition, Asahina et al. (2003) showed that no active palmar sweating responses were observed with the ratemeter in a 21-year-old female patient with bilateral restricted amygdala lesions caused by idiopathic subacute limbic encephalitis. These findings suggest a possibility that active palmar sweating responses measured by the ratemeter may become a useful tool in obtaining one of the biological parameters for evaluating amygdala-related emotional processing and associative learning.

The palmar active sweating responses are controlled physiologically by neural activities of neo- and limbic-cortex centers including amygdala, hippocampus, and prefrontal cortex and the activities of sudomotor pathways from the centers to the brain stem, to the spinal cord, and to the peripheral cholinergic sympathetic nerves fibers [Kuno, 1956; Ohhashi et al., 1998]. The central mechanisms of the palmar sweating responses are also known to be affected to some extent by the thermoregulatory mechanisms [Ogawa, 1975]. The functional properties of eccrine sweat glands in the palms also contribute to changes in the active sweating responses [Kuno, 1956]. To establish more selective and more quantitative clinical tests with the palmar sweating responses for evaluating amygdala-related emotional processing and associative learning, we have needed to understand comprehensively crucial roles in physiological factors affecting the palmar active sweating responses.

Recently, we demonstrated that handgrip exercise produced reproducible responses of active palmar sweating in humans [Kobayashi et al., 2003]. In the palmar skin, it is well known that the sweating rate can increase without changes in the internal temperature [Kondo et al., 1997, 1999; Van Beaumont & Bullard, 1963, 1966]. The changes in the sweating rate may be due to non-thermal factors involving activation of mechanosensitive or metabosensitive receptors in exercising muscles [Kondo et al., 1997; Van Beaumont & Bullard, 1963] or emotional or mental stimulation [Kuno, 1956]. However, the relationship between the handgrip exercise-mediated palmar sweating responses and the magnitude of the handgrip exercise is not well understood.

In addition, it is well known that lying on one side produces a significant increase in the thermal stimulation sweating responses over the upper part of the body and a simultaneous decrease in the sweating responses over the lower part of the body. This phenomenon is called as the “hemihidrotic reflex” [Takagi & Sakurai, 1950; Kuno, 1956; Tadaki et al., 1981]. Another sweating reflex due to changes in body posture is well known. When a subject changes his posture from supine to erect, the thermal stimulation-mediated sweating responses on the upper part of the body increase significantly while those on the lower part decrease. Various studies have suggested that the phenomenon may be produced as a reflex through the spinal cord, but without affecting higher center mechanisms [Ogawa et al., 1979]. However, little is known about the hemihidrotic reflex in the context of palmar active sweating responses.

Therefore we have attempted to elucidate the crucial roles played by physical factors such as handgrip intensity, posture, pressure on the skin of the back, and ambient temperature on the palmar active sweating responses in humans.

2. Materials and Methods

2.1. Subjects

Thirty-five right-handed male (n=5) and female (n=30) volunteer students in our school of health science (20.2 ± 1.3 yr. old) participated in the present study. Institutional review board approval for human subjects in this study was obtained. Written informed consent was obtained from all participants prior to enrolling in this study. All subjects refrained from the consumption of alcohol, tobacco, or caffeine for at least 12 hrs prior to the experiment. No subject was taking medication at the time of the study. All experiments were performed at the same time of day to avoid any diurnal effects [Aoki et al., 1997].

2.2 Measurements

We measured responses of active palmar sweating in humans by using the newly developed ratemeters (SKD-2000, Skinos Co. Ltd., Nagoya, Japan) attached to left (contra-lateral) and right (ipsi-lateral) palmar surfaces of the thumbs (contacted area 1 cm^2) of all subjects. The ratemeter is small and portable enough to use clinically at the bed-side of patients in hospital because a huge cylinder of dry nitrogen gas is not needed. Through A/D conversion and micro-computation, the absolute amount of palmar perspiration can be recorded as loss of water per constant area and constant time on a chart recorder and then stored into a personal computer. The stored data were analyzed with a commercial software program (Hyper Wave, Kissei Komtec Co. Ltd., Matsumoto, Japan).

2.3.1. Protocol I

Fourteen healthy subjects (2 males, 12 females; 20.7 ± 1.4 yr. old) participated in the examination to elucidate the effects of exercise intensity and/or posture (seated or supine position) on the handgrip exercise-mediated responses of active palmar sweating. Each subject was relaxed at all times during the experiment in a silent air-conditioned room (ambient temperature, 22.1 ± 1.6 °C and relative humidity, 31.8 ± 3.7 %). After a first 30-min rest, each subject performed two maximal voluntary contractions (MVC) of the right hand using a handgrip dynamometer. We used the higher value to determine the relative workload (%MVC). In order to memorize physically the force of the handgrip, all subjects repeatedly tried the 5-s handgripping exercise at 25, 50, 75, and 100% MVC. Subsequently, all subjects seated themselves on comfortable chairs without back-support and then rested again for ~30 min before starting the isometric handgrip exercises (IHG) with the right hand. The subject performed the 5-s IHG at 100, 75, 50, and 25% MVC in this decreasing order at 3-min intervals. The 3-min interval is known to be suitable for obtaining reproducible responses of active palmar sweating to the IHG [Kobayashi et al., 2003]. The

IHG-mediated responses of active palmar sweating were evaluated at ipsi-(right) and contra-lateral (left) palmar surfaces of the thumbs in each subject. The examination with the same protocol was performed with each subject in a supine position. A rest of at least 60-min was granted between the trials of the examination.

In preliminary studies, all subjects were instructed to repetitively perform physical tasks. Almost all subjects (10 of 14 subjects) showed significant active palmar sweating response during the oral explanation of performance of the task (Fig. 1). So we have attempted to independently measure active palmar sweating responses during oral explanation of the task and during actual operation of the task. Thus we first evaluated the palmar sweating response in each subject for 1-min during oral explanation of the task. Next, we continuously measured the palmar sweating response in each subject for 2 min during performance of the task (Fig. 1).

2.3.2 Protocol II

Ten male (n=2) and female (n=8) right-handed subjects (20.3±1.5 yr. old) participated in the examination to study the effects of exercise intensity and/or pressure on the skin of the back on the handgrip exercise-mediated responses of active palmar sweating. Each subject was relaxed at all times during the experiment in a silent air-conditioned room (ambient temperature, 25.5±0.4°C and relative humidity, 37.0±3.5%). All subjects were seated on comfortable chairs with back-support and then rested without pressing the skin of the back on the back-support for ~30min before starting the IHG of the right hand. The same examination procedure and data analyses as those in protocol I were adopted in the protocol.

An examination with the same protocol was also performed on each subject who for a period of 30min with the skin of the back pressed to the back-support of the chairs.

2.3.3 Protocol III

Eleven healthy male (n=1) and female (n=10) right-handed subjects (19.7 ± 0.9 yr. old) participated in the examination to elucidate on the effects of ambient hyperthermic conditions and/or pressure on the skin of the back on the handgrip exercise-mediated responses of active palmar sweating. Firstly, each subject relaxed in a silent air-conditioned room (temperature, 22.5 ± 0.8 °C and relative humidity, 37.0 ± 6.5 %). After an initial first 30-min rest, all subjects were seated on comfortable chairs with back-support and then rested without pressing the skin of the back to the back-support for ~30 min before starting the IHG of the right hand. Under ambient normothermic conditions (~23 °C), the subject performed the 5-s handgrip exercises at 100, 50, and 25% MVC in this decreasing order every 3-min. The relative workload of the IHG in each subject was memorized physically in the same manner as that adopted in protocol I. The same data analyses as those in protocol I were done in each subject. An examination with the same protocol was performed for each subject who pressed the skin of the back to the back-support of the chairs. A rest of at least 60-min was granted between trials of the examination.

Next, under ambient hyperthermic conditions (temperature, 30.0 ± 1.3 °C and relative humidity, 32.3 ± 2.5 %), the effects of pressure on the skin of the back on the IHG-mediated responses of active palmar sweating were also determined at the ipsi- and contra-lateral surfaces of the thumbs. The same examination procedure was used as that adopted during ambient normothermic conditions.

2.4. Data analysis

Data were continuously collected throughout the protocols at a sampling rate of 50 Hz. The loss of water per constant skin-areas of the palm and constant time was calculated as follows: the IHG-mediated response of active palmar sweating minus basal perspiration (defined as the value of loss of water obtained at the starting point of active sweating). All data show the mean ± standard error of the mean. The data were analyzed by using repeated measures two- or three-way analysis of variance. Scheffe's or Fisher's tests or Multiple post-hoc comparison tests were conducted to identify paired differences when a significant main factor was identified. Differences were considered statistically significant at $P<0.05$.

3. Results

3.1. Pre-operational response of active palmar sweating to IHG

Figure 1 shows representative traces of pre-operational responses of active palmar sweating to the IHG obtained from a single 24-year-old female subject seated on a chair without back-support during normothermic conditions (~22 °C). Ipsi- and contra-lateral rapid and oscillatory active palmar sweating responses started simultaneously with oral explanation of the physical task (Fig. 1, black arrows). We defined an active palmar sweating response prior to starting the IHG as pre-operational response. The pre-operational response terminated within 1-min after the oral explanation was given and then returned to the control of basal perspiration. Pre-operational response was significantly reduced by trials. Thus the 1st pre-operational responses to the explanation of physical task are maximal at ipsi- and contra-lateral palmar surfaces of the thumbs. The 2nd, 3rd, or 4th ones at ipsi- and contra-lateral palmar surfaces are significantly smaller than those obtained in the 1st trial. Such data are summarized in the upper panel of figure 2 (n=14).

At 1-min after oral explanation of the physical task was given, the subject was informed by a verbal start of "yes", and then began to perform the IHG. Active palmar sweating responses occurred simultaneously on ipsi- and contra-lateral palmar surfaces of the thumbs

(Fig. 1, white arrows). We defined active palmar sweating during operation of the physical task as operation-mediated response.

3.2. Effects of exercise intensity on IHG-mediated response of active palmar sweating

Figure 1 also demonstrates representative traces of the effects of exercise intensity on the IHG-mediated responses of active palmar sweating in a female subject in a seated position under normothermic conditions (~22 °C). The IHG of the right hand caused exercise intensity-dependent pre-operational and operation-mediated responses of active palmar sweating in the right (ipsi-lateral response) and left (contra-lateral response) thumbs of the subject.

The lower panel of figure 2 summarizes the effects of exercise intensity on the operation-mediated responses of active palmar sweating to the IHG in the ipsi (right)- and contra (left)-lateral palmar surfaces of the thumbs (n=14). In the ipsi-lateral response, the absolute amount of water loss produced by 100%, 75%, 50%, and 25% MVC was 0.332 ± 0.047, 0.224± 0.041 ($p<0.001$ vs 100% MVC), 0.185 ± 0.035 ($p<0.0001$ vs 100% MVC), and 0.121 ± 0.023 ($p<0.0001$ vs 100% MVC) mg/cm^2/min, respectively. In the contra-lateral response, the amount of water loss produced by 100%, 75%, 50% and 25% MVC was 0.261 ± 0.038, 0.182 ± 0.034 ($P<0.01$ vs 100% MVC), 0.164 ± 0.035 ($p<0.001$ vs 100% MVC), and

0.094 ± 0.021 ($P<0.0001$ vs 100% MVC) $mg/cm^2/min$, respectively. Thus the IHG-mediated ipsi- and contra-lateral responses of active palmar sweating were dependent upon the exercise intensity in all subjects in the seated position.

In preliminary experiments, the operation-mediated response of active palmar sweating to the IHG was confirmed to be reproducible, resulting in no habituation.

3.3. Effects of supine position on IHG-mediated responses of active palmar sweating

Figure 3 summarizes the effects of supine position on the operation-mediated responses of active palmar sweating in the ipsi- and contra-lateral palmar surfaces of the thumbs (n=14). Similar to the seated position, the exercise intensity-dependent operation-mediated responses of active palmar sweating to the IHG was significant in all subjects. In the ipsi-lateral response (n=14), the absolute amount of water loss produced by 100%, 75%, 50%, and 25% MVC was 0.244 ± 0.048, 0.125 ± 0.030 ($p<0.001$ vs 100% MVC), 0.085 ± 0.025 ($p<0.0001$ vs 100% MVC), and 0.041 ± 0.012 ($P<0.0001$ vs 100% MVC) $mg/cm^2/min$, respectively. A dependence on exercise intensity in the IHG-mediated responses of active palmar sweating was also observed on the contra-lateral palmar thumbs of all subjects, with 100%, 75%, 50%, and 25% MVC being 0.187 ± 0.035, 0.091 ± 0.020 ($p<0.001$ vs 100% MVC), 0.058 ± 0.015 ($P<0.0001$ vs 100% MVC), and 0.030 ± 0.010 ($P<0.0001$ vs 100% MVC) $mg/cm^2/min$, respectively.

At each exercise intensity, the amount of water loss produced by the IHG in the seated position was significantly larger than that in the supine position (Fig. 4, n=14). This significant difference in the IHG-mediated responses of active palmar sweating between the seated and supine positions was observed not only ipsi-laterally, but also contra-laterally (Fig. 4, n=14). Basal ipsi- and contra-lateral perspiration, defined as the value of loss of water obtained at the start point of active sweating, was significantly smaller in the supine position than in the seated position (Table 1). In contrast, no significant difference in the strength of voluntary contractions at each workload was observed between the sitting and supine positions (Table 2).

3.4. Effects of pressure on the skin of the back in IHG-mediated responses of active palmar sweating

When subjects move from a seated to a supine position, inputs from arterial and cardiopulmonary barorecetors and from graviceptors are affected. In order to investigate the isolated effect of pressure on the skin of the back on IHG-mediated responses without these confounding inputs from baroreceptors and graviceptors, we left subjects in the seated position while simply having them apply pressure to the back.

Figure 5 summarizes the effects of pressure on the skin of the back on the operation-mediated responses of active palmar sweating in the ipsi- and contra-lateral palmar surfaces of the thumbs (n=10). Significant differences in the IHG-mediated responses between those without pressure on the skin of the back and those with were observed not only for the ipsi-lateral palmar surfaces of the thumbs. Basal ipsi- and contra-lateral perspiration in the seated position with pressure on the skin of the back was significantly less than that obtained without pressure on the skin of the back (Table 1). In contrast, no significant difference in the strength of voluntary contractions at each workload was observed with or without pressure on the skin of the back (Table 2).

Similar to the supine position, the significant dependence on exercise intensity in the IHG-mediated responses of active palmar sweating was also observed on the ipsi- and contra-lateral palmar thumbs of all subjects in the seated position when pressure was applied on the skin of the back (Fig. 5, black columns).

3.5. Effects of ambient hyperthermic conditions on IHG-mediated responses of active palmar sweating

Figure 6 summarizes the effects of ambient hyperthermic conditions (30.0 ± 1.3 °C) on operation-mediated responses of active palmar sweating to the IHG in subjects in the seated position with or without pressure on the skin of the back (n=11).

In contrast to results under ambient normothermic conditions (Fig. 5), no significant effects of pressure on the skin of the back on the IHG-mediated responses of active ipsi- and contra-lateral palmar sweating were observed under ambient hyperthermic conditions (~ 30 °C). In the ipsi-lateral palmar surfaces of the thumbs in the seated position without pressure (n=11), the absolute amount of water loss produced by 100%, 50%, and 25% MVC was 0.299 ± 0.068, 0.163 ± 0.035, and 0.127 ± 0.029 $mg/cm^2/min$, respectively. In the ipsi-lateral response in the seated position with pressure (n=11), the amount of water loss produced by 100%, 50%, and 25% MVC was 0.179 ± 0.042 ($p<0.05$ vs without pressure), 0.109 ± 0.022 (NS vs without pressure), and 0.099 ± 0.026 (NS vs without pressure) $mg/cm^2/min$, respectively.

In the contra-lateral responses, the amount of water loss produced by 100%, 50%, and 25% MVC in the seated position with and without the pressure was 0.175 ± 0.031 and 0.135 ± 0.032 (NS), 0.118 ± 0.034 and 0.100 ± 0.030 (NS), and 0.097 ± 0.028 and 0.097 ± 0.031 (NS) $mg/cm^2/min$, respectively.

Similarly to normothermic conditions, no significant difference in the strength of voluntary contractions was observed in the seated position without or with pressure (Table 2).

In contrast to the supine position, no significant difference in basal perspiration was observed between ambient normothermic or hyperthermic conditions (Table 1).

4. Discussion

The major findings of the present experiments were as follows: (1) Oral explanation only of the IHG caused rapid and oscillatory responses of active palmar sweating (pre-operational response) in almost all subjects (10 of 14 subjects). The IHG-mediated pre-operational responses of active palmar sweating were observed ipsi- and contra-laterally and were significantly reduced through repetitive trials of the oral explanation. (2) The IHG-mediated ipsi- and contra-lateral responses of active palmar sweating were significantly reduced by lowering of the strength of voluntary contractions (100-25% MVC) in the seated and supine positions. In contrast, the IHG-mediated operational responses of active palmar sweating were reproducible, resulting in no habituation. (3) The IHG-mediated ipsi- and contra-lateral responses of active palmar sweating were significantly decreased by changing the body posture from a seated to a supine position. (4) The procedure of applying pressure on the skin of the back also caused a significant reduction in the IHG-mediated ipsi- and contra-lateral responses of active palmar sweating. (5) Ambient hyperthermic conditions (~30 °C) significantly diminished the pressing on the back-mediated reduction of the IHG-mediated responses of active palmar sweating.

These findings suggest that the increase in operation-mediated responses to the IHG is dependent on exercise intensity and that the IHG-mediated ipsi- and contra-lateral responses of active palmar sweating are significantly reduced by changing posture from a seated to a supine position or by pressing the skin of the back, the reduction of which is significantly diminished under ambient hyperthermic conditions.

The present findings also suggest that the IHG produces a clear feedforward pre-operational response of active palmar sweating during oral explanation of the physical task, prior to starting actual operation of the task. The evidence is in agreement with our previous study in that oral explanation of physical stimulation through many languages seems to activate the limbic system including amygdala with various feelings of anxiety or unpleasantness and then to produce the response of active palmar sweating in humans [Kobayashi et al., 2003].

It is noteworthy that the present experiments were conducted in healthy subjects whose sweat glands were assumed to be normal. This assumption may affect any clinical testing where sweat glands are directly impaired, in essence giving us a false-positive result of reflex dysfunction. Therefore further investigation will be needed in the future to evaluate the usefulness and significance of the creative clinical test suggested to detect a measurable difference between healthy subjects and patients with suspected autonomic dysfunction.

In conclusion, in order to increase the precision of clinical tests for evaluating amygdala-mediated emotional processing and associative learning, it is important to keep ambient temperature under normothermic conditions, while also maintaining constant handgrip force and posture. In addition, we should take into account the pre-operational response of active palmar sweating to IHG.

4.1. Effect of exercise intensity on the IHG-mediated response of active palmar sweating

In non-glabrous skin, isometric handgrip exercise (IHG; 20~60% MVC, 60-120 s) increases heart rate, mean arterial pressure, sweating rate, and sympathetic nerve activity to skin and muscle [Nishiyasu et al., 1994; Rowell & O'Leary, 1990; Saito et al., 1990; Shibasaki et al., 2001; Vissing et al., 1991]. These physiological responses associated with the IHG are related to mechanisms involving central command such as stimulation from the parallel activation of motor and autonomic pathways and the activation of mechanosensitive or metabosensitive receptors in exercising muscle [Crandall et al., 1995, 1998; Kondo et al., 1998,1999; Rowell & O'Leary, 1990].

In the present study, we first demonstrated that the IHG caused a quick and significant increase in sweating rate in the contra-lateral as well as the ipsi-lateral palmar surface of the thumb under the ambient normothermic conditions (~22 °C). We also demonstrated clearly that the IHG-mediated ipsi- and contra-lateral responses of active palmar sweating were dependent upon exercise intensity. Kondo et al [2000] also demonstrated that IHG for 60 s produced an increase in sweating rates of the forearm and palm under ambient hyperthermic conditions (~35 °C). There was a difference in time course of the sweating rate between the two sites. Thus the sweating rate on the palm showed a plateau after an abrupt increase, whereas the sweating rate on the forearm increased progressively during the exercise. Through measurements of skin blood flow and sweating rate, Saad et al. [2001] also reported that glabrous skin showed a more marked reflex response to the IHG than non-glabrous skin. In fact, the IHG increases sympathetic muscle nerve activity [Mitchell & Victor, 1996].

No paper except the present study, however, has demonstrated that the IHG can produce a significant increase in sweating rate on the palmar surface of the contra-lateral thumb, the skeletal muscles of which are not at all stimulated mechanically. These findings may suggest that the central command including spinal sudomotor center and/or the activated condition of sympathetic cholinergic nerve fibers may contribute to the modulation of contra-lateral palmar sweating responses during 5-s IHG. However, it remains unanswered which of these mechanisms are responsible for the increase of sweating rate in glabrous skin such as the palm during the IHG demonstrated in the present study.

4.2. The hemihidrotic reflex produced by pressure on the skin of the back in active palmar sweating response

In the present experiments, a change in posture from a seated to supine position or pressure on the skin of the back caused a significant reduction of the IHG-mediated responses of active palmar sweating on ipsi- and contra-lateral palmar surfaces of the thumbs. These findings suggest the existence of a hemihidrotic-like reflex due to change in posture or pressing the skin of the back in the IHG-mediated responses of active palmar sweating. The findings may be compatible with the observation that pressure on one side of the chest produces a significant reduction in mental arithmetic-mediated sweating responses on the ipsi-lateral palm [Takagi & Sakurai, 1950].

In addition, ambient hyperthermic conditions (~30 °C) caused a significant decrease of the pressing on the back-mediated reduction of the IHG-mediated responses of active palmar sweating on the ipsi- and contra-lateral palmar surfaces of the thumbs (Fig. 6). However, ambient hyperthermic conditions caused no significant effect on basal perspiration in the palms (Table 1). These data may be a first demonstration to give us insights for evaluating the central command and nervous pathways in the spinal cord involved in the hemihidrotic reflex. Further investigation, however, will be needed to elucidate nervous mechanisms of the hemihidrotic reflex and the crucial role of hyperthermia on the nervous pathways involved in the IHG-mediated sweating responses in the palms of humans.

In non-glabrous skin, it is well known that skin blood flow is regulated through two branches of the sympathetic nervous system; a noradrenergic vasoconstrictor system and a separate sympathetic active vasodilator system [Roddie, 1983]. One or both of these systems may contribute to the regulation of cutaneous circulation during the IHG. In ambient normothermia, changes in skin blood flow during the exercise have been specifically attributed to changes in vasoconstrictor activity [Blair et al., 1960], whereas in ambient hyperthermia, changes in skin blood flow could be attributed to increases in vasoconstrictor activity and/or changes in active vasodilator activity [Kellogg et al., 1990, 1991].

On other hand, regarding glabrous skin such as the palm and sole, it is generally agreed that the skin lacks inputs from active vasodilator nerves [Johnson et al., 1995]; therefore, reflex control of the skin blood flow in those regions is thought to be regulated entirely by the noradrenergic vasoconstrictor system. The skin blood flow in glabrous skin is also characterized by large spontaneous fluctuations, which are a manifestation of changes in blood flow through arteriovenous anastomoses [Bergersen, et al., 1997, 1999]. Thus the vasomotor control in glabrous skin, rich in arteriovenous anastomoses, may differ from that in non-glabrous skin. However, it remains unknown whether the IHG-mediated decrease in the sudomotor nerve activity in glabrous skin can be produced in ambient hyperthermic conditions. Further investigation will be needed to elucidate in detail the effects of ambient hyperthermic conditions on cutaneous vasomotor and sudomotor nervous activities innervated in glabrous skin and on the central command related to the IHG-mediated responses of active palmar sweating.

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Table 1: Basal perspiration (mg/cm^2/min) of palmar surfaces of the thumbs in humans.

	Ipsi-lateral palms		Contra-lateral palms	
Protocol I	seated	supine	seated	supine
(n=14)	0.26±0.06	0.21±0.05***	0.22±0.06	0.17±0.04***

*** p<0.001 vs value obtained with the seated position

	Ipsi-lateral palms		Contra-lateral palms	
Protocol II (the seated position)	without pressure	with pressure	without pressure	with pressure
(n=10)	0.18±0.08	0.13±0.05***	0.23±0.09	0.18±0.09***

*** p<0.001 vs value obtained without pressure on the skin of the back

	Ipsi-lateral palms		Contra-lateral palms	
Protocol III	normothermic condition	hyperthermic condition	normothermic condition	hyperthermic condition
(n=11)	0.16±0.08	0.17±0.095^{NS}	0.18±0.12	0.17±0.09^{NS}

NS vs value obtained with ambient normothermic conditions

Table 2:

Protocol I: The strength of 100, 75, 50 and 25 % maximal voluntary contractions (MVC) in subjects in seated or supine position in ambient normothermic conditions (n=14).

	seated position	supine position
100%MVC	24.2 ± 1.6 (Kg)	21.5 ± 1.7 (Kg)^{NS}
75%MVC	18.1 ± 1.5 (Kg)	16.0 ± 1.8 (Kg)^{NS}
50%MVC	14.2 ± 1.3 (Kg)	12.1 ± 1.6 (Kg)^{NS}
25%MVC	8.5 ± 1.0 (Kg)	7.2 ± 1.4 (Kg)^{NS}

NS vs. value obtained with the seated position

Protocol II: The strength of 100, 75, 50 and 25 % maximal voluntary contractions (MVC) in subjects in a seated position with or without pressure on the skin of the back in ambient normothermic conditions (n=10).

	without pressure on the skin of the back	with pressure on the skin of the back
100%MVC	27.9 ± 2.2 (Kg)	28.4 ± 1.8 (Kg)^{NS}
75%MVC	22.6 ± 1.6 (Kg)	22.0 ± 1.1 (Kg)^{NS}
50%MVC	15.8 ± 1.0 (Kg)	16.0 ± 1.1 (Kg)^{NS}
25%MVC	10.2 ± 1.1 (Kg)	9.8 ± 1.0 (Kg)^{NS}

NS vs. value obtained without pressure on the skin of the back

Protocol III: The strength of 100, 50 and 25 % maximal voluntary contractions (MVC) in subjects in the seated position with or without pressure on the skin of the back during ambient hyperthermic conditions (n=11).

	without pressure on the skin of the back	with pressure on the skin of the back
100%MVC	23.1 ± 1.5 (Kg)	21.6 ± 2.3 (Kg)^{NS}
50%MVC	14.1 ± 1.5 (Kg)	12.3 ± 1.3 (Kg)^{NS}
25%MVC	7.7 ± 1.1 (Kg)	7.4 ± 0.9 (Kg)^{NS}

NS vs. value obtained without pressure on the skin of the back

Legends

Figure 1. Representative recordings of ipsi- and contra-lateral responses of active palmar sweating to 100, 75, 50 and 25% maximal voluntary contraction (MVC) in a 24-year old female subject seated on a chair without back-support. The black arrows show the point at which oral explanation of the task of isometric handgrip exercise (IHG) was given to the subject under ambient normothermic conditions (~22 °C). The white arrows denote the point at which the subject was informed of the start signal "yes" and then began the 5-s IHG.

Figure 2. Effects of exercise intensity (100%, 75%, 50% and 25% MVC) under normothermic conditions (~22 °C) on the pre-operational (upper panel) and operation-mediated (lower panel) responses of active palmar sweating to the IHG on the ipsi- (left-half panel) and contra- (right-half panel) lateral palmar surfaces of the thumbs of the subjects (n=14) in the seated position. * $p<0.05$, ** $p<0.01$, *** $p<0.001$, †<0.0001, ns, not significant (two-way repeated measures ANOVA and Scheffe's or Fisher's tests).

Figure 3. Effects of exercise intensity (100%, 75%, 50% and 25% MVC) under normothermic conditions (~22 °C) on the operation-mediated responses of active palmar

sweating to IHG on the ipsi-(left panel) and contra-lateral (right panel) palmar surfaces of the thumbs of subjects (n=14) in the supine position. * $p<0.05$, ** $p<0.01$, *** $p<0.001$, †<0.0001, ns, not significant (two-way repeated measures ANOVA and Scheffe's or Fisher's tests).

Figure 4. Effects of the seated (white columns) versus supine (black columns) position under normothermic conditions (~22 °C) on the operation-mediated responses of active palmar sweating to the IHG (100%, 75%, 50% and 25% MVC) on the ipsi- (left panel) and contra-lateral (right panel) palmar surfaces of the thumbs of the subjects (n=14). * $p<0.05$, ** $p<0.01$, *** $p < 0.001$, ns,, not significant (two-way repeated measures ANOVA and Scheffe's or Fisher's tests).

Figure 5. Effects of pressure on the skin of the back (black columns) under normothermic conditions (~25°C) on the operation-mediated responses of active palmar sweating to the IHG (100%, 75%, 50% and 25% MVC) on the ipsi-(left panel) and contra-lateral (right panel) palmar surfaces of the thumbs of the subjects in the seated position (n=10). * $p<0.05$, ** $p<0.01$, ns, not significant (two-way repeated measures ANOVA and

Scheffe's or Fisher's tests).

Figure 6. Effects of pressure on the skin of the back (black columns) under ambient hyperthermic conditions (~30 °C) on the operation-mediated responses of active palmar sweating to the IHG (100%, 50% and 25% MVC) on the ipsi- (left panel) and contra- (right panel) lateral palmar surfaces of the thumbs of the subjects in the seated position (n=11). * $p<0.05$, ns, not significant (three-way repeated measures ANOVA and Multiple post-hoc comparison tests).