Regional differences in temperature sensation and thermal comfort in humans

Mayumi Nakamura,1 Tamae Yoda,1 Larry I. Crawshaw,5,6 Saki Yasuhara,2 Yasuyo Saito,2 Momoko Kasuga,1 Kei Nagashima,2,3 and Kazuyuki Kanosue1,2,3

1Faculty of Sport Sciences, 2Faculty of Human Sciences, and 3Consolidated Research Institute for Advanced Science and Medical Care, Waseda University, Tokorozawa, Saitama, Japan; 4Faculty of International Liberal Arts, Dokkyo University, Soka, Saitama, Japan; 5Department of Biology, Portland State University, Portland, Oregon, and 6Department of Behavioral Neuroscience, Oregon Health and Science University, Portland, Oregon

Submitted 31 March 2008; accepted in final form 2 October 2008

Sensations evoked by thermal stimulation (temperature-related sensations) can be divided into two categories: “temperature sensation” and “thermal comfort.” Although several studies have investigated regional differences in temperature sensation, less is known about the sensitivity differences in thermal comfort for the various body regions. In the present study, we examined regional differences in temperature-related sensations with special attention to thermal comfort. Healthy male subjects sitting in an environment of mild heat or cold were locally cooled or warmed with water-perfused stimulators. Areas stimulated were the face, chest, abdomen, and thigh. Temperature sensation and thermal comfort of the stimulated areas were reported by the subjects, as was whole body thermal comfort. During mild heat exposure, facial cooling was most comfortable and facial warming was most uncomfortable. On the other hand, during mild cold exposure, neither warming nor cooling of the face had a major effect. The chest and abdomen had characteristics opposite to those of the face. Local warming of the chest and abdomen did produce a stronger comfort sensation during whole body cold exposure. The thermal comfort seen in this study suggests that if given the chance, humans would preferentially cool the head in the heat, and they would maintain the warmth of the trunk areas in the cold. The qualitative differences seen in thermal comfort for the various areas cannot be explained solely by the density or properties of the peripheral thermal receptors and thus must reflect processing mechanisms in the central nervous system. The costs of publication of this article were defrayed in part by the payment of page charges. The article must therefore be hereby marked “advertisement” in accordance with 18 U.S.C. Section 1734 solely to indicate this fact.

http://www.jap.org

8750-7587/08 $8.00 Copyright © 2008 the American Physiological Society
The face tended to show stronger discomfort during heat exposure than other areas of the body, and the abdomen tended to show stronger discomfort during cold exposure. These tendencies are interesting but not conclusive, because the experiment was done only with whole body heat or cold exposure. Thus $T_{sk}$ differed depending on body area, which made an accurate comparison of sensation in different areas difficult.

Understanding how the elicitation of thermal comfort, local as well as whole body, differs among certain body regions is the goal of this study. The information will be valuable not only for physiological understanding but also for the design of a comfortable environment and efficient clothing. The results will also aid in the optimization of medical and nursing practices. To these ends, we examined regional differences in temperature sensation and thermal comfort by applying local temperature stimulation during whole body exposure to mild heat or cold. We paid special attention to the face and abdomen, because as noted above, these areas showed unusual tendencies in thermal comfort in previous studies.

METHODS

Experiment 1 (Mild Heat Exposure)

Subjects. Eleven healthy male subjects (mean ± SE: age 23.0 ± 0.7 yr, weight 66.2 ± 1.7 kg, height 1.73 ± 0.02 m) participated in this study. Each subject gave informed consent for the experimental protocol, which was approved by the Human Research Ethics Committee in the Faculty of Sport Sciences, Waseda University. The experiments were conducted in accordance with the Declaration of Helsinki. Subjects were instructed to avoid alcohol from the evening before participation in the experiment. Experiments were conducted in accordance with the Declaration of Helsinki. Subjects were instructed to avoid alcohol from the evening before participation in the experiment.

Experimental procedure. The experiments were done in the period from November to December 2006. Subjects arrived at the laboratory at 9:30 AM or 2:30 PM, changed to short pants (only), and entered a climatic chamber that was maintained at 32.5 ± 0.5°C (SE) with a relative humidity of 50%. Subjects rested in a sitting position while all measuring devices and thermal stimulators were applied. About 1.5 h after arrival of the subjects, the local warming and cooling protocol was initiated with water-perfused stimulators (0.027 m²) made with vinyl tubes 7 mm in diameter (Fig. 1). Thermally conductive sheet (GP1-0.5, Kitagawa Industries) of 0.027 m² was stuck to the contacting surface of the stimulator so as to facilitate heat conductance. The perfusion water for the basal condition was set at 35°C, for warming at 42°C, and for cooling at 25°C, and it was supplied to the stimulators from three thermostatic bath/circulators (model RE 206, Ecoline low-temperature thermostats, Lauda Dr. R. Wobser). Flow to the stimulators was controlled using three-way valves. The areas stimulated were the face, chest, abdomen, and thigh (Fig. 2). Each stimulus lasted 90 s. The interval between stimulation of different areas was 4.5 min (Fig. 3). The order of stimulation of the four areas was randomized, and the order of cooling and warming was balanced among all subjects.

Measurements. Temperature sensation and thermal comfort of the stimulated area, and whole body thermal comfort were reported by the subject in the period from 120 s before to 90 s after each local stimulation whenever any change in the sensations was felt. The sensations were reported by rotating each of dials located in front of the subject and numbered from $−10$ ("maximal cold" or "maximal uncomfortable") to 10 ("maximal hot" or "maximal comfortable"); 0 indicated "neutral." The experiment was actually done with Japanese words. In the scale, the only term cold (samui or tsumetai in Japanese) or "uncomfortable (fukai)" were indicated at the number $−10$, "hot (atsui)" or "comfortable (kai)" at 10, and "neutral (chu-ritsu)" at 0. No other word was indicated on the scale. The setting of the dial was measured as a voltage every 5 s and averaged over 10 s. Core temperature ($T_{co}$) was recorded with a telemetry system (Core-Temp2000, HTI Technologies) every 20 s and averaged over 60 s. For this record, a transmitter pill was swallowed 1.5 h before the initiation of local stimulation. $T_{sk}$ was recorded with copper-constantan thermocouples every 5 s at forehead, chest, abdomen, back, upper arm, forearm, hand, thigh, lower leg, and foot for the calculation of mean skin temperature ($T_{sk}$), and it was recorded at two points under each stimulation device. Mean $T_{sk}$ was calculated with the formula of Hardy and DuBois (16) and averaged over 60 s. The $T_{sk}$ of each stimulated area was obtained by averaging two temperatures at the area over 10 s.

Statistical analysis. Temperature-related sensations and the difference in $T_{co}$, and in mean $T_{sk}$ during each area’s stimulation were analyzed using two-way repeated-measures ANOVA followed by the Tukey test for the significance of individual values. The $T_{co}$ at the start of stimulation, changes in $T_{sk}$ ($4T_{sk}$), and changes in temperature-related sensations of the four stimulated areas were analyzed using one-way repeated-measures ANOVA, followed by a Tukey test. All values are presented as means ± SE, and significant difference was set at a level of $P < 0.05$.

Experiment 2 (Mild Cold Exposure)

The experiments were done in the period from February to March 2007. Ten healthy male subjects (age 21.5 ± 0.5 yr, weight 64.9 ± 1.8 kg, height 1.73 ± 0.02 m) participated in this study. Subjects sitting in the climatic chamber at 21.3 ± 0.1°C with a relative humidity of 50% were locally cooled and warmed with the same water perfused stimulators as in experiment 1. In this condition, overall $T_{sk}$ was lower than that during the mild heat exposure of experiment 1. Therefore, water temperature for the basal condition was set at 33°C, 2°C lower than for experiment 1.

In a preliminary experiment, local stimulation temperatures as in experiment 1 (25°C for cooling, and 42°C for warming) were tested, but the subjects reported only weak sensations following local cooling of the four areas. For this reason, the water source for local cooling was set at 22°C, 3°C lower than in experiment 1. The water source temperature for local warming was the same as in experiment 1, 42°C. The other experimental methods, protocol, and statistical analysis were as in the experiment 1.

RESULTS

Experiment 1 (Mild Heat Exposure)

Local cooling. $T_{co}$ during the 30 min of local cooling trials was 37.3 ± 0.1°C, and it remained unaltered during the period of local stimulations. Mean $T_{sk}$ was also the same (34.4 ± 0.1) when local cooling was initiated at each of the local areas.
Although the local basal $T_{sk}$ of the stimulated areas differed by 1°C, $T_{sk}$ for the face was significantly higher than for the chest ($P < 0.05$), abdomen and thigh ($P < 0.01$), and significantly lower for the thigh than for the abdomen ($P < 0.05$), face and chest ($P < 0.01$; Fig. 4A). The magnitude of local $\Delta T_{sk}$ during 90 s of cooling was greater for the thigh than for the abdomen ($P < 0.05$), face and chest ($P < 0.01$; Fig. 4B).

Before local cooling, subjects reported “slightly hot” for local temperature sensation and “slightly uncomfortable” for local comfort (open bars in Figs. 4C left and D left). Neither sensation differed significantly among the four areas to be stimulated. At the end of 90 s of cooling, subjects reported a definite “cold” sensation (score $-4.8 \pm 0.3$) with no significant difference among the four areas (solid bars in Fig. 4C left). Nor was a significant difference observed among the magnitude of change in local temperature sensation ($\Delta$local temperature sensation) during 90 s of cooling of the four stimulated areas (Fig. 4D left). The concurrent estimations of local thermal comfort, however, did depend on the area stimulated. While facial cooling produced a strong “comfortable” feeling, abdominal cooling produced no local comfort, and the difference between face and abdomen was significant ($P < 0.01$; solid bars in Fig. 4D left). And chest or thigh cooling produced a sufficient change in comfort score to convert uncomfortable to comfortable. The magnitude of change in local thermal comfort ($\Delta$local thermal comfort) during 90 s of cooling of the four stimulated areas was greater for the face than for the chest ($P < 0.05$), and abdomen ($P < 0.01$; Fig. 4D right).

As for whole body thermal comfort, the subjects reported very similar “uncomfortable” responses just before local cooling of each area (open bars in Fig. 4E left). After local cooling, the changes in whole body thermal comfort ($\Delta$whole body thermal comfort) differed depending on the area cooled. During facial cooling, “uncomfortable” changed to “comfortable.” This effect was observed also for thigh cooling but not for chest or abdominal cooling (Fig. 4E left). The score of whole body thermal comfort at the end of cooling was significantly higher for the face than for the abdomen ($P < 0.05$; solid bars in Fig. 4E left). The magnitude of $\Delta$whole body thermal comfort during 90 s of cooling was greater for the face than for the abdomen ($P < 0.01$; Fig. 4E, right).

Local warming. $T_{co}$ during the 30 min of local warming trials was $37.3 \pm 0.1^\circ$C, and mean $T_{sk}$ during the same 30 min of local warming trials was $34.3 \pm 0.1^\circ$C. Neither value differed for any time period during stimulation of the four areas. At the start of warming, local $T_{sk}$ of the stimulated areas was significantly higher for the face than for the chest ($P < 0.05$), abdomen, and thigh ($P < 0.01$), and it was significantly lower for the thigh than for the abdomen ($P < 0.05$), face, and chest ($P < 0.01$; Fig. 5A). The magnitude of local $\Delta T_{sk}$ during 90 s of warming was greater for the thigh than for the abdomen ($P < 0.05$), face, and chest ($P < 0.01$; Fig. 5B).

Before local warming, subjects reported “slightly hot” for the local temperature sensation and “slightly uncomfortable” for local comfort (open bars in Fig. 5C left and D left). The two types of sensation did not significantly differ among the four areas. At the end of 90 s of warming, subjects reported a distinct “hot” sensation that was significantly stronger for the face than for the thigh ($P < 0.05$; solid bars in Fig. 5C left). The magnitude of $\Delta$local temperature sensation during 90 s of warming of the four stimulated areas was greater for the face than for the thigh ($P < 0.05$; Fig. 5C right). And local thermal discomfort increased. This effect was stronger for the face than for the chest ($P < 0.05$, solid bars in Fig. 5D). Although the magnitude of $\Delta$local thermal comfort was greater for the face, a significant difference was not observed among the four areas stimulated (Fig. 5D right).

For whole body thermal comfort, subjects reported “uncomfortable” just before local warming of each area without any significant difference among the four areas (open bars in Fig. 5E left). Local warming increased the “uncomfortable” feeling except for chest warming. Although this effect was stronger for facial warming, a significant difference was not observed among the four areas stimulated (solid bars in Fig. 5E left and 5E right).

Experiment 2 (Mild Cold Exposure)

Local cooling. $T_{co}$ during the 30 min of local cooling trials was $37.1 \pm 0.1^\circ$C, and mean $T_{sk}$ during the same 30 min of local cooling trials was $34.3 \pm 0.1^\circ$C, and mean $T_{sk}$ during the same 30 min of local cooling trials was $34.3 \pm 0.1^\circ$C. Neither value differed for any time period during stimulation of the four areas. At the start of warming, local $T_{sk}$ of the stimulated areas was significantly higher for the face than for the chest ($P < 0.05$), abdomen, and thigh ($P < 0.01$), and it was significantly lower for the thigh than for the abdomen ($P < 0.05$), face, and chest ($P < 0.01$; Fig. 5A). The magnitude of local $\Delta T_{sk}$ during 90 s of warming was greater for the thigh than for the abdomen ($P < 0.05$), face, and chest ($P < 0.01$; Fig. 5B).

Before local warming, subjects reported “slightly hot” for the local temperature sensation and “slightly uncomfortable” for local comfort (open bars in Fig. 5C left and D left). The two types of sensation did not significantly differ among the four areas. At the end of 90 s of warming, subjects reported a distinct “hot” sensation that was significantly stronger for the face than for the thigh ($P < 0.05$; solid bars in Fig. 5C left). The magnitude of $\Delta$local temperature sensation during 90 s of warming of the four stimulated areas was greater for the face than for the thigh ($P < 0.05$; Fig. 5C right). And local thermal discomfort increased. This effect was stronger for the face than for the chest ($P < 0.05$, solid bars in Fig. 5D). Although the magnitude of $\Delta$local thermal comfort was greater for the face, a significant difference was not observed among the four areas stimulated (Fig. 5D right).

For whole body thermal comfort, subjects reported “uncomfortable” just before local warming of each area without any significant difference among the four areas (open bars in Fig. 5E left). Local warming increased the “uncomfortable” feeling except for chest warming. Although this effect was stronger for facial warming, a significant difference was not observed among the four areas stimulated (solid bars in Fig. 5E left and 5E right).

Experiment 2 (Mild Cold Exposure)

Local cooling. $T_{co}$ during the 30 min of local cooling trials was $37.1 \pm 0.1^\circ$C, and mean $T_{sk}$ during the same 30 min of
cooling trials was 29.4 ± 0.2°C. Neither value differed for any time period during stimulation of the four areas. The difference in local Tsk values at the start of local cooling among the stimulated areas was more prominent than in experiment 1, and significant differences were observed for all combinations of the four areas (P < 0.01; Fig. 6A). The Tsk was highest for the face (34.9 ± 0.1°C) and lowest for the thigh (33.1 ± 0.1°C). The magnitude of local ΔTsk during 90 s of cooling was greater for the thigh than for the other three areas (P < 0.01; Fig. 6B).

Before local cooling, subjects reported sensations close to “neutral” both for local temperature sensation and for thermal comfort (open bars in Fig. 6C and D left). Neither sensation

**Fig. 4. Local skin temperature and temperature-related sensations during local cooling of 4 areas in mild heat exposure experiment. A: local Tsk at the start of cooling. B: magnitude of local ΔTsk during 90 s of cooling. C left: local temperature sensation of areas stimulated (stim). C right: magnitude of local temperature sensation changes during 90 s of cooling of areas stimulated. D left: local thermal comfort of areas stimulated. D right: magnitude of local thermal comfort changes during 90 s of cooling of areas stimulated. E left: whole body thermal comfort during the stimulation of each area. E right: magnitude of whole body thermal comfort changes during 90 s of cooling of areas stimulated. In left graph of C–E, open bars show the sensations before stimulation and solid bars show the sensations at the end of stimulation. Values are means ± SE for 11 subjects. *P < 0.05; **P < 0.01, significant differences among the 4 stimulated sites.
differed significantly among the four areas. At the end of 90 s of cooling, subjects reported a definite “cold” sensation (score = 4.1 ± 0.3), and no significant difference was observed among the four areas (solid bars in Fig. 6C left). The magnitude of Δlocal temperature sensation during 90 s of cooling of the four stimulated areas was greater for the abdomen than for the face (P < 0.05; Fig. 6C right). For local thermal comfort, whereas facial cooling produced no local “uncomfortable” feeling, cooling of the other body surfaces produced clear “uncomfortable” feeling (solid bars in Fig. 6D left). Local
discomfort at the end of cooling was significantly stronger for the abdomen and thigh than for the face \((P < 0.01);\) solid bars in Fig. 6D left). The magnitude of \(\Delta T_{sk}\) local thermal comfort changes during 90 s of cooling of areas stimulated. D right: magnitude of local thermal comfort changes during 90 s of cooling of areas stimulated. E left: whole body thermal comfort during the stimulation of each area. E right: magnitude of whole-body thermal comfort changes during 90 s of cooling of areas stimulated. In left graph of C–E, open bars show the sensations before stimulation and solid bars show the sensations at the end of stimulation. Values are means \(\pm SE\) for 10 subjects. *\(P < 0.05;\) **\(P < 0.01,\) significant differences among the 4 stimulated sites.
significant difference among the four areas (solid bars in Fig. 6E left). The whole body “uncomfortable” sensation was increased by local cooling, but significant differences between the stimulated areas were not observed (solid bars in Fig. 6E left and 6E right).

Local warming. \(T_c\) during the 30 min of local warming trials was \(37.1 \pm 0.1^\circ C\) and mean \(T_a\) during the same 30 min of local warming trials was \(29.3 \pm 0.2^\circ C\). Neither value differed for any time period during stimulation of the four areas. At the start of warming, significant differences in local \(T_a\) values among the stimulated areas were observed in all combinations of the four stimulated areas (\(P < 0.01\); Fig. 7A). The magnitude of local \(\Delta T_a\) during 90 s of local warming was greater for the thigh than for the other three areas (\(P < 0.01\); Fig. 7B).

Before local warming, subjects reported sensations close to “neutral” both for local temperature sensation and local comfort (open bars in Fig. 7C left and D left). Neither type of sensation differed significantly among the four areas. At the end of 90 s of warming, subjects reported a distinct “hot” sensation (score 3.5 \(\pm 0.2\)), and no significant difference was observed among the four areas (solid bars in Fig. 7C left). Nor was a significant difference observed among the magnitude of \(\Delta T_a\) during 90 s of warming of the four stimulated areas (Fig. 7C right). The concurrent estimations of local thermal comfort, however, did depend on the area stimulated. Although warming of the abdomen and chest produced a definite “comfortable” feeling, facial warming had only a little effect that was weaker than chest (\(P < 0.05\)) and abdomen (\(P < 0.01\); solid bars in Fig. 7D left). The magnitude of \(\Delta T_a\) thermal comfort during 90 s of warming of the four stimulated areas was greater for the abdomen than for the face (\(P < 0.01\); Fig. 7D right).

For whole body thermal comfort, subjects reported “uncomfortable” just before local warming of each area without any significant difference among the four areas (open bars in Fig. 7E left). Whole body discomfort was decreased by local warming. Although this effect was stronger for the chest and abdominal warming, a significant difference was not observed among the four areas stimulated (solid bars in Fig. 7E left and Fig. 7E right).

**DISCUSSION**

In the present study, four body surfaces of equivalent area (0.027 m²) were heated or cooled, and the ensuing temperature-related sensations were analyzed with special attention to thermal comfort in healthy male subjects. Definite regional differences in local thermal comfort were observed. During mild heat exposure, when the subjects’ whole body sensation was “uncomfortable,” local cooling was most comfortable and local warming was most uncomfortable when applied to the face (Figs. 4D and 5D). On the other hand, during mild cold exposure, in which whole body thermal comfort was “uncomfortable,” neither warming nor cooling of the face had a major effect (Figs. 6D and 7D). The chest and abdomen had characteristics opposite to those of the face. Local cooling of these areas did not produce explicit comfort even during whole body heat exposure (Fig. 4D). But local warming of the chest and abdomen did produce strong comfort during whole body cold exposure (Fig. 7D). This effect was more prominent for the abdomen than for the chest.

**Effect of Adapting Temperature and Stimulus Magnitude**

Although the areas locally stimulated were adapted to 35 or 33°C before stimulation, local \(T_a\) values at the start of stimulation were not necessarily the same. In the mild heat exposure experiment, the \(T_a\) values were in the range of 35–36°C, but they were highest in the face and decreased, in order, from chest, to abdomen, to thigh (Figs. 4A and 5A). Although the magnitudes of thermal stimulation (\(\Delta T_a\)) were larger in the reverse order both for heating and cooling, there was no significant difference among the face, chest, and abdomen (Figs. 4B and 5B). The difference in the \(\Delta T_a\) values among the various areas is likely caused by differences in skin blood flow due to vasomotor status and tissue vascularity. For the ambient temperature utilized in the heat exposure (experiment 1), the skin vessels of all areas would be expected to be vasodilated. In the mild cold exposure experiment, differences in local \(T_a\) values and \(\Delta T_a\) values were more prominent (Fig. 6, A and B, and 7, A and B), probably due to cold-induced skin vasoconstriction that was stronger for the chest and thigh than for the face and abdomen.

When skin is warmed at a constant rate of temperature change, starting from various levels of temperature adaptation, the response magnitude of skin warm fibers is larger at higher adapting temperatures (15, 19). Furthermore, warm sensations are more sensitive at higher adapting temperatures, and cold sensations are more sensitive at lower adapting temperatures (17). In the present study, despite differences in \(T_a\) values and \(\Delta T_a\) values, we could find little difference in temperature sensation among the four areas (Figs. 4C, 5C, 6C, and 7C). Additionally, the regional differences in thermal comfort never correlated with differences in \(T_a\) values or \(\Delta T_a\) values; e.g., thermal comfort was never stronger for the thigh, although the \(\Delta T_a\) of the thigh was always larger than that of other areas. Regional differences in thermal comfort observed in the present study, therefore, cannot be explained simply by invoking the slight differences in local temperature produced by the thermal stimulation.

**Mechanism for the Regional Difference in Thermal Comfort**

It is generally assumed that inputs from the same warm or cold skin thermoreceptors are utilized for both temperature sensation and thermal comfort, although there is no direct experimental evidence for this supposition. Although it is difficult to quantitatively evaluate differences in the density of skin thermoreceptors in humans, the density of hot and cold spots would be expected to correlate positively with the density of warm and cold receptors (17). The distribution of peripheral warm and cold spots over the body surface is not uniform (22, 33, 39, 40), and the face is one of the areas where both warm and cold spots are particularly dense. Although this high density might be invoked to explain the strong thermal comfort produced by facial stimulation in the heat exposure experiment, the same facial stimulation produced only a slight change in thermal comfort during cold exposure. Similarly, the chest and abdomen have particularly dense cold spots (39). Although thermal stimulation, especially warming, of these areas produced a distinct change in thermal comfort during
cold exposure, the same stimulation during heat exposure had a minor effect. Thus the location-dependent effect of thermal stimulation on thermal comfort cannot be explained simply by the density of cold or warm spots. Additionally, it should be noted that regional differences in temperature sensation were not seen with stimulation that did produce regional differences in thermal comfort. The above observations make it unlikely that regional differences in thermal comfort can be entirely explained by the properties and distribution of peripheral thermoreceptors. A more plausible explanation is that central nervous processing is responsible for the production of the regional differences in thermal comfort. Feelings of warmth and cold correlate with neural activity in insular cortex (13, 32), and the amygdala, mid-orbitofrontal and pregenual cingu-
late cortex, and ventral striatum have been implicated in the
 genesis of thermal comfort (18, 34). We speculate that a central
 nervous system map weighing the input from each body area
 would be involved in the production of regional differences in
 thermal comfort.

 It is well known that thermal comfort is affected by the
 thermal state of the body (4, 5, 11, 21, 24, 25, 27). The same
 hand warming produces a comfortable or uncomfortable feel-
 ing depending on whether the individual is hypothermic or
 hyperthermic. Thus a thermal stimulation is felt comfortable
 when it serves to regain normal body temperature, and felt
 uncomfortable when it worsens internal thermal conditions.
 Somehow, the central nervous system processes sensory input
 so that it is perceived as comfortable or uncomfortable depend-
 ing on the thermal status of the body. Interestingly, the direc-
 tion of this alteration in hedonic valence is not uniform for all
 body areas. As we showed, feelings of comfort in the face are
 very sensitive to local temperature stimuli in the heat, but they
 are less sensitive in the cold. The abdomen demonstrates the
 opposite tendency. It will be of interest to determine how this
 alliesthesia (8) occurs and how regional differences between
 sensation and comfort are created.

 Meaning of the Regional Difference in Thermal Comfort

 Thermal comfort and discomfort are specific aspects of the
 pleasure-pain system of animals. In an overall sense, comfort
 and discomfort (including pain) function to interrupt other
 ongoing behaviors to focus the organism on a particular,
 significant threat to its well-being. What is the function of the
 regional difference in thermal comfort? It is well known that
 even in homeothermic animals, the magnitude of temperature
 fluctuation inside the body in different thermal environments is
 dependent on the particular body part (2). The temperature of
 the body core fluctuates only slightly, whereas that of the
 periphery, such as arms and legs, shows large changes. The
 basic function of temperature regulation must be to maintain
 the temperature of the body core because the vital organs are
 located there. Regional differences in thermal comfort can be
 considered in this light.

 The head contains the brain, which possesses a high, con-
 tinuous rate of heat production. The human brain is particularly
 susceptible to heat damage and can only tolerate temperatures
 up to about 40.5°C, while organs of the torso core temperatures
 can tolerate temperatures that exceed 42°C (41). It is critical
 for organism viability that heat be rapidly removed from the
 head area, and special systems to cool the brain are suggested
to exist in humans (9, 29) and are well documented in many
 animals (41). In humans, venous blood from the scalp and the
 face is posited to flow, via the emissary veins, into the brain
during hyperthermia at a rate sufficient to produce selective
 brain cooling (9, 29). A hot face would further heat an already
 overheated brain. Preference for a low facial temperature in the
 heat would help avoid heat-induced damage to the brain.

 Preference for a warm abdomen similarly must reflect im-
 portant aspects of the organism’s need to conserve and produce
 heat. For most mammals, the abdomen and inner thighs are
 thinly furred areas that can be utilized to dissipate heat during
 exercise or in a hot environment. In the cold, mammals curl up,
 which greatly decreases the surface area and shields the thinly
 furred areas (26). Although humans are not furred, they do
 benefit from a fetallike position in the cold, which minimizes
 the surface area for heat loss. The adoption of this posture
 warms the abdomen, and the pleasant feelings that ensue must
 contribute to the initiation and maintenance of this postural
 adjustment. Furthermore, a warm abdomen facilitates diges-
tion, which in the act of altering chemical energy into forms
 that the body can utilize to produce heat (and all its other
 functions), also releases substantial amounts of heat in the
 process (41).

 Thermal Comfort and Autonomic Thermoregulation

 Previous works have repeatedly found that, per unit area of
 skin, facial temperature exerts the largest peripheral influence
 on autonomic thermoregulation (7, 12, 14, 28). The effect is
 not dependent on the ambient temperature. Heating the face in
 a warm environment produces a considerably greater increase
 in sweat rate than heating other skin areas (12, 28), whereas
 cooling the face in a warm environment produces a consider-
 ably greater decrease (12, 14). Belding et al. (7) also found that
 at low ambient temperatures, warming the face induced per-
 iperal vasodilatation, whereas warming the same area of the
 chest or a much larger area of the leg had no effect. Such a
 strong, consistent facial sensitivity might be explained by a
 high density of thermoreceptors (cold and warm spots) in the
 face.

 However, for thermal comfort, the predominance of facial
 thermosensitivity is dependent on the ambient temperature. The
 whole ody comfort sensation is likely the primary input for
 behavioral thermoregulation and if an individual is in a situa-
tion where feelings of comfort can be acted on, it is possible to
 maintain without utilizing the energy and fluid resources nec-
 essary for autonomic regulation. The different regional sensi-
tivities of thermal comfort and autonomic thermoregulation
 could indicate that autonomic and behavioral temperature reg-
 ulation are controlled separately in the central nervous system.
 The ability to regulate body temperature by behavioral (but not
 autonomic) means remains in animals whose medial preoptic
 area/anterior hypothalamus has been lesioned (10, 23, 35).
 Indeed, it has recently been reported that the afferent neuronal
 pathways for discriminative sensation or localization of a
 thermal stimulus and for homeostatic control of body tempera-
ture are separate (30).

 The comfort sensations seen in this study indicate that if
 given the chance, humans would preferentially cool the head in
 the heat, and they would maintain the warmth of the abdomen
 in the cold. These regional differences in the thermal comfort
 are consistent with the biological roles of each body part. The
 qualitative differences seen in thermal comfort for the various
 areas cannot be explained solely by the density or properties of
 the peripheral thermal receptors. It seems certain that these
 differences are due to dissimilar neuronal pathways and pro-
 cessing in the central nervous system. We investigated only
 dynamic responses in this study during the 90 s of thermal
 stimulation. Comfortableness occurs when discomfort disap-
ppears, and it does not continue for a long time (20). It would
 be interesting to see how the regional differences in thermal
 comfort were altered by longer periods of thermal stimulation.
 Because we tested only in mild heat and cold ambient tem-
 peratures, and only in male subjects, it would be interesting to
 know how these regional differences in thermal comfort might
be changed under different thermal condition and/or in female subjects. Furthermore, in the present study, we only tested four areas. It would be valuable to examine the thermal and comfort sensitivities of other body areas, such as hands and feet, and consider how the properties of each area’s thermal and comfort sensations related to the physiological functions subserved by that particular area.

ACKNOWLEDGMENTS

The authors thank Megumi Nishiba for technical assistance, and Dr. Stan Hillman for his helpful ideas.

GRANTS

This study was partly supported by Waseda University Grant for Special Research Projects (no. 2006A-108); by the “Establishment of Consolidated Research Institute for Advanced Science and Medical Care” Project, Ministry of Education, Culture, Sports, Science and Technology, Japan; and by the Grant-in-Aid for Science Research from the Ministry of Education, Science and Culture of Japan (no. 186590620).

REFERENCES