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Thermal sensation: a mathematical model based on neurophysiology

Abstract Thermal sensation has a large influence on thermal comfort, which is an important parameter for building performance. Understanding of thermal sensation may benefit from incorporating the physiology of thermal reception. The main issue is that humans do not sense temperature directly; the information is coded into neural discharge rates. This manuscript describes the development of a mathematical model of thermal sensation based on the neurophysiology of thermal reception. Experimental data from two independent studies were used to develop and validate the model. In both studies, skin and core temperature were measured. Thermal sensation votes were asked on the seven-point ASHRAE thermal sensation scale. For the development dataset, young adult males ($N = 12$, 0.04Clo) were exposed to transient conditions; T_{air} 30–20–35–30°C. For validation, young adult males ($N = 8$, 1.0Clo) were exposed to transient conditions; T_{air} : 17–25–17°C. The neurophysiological model significantly predicted thermal sensation for the development dataset ($r^2 = 0.89$, $P < 0.001$). Only information from warm-sensitive skin and core thermoreceptors was required. Validation revealed that the model predicted thermal sensation within acceptable range (root mean squared residual = 0.38). The neurophysiological model captured the dynamics of thermal sensation. Therefore, the neurophysiological model of thermal sensation can be of great value in the design of high-performance buildings.

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Key words: Thermal sensation; Thermal reception; Neurophysiology; Neural integration; Mathematical model; Building design.

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Practical Implications

The presented method, based on neurophysiology, can be highly beneficial for predicting thermal sensation under complex environments with respect to transient environments.

Introduction

Thermal comfort, determined by the influence of the indoor environmental parameters on thermal sensation, is regarded as an important performance indicator of building performance. Therefore, accurate mathematical models of thermal sensation are extremely useful in design of new high-performance buildings. Recently, de Dear (2011) reintroduced the concept of ‘thermal alliesthesia’, which deals with the neurophysiological mechanisms responsible for thermal sensation. According to de Dear, with the concept of alliesthesia it should be possible to explain in the future: ‘why occupants of today’s so called sustainable buildings can enjoy positive indoor environmental

quality in indoor climates that would have failed the criteria established under yesterday’s standards of thermal comfort’.

In this study we aim to expand the synthesis between neurophysiology and mathematical modeling to make a better prediction of the thermal sensation. One of the key principles in the neurophysiology of thermal reception is that humans do not sense temperature directly. Temperature information is coded into the firing rate of temperature-sensitive neurons (thermoreceptors). These neurons are found all over the body. Two types of thermoreceptors can be distinguished: ‘cold’ or ‘warm’ sensitive (see Figure 1). Skin contains both types of thermoreceptors, whereas deeper laying tissues (e.g., intestines, spinal cord, and hypothalamus)

Fig. 1 Averaged steady state neuron discharge rate vs. skin temperature for cold sensitive (gray line) and warm sensitive (black line) neurons of cat tongue (after (Mekjavic and Morrison, 1985; Zotterman, 1953))

contain mostly warm-sensitive thermoreceptors (Boulant, 2006).

The main hypothesis is that through simulation of the neurophysiological pathways the dynamics of thermal sensation can be captured. Therefore, we developed a new model for thermal sensation based on the neurophysiology of thermal reception and integration through neural pathways.

Context

Both thermal comfort and energy use play an important role in the performance of a building. About one-third of the primary energy used in developed countries is consumed by heating, ventilating, and air conditioning in residential, commercial, and public buildings (IEA, 2007). This reveals the high importance of reducing the energy use in buildings. However, satisfaction of the occupants with their thermal environment mainly determines the success of the application of low-energy Heating Ventilation and Air Conditioning (HVAC) systems. Much effort has been taken to design optimal energy HVAC systems; this resulted in among others, low temperature heating systems, high temperature cooling systems, different ventilation principles, etc. However, the Annex 37 (Juusela, 2003) study revealed that an optimal energy use does not always result in an increased comfort level. Non-uniform thermal conditions, which may occur owing to application of low-energy systems, can be responsible for discomfort [e.g., a low temperature floor heating system in combination with natural ventilation (Boerstra et al., 2000)]. Contrary, Arens et al. (2006) concluded that through asymmetrical and transient thermal environments, higher levels of thermal comfort could be achieved in comparison with steady-state uniform environments. Regarding transient environments, de Dear and Brager

(2001) concluded that satisfaction with the thermal environment does not mean that this environment has to be controlled at a constant indoor air temperature (de Dear and Brager, 2001). A study by Schellen et al. (2010) confirmed this statement. Furthermore, compared to a constant temperature, allowing the temperature to drift could be a means to reduce energy use.

To adequately design optimal environmental conditions in the future, both in an energy-friendly and comfortable way, more knowledge on the interaction between the system, indoor climate, and the human body is indispensable.

Thermal sensation

Thermal sensation and satisfaction with the thermal environment is a complex phenomenon, and therefore complicated to predict in the design phase. Owing to the large differences between persons, both psychological and physiological, it is difficult to satisfy everyone in the same room. Many researchers have studied the parameters that affect thermal sensation with the objective of developing a model to predict thermal sensation. The most used and referred model is the predicted mean vote (PMV) model of Fanger (1970). This model is included in current building standards to predict thermal sensation, and therefore often used to assess the thermal comfort in the design phase. This model intended to be a method that could be used by HVAC engineers to determine the optimum environmental conditions (combination of air temperature, mean radiant temperature, relative humidity, mean air velocity, activity level, and clothing) to satisfy the largest possible percentage of a given group of occupants. It was assumed that a person is most comfortable in a thermal neutral condition, which is defined as the condition wherein a person does not prefer either a colder or warmer environment.

Although this method is frequently used and implemented in building regulations, many researchers showed the limitations of the model, e.g., for differences between subpopulations (males/females, young/older people, etc), thermal neutrality, expected discomfort, and driving mechanisms (dependent parameters), for thermal comfort (de Dear and Brager, 2001; Humphreys and Hancock, 2007; Nakano et al., 2002; Parsons, 2002; Schellen et al., 2010; Van Hoof, 2008).

According to de Dear (2011), the PMV theory from Fanger led to the thermal comfort mantra 'cool, dry, still indoor air', which was achieved by static isothermal indoor climates. As described above, a growing interest is on dynamic non-uniform environments as they can provide an energy-saving potential, more comfortable environment, and probably healthier environment (de Dear, 2011; Johnson et al., 2011). The above-mentioned studies indicate there is a need for new sensation models that cope with dynamic,

transient environments and individual effects and requirements.

de Dear et al. (1993) showed with a mathematical simulation that the discharge rate of skin thermoreceptors correlated to the change in thermal sensation during sudden temperature transitions (de Dear et al., 1993). Hence simulating the actual physiology of humans (i.e., neuron discharge rate instead of using skin temperatures) can be highly beneficial when designing buildings while optimizing energy costs and thermal comfort.

Neurophysiology of thermal reception

Most knowledge of thermoreceptor responses comes from experiments on isolated nerves of anesthetized animals (e.g., cats, rabbits, and primates); nevertheless, the fundamental properties of thermoreception also have been confirmed in man (Hensel, 1981). Still, the exact neuron discharge rate vs. temperature may differ substantially between species or between tissues. However, the general characteristics of thermoreception are assumed to be sufficient to serve the purpose of this study.

Zotterman et al. (1953) reported the averaged non-linear characteristic of thermoreceptor firing rates from steady-state temperature experiments on cat tongue. The maximum steady-state discharge rate for cold-sensitive receptors lies around 25°C (11 impulses/s) and for warm-sensitive receptors the maximum firing rate lies around 38°C (4 impulses/s) (Dodt and Zotterman, 1952, Zotterman, 1953). Contrary, other researchers showed that in cat nose the maximum steady-state discharge rate for cold-sensitive receptors was at 27°C (9 impulses/s) and for warm-sensitive neurons the maximum was at 46°C (36 impulses/s) (Hensel and Kenshalo, 1969). Therefore, it can be concluded that thermoreceptor data reported in literature differ considerably.

In addition to the steady-state discharge rate, time-dependent changes in skin temperature (i.e., direction and rate of temperature change) also influence the discharge rate. For instance, warm-sensitive neurons increase their discharge rate when heated, and even more when strongly heated, whereas during cooling the discharge rate of warm-sensitive neurons is decreased (Figure 2).

The neural pathway from local thermal reception to thermal sensation is described in literature as follows (Craig et al., 2000; Morrison, 2011). (i) The thermoreceptors bring the information to the spinal cord (i.e., from peripheral skin and deep body tissues) and to the trigeminal nucleus (i.e., from face skin). (ii) From the dorsal horn (top of spinal cord) and trigeminal nucleus, second-order neurons project to the thalamus. This is a different pathway than for thermoregulation, because for thermoregulation the secondary neurons connect to

Fig. 2 Schematic view of dynamic neuron discharge rate of temperature sensitive neurons. With increasing temperature warm thermoreceptors show an initial overshoot in discharge rate and cold thermoreceptors show an initial undershoot. Vice versa for decreasing temperature. Modified from Hensel (1981)

the hypothalamus instead of the thalamus (Benzinger, 1969; Morrison, 2011). (iii) The thalamus projects to the insular cortex, which is presumed to be the brain area for perception and localization of thermal stimulus intensity (Craig et al., 2000).

Methods

The mathematical model developed in this study uses experimentally measured skin and core temperature as input variables. Temperature recordings were then transduced to their equivalent neuron discharge rate. Finally, the neuron discharge rates were correlated to the experimentally measured sensation votes.

Experiments

In this study, two data sets of independent experiments were used. The first data set was used for development of the model; the second data set was used for validation. In both studies, core temperature was measured with an ingested telemetric pill (Cortemp, HQ Inc., Palmetto, FL, USA). The skin temperatures were measured according to ISO 9886 (2004) by wireless iButtons (Thermochron iButton_DS1291H, Dallas Maxim) at the 14-points as proposed by ISO 9886 (2004) (Parsons,

Table 2 Subject characteristics in experiments used for model development and for validation

	Model development ($N = 12$)	Validation ($N = 8$)
Age (year)	24.9 ± 1.0	23.6 ± 1.2
Mass (kg)	76.1 ± 3.3	82.7 ± 8.6
Height (m)	1.80 ± 0.02	1.83 ± 0.11
Body fat (%)	16.7 ± 1.4	14.5 ± 3.3
BMI (kg/m ²)	23.4 ± 0.9	24.8 ± 3.1

2003; Van Marken Lichtenbelt et al., 2006). Thermal sensation votes were asked on a continuous seven-point thermal sensation interval scale, where each point on the line could be marked (ASHRAE, 2005). As a result, the thermal sensation could be assessed within ±0.05 scale unit of accuracy. The AHRAE thermal sensation scale is represented in Table 1.

For the development dataset, male participants were lying and wearing shorts only (0.04Clo). Firstly, participants were exposed to baseline air temperature (30°C, 0.5 h). Next, participants were exposed to mild cold followed by warm conditions (20°C, 1 h; 35°C, 1 h). Finally, participants were exposed to baseline conditions again for 1 h (Kingma et al., 2011). For the validation data set, male participants were sedentary and dressed (1.0 clo, including desk chair). The participants were exposed to a transient condition; temperature range: 17–25°C, duration: 8 h, temperature drift: first 4 h: +2°C/h, last 4 h: –2°C/h (Schellen et al., 2010). Thus, participants were exposed to considerably different conditions in both datasets. Subject characteristics are shown in Table 2.

Modeling of thermal reception and neural pathways

For the development phase of the thermosensation model, skin temperature and core temperature recordings were used. First, the discharge rates of skin cold (C) and warm (W) thermal receptors and core warm (H_{warm}) receptors were calculated as described below.

Calculation of neuron discharge rate

As described in the introduction, different thermoreceptor data exist in literature. However, with respect to

Table 1 Seven-point ASHRAE thermal sensation scale (ASHRAE, 2004)

Thermal sensation	Corresponding term
–3	Cold
–2	Cool
–1	Slightly cool
0	Neutral
+1	Slightly warm
+2	Warm
+3	Hot

mathematical modeling of thermoreceptor data, only a study by Mekjavic and Morrison (1985) was found (Mekjavic and Morrison, 1985). They based their mathematical neuron discharge rate model on the thermoreceptor data presented by Zotterman (1953). Therefore, the *simulated* discharge rate of temperature-sensitive neurons at the periphery is modeled as a steady-state discharge rate and dynamic response to temperature changes and according to Mekjavic and Morrison (1985):

$$c_t = (1/\Delta t) \sum_j (S_{t-\Delta t} + (A_0(1 - \exp(-j/K)) + DA(\exp(-j/K_e) - \exp(-j/K_i)))) \quad (1)$$

Here, c_t is the discharge rate for cold-sensitive neurons at timepoint t (w_t for warm-sensitive neurons), Summation over j from $j=0$ to $\Delta t - 1$, $S_{t-\Delta t}$ is the steady-state neuron discharge rate at $t = t - \Delta t$, A_0 and A are gain factors that depend on the difference of steady-state discharge rates between two moments of time ($A_0 = S_{t-\Delta t} - S_t$ and $A = 5.0 S_{t-\Delta t} |A_0|$). $K = 5.5$, $K_i = 3.3$, and $K_e = 5.5$ are static, inhibitory, and excitatory gain factors, respectively. D is a sign operator indicating an excitatory or inhibitory response. When cold-sensitive neurons are heated, D is negative, when the same neurons are cooled, D is positive and vice versa for warm-sensitive neurons. The steady-state discharge rate of neurons is calculated as:

$$S_t = \sum_j x_j T^j \quad (2)$$

where x_j is the j -th order coefficient as given in Table 3 and T is the local temperature. The steady-state response of core temperature neurons is also calculated according to Mekjavic and Morrison (1985) by shifting measured core temperature by –2°C.

Local skin temperatures were used instead of mean skin temperature; using mean skin temperature would lead to significant errors in calculation of the average

Table 3 Coefficients to calculate the static neuron discharge rate of cold and warm sensitive neurons [values are modified from Mekjavic and Morrison (1985)]

Coefficient	Cold sensitive neuron	Warm sensitive neuron
x_0	–0.19005313e-6	0.1526647e-5
x_1	0.85318078e-5	–0.5147704e-4
x_2	–0.16974919e-5	0.7707699e-3
x_3	0.19724509e-4	–0.67475955e-2
x_4	–0.14833377e-3	0.38244284e-1
x_5	0.75486723e-1	–0.14664175e-0
x_6	–0.26343323e-0	0.38526706e-2
x_7	0.62289589e-2	–0.68496075e-4
x_8	–0.95563808e-4	0.78889647e-6
x_9	0.85949930e-6	–0.53173142e-8
x_{10}	–0.34432887e-8	0.15936041e-10

discharge rate of temperature-sensitive neurons, owing to the nonlinear characteristic of neuron discharge rate vs. temperature. For instance, the average discharge rate of two cold-sensitive neurons with temperature ($T_1 = 20^\circ\text{C}$ and $T_2 = 30^\circ\text{C}$) is not equal to the discharge rate of a neuron with temperature $T_{\text{mean}} = 25^\circ\text{C}$ (see Figure 1). Local neuron discharge rates are integrated at the spinal cord. This is calculated by averaging neuron discharge rate over skin positions ($P_{\text{warm}} = \Sigma W/n$ and $P_{\text{cold}} = \Sigma C/n$). Here, P_{warm} and P_{cold} (P stands for peripheral) are the averaged (i.e., integrated) peripheral warm and peripheral cold discharge rates and n is the number of positions where skin temperature is experimentally measured. From the horn (i.e., top of spinal cord), second-order neurons project to the thalamus and from the thalamus further to the insular cortex. There the thermal information from the body core (H_{warm}) and skin (P_{cold} and P_{warm}) is integrated. Some hypotheses on the neural pathways involved in thermal sensation exist (Chatonnet et al., 1966; de Dear, 2011). Therefore, we developed several models where the subject averaged thermal sensation vote was used as a dependent variable (see Table 4). Each model represents a different hypothesis, or assumption, of the neural pathway involved in thermal sensation. All variables are expressed in the discharge rate unit ‘impulses per second’. Therefore, the model coefficient signs define excitation and inhibition within the neural pathway, a positive sign denotes excitation and a negative sign denotes inhibition. The first model is based on the assumption that only skin thermoreception contributes to thermal sensation (de Dear, 2011). The second model assumes that all three forms of thermoreception (i.e., skin cold thermoreception, skin warm thermoreception, and core warm thermoreception) project individually to the thermal sensation (Chatonnet et al., 1966). The third model assumes that core body thermoreception and skin warm thermoreception contribute to thermal sensation. Finally, the fourth model assumes that core body thermoreception and skin cold thermoreception contribute to thermal sensation.

The neuron discharge rates were correlated to the experimentally measured sensation votes by multiple regression analysis. All calculations were performed

using *Matlab 2010a for Mac*. Only one model was selected for validation against the independent data set. Model selection for validation was based on the following criteria: (i) all β -coefficients significantly differed from zero (ii) highest explained variance (i.e., highest r^2 -value).

Validation

The thermo sensation model was validated by calculation of the root mean squared residual (RMSR) between model prediction and measured sensation votes of the validation data set. The model prediction quality was considered acceptable when $\text{RMSR} < 1$, thus the model prediction should be within 1-scale points of the measured sensation vote. This value was based on a power calculation to have 95% chance to detect a significant error in model prediction using $N = 8$ subjects for validation. Given the variation in sensation votes as estimated from the development dataset, a statistical detection power of 95% is feasible when the average prediction error ≥ 1 -scale unit. The power calculation for the ‘one-sample test’ is as follows:

$$Z_\gamma = (n\delta^2/\sigma^2)^{0.5} - Z_{0.5\alpha}. \quad (3)$$

Here, Z_γ is the value of the standard normal distribution corresponding to the type II error rate (power = $1 - \gamma = 0.95$), n is the sample size ($N = 8$), δ is the prediction error, σ is the standard deviation as estimated from the development dataset, and $Z_{0.5\alpha}$ is the value of the standard normal distribution corresponding to the type I error rate ($\alpha = 0.05$).

Model prediction was performed by repetition of the thermoreceptor discharge rate calculation procedure as described in the model development phase. However, now, skin and core temperature data from the validation data set were used.

Results

Model development phase

Regression analysis revealed that all models, each with different assumptions on the neural pathways, significantly explained the thermal sensation vote (see Table 5). However, only in model 3 and model 4 did all β -coefficients differ significantly from zero. In models 2 through 4, the core warm thermoreception pathway had a significant negative contribution to the thermal sensation. Hence, during the mild thermal challenge, a decrease in core temperature related to a warm thermal sensation. In model 3, the skin warm thermoreception pathway had a significant positive contribution to the thermal sensation. Thus, warm or heated skin related to a warm thermal sensation. Vice

Table 4 Thermosensation models that were tested on experimental data

$S = \beta_0 + \beta_1 P_{\text{cold}} + \beta_2 P_{\text{warm}}$	(1)
$S = \beta_0 + \beta_1 H_{\text{warm}} + \beta_2 P_{\text{cold}} + \beta_3 P_{\text{warm}}$	(2)
$S = \beta_0 + \beta_1 H_{\text{warm}} + \beta_2 P_{\text{warm}}$	(3)
$S = \beta_0 + \beta_1 H_{\text{warm}} + \beta_2 P_{\text{cold}}$	(4)

S is the thermal sensation vote as defined on the seven-point ASHRAE scale for thermal sensation. H_{warm} (impulse/s) is the neuron discharge rate corresponding to measured core temperature. P_{cold} (impulse/s) is the averaged neuron discharge rate of skin cold sensitive thermoreceptors. P_{warm} (impulse/s) is the averaged neuron discharge rate of skin warm sensitive thermoreceptors.

Table 5 Regression coefficients $\pm$ 95% CI (β 's) with the corresponding variable, explained variance (r^2), and P -value of sensation models during development phase

Model	β_0	β_1	β_2	β_3	r^2	P -value
1	-0.12 ± 55.1	-0.6 ± 4.3 (P_{cold})	1.9 ± 9.6 (P_{warm})		0.81	$<1.8 \times 10^{-6}$
2	36.4 ± 49.6	-14.8 ± 9.6 (H_{warm})*	0.7 ± 3.5 (P_{cold})	3.9 ± 7.7 (P_{warm})	0.89	$<2.1 \times 10^{-7}$
3	$44.0 \pm 32.8^*$	-14.3 ± 9.0 (H_{warm})*	2.3 ± 0.9 (P_{warm})*		0.89	$<2.5 \times 10^{-8}$
4	$56.1 \pm 30.7^*$	-13.9 ± 9.4 (H_{warm})*	-1.0 ± 0.4 (P_{cold})*		0.87	$<8.2 \times 10^{-8}$

* $P < 0.05$. **Fig. 3** (a) Averaged sensation votes and model fit (Model 3) of the development data set. Error bars represent the standard deviation. (b) Thermal condition to which participants were exposed **Fig. 4** (a) Averaged sensation votes and model prediction (Model 3) on the validation data set. Error bars represent the standard deviation. (b) Thermal condition to which participants were exposed

versa, in model 4, the skin cold thermoreception pathway had a significant negative contribution to the thermal sensation, such that cold or cooled skin related to a cold thermal sensation. The measured sensation votes and the prediction of model 3 on the development data set are shown in Figure 3.

Model validation phase

Model 3 was selected for the validation phase as it best explained the variation ($r^2 = 0.89$). The sensation

votes of the validation set and the model prediction are shown in Figure 4. The root mean square error (RMSR) of the thermal sensation prediction on the validation set was 0.38, which means that on average there was a 0.38 prediction error in thermal sensation. The maximum error observed was 1.16 scale points at the beginning of the experiment. The minimum error observed was 0.02 scale points at $t = 100$ min. In general, the model predictions were within the standard deviation of the measurements.

Discussion

In this study, a mathematical model of thermal sensation based on neurophysiology was validated on an independent dataset. The results indicate that the simulation of the neural pathways was able to capture characteristics of thermal sensation. Such a model of human thermal sensation can be of great value in designing of high-performance buildings.

A comfortable environment could be described as an environment where the average rating of a group of persons is between -1 and $+1$ on the ASHRAE thermal sensation scale (Fanger, 1970; Parsons, 2003). The model developed in this study was able to predict thermal sensation within 0.5-scale unit accuracy for both datasets (development and validation). Foda et al. (2011) found for four different thermal sensation models a discrepancy between predicted and measured overall thermal sensation within ± 1.0 scale unit. Thus, the model presented in this paper provides a greater accuracy and therefore more detailed information can be obtained regarding the overall thermal sensation. In practice, this could be beneficial because small deviations from a neutral thermal sensation (i.e., an overshoot or undershoot in thermal sensation) could provide a more comfortable thermal environment (Humphreys and Hancock, 2007; Van Hoof, 2008).

In current building practice, the PMV model of (Fanger, 1970) is used to predict the future thermal sensation of occupants. However, as mentioned in the introduction this model has limitations regarding the prediction of thermal sensation (e.g., for different subpopulations). Van Hoof et al. (2010) concluded in an extensive literature review that multi-segmental models of human physiology have a large potential to predict high-resolution thermal sensation of occupants in both the design phase of a building and laboratory conditions (Van Hoof et al., 2010). Especially, a large potential exists for complex environments regarding non-uniform and transient conditions which, in the end, could turn out to be the most comfortable environments (de Dear, 2011). However, van Hoof et al. also concluded that it is a great challenge to link the outcomes of a thermophysiological model to thermal sensation.

Until now, few studies have been available where physiological responses are related to thermal sensation. All current models require a body temperature setpoint to simulate thermal sensation. Fiala (1998) developed the dynamic thermal sensation (DTS) model to predict the dynamic thermal sensation based on core temperature, mean skin temperature, and rate of change in mean skin temperature (Fiala, 1998). Another study conducted by Zhang et al. (2010a,b,c) related physiological responses to local thermal sensation based on differences between local skin temperature and the setpoint of skin temperature for a specific

body part, rate of change in local skin temperature, and rate of change in core temperature (Zhang et al., 2010a,b,c). Although these models show promising results, one could argue whether setpoints are a good representation of the physiology behind thermoregulation or thermal sensation (Cabanac, 2006; Romanovsky, 2007).

In this study, a thermal sensation model was developed based on the neurophysiology of thermal reception and neural integration. Several hypotheses of the neural pathways that predict thermal sensation were tested (see Table 5). Interestingly, the best model only required thermal information from warm-sensitive receptors of skin and core. The reason for this becomes clear after analysis of simulated core and skin thermoreception over time. Figure 5 shows the simulated neuron discharge rate for core warm receptors (H_{warm}) and integrated skin cold (P_{cold}) and warm (P_{warm}) receptors. The signals of P_{cold} and P_{warm} are almost mirrored images of each other; therefore, both signals contain the same information. It is possible that in more extreme situations (colder, hotter, or larger temperature changes), information of both cold and warm skin receptors is necessary to correctly predict thermal sensation. For instance, when skin temperature decreases below 26°C , temperature information is dominated by the discharge rate of skin cold-sensitive thermoreceptors (Figure 1): the discharge rate of warm-sensitive thermoreceptors decreases to zero. Likewise, above 35°C , virtually no skin cold thermoreceptor input is generated, and all information is coded by skin warm thermoreceptors (Figure 1). In more neutral environments, however, skin warm and cold thermoreceptors seem to reveal the same. To the best of our knowledge, only one other study correlated thermal reception to thermal sensation (de Dear et al., 1993). de Dear et al. showed that the change in thermal sensation correlated to the discharge rate of both cold and warm skin thermoreceptors during a sudden ambient temperature transition. The authors did not report correlations to absolute sensation votes. The results presented in this paper suggest that apart from skin thermal reception, absolute thermal sensation is also dependent on warm core thermoreceptors. It could be that skin thermoreceptors correlate well to changes in thermal sensation, yet the core thermoreceptors are important for an absolute 'basal' level of thermal sensation. We will again illustrate this with Figure 5. This figure shows that there is a delayed response of the core thermoreceptors relative to the skin thermoreceptors ($t = 30\text{--}90$ min). The warm core thermoreceptors decrease their discharge rate (Figure 5, Top), while skin thermoreception already returned to near baseline values (Figure 5, Bottom). Note that the delay of core thermoreception might differ depending of the exact site and method of core temperature measurement (Benzinger, 1969; Teunissen et al., 2011). Owing to the

Fig. 5 Simulated thermoreceptor discharge rates of: (a) skin cold thermoreceptors (P_{cold}); (b) core warm thermoreceptors (H_{warm}); and (c) skin warm thermoreceptors (P_{warm}). (d) The thermal condition participants were exposed to

slow response, abdominal core thermoreception cannot be associated with thermal sensation during sudden ambient temperature transitions. However, during rewarming, the afterdrop in core temperature is clearly visible in the core warm thermoreception. An afterdrop in core temperature is caused by the return of cooled blood from the peripheral tissues (Severens et al., 2007). Although the range of the discharge rate change for core warm thermoreceptors is not as large as for skin warm thermoreceptors (H_{warm} : 3.4–3.5 pulse/s and P_{warm} : 1.9–3.1 pulse/s), the associated weight (β) is considerably larger for core thermoreception than for skin thermoreception ($\beta_{H_{\text{warm}}} = -14.3$ and $\beta_{P_{\text{warm}}} = 2.3$), which evens out the difference in discharge rate. Hence, core thermoreception has a large long-lasting influence on thermal sensation and skin thermoreception has a fast changing influence on thermal sensation. The negative sign of the core warm thermoreception pathway model coefficient may seem counter-intuitive at first, because it suggests that a decrease in core temperature relates to a warm thermal sensation. However, during the mild thermal challenge, core temperature remained stable during mild cold, yet during rewarming, core temperature dropped on average by 0.3°C (Kingma et al., 2011). A paradoxical decrease in core temperature during rewarming or an increase in core temperature during mild cold has been described in physiological literature (Benzinger, 1969;

Sessler, 2000). The inverse relation between core temperature change and thermal sensation during a mild thermal challenge might be part of thermal alliesthesia, as during stable conditions a high core temperature is associated with to a warm thermal sensation and thermal discomfort (Mayer, 1993). Another issue for thermal alliesthesia relates to the dominance of thermoreception to thermal sensation. When the thermal environment continuously changes, there is a large contribution of thermoreception to the overall thermal sensation. This can be explained by the importance of detecting changes in the thermal environment to maintain thermal homeostasis. However, when the ambient environment is more stable, the relative influence of non-thermal factors may increase. Therefore, thermoreception and thermal sensation may have a stronger coupling during thermal transients relative to stable thermal conditions. Overall, this suggests that the currently developed model may be suitable for predicting thermal sensation during transient thermal conditions, yet less so during stable thermal conditions.

The model presented in this study relies on *simulated* neuron discharge rate. In literature, different experimentally measured thermoreceptor data exist. For instance, a study by Hensel and Kenshalo (1969) showed a near 10-fold increase in the maximum steady-state discharge rate of warm-sensitive neurons

in comparison with the data presented by Zotterman (1953) (36 impulses/s vs. 4 impulses/s, respectively). Especially during transient conditions, such differences could have a large impact on model performance, which is mainly because the magnitude of the dynamic response scales with the difference between two steady-state discharge rates. For instance, when a warm-sensitive neuron is heated using the data presented by Hensel and Kenshalo (1969), a higher steady-state discharge rate would also result in a larger dynamic response. Vice versa, when a warm-sensitive neuron is cooled, its discharge rate is also suppressed more. Theoretically, cooling could even nullify the discharge rate of warm-sensitive neurons, leaving only cold-sensitive neurons to obtain information on the thermal status of the body. Therefore, future studies should elucidate how using different thermoreceptor data might alter the results of this study.

In summary, the neurophysiological approach for developing a mathematical thermal sensation model as presented in this paper offers a method to predict the thermal sensation under complex non-uniform and transient mild thermal environments. Furthermore, this approach can be extended to a thermal sensation prediction on a local body part level; however, more research is needed for this. Therefore, future work should focus on:

- relative importance of specific skin areas to whole body thermal perception,
- relative importance of core temperature measurement site to thermal perception,
- thermoreception in more extreme environments (e.g., colder, warmer, and larger temperature changes),
- steady-state thermoreception characteristics,
- inclusion of other subpopulations such as, females, older people, or people with obesity,
- application of local thermoreception to local comfort.

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Conclusion

In this study, a new model for predicting thermal sensation is developed. This model is based on the neurophysiology of thermal reception. The model is validated on an independent dataset. The only dependent parameters for thermal sensation in the model are core body warm thermoreception and skin warm thermoreception. The model was capable to significantly predict thermal sensation within 0.5-scale unit accuracy for both the development dataset and the validation dataset. In current building practice, an accuracy of ± 1.0 is considered as acceptable. Though, rather small deviations from optimum (neutral), < 1.0 -scale unit could provide a more comfortable thermal environment and occupants would therefore be more satisfied with their environment. The presented method can be highly beneficial for predicting thermal sensation under complex environments with respect to non-uniform and transient environments, especially in combination with thermophysiological models to link physiological responses to thermal sensation. Therefore, the neurophysiological model of thermal sensation can be of great value in the design of high-performance buildings.

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