Dynamics and Perception in the Thermal Grill Illusion

Shriniwas Patwardhan¹, Anzu Kawazoe², David Kerr³, Masashi Nakatani⁴, and Yon Visell¹,²

Abstract—A basic challenge in perception research is to understand how sensory inputs from physical environments and the body are integrated in order to facilitate perceptual inferences. Thermal perception, which arises through heat transfer between extrinsic sources and body tissues, is an integral part of natural haptic experiences, and thermal feedback technologies have potential applications in wearable computing, virtual reality, and other areas. While physics dictates that thermal percepts can be slow, often unfolding over timescales measured in seconds, much faster perceptual responses can occur in the thermal grill illusion. The latter refers to a burning-like sensation that can be evoked when innocuous warm and cool stimuli are applied to the skin in juxtaposed fashion. Here, we show that perceptual response times to the thermal grill illusion decrease systematically with perceived intensity. Using results from behavioral experiments in combination with a physics-based description of tissue heating, we develop a simple model explaining the perception of the illusion through the evolution of internal tissue temperatures. The results suggest that improved understanding of the physical mechanisms of tissue heating may aid our understanding of thermal perception, as exemplified by the thermal grill illusion, and might point toward more efficient methods for thermal feedback.

Index Terms—Haptics, Thermal Perception, Thermal Grill Illusion, Response Time, Heat Equation, Simulation

1 INTRODUCTION

THERMAL cues play important roles in the haptic perception of objects [1], especially in material discrimination [2]. Thermal feedback is also of growing interest in medicine, human-computer interaction, wearable technologies, and virtual reality, where it may be used enhance interactive experiences, such as touching virtual objects objects [3]. However, the engineering and application of thermal displays is still improving, aided by advances in technologies [4] and knowledge of human factors [5].

Thermal touch involves the perception of the temperature or properties of objects through the exchange of heat through contact with the skin. The normal temperature of human skin in homeostasis is between 31 and 35 °C. Temperatures are perceived as warm (31 to 35 °C), painfully hot (> 45 °C), cool (31 to 35 °C), or painfully cold (< 15 °C). These sensations are mediated by thermoreceptive afferent nerve fibers innervating the skin [6], as well as nociceptive afferents associated with painful temperatures [7], [8].

Thermal touch is dynamic. Heat is exchanged at rates that depend on the temperature difference between the skin and the stimulus, and on thermal transport within both bodies. The rate of thermal transport in soft materials, such as the skin, is limited by the dynamics of elastic vibrations, or phonon transport. From kinetic theory, thermal conductivity, k, is proportional to \( \sqrt{E/\rho} \), where E is the elastic modulus and \( \rho \) the density [9]. Thus, soft materials like skin are intrinsically insulating, lengthening the time for heat exchange, and partly explaining why thermal perception at non-noxious temperatures is often slow, associated with timescales measured in seconds [5]. In contrast, as shown here, the thermal grill illusion can elicit rapid responses even at moderate temperatures.

Thermal perception is also spatially dependent, because thermal contacts and temperatures vary across the skin, and because the internal temperature of the skin varies with position. Due to spatial summation, a larger area of stimulation leads to greater intensity of sensation. Input from both cold and warm thermoreceptors contributes to perception, and when heat exchange with the skin is spatially non-uniform, can lead to integration of input from different thermoreceptor types. While not fully understood, the perceptual integration of thermal signals in space or time, and their interaction with other tactile modalities (such as nociception), has been found to give rise to different perceptual effects.

The present investigation addresses one such effect, the thermal grill illusion, and its ability to rapidly elicit intense sensations [7]. The thermal grill illusion (TGI) was discovered by Torsten Thunberg (1896), who reported that innocuous warm and cool stimuli applied simultaneously to the skin by means of interlocking spiral tubes elicited burning sensations like those that accompany cold pain [11]. While touching either the warm or cool stimuli in isolation elicits little discomfort, touching both simultaneously can elicit a “burning” sensation [12], [13]. The illusion can be experienced by using shapes other than spiral tubes – alternating bars, checkerboard patterns, or grids. The thermal grill illusion does not change greatly with the number of temperature regions or their spacing [14].

1. This paper is based on a recent conference paper by the authors [10], in revised and extended form.

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1 Department of Electrical and Computer Engineering, University of California Santa Barbara, USA
2 Media Arts and Technology Program, University of California Santa Barbara, USA
3 Sansum Diabetes Research Institute, Santa Barbara, USA
4 Faculty of Environment and Information Studies, Keio University, Kanagawa, Japan
Currently, the most accepted physiological explanation ascribes the thermal grill illusion to interactions between different thermally sensitive afferent pathways in early somatosensory processing \[15]. According to this theory, touching the cold terminal of a thermal grill, normal discharge from coolness sensitive A\(\delta\) afferent fibers is suppressed due to the spatial summation of inputs that signal warmth in other (possibly proximal) skin regions \[15]. In the absence of such warm inputs, the A\(\delta\) inputs inhibit the activity of polymodal C-nociceptive afferent fibers, which otherwise cause burning sensations at only noxious cold temperatures \(< 15^\circ\text{C}\). When A\(\delta\) input is suppressed by input from nearby warm regions, a burning sensation occurs at merely cool \(< 24^\circ\text{C}\) temperatures. Brain imaging studies reveal that the thermal grill and the noxious hot and cold stimuli produce similar patterns of activation in the anterior cingulate cortex, whereas the warm and cool components of the thermal grill do not \[16\]. Complicating these characterizations, recent research indicates that thermal grill-like illusions can occur across spatially non-adjacent skin regions, and that the effects can be modulated by body posture, suggesting that integration at the cortical stage of neural processing might best explain the effect \[17\], \[18\], \[19\].

While response times for homogeneous thermal stimuli are often slow below noxious temperatures \[9\], the TGI can elicit rapid and intense responses even at moderate (warm and cool) temperatures. One reason may be the involvement of both myelinated A\(\delta\) fibers, that transmit fast propagating neural signals (speed 2 to 30 m/s), and unmyelinated C fibers, which conduct more slowly (2 m/s or less). The properties of each can have important perceptual consequences \[20\], \[21\], affecting the dynamic perception of thermal grill stimuli \[22\]. As noted above, tissue heating is relatively slow at innocuous temperatures, and this may also be an important factor for understanding the time dependence of TGI perception.

Recent studies have shed light on the perception of TGI stimuli, including responses in regimes that do not elicit burning sensations \[23\], duration and site dependence \[22\], and dynamic responses captured during the time-course of application \[24\]. Nonetheless, an integrated understanding of the underlying mechanisms, including tissue heating and neural integration, is lacking. Addressing this gap could be of broader relevance to the understanding of thermal perception, since similar sensory resources and processes are thought to be involved.

To investigate thermal display via the TGI, and time-dependent properties of the perception of the latter, we developed a new thermal grill display device capable of presenting a range of thermal grill temperatures under computer control. We used this device to undertake a psychophysical experiment in which we measured response time and perceived intensity as participants felt thermal grills, and analyzed the results to elucidate the relation between stimulus parameters, perceived intensity, and response times.

In order to relate our perceptual findings to tissue heating, we compared them with predictions of a model of internal heating of the skin. Jones and Ho previously proposed a thermal model that predicts the temporal response of the skin surface during contact with a surface at constant temperature \[1\], \[25\]. However, internal heat transfer is not captured in this model, and may be physiologically significant, since thermoreceptive afferents lie below the most superficial layers of skin \[26\]. Furthermore, the Jones-Ho model does not account for tissue heating due to contact with objects whose surface temperature varies with position, as in the TGI. Models of tissue heating have shed light on time-dependent heating and cooling phenomena \[27\], \[28\], underlining the value of such methods.

Here, we based our analysis on a physical description of spatial and temporal heating in body tissues, derived from the Pennes bioheat equation \[29\]. Using results of analytical and numerical modeling, we derived an simple model explaining the perception of the TGI through the time-evolution of internal tissue temperatures.

### 2 Thermal Grill Display Design

We designed a new electrothermal display device to empirically investigate factors reflecting how the thermal grill stimuli are perceived, and to explore the use of these stimuli in human-computer interfaces. The device is comprised of a thermal grill surface, with heating apparatus, controller, sensors, and computer.

The thermal grill surface is made of aluminum bars, each having dimensions \(6 \times 6 \times 15 \text{ mm}\). A total of 6 such bars are used. They are separated by 6 mm and arranged in an alternating pattern (Figure 1). In typical operation, half of the bars are heated (using a Peltier element on one side) and the remaining half are cooled (using that from the other side), but the bars may also be used to uniformly heat or cool. The heating and cooling is done using Peltier devices (TEC1-12706 ThermoElectric Peltier Cooler 12 Volt, 92 Watt), semiconductor thermoelectric heat pumps that move heat from one side to another when an electric potential is applied across their terminals, causing one side to heat and the other to cool (Figure 2). An opposing side is maintained close to room temperature via a heat sink to ensure efficient operation. We employed two heat sinks to ensure that the Peltier elements could be positioned away from the touched grill area, which ensured that the warm and cool elements remained well decoupled. The temperature of the grill elements is monitored using surface temperature.
Fig. 2: Thermal grill display device. Peltier thermoelectric pumps are electronically controlled independently for each of the two sets of grill elements. A microcontroller sends control signals to the Peltier elements and reads signals from the temperature sensors. Heat sinks allow the thermoelectric device to operate relative to room temperature. Temperature sensors are affixed to the bottom of the touched portion of the grill. The temperature of the top surface of the device was calibrated in order to ensure that the specified temperature is felt by the skin on contact with the device.

Fig. 3: The thermoelectric haptic device used for the experiment. The participant kept their hand on the thermal grill and their responses were recorded.

In order to validate the performance of the device, we measured the temperature on the top surface using a contactless thermal probe and calibrated the temperature sensors to this value, ensuring that the measured temperature reflects what is felt at the surface.

In order to validate the performance of the device, we measured the temperature on the top surface using a contactless thermal probe and calibrated the temperature sensors to this value, ensuring that the specified temperature that is felt by the skin on contact with the device was within approximately \( \pm 1^\circ C \) of the specified temperature. The temperature control loop and sensor monitoring (sample frequency 100 Hz) is performed via a microcontroller (Arduino Uno, Arduino SRL, Italy), and commanded by desktop computer via serial communication. When a new temperature is commanded, it takes approximately one minute for a stable target temperature to be reached. We allowed for three minutes in the experiment below.

3 Time-dependent perception of the TGI

We designed a psychophysical experiment to apply this display, and to investigate the dynamics of thermal perception in the thermal grill illusion – and in particular the relation between the intensity of the sensations that it produced and the time that it took for these sensations to be elicited. In it, we assessed both intensity and reaction time, and analyzed the results to determine how they were related to the temperatures of the warm and cool bars.

Fig. 4: Temperature Settings for the thermal grill used in the study. Hot temperatures were varied between 31 to 40°C and cold temperatures were varied between 14 to 23°C. Four combinations each for hot and cold temperatures give 16 thermal grill settings.

3.1 Apparatus

The apparatus consisted of the thermal grill display device described in the previous section. We measured the response times during using an electronic sensor (switch), which was recorded when the surface was touched and released by the hand of the participant. The ambient temperature during the experiment was climate controlled within a range from 20 and 22°C. The experiment was run under computer control using Python-based psychophysics software (PsychoPy, University of Nottingham, UK), which selected the stimuli, commanded the thermal grill display, displayed the graphical user interface, and recorded participant responses.
3.2 Methods and Stimuli

During the experiment, subjects felt the thermal grill (Figure 3) at various temperature settings, consisting of the temperature of warm and cool elements (see Figure 4). Their response time and perceived intensity was recorded. The temperature settings of the thermal grill were changed between trials. There were a total of 16 temperature combinations (Figure 4). These temperature combinations were chosen to be well within the limits of thermal pain, so as that the individual elements were not perceived to be painful. The participants felt the thermal grill at the minimum and maximum settings prior to the experiment, in order to remove individual bias towards rating the perceived intensity.

3.3 Participants

A total of 10 participants volunteered for the experiment, five were female and five male, with ages ranging from 22 to 29 years old. Participants were compensated with $10 for their time. Participants reported no condition affecting normal use or sensation in the hands. All reported being right-hand dominant. All subjects gave informed consent. The experiments were approved and conducted according to the human subjects research policies of the University of California, Santa Barbara. Prior to the experiment, participants completed a short survey collecting anonymous demographic and screening information.

3.4 Procedure

Prior to the experiment, participants were asked to touch the thermal grill at the maximum and minimum temperature differential, and to rate the intensity of each trial using a continuous visual analog scale on a computer. The total duration for each participant was 1 hour including a three minute break time between each temperature setting. This break time also enabled the thermal grill to reach a stable temperature.

The experiment was conducted in a quiet environment to limit distractions. Participants were seated at a desk equipped with a computer interface and the thermal grill. Participants completed a brief guided training phase before they proceeded to the main part of the experiment, during which they felt the thermal grill at the minimum (smallest temperature difference) and maximum (largest temperature difference) settings, and were informed that these corresponded to the least and most intense stimuli. During each trial, participants placed their palm flat on the grill. Participants were instructed to remove their hand from the display as soon as they felt a burning sensation similar to the one that they felt for the largest temperature difference stimulus, which they felt during the acclimation phase (see Methods and Stimuli). The response time was given by the time between initial contact and the removal of the hand, as recorded by the switch. If they did not respond within 10 seconds, participants were prompted to remove their hand from the display. Participants then rated the intensity using a continuous slider (visual analog scale), ranging from 0 (least intense) to 1 (most intense). Subsequent trials proceeded similarly. We proceeded with three trials at each temperature setting, in succession, since no delay was required between them, and this permitted significantly more data to be collected, and averaged responses from the three. Different temperature settings were presented in random order. There were a total of 16 such settings in the experiment. The procedure was computer automated, and provided automated prompts indicating when the thermal grill should be felt in each experimental condition.

Fig. 5: Perceived intensity and response time to thermal grill stimuli, data from all subjects and all trials in the experiment. The horizontal axis represents the temperature differential of the thermal grill. The vertical axis represents perceived intensity, from 0-1, on a scale rated according to extremal settings felt before the experiment. The perceived intensity shows a sigmoidal relationship with the temperature differential. (b) As in (a), except that the vertical axis represents the response time in seconds.
3.5 Results

The rated intensity \( I(\Delta T) \) increased, on average, monotonically with the temperature difference between warm and cool elements (Figure 5). The relationship between intensity and temperature difference was sigmoidal in shape. Fitting intensity \( I \) as a function of temperature difference \( \Delta T \) with a sigmoidal function

\[
I(\Delta T) = a(b + e^{-c\Delta T})^{-1} + d
\]

indicated a positive effect of temperature difference on intensity \( (p < 0.01) \). The \( R^2 \) value for the fit was 0.89. Differentiating this fitting function revealed that the maximum rate of increase in perceived intensity occurred at temperature difference \( \Delta T = 17^\circ C \).

On average, response time \( t_R \) decreased monotonically with temperature difference (Figure 5c). We modeled the relationship via a sigmoidal function \( t_R(\Delta T) = a(b + ce^{-d\Delta T})^{-1} + f \) and determined that the relationship was significant \( (p < 0.01) \) and that the \( R^2 \) value was 0.768. From the data, at the highest temperature difference, the response time was fastest. At the lowest temperature differences, the results reflect a mix of trials in which participants withdrew their hand based on what they felt and others in which they were prompted to do so after 10 seconds had elapsed. Nonetheless, a decrease in response time is seen with increasing temperature at these levels. Here too, the rate of decrease was fastest near 17\(^\circ\) C. For each increase in \( \Delta T \) by one degree, the response time decreased by 0.506 seconds, on average.

Across all temperature differences used in the experiment, there was, on average, a decrease in response time with intensity (Figure 5). The relationship was approximately linear, and a linear fit yielded an \( R^2 \) value of 0.673. The lowest uncertainty was for the highest temperature differences (\( \Delta T = 26^\circ C \)), for which all data points clustered around a mean response time of approximately 1.5 seconds and an intensity of 0.9.

3.6 Perception Experiment: Discussion

The results (Figure 5b) indicate that as the temperature difference \( \Delta T \) between the warm and cool bars increased, the perceived intensity increased, on average, while the response time \( t_R \) decreased. This suggests that the thermal grill illusion is not a digital phenomenon, and that there is a proportional effect of temperature difference on both intensity and response time, for temperatures in the range studied here. This is also consistent with prior observations [30], that the strength of the thermal grill illusion depends on the cold-warm differential rather than the individual cool and warm temperatures. The sigmoidal functions that we fit to the data may, in principle, be used in order to predict the intensity and response time to thermal grill stimuli as the temperature difference is varied, but the results likely also depend on factors including the surface area of contact [31]. Nonetheless, we expect qualitatively similar results to hold for thermal grill displays of different dimensions or configuration. The variability in intensity and response time were smallest (excluding limiting effects on response time measurements, see above) at the highest temperatures. The ratings and response times varied little among the entire participant population, underlining the robustness of this effect.

4 Modeling spatiotemporal tissue heating

We next sought to relate the perceptual results to the proximal thermal stimuli felt by participants. Because the internal temperature of hand tissues could not be directly measured, we developed analytical and numerical models of tissue heating.

Modeling heat transfer in the regimes of interest required that we make several simplifying assumptions in order to avoid complexities arising from the anatomy and physiology of the hand. First, we adopted a homogenized model, characterized by average tissue properties. We neglected differences between soft tissue layers (Figure 7). We also neglected heat conduction in the vascular network, a process known as perfusion, which is itself temperature-dependent [32]. Since the temperatures of interest are nonnoxious, we also neglected the possibility of irreversible thermal damage. With these simplifications in mind, we developed an analytical description, before proceeding to a numerical solution that we used to compare with the results of the perception experiment.

4.1 Mathematical model of internal tissue heating

An accepted physical model of tissue heating due to thermal contact with body tissues is the time-dependent bioheat equation [1], as introduced by Pennes [29]. It is written

\[
\rho c_p \frac{\partial T}{\partial t} = k \nabla^2 T + \omega \rho_b c_h (T_a - T) + q_{met} + q_{ext}.
\]

Here, \( T = T(x, y, z, t) \) is the temperature of skin tissues at point \((x, y, z)\) and time \(t\), \( k \) is the effective thermal conductivity of skin, \( \rho \) and \( \rho_b \) are the effective densities of
For the purpose of modeling tissue heating in the TGI, we assumed the thermal stimulus to vary along one surface dimension, \( x \), described by a boundary condition, \( T_{\text{top}}(x) \), which began at time \( t = 0 \). This yields a problem with two spatial dimensions, displacement \( x \) and depth \( y \), and time \( t \), whose solution \( T(x, y, t) \), describes the spatiotemporal tissue temperature distribution, and satisfies \( T(x, y, 0, t) = T_{\text{top}}(x) \) for \( t > 0 \). The time-dependent heat equation \(^1\)

\[
\frac{\partial^2 T(x, y, t)}{\partial x^2} + \frac{\partial^2 T(x, y, t)}{\partial y^2} = \frac{\rho c}{k} \frac{dT(x, y, t)}{dt}
\]  

\( (2) \)

We adopted values of \( \rho, c \), and \( k \) that are typical of human skin in-vivo, as reported in Table 2\(^3\).\(^4\).\(^5\).

Our goal is thus to determine the temperature distribution associated with a boundary condition, \( T(x, y_0, t) = T_{\text{top}}(x)\Theta(t) \), where \( \Theta(t) \) is the Heaviside step function. For thermal grill stimuli, we took \( T_{\text{top}}(x) \) to be a temperature profile corresponding to alternating hot and cold values, \( T_h \) and \( T_c \), see Fig. 8\(^6\), with other boundaries maintained at ambient body temperature, \( T_A \). The boundary conditions are summarized in Table 1. This simplified boundary condition eased the development of analytical solutions, but omits gaps between warm and cool bars in our display. In our device, these gaps improved thermal insulation. Omitting them could thus affect model predictions. However, similar perceptual responses have been observed in prior studies with gapless TGI stimuli. In addition, tissues directly below the warm-cool boundaries are similarly proximal to both temperatures, yielding little net heating, a condition that is similar to what would occur under a gap.

This problem can be solved using standard methods. First, the heat equation is linear, enabling us to use superposition to subtract the constant ambient body temperature \( T_A \), and model the response through a tissue temperature variable \( T(x, y, t) = T(x, y, t) - T_A \), where \( T \) now refers to the true tissue temperature. This yields boundary conditions \( T(x, y, t) = 0 \) for \( x = 0, x = w \) and \( y = d, \) and \( T_{\text{top}}(x) - T_A = T_{\text{top}}(x) \), see Figure 9. Under thermal grill conditions, we assumed the bars to be equally warmer and cooler (respectively) than skin temperature \( T_A \), so that the boundary conditions are \( T(x, 0, t) = \pm T_h \) within each surface domain of width \( a \).

\[
T_{\text{top}}(x) = \pm T_h \text{ if } x_n < x < x_{n+1}, \\
x_n = na, \ n = 0, 1, 2, \ldots, N
\]

We fixed the initial condition to be \( T(x, y, 0) = 0 \), so that the initial tissue temperature was \( T_A \). In this case, symmetry dictates that the temperature \( T(x, x_n, y, t) = 0 \) for positions \( x_n \) at the boundary between heating elements, for all \( y \) and all \( t \). The solution to this problem is obtained by solving the heat equation within each domain \( x_n < x < x_{n+1} \) of width 10 mm (Figure 9), with boundary conditions \( T(0, y, t) = T(a, y, t) = 0 \) and \( T(x, 0, t) = \pm T_h \). Since the heat equation is linear in \( T \), the solutions \( T(x, y, t) \pm T_h \) with boundary conditions \( T_h \) and \( -T_h \) are related by

\[
T(x, y, t)|_{T_h} = T(x, y, t)|_{-T_h}
\]

We divided the problem into its steady state and transient components. The complete solution can be written \( T(x, y, t) = T^S(x, y) + T^T(x, y, t) \), where \( T^S(x, y) = \lim_{t \to \infty} T(x, y, t) \) is the steady state solution and \( T^T(x, y, t) \) is the transient part. The steady state solution can be readily obtained when the temperature of the boundaries is held constant. It satisfies the time-independent heat equation,

\[
\frac{\partial^2 T}{\partial x^2} + \frac{\partial^2 T}{\partial y^2} = 0,
\]

which is Laplace’s equation in two dimensions. The solution with TGI boundary conditions is obtained using the method of separation of variables \(^3\)

\[
T^S(x, y) = \pm T_h \sum_{n=1}^{\infty} \sum_{m=1}^{\infty} C_{n, m} \sin \left( \frac{n \pi x}{a} \right) \sin \left( \frac{m \pi (y - b)}{a} \right) e^{\lambda t}
\]

where the sign is positive or negative for warm or cool bars respectively. The steady-state solution over the entire domain is then obtained by concatenating the piecewise solutions for domains \( ma \) \( < x < (m + 1) a \), where \( m = 0, 1, \ldots, 5 \).

The transient part of the solution, \( T^T(x, y, t) \), can also be obtained using the method of separation of variables, and may be written in the following form:

\[
T^T(x, y, t) = \sum_{n=1}^{\infty} \sum_{m=1}^{\infty} C_{n, m} \sin \left( \frac{n \pi x}{a} \right) \sin \left( \frac{m \pi y}{b} \right) e^{\lambda t}
\]

\( (5) \)
Fig. 8: Boundary conditions for hand touching thermal grill. Top panel: The top boundary is held at the temperature of the thermal grill, while the other three are held at ambient body temperature. Bottom panel: The same boundary conditions after subtracting ambient body temperature $T_A$ from all sides.

TABLE 1: Boundary conditions for heat equation over the domain corresponding to the volume of body tissue near the surface of the skin after subtracting ambient body temperature $T_A$ from all the sides.

<table>
<thead>
<tr>
<th>x</th>
<th>y</th>
<th>Temperature $T(x, y, t)$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Left Boundary</td>
<td>$x = 0$</td>
<td>$0 \leq y \leq b$</td>
</tr>
<tr>
<td>Right Boundary</td>
<td>$x = a$</td>
<td>$0 \leq y \leq b$</td>
</tr>
<tr>
<td>Bottom Boundary</td>
<td>$0 \leq x \leq a$</td>
<td>$y = 0$</td>
</tr>
<tr>
<td>Top Boundary</td>
<td>$0 \leq x \leq a$</td>
<td>$y = d$</td>
</tr>
</tbody>
</table>

where

$$\lambda = -\frac{k}{\rho c} \left( \frac{(n\pi)^2}{a^2} + \frac{(m\pi)^2}{b^2} \right)$$  \hspace{1cm} (6)

$$C_{n,m} = \frac{4}{ab} \int_0^b dy \sin \left( \frac{m\pi y}{b} \right) \left( T(x, y, 0) - T_{ss}(x, y) \right)$$

$$\times \int_0^a dx \sin \left( \frac{n\pi x}{a} \right)$$  \hspace{1cm} (7)

4.2 Numerical Simulations of Dynamic Tissue Heating

The analytical expressions for the temperature distribution, $T(x, y, t)$, illustrate the spatial and temporal dependence of tissue heating in response to TGÎ stimuli, including a repeated pattern of position dependence, $x$, and an exponential decay in time toward a steady-state solution, $T_S(x, y)$, governed by a time-constant proportional to $k/(\rho c V)$, where $V = ab$ is the domain size. However, these expressions are inconvenient for quantitative evaluation, due to the infinite sums and integrals. Instead, we quantitatively estimated tissue heating using finite element method numerical simulation. We modeled the problem domain using a rectangular mesh with dimensions $3858 \times 2060$. We used values for the thermal conductivity, $k$, heat capacity, $c$, and mass density, $\rho$ based on representative values for human skin in vivo (Table 2 based on [34]).

The simulation spans ten seconds, matching the maximum response time, and we captured the results at 50 instants with a sample period of 200 ms. The initial conditions and boundary conditions matched those described above. The time-dependent solution is shown for five instants in time in Figure 10 shown relative to the nominal range of depths of thermoreceptive afferents. Thermoreceptors lie at the regions of the dermis nearest to the epidermis, shown here as 1-3 mm, but depending in general on body location and other factors. The numerical solutions reflect the imposed surface temperature boundary conditions, and exhibit the $x$-dependent periodicity, exponential decrease in amplitude with depth, and time-dependence, including convergence toward an apparent steady-state at large times, $t$, that were predicted by the analytical solutions developed in Section 4.1.

5 From Tissue Heating to Perception

In order to obtain insight into the relation between the time-course of internal tissue heating and the perception of the thermal grill illusion, we combined the physical model of tissue heating developed in Section 4 with the experimental results from Section 3 in order to formulate a minimal model of perception that relates the perceived intensity of the thermal grill to time-dependent temperature gradients in the skin.

TABLE 2: Parameters used for the numerical simulation

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Simulation time</td>
<td>10 seconds</td>
</tr>
<tr>
<td>Frame rate</td>
<td>200 ms</td>
</tr>
<tr>
<td>Mesh size</td>
<td>$3858 \times 2060$</td>
</tr>
<tr>
<td>Maximum depth simulated</td>
<td>20 mm</td>
</tr>
<tr>
<td>Temperature at top boundary</td>
<td>$\pm T_h = \pm 38^\circ C$</td>
</tr>
<tr>
<td>Temperature at other boundaries</td>
<td>$0^\circ C$</td>
</tr>
<tr>
<td>Thermal conductivity of tissue</td>
<td>$k = 0.3 \text{ W m}^{-1}\text{ C}^{-1}$</td>
</tr>
<tr>
<td>Mass density of tissue</td>
<td>$\rho = 10^3 \text{ kg m}^{-3}$</td>
</tr>
<tr>
<td>Heat capacity of tissue</td>
<td>$c = 3 \times 10^3 \text{ J kg}^{-1} \text{ C}^{-1}$</td>
</tr>
</tbody>
</table>
Fig. 10: Time-dependent numerical solution for tissue heating at instants spanning ten seconds of the simulation, illustrating progressive heating of underlying tissues. The dashed black lines indicate the approximate range of depths of the epidermis-dermis interface, $1 \leq \Delta t \leq 3$ mm.

5.1 Predicting internal tissue temperatures associated with the responses

We first analyzed results of the time-dependent numerical solutions $T(x, y, t; \Delta T)$ of the heat equation, which were based on thermal grill boundary conditions matching each grill temperature difference, $\Delta T - T_h - T_c$, used in the experiment (see Figure 10).

To determine the tissue state at the time participants responded to the thermal grill, we evaluated the numerically-determined tissue temperature distribution at thermoreceptor depths, and at the response time $t_R(\Delta T)$ predicted by our fit to the ensemble of experimental data. The thermoreceptor depths, from 1 to 3 mm, corresponded to the nominal range of thermoreceptive afferents in glabrous skin, below the epidermal strata (corneum, lucidium, granulosum, spinosum, basale) [26], [36]. The corresponding values of $\Delta T$ and $t_R(\Delta T)$ were obtained from the behavioral data, as reported in Table 3.

We inferred the internal tissue state by evaluating the simulation at the respective response time $t_R(\Delta T)$, yielding values $T(x, y_T, t_R; \Delta T)$, as shown in Figure 11. The values increase in magnitude with temperature difference, $\Delta T$, despite the much shorter heating time $t_R$ associated with highest values of $\Delta T$ (Figure 11). This was true for all seven values of $\Delta T$, and four different depths $y_T$, and seemed to mirror the increase in perceptual intensity of TGI stimuli, which occurred even when the heating time was short. Variations in temperature with position $x$ were slower at greater depths, due to the smoothing effect of thermal diffusion.

5.2 Relating temperature gradients to perception

The magnitude of the internal temperature variations increased until the time of response, at which the hand was withdrawn. In view of the observed increase in TGI intensity with temperature differences, we hypothesized that intensity increased monotonically with the magnitude of internal temperature differences. The latter could be sensed through the integration of inputs from adjacent thermoreceptors arranged along the grill direction. We measured temperature differences via the magnitude of the time-dependent

![Fig. 11: Simulated temperatures $T(x, y_T, t_R; \Delta T)$ as a function of displacement $x$ along the direction of the thermal grill, at different tissue depths $y_T$, associated with those of thermoreceptive afferents. Each curve represents a prediction of the simulation at the mean time, $t_R$, that participants responded to stimuli with temperature difference $\Delta T$ (range 8 to 26 °C). Temperatures are expressed relative to pre-stimulation ambient temperature, $T_A$, in the tissue. Corresponding temperature difference and response time values are shown in Table 3.](image-url)
internal tissue temperature rate of change, \(G(x, y, t; \Delta T)\), along the grill direction, where
\[
G(x, y, t; \Delta T) = \frac{\partial T(x, y, t; \Delta T)}{\partial x}.
\]

The maximum value of this gradient at the effective depth \(y_T\) of the thermoreceptors is attained for positions \(x_d = ma\) (where \(m = 1, 2, 3, 4\), which lie below the grill boundary; see Figure 8. At the response time \(t_R\), we hypothesized that the perceived TGI intensity is determined by the value of the temperature gradient magnitude, \(G(x_d, y_T; t_R; \Delta T)\), at time \(t_R\). Since perceived intensity \(I(\Delta T)\) was rated in an interval from 0 to 1, we modeled the relationship between intensity and temperature gradient via a saturation function, \(\sigma(z)\), such that \(0 \leq \sigma(G) \leq 1\). The prediction for the perceived intensity, \(I(\Delta T)\), is thus
\[
I(\Delta T) = \sigma(G(x_d, y_T; t_R; \Delta T)).
\]

For fixed \(t_R > 0\), the value of \(\sigma(G)\) increases with temperature difference, and for fixed temperature difference, it increases in magnitude with time \(t_R\). We evaluated the proposed relationship using data from the behavioral experiment. We took the saturating function, \(\sigma(z)\), to be of sigmoidal form, \(\sigma(z) = c_1/(c_2 + \exp(-c_3 z))\), and fit the parameters to the experimental data. The results (Figure 12) qualitatively matched our predictions. The model yielded an \(R^2\) value of 0.89, indicating that it explains a large proportion of the variability in the response data.

Although this model is simplified, the results suggests that accounting for the dynamics of internal tissue heating can provide insight into TGI perception.

<table>
<thead>
<tr>
<th>Temperature Difference (\Delta T), °C</th>
<th>Response time (t_R(\Delta T)), s</th>
</tr>
</thead>
<tbody>
<tr>
<td>8</td>
<td>10</td>
</tr>
<tr>
<td>11</td>
<td>9.5</td>
</tr>
<tr>
<td>14</td>
<td>8</td>
</tr>
<tr>
<td>17</td>
<td>4.5</td>
</tr>
<tr>
<td>20</td>
<td>4.2</td>
</tr>
<tr>
<td>23</td>
<td>3</td>
</tr>
<tr>
<td>26</td>
<td>1.5</td>
</tr>
</tbody>
</table>

TABLE 3: Temperature differences and response times, estimated from the ensemble of experiment results (Figure 3), as used in the comparison with model predictions. In modeling the relationship between internal temperatures and perceived intensity (Figure 12), the numerical solution for \(T(x, y, t; \Delta T)\) was evaluated for each \(\Delta T\) shown at the response time \(t_R(\Delta T)\) listed in the table.

### 6 Discussion

The perception experiment demonstrated that response times varied inversely with the temperature differences. They were consistently long for the lowest temperature differences studied: Below about 20°C, the vast majority of responses took longer than three seconds. At the highest temperature differences (23 to 26°C), response times were almost always short, generally between 300 ms and 2.5 s. Participants feeling these stimuli responded rapidly, removing their hands soon after first touching the display. Furthermore, the short response times stand out when compared with the relatively large propagation times associated with C fiber afferents. The latter have low neural conduction speeds of less than about 2 m/s, which implies that there is a minimum delay time on the order of 500 ms before a signal from a thermosensitive C-fiber afferent could be integrated with input from nearby afferents. This is too slow to account for the fast response times in our experiment. In contrast, conduction speeds for Aδ afferents are faster, up to 30 m/s.

The difference in conduction speeds between these pathways may be relevant to understanding the dynamics of perception in the thermal grill illusion because, according to currently accepted explanations, the illusion arises due to a reduction of normal discharge in cold-sensitive Aδ afferents, which are suppressed due to spatial summation of inputs from warmer skin regions. Aδ discharge is thought to have a disinhibiting effect on polymodal C-nociceptive fibers, preventing them from signaling pain in response to cool stimuli. In view of this, the rapid responses elicited by the TGI suggest that first order Aδ fibers may play a gating role. Signals from these afferents are first to reach the central nervous system. Once there, they can disinhibit C-fiber activity, yielding TGI sensations.

An interesting corollary is that temporal and spatial integration may be inextricably linked. Plausibly, because of the slow propagation speed of C-fiber afferents, input from Aδ afferents will arrive at the central nervous system simultaneous with C-fiber afferent activity elicited by an earlier peripheral stimulus, as much as one second earlier. This suggests that the TGI involves a neural integration across a relatively long period of time, in addition to the spatial integration to which it is more often attributed.
7 CONCLUSIONS

In this study, we investigated the perception of the thermal grill illusion by developing a mathematical model of tissue heating, designing a new thermal display, and conducting a psychophysical experiment. We assessed the intensity of responses elicited by TGI stimuli, and measured associated response times. The responses were highly stereotyped. As the temperature difference increases, the intensity increases monotonically, while the response time decreases monotonically. A comparison of the psychophysical results with a model of tissue heating suggests that internal tissue temperature may predict perceived intensity. Under currently accepted explanations, the thermal grill illusion depends on tissue heating, neural processing, and the spatial distribution of thermal stimuli. Existing models do not account for internal temperatures of tissues, and the results of this study could help to inform models accounting for these factors.

However, findings from recent studies of the TGI suggest that this explanation may be oversimplified. TGI-like effects have been demonstrated to be elicited by stimuli in which heating and cooling are applied to skin regions that are not necessarily adjacent [17], [18], [19], including the distal ends of adjacent fingers, and that the effect can also be modulated by body posture. In view of these findings, the temperature-gradient-dependence proposed in our model could be viewed as a proxy for temperature differences between tissue regions that need not be adjacent, and that could be calculated at later stages of neural processing. Further research is thus needed in order to clarify the thermal and neural mechanisms underlying the thermal grill illusion.

Despite the intriguing findings of this research, there are several areas in which this study could be improved. In the perception experiment, we assumed an upper bound of 10 seconds on the response times, and imposed this on the results in order to ensure that the experiment terminated in a reasonable amount of time. However, at the lowest temperature differences, it is likely that, for some subjects, no TGI percept was felt.

Our analysis of the relation between tissue heating and perceptual responses was based on a physical model of heat transfer. It suggests that the magnitude and time course of internal tissue heating is significant for understanding responses to the thermal grill illusion. However, this model includes a number of simplifications. A more detailed model of neural transduction, propagation, and integration, as well as thermal processes including blood perfusion and internal heating is needed, and could lead to an improved computational model of the TGI, and possibly of thermal perception. We hope to address this in future work.

The thermal grill illusion is an evocative example of sensory integration, from ambient physics to the nervous system. It is also an interesting example of fast perceptual processing of thermal stimuli. A greater understanding of these phenomena could inform future thermal displays with better performance and wider applications than are currently envisaged.

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Yon Visell received the PhD Degree in Electrical and Computer Engineering from McGill University (2011), and MA and BA degrees in Physics (Univ. Texas-Austin, Wesleyan Univ.). Since 2015, he is Assistant Professor of Media Arts and Technology, Electrical and Computer Engineering, and Mechanical Engineering (by courtesy) at the University of California, Santa Barbara, where he directs the RE Touch Lab. Assistant Professor (2012-2015) in the ECE Department at Drexel University. Post-Doctoral Fellow (2011-2012) at the Inst. of Intelligent Systems and Robotics, Universite Pierre et Marie Curie. He has been employed in industrial R&D for sonar, speech recognition, and music DSP at several high-technology companies. His research interests include haptic perception, haptic engineering, and robotics.