

Coolness both underlies and protects against the painfulness of the thermal grill illusion



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ABSTRACT

We investigated the contributions of warm and cool signals in generating the thermal grill illusion (TGI), a phenomenon in which interlaced warm and cool bars generate an experience of burning, and under some conditions painful, heat. Each subject underwent 3 runs, 2 of which tested the effects of preadapting subjects to the grill's warm or cool bars (while the interlaced bars were thermally neutral) on the subsequent intensity of the illusion. In a control run, all bars were neutral during the adaptation phase. Thermal visual analogue scale ratings during the warm and cool adaptation periods revealed significant and equivalent adaptation to the 2 temperatures. Adaptation to the grill's cool bars significantly reduced pain and perceived thermal intensity of the TGI, compared to the control condition, while adaptation to the grill's warm bars had little effect. These results suggest that the cool stimulus triggers the pain signals that produce the illusion. The inability of warm adaptation to attenuate the TGI is at odds with theories suggesting that the illusion depends upon a simple addition of warm and cool signals. While the grill's cool bars are necessary for the TGI's painfulness, we also observed that the more often a participant reported feeling coolness or coldness, the less pain he or she experienced from the TGI. These results are consistent with research showing that cool temperatures generate activity in both thermoreceptive-specific, pain-inhibitory neurons and nociceptive dorsal horn neurons.

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1. Introduction

The thermal grill illusion (TGI) is generated by pairing warm and cool. Combining mild warm and cool often produces an experience of innocuous heat [1,11–13]; but, as the temperatures are made more extreme (albeit still innocuous), the illusion becomes painfully hot to most individuals [3,7,9,16–18]. Although the illusion was discovered by Thunberg over a century ago [21], there is still no consensus on how it is coded.

Two different theoretical perspectives characterize modern thinking about the TGI. According to Craig and Bushnell [7], the grill's cool bars stimulate both A δ cool and C nociceptive afferents, which send signals to thermoreceptive-specific (COOL) and heat-pinch-cold (HPC) second-order neurons in the dorsal horn, respectively. Normally, the first of these signals masks the second [10,22]. However, single-cell recordings in cat dorsal horn showed

that interlaced warm bars selectively reduced the firing of COOL neurons [7]. Thus, they proposed that the TGI is due to a disinhibition of HPC nociceptive signals via warmth's inhibition of pain-inhibitory COOL signals.

In contrast, some psychophysical results suggest that the interaction between the grill's warm and cool stimuli might be additive. Green [12] showed that the intensity of the TGI is similar to the sum of the perceived intensities of the warm and cool component temperatures. Bouhassira and colleagues [3] later found that, for a given cool temperature, the illusion increases if the warm bars are made warmer. This could be explained by increased inhibition of COOL neurons at warmer temperatures. However, they also found that, for a given warm temperature, the illusion increases if the cool temperature is decreased. Since the rates of both COOL and HPC neurons increase similarly throughout the range of temperatures employed [8], the disinhibition theory appears to be at odds with this result. Instead, the symmetrical result of increasing the TGI by making either of the 2 temperatures more extreme suggests that warm and cool signals might be adding to one another to produce the illusion.

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The current study utilized thermal adaptation to disentangle the relative contributions of warm and cool in generating the TGI. The addition theory states that the strengths of the warm and the cool signals are equally important for the illusion [3,12]; thus, it predicts similar reductions in the TGI following adaptation to either temperature. The disinhibition theory predicts different results following warm or cool adaptation. Since warmth is thought to inhibit cool signals and unmask an underlying nociceptive signal [7,9], adaptation to warmth should reduce the illusion by reducing the inhibition on COOL neurons. Since both COOL and HPC neurons respond to the cool bars of the grill, cool adaptation should fatigue both neuronal populations. Furthermore, the cool adapting stimulus will excite COOL neurons more than HPC neurons [8] and may therefore adapt them to a greater extent. Thus, based on the disinhibition theory, adaptation to cool could be expected to either have no effect or to slightly increase the illusion since the pain-inhibitory cool signals should be dampened at least as much as the pain-excitatory nociceptive signals.

2. Methods

2.1. Participants

Twenty-six undergraduate students participated in the study. Recruiting was carried out through the University of North Carolina Psychology Department's participant pool Web site. Age of participants ranged from 18 to 23 years ($M = 20.5$; $SD = 1.9$). The study was approved by the University's institutional review board and written informed consent was obtained. Participants were compensated with research participation credit for an Introductory Psychology course for their participation.

2.2. Experimental design

Each subject participated in 3 separate runs. Each run consisted of a 3-minute adaptation phase, followed by a test phase. The test phase was identical in all 3 runs, with interlaced warm (42°C) and cool (18°C) bars, but the adaptation phase differed across runs. During the *cool adaptation run*, half of the bars were at the cool temperature (18°C) that was later used to produce the TGI, while the interlaced bars were held at a neutral temperature (32°C). The *warm adaptation run* consisted of warm bars (42°C) interlaced with neutral bars (32°C). Following the adaptation period in each of these runs, the neutral bars were heated or cooled to produce the test stimulus (ie, 18°C bars interlaced with 42°C bars). Each subject also participated in a neutral adaptation run; in this case, all of the bars were held at 32°C during the adapting period. It should be noted that the subject's forearm remained in place throughout the run, so that the adapted regions of skin were still positioned over bars of the adapting temperature during testing of the TGI. The order of runs was counterbalanced across subjects (Fig. 1).

2.3. Apparatus

2.3.1. Thermal grill

The thermal grill apparatus consisted of 12 pieces of copper tubing (length 33 cm; diameter 1 cm; thickness 0.4 mm) that were secured onto the top of a plastic holder (Fig. 2). Each bar rested in a trough (1.25 cm wide and 0.5 cm deep) and was separated from its neighbor(s) by 0.5 cm. In order to gain thermal control over the bars, 2 sets of plastic tubing through which water could be circulated were connected to the ends of the bars. Set 1 was comprised of the odd-numbered bars and Set 2 the even-numbered bars. The 2 sets of bars also had separate intake tubes that were connected to

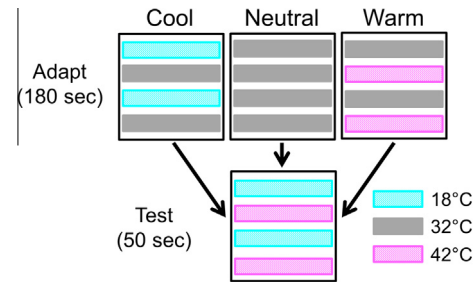


Fig. 1. Experimental design. Each run, including cool adaptation, warm adaptation, and neutral adaptation, consisted of a 3-minute adaptation phase (Adapt) followed by a 50-second presentation of the thermal grill illusion (Test) stimulus. The subject rated perceived thermal intensity throughout the adaptation phase and for the first 30 seconds of the test phase. Then, following a 5-second countdown, the subject rated the painfulness of the TGI for 15 seconds.

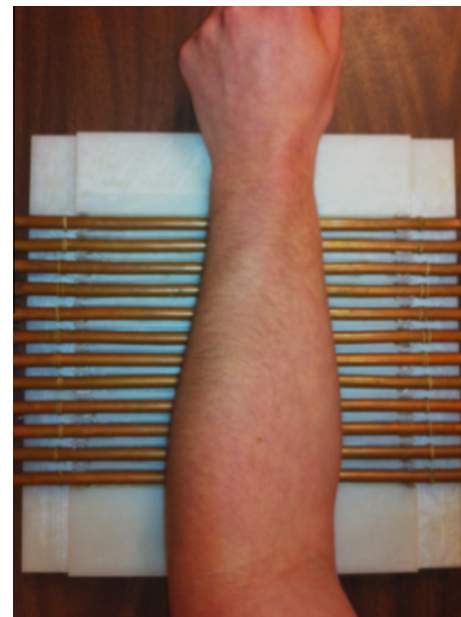


Fig. 2. Thermal grill. The subject placed his or her left forearm of the grill, as shown. See text for a detailed description of the apparatus.

bars 1 and 2. Each intake was connected to a thermally insulated 19-L tank that was positioned on a shelf 0.65 m above the tabletop. Each set of tubes had an outtake that passed water into a receptacle on the floor. Two thermistor probes (YSI 400 series) were used to record bar temperatures during experiments. They were attached to small sections of copper tubing that were inserted into the flow lines, near the grill.

Based on preliminary testing, we determined warm and cool temperatures that produced a moderately intense TGI but were not perceived to be painful on their own. These bar temperatures were 42°C and 18°C .

In a calibration, we made repeated measurements in one individual of the skin-thermode interface temperatures produced by these bar-surface temperatures. These tests used a K/J Thermometer (421502; Extech Instruments Corp., Nashua, NH, USA), with a K-type bead thermocouple (TP870; Extech Instruments Corp.). The thermocouple was positioned (over a thin layer of epoxy) on a copper bar that was inserted in the apparatus in place of the fourth bar of the grill. The skin of the volar forearm rested on the apparatus and the temperature was allowed to stabilize. These measurements revealed that the skin-thermode interface temperatures

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