IEEE Access
Multidisciplinary ⋮ Rapid Review ⋮ Open Access Journal

Received 26 January 2024, accepted 4 April 2024, date of publication 22 April 2024, date of current version 7 May 2024.

Digital Object Identifier 10.1109/ACCESS.2024.3392276

RESEARCH ARTICLE

Extrapolation of Thermal Sensation: Warm–Cold Stimulus Pair Elicits a Sense of Warmth Outside the Stimulus

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This research was supported by the Japan Society for the Promotion of Science (JSPS) KAKENHI Grant-in-Aid for Scientific Research (A) Grant Number JP19H01121.

This work involved human subjects or animals in its research. Approval of all ethical and experimental procedures and protocols was granted by the Research Ethics Committee of Osaka University.

ABSTRACT Touching a warm stimulator with the base of the finger and a cold stimulator with the middle of the finger causes a sense of warmth at the fingertip outside the cold stimulator, revealing Extrapolation of Thermal Sensation (ETS). Although the ETS shares similarities with the Thermal Grill Illusion (TGI) regarding spatial thermal integration, the spatial distributions of the sensations are different. The TGI is limited to the inside boundaries that envelope physical stimuli, whereas the ETS crosses the boundaries. Although TGI is reproduced accompanied by overestimation of the cold stimulus, which is influenced by the spinal segmental distance between warm and cold stimuli, it remains to be seen whether ETS carries out the same. The study investigated the ETS and TGI using simultaneous warm, cold, and neutral stimulation of the fingers or lower leg. To show the difference between the ETS and TGI, we manipulated the segmental distance between warm and cold stimuli and observed the resulting perceived temperatures of the neutral and cold stimulators. The perceived temperatures of the ETS and TGI varied in units of segmental distance. However, the ETS was not reproduced where the TGI was. Thus, we conclude that the mechanism of the ETS is different from that of the TGI. The experimental results suggest that a non-uniform intersegmental connection contributes to the lower reproducibility of ETS on the lower leg.

INDEX TERMS Extrapolation of thermal sensation, thermal grill illusion, thermal referral.

I. INTRODUCTION

Spatially continuous thermal perception is integrated from spatially discrete thermal sensation. For example, free nerve endings, which function as thermoreceptors that code changes in temperature on the skin surface, can be observed as warm and cold spots with almost no overlap [1], [2]. The responses of the thermoreceptors ascend to the spinal cord, where the dorsal root ganglion cells form a discrete structure called the spinal segment in the dorsal root, which further forms the dermatome of the skin [3]. Thus, while spatial discreteness is maintained during the ascent from the periphery, the thalamus and somatosensory cortex above the spinal cord reproduce the spatial continuity of the stimulus, which is consistent with the site of the body [4]. This neurophysiological finding indicates that the thermal sensation is a spatially continuous perceptual phenomenon based on spatially discrete observations.

A sense of warmth has been reported to arise between spatially discrete warm stimuli, known as Thermal Referral (TR) [6], [7], [8], [9], [10], [11], [12], [13], [14] (Fig.1 a). Additionally, the Thermal Grill Illusion (TGI) is a phenomenon in which multiple pairs of spatially distributed warm and cold stimuli induce a burning sensation or pain [5],

The associate editor coordinating the review of this manuscript and approving it for publication was Okyay Kaynak.

[15], [16], [17], [18], [19], [20], [21], [22], [23], [24], [25], [26] and the spatial gradient of the thermal stimuli is not perceptually reproduced. From this perspective, TR and TGI are spatially interpolated phenomena of thermal sensation. Furthermore, using a warm-cold stimulus pair, Fardo found that cold stimulation reproduced an overestimation as if it were a more neutral stimulus [27] (Fig.1 b). The overestimation of cold stimuli is dependent on the spatial spacing of the warm-cold stimulus pair and contributes to the units of the dermatome. That is, the mechanism underlying the spatial interpolation of thermal sensations is structured in dermatomes [27]. However, the spatial extrapolation of thermal sensation needs to be studied further and has not been observed in dermatomes.

The fact that a spatially continuous thermal sensation arises from spatially discrete warm and cold points can be understood as a thermal sensation mechanism that solves the estimation problem of deriving spatially continuous quantities from spatially discrete observations. From an analytical point of view, the thermal sensation mechanism also relies on an equivalent basis decomposition mechanism, just as many continuous signals are represented by the superposition principle of basis functions via orthogonal transformations. Similar to the Fourier transform, which is an orthogonal transform, also has sine and cosine functions as basis functions, which ensure perfect reproducibility of signals by means of even and odd function pairs. Assuming that the aforementioned ''interpolation'' phenomenon of thermal sensation establishes a spatially uniform perception, that is, the role is even-functional as the default function that converts temperature stimuli into perception, then the default function that establishes a spatially uniform thermal sensation is an unknown odd function. If the Extrapolation of Thermal Sensation (ETS) can be understood as the role of this unknown odd function, then it is predicted that the ETS will become a pair of TGI phenomena, providing mathematical completeness to the thermal sensation mechanism.

In this study, we focus on previously discovered ETS [28], [29]. We compare ETS with TGI by observing the resulting sensation at the bodily location of the stimulus using a pair of simultaneous warm, cold, and neutral stimuli. We investigate the ETS mechanism by comparing it with TGI and investigate whether ETS has the same segmental effect on the fingers and lower leg. Animal testings have shown that in the C7 segment, corresponding to the hand, nerve fibers rapidly decrease beyond one to two segments from their originating nerve root [30]. In contrast, in the lumbosacral segments, the distribution of nerve fibers may remain relatively uniform [30]. Considering the varying strengths of lateral connections across spinal segments, we focus on the fingers and lower leg as target locations for stimulation.

Warm and cold stimuli are considered to be integrated across the nearest one to two spinal segments through short-range intersegmental connections known as the Lissauer tract. Studies have observed this spatial thermal integration in the upper arm and lower back [27]. However,

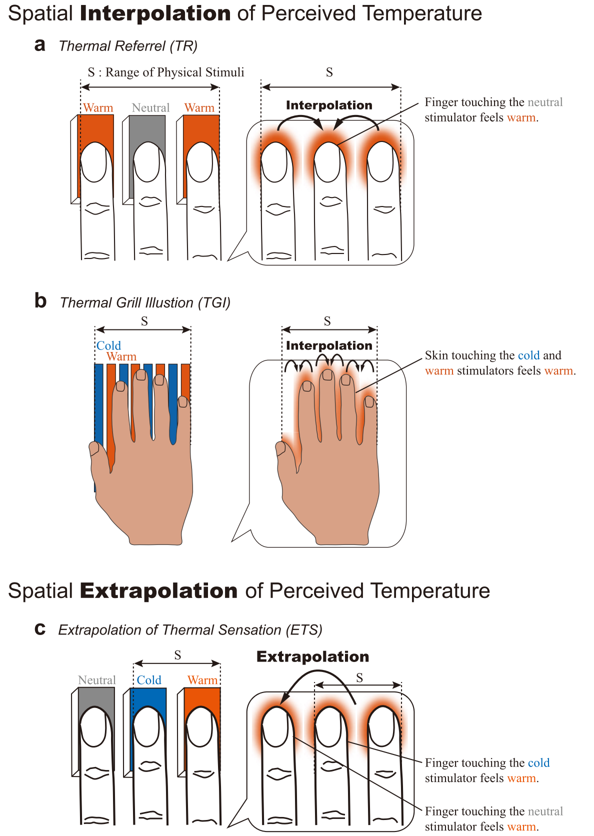

FIGURE 1. Schematic representations of thermal illusions. (a) Thermal Referral (TR). (b) Thermal Grill Illusion (TGI). Dotted lines represent boundaries that envelop physical stimuli. Thermal illusions such as TR and TGI have a common characteristic. That is, the sensation is limited inside the boundaries that envelop physical stimuli. (c) Extrapolation of Thermal Sensation (ETS). A sense of warmth at the index finger is perceived when the ring finger touches a warm stimulator, and the middle finger touches a cold stimulator. ETS is a phenomenon that crosses physical boundaries.

there is limited research on how the Lissauer tract influences the strength of lateral connections, particularly in terms of the density of connections to second-order neurons in the neighboring spinal segments. This study describes the role of these lateral connections in thermal integration, based on the findings of previous research [27]. Moreover, this study explores the effect of the Lissauer tract on the lateral connection strength and density of connections to second-order neurons in neighboring segments. Therefore, we elucidate the role of lateral connections in thermal integration, thereby advancing our understanding of sensory perception mechanisms based on prior research [27].

II. MATERIALS AND METHODS

A. PARTICIPANTS

A total of 47 healthy volunteers participated in Experiment 1 (n = 13, all men), Experiment 2 (n = 13, 11 men), Experiment 3 (n = 4, all men), Experiment 4 (n = 13, all men), and Experiment 5 (n = 4, all men). All participants were aged between 23 and 30 and met the following exclusion criteria:

individuals experiencing pain and chronic diseases related to neurological, rheumatological, psychiatric, and cancer-related problems. Moreover, all participants self-reported as right-handed. The experimental procedures were approved by the Research Ethics Committee of Osaka University and were conducted in accordance with the guidelines outlined in the Declaration of Helsinki.

B. EXPERIMENT 1

First, we confirmed that ETS varied in units of segmental distance. This phenomenon was initially reported based on the reproducibility of the sense of warmth, which did not quantify the perceived temperature resulting from ETS. To address these limitations, we adopted the adaptive staircase method to quantitatively assess the perceived temperature at the target location based on physical stimuli (temperature) applied to neighboring stimulation sites on the skin. Our methodology was based on a factorial within-subjects design that involved the following:

1) TEMPERATURE COMBINATION

The "control" condition had all three stimulators set to 30°C, while in the "ETS" condition, the warm, cold, and neutral stimulators were set to 42°C, 18°C, and 30°C, respectively.

2) SEGMENTAL DISTANCE

We varied the placement of the warm and cold stimulators, within the same dermatome, across adjacent dermatomes, or across nonadjacent dermatomes, denoted as $D_{sg} = 0$, $D_{sg} = 1$ and $D_{sg} = 2$, respectively.

3) ARRANGEMENT

The neutral stimulator was alternately placed on the fingertip or base of the finger.

To investigate the segmental hypothesis, we varied the spatial arrangement of the three stimulators to apply thermal stimuli within the same dermatome or across different dermatomes. This approach is based on Keegan's work, which is known for clearly defining the dermatomal boundaries [32], [33], [34]. The detailed layout of the dermatomes is depicted in Fig. 2a. Specifically, the C6 and C8 dermatomes correspond to the areas of the hand near the thumb and little finger, respectively. The C6 dermatome primarily covers the thumb (D1), whereas C7 encompasses the central part of the hand, including the index (D2) and middle fingers (D3). The C8 dermatome extends over areas corresponding to the ring (D4) and little fingers (D5). In our experiment, we placed the cold and neutral stimulators in the same dermatome.

We precisely defined the placement of the Peltier modules at three distinct locations on the finger: the base of the finger (just below the proximal phalanges), middle of the finger (just below the middle phalanges), and fingertip (just below the distal phalanges). To ensure accuracy, the edge of each Peltier module was aligned with the corresponding crease. The finger posture was determined by the participants. Therefore, the spatial arrangement of the Peltier modules was not controlled, except for the alignment of the edges of the Peltier modules with the creases. We conducted experiments under four arrangement conditions for $D_{sg} = 0$ and $D_{sg} = 1$. Additionally, in the $D_{sg} = 2$ condition, two arrangement conditions were explored, as illustrated in Fig.2 b-d.

To further validate earlier research on TGI [27], we examined how the participants perceived the temperature of the cold stimulator. Our study adopted a factorial within-subject design comprising the following:

4) TEMPERATURE COMBINATION

"TGI," in which the warm, cold, and neutral stimulators were 42°C, 18°C, and 30°C, respectively. The target location was a cold stimulator.

5) SEGMENTAL DISTANCE

We placed warm and cold stimulators in various arrangements, within the same dermatome, across adjacent dermatomes, and across nonadjacent dermatomes.

The cold stimulator was tested under b1, c1, and d1 conditions (Fig.2 b-d) (1 temperature combination × 3 segmental distances) to investigate the TGI effect.

Each participant underwent testing over four days. On one day, ETS was evaluated across all conditions, with a repeat assessment on another day. This protocol was also used to examine the TGI effect. The conditions were tested in random order. Each staircase consisted of 15 trials, starting with a 30°C stimulus on the corresponding target location of the left hand. The temperature of the first step was 3°C, which decreased to 2°C after the first reversal point. After the third reversal point, the step size was set at 1°C. The average of the last four reversal points for each staircase was used to determine the perceived temperature of the target location. To avoid painful sensations, the highest and lowest temperatures did not exceed 45°C and 15°C, respectively. The experiment was conducted in a room with a constant temperature of 25°C. Before beginning, participants placed their hands on a hot plate. At the sound cue, participants removed their hands and simultaneously touched the three stimulators with each hand for 5 s. Following another cue, they compared the temperature of the target locations on both hands and reported whether the target location on the right hand was warmer than that on the left hand. To study the segmental effects of the ETS and TGI, each condition involved two staircases, totaling 46 staircases.

C. EXPERIMENT 2

In Experiment 1, we confirmed that ETS varied in units of segmental distance. However, this did not rule out the possible role of physical distance in ETS. Thus, we investigated ETS under a controlled inter-stimulus distance. This procedure was based on the method described in Experiment 1. Three stimulators were taped and each was applied to the same hand. Thus, the two adjacent stimulators were each 20 mm wide because of the width of the water tank for each

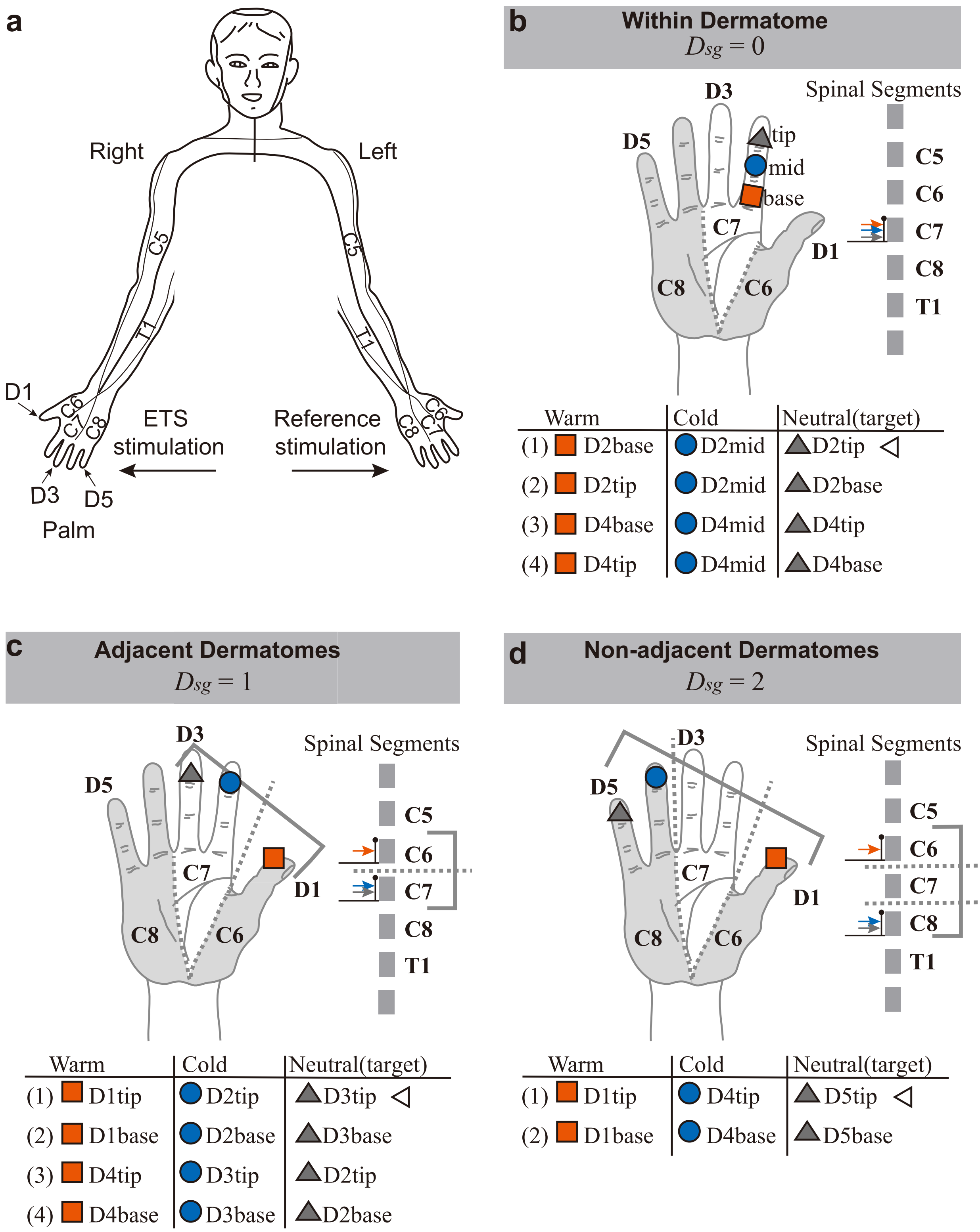

FIGURE 2. Experimental conditions in Experiment 1. (a) Dermatomes are sketched based on the work of Keegan and Garrett [32]. Using the adaptive staircase method, participants compared the thermal sensation of the skin area touching the neutral stimulator of the right hand (the target location) with that of the left hand. (b) Warm (red square) and cold (blue circle) stimulators were within the same dermatome ($D_{sg} = 0$). (c) Warm and cold stimulators were across the two adjacent dermatomes ($D_{sg} = 1$). (d) Warm and cold stimulators were across non-adjacent dermatomes ($D_{sg} = 2$). The neutral (gray triangle) and cold stimulators were kept within the same dermatome in all conditions. Only combinations with the ◁ mark are depicted in the figure.

stimulator. We followed a 4 × 2 full-factorial within-subjects design.

1) TEMPERATURE COMBINATION

"control," in which the three stimulators were 30°C; "warm," in which the temperature of the warm stimulator was raised from the baseline of 30°C to 42°C; "cold," in which the temperature of the cold stimulator was lower to 18°C; and "ETS," in which the warm, cold, and neutral stimulators were 42°C, 18°C, and 30°C, respectively.

2) SEGMENTAL DISTANCE

The $D_{sg} = 0$ and the $D_{sg} = 1$ conditions were tested. In the $D_{sg} = 0$ condition, warm, cold, and neutral stimulators were applied to the fingertip, middle, and base of D2, respectively. In the $D_{sg} = 1$ condition, three stimulators were applied to D4, D3, and D2 bases. During the experiment, a neutral stimulator was maintained at the base of D2.

Eight conditions (4 temperature combinations × 2 segmental distances) were applied in a random order. Each condition involved two staircases. Therefore, only 16 staircases are included in this study.

D. EXPERIMENT 3

In Experiment 2, we quantified the perceived temperature of the neutral area resulting from ETS on the fingers. In Experiment 3, we aimed to confirm the spatial characteristics of the sensation resulting from ETS by examining the perceptual distribution on the fingers. Considering that the sensation induced by ETS was nonverbal, we instructed the participants to sketch their thermal sensations. They sketched the sensation on the palm side from the top and two sides.

The $D_{sg} = 0$ and the $D_{sg} = 1$ conditions were tested in Experiment 3. In the $D_{sg} = 0$ condition, a warm-cold-neutral stimulus pair was applied to the fingertip, middle, and base of D2, respectively (Fig.2 b2). In the $D_{sg} = 1$ condition, three stimulators were applied to bases of D4, D3, and D2 (Fig.2 c4). Under both conditions, a neutral stimulator was held at the base of D2. The touching edge of the Peltier module was aligned with the corresponding crease. The stimulus presentation time was 15 s to ensure that the participants could obtain the perceptual distribution of all five fingers. The participants were instructed to draw the shape and field of the warm, cold, and neutral sensations using red, blue, and gray circles, respectively. Overlapping of circles was allowed to account for the possible overlap of sensations. Circles outside the body were also allowed as the boundaries of sensations may extend spatially beyond the body.

E. EXPERIMENT 4

In experiments 1-3, we investigated the perceptual characteristics of ETS on the fingers. In experiments 4 and 5, we explored these characteristics in the lower leg to investigate whether the segmental effect of ETS is independent of body parts. We followed a factorial within-subjects design.

1) TEMPERATURE COMBINATION

"control" and "ETS" conditions were tested.

2) SEGMENTAL DISTANCE

Based on the work of Keegan and Garrett [32], [33], [34], the stimulators were arranged in a way that allowed the delivery of two warm and cold stimuli either within the dermatome or across dermatomes.

3) ARRANGEMENT

The stimuli were applied to the anterior and posterior right lower leg.

The dermatomal boundary of the anterior lower leg descends from the medial femoral condyle above the knee to the medial malleolus (Fig.3 a). Within this anatomical region, the lateral portion is innervated by the L5 dermatome, whereas the medial portion receives sensory innervation from the L4 dermatome. $D_{sg} = 0$, $D_{sg} = 1$, and $D_{sg} = 2$ were tested. In the $D_{sg} = 0$ condition, the stimulus pair was applied vertically to the L4 dermatome. In the $D_{sg} = 1$ condition, the stimulus pair was applied horizontally, 10 cm below the patella, where the dermatomal boundary evenly divides the lower leg. Warm stimuli were applied to the L5 dermatome, whereas cold and neutral stimuli were applied to the L4 dermatome. In the $D_{sg} = 2$ condition, two adjacent stimulators were spaced 40 mm apart. Warm stimuli were applied to the S1 dermatome, whereas cold and neutral stimuli were applied to the L4 dermatome.

The dermatomal boundary of the posterior lower leg descends vertically from the middle gluteus maximus. The lateral part is the S1 dermatome and the medial part is the S2 dermatome. In the $D_{sg} = 0$ condition, the stimulus pair was applied vertically to the S1 dermatome. In the $D_{sg} = 1$ condition, the stimulus pair was applied horizontally, 10 cm below the knee. Warm stimuli were applied to the S2 dermatome, whereas cold and neutral stimuli were applied to the S1 dermatome. In the $D_{sg} = 2$ condition, two adjacent stimulators were spaced 40 mm apart. Warm stimuli were applied to the L4 dermatome, whereas cold and neutral stimuli were applied to the S1 dermatome.

The location of the neutral stimuli was maintained under $D_{sg} = 0$ and $D_{sg} = 1$ conditions. Eight conditions (2 temperature combinations × 2 segmental distances × 2 arrangements) were tested.

Moreover, the perceived temperature of a cold stimulator was tested to verify the segmental effect of TGI on the lower leg. We followed a factorial within-subjects design.

4) TEMPERATURE COMBINATION

"TGI," in which the warm, cold, and neutral stimulators were 42°C, 18°C, and 30°C, respectively. The target location was the cold stimulator.

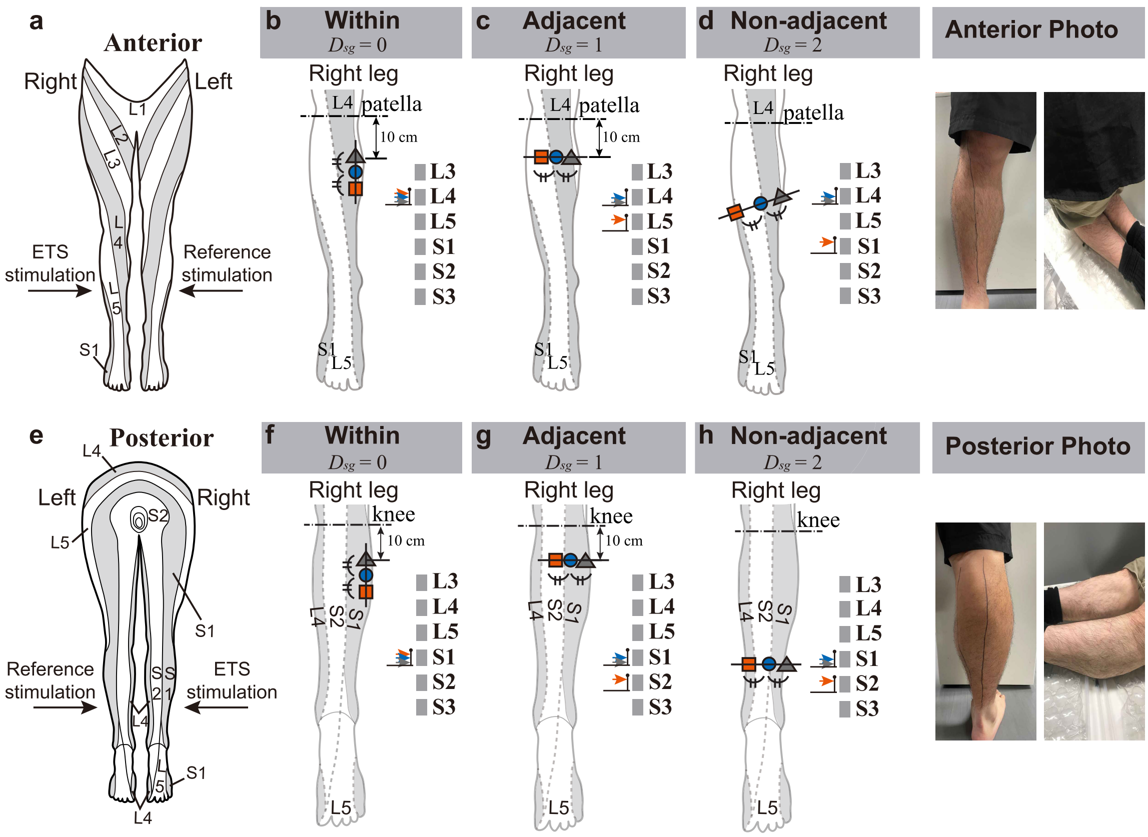

FIGURE 3. Experimental conditions in Experiment 4. Dermatomes are sketched based on the work of Keegan and Garrett [32]. The generation of ETS was investigated at both the anterior and posterior lower leg, while the physical distance between every two adjacent stimulators was equidistant. (b-d) Warm (red square) and cold (blue circle) stimulators were applied to the anterior lower leg. (f-h) Warm and cold stimulators were applied to the posterior lower leg.

5) SEGMENTAL DISTANCE

Warm and cold stimulators were placed within the same dermatome or across adjacent dermatomes or across nonadjacent dermatomes.

6) ARRANGEMENT

The stimuli were applied to the anterior and posterior right lower leg.

Therefore, 6 conditions (1 temperature combination × 3 segmental distances × 2 arrangements) were randomly tested.

The procedure was the same as that for Experiment 1. Each participant underwent a four-day test. Using the adaptive staircase method, participants compared the thermal sensation of the skin area touching the neutral stimulator of the right leg (target location) with that of the left leg. Each condition involved two staircases. A total of 28 staircases were included.

F. EXPERIMENT 5

We further investigated the characteristics of the resulting ETS by examining the perceptual distribution in the posterior lower leg. The procedure was the same as that described in Experiment 3. $D_{sg} = 0$ and $D_{sg} = 1$ conditions were tested. The stimulus pair was applied vertically under the $D_{sg} = 0$ condition. The stimulus pair was applied to the S1 dermatome. Under the $D_{sg} = 1$ condition, warm stimuli were applied to the S2 dermatome, whereas cold and neutral stimuli were applied to the S1 dermatome.

G. APPARATUS AND DATA ANALYSIS

Six thermal units were used in this study. Each thermal unit had a Peltier module, heat sink, and water tank. To facilitate heat dissipation, we used a 25 mm × 15 mm × 15 mm heat sink that effectively conducted the heat generated by the 15 mm × 15 mm Peltier modules in a 30 mm × 20 mm × 12 mm water tank (see Fig. S1). The cooling surface area was 2400 mm^2. We used pumps to circulate water at a flow rate of 1 m/s to extract waste heat. A microcontroller (mbed NXP LPC1768, NXP Semiconductors Taiwan Ltd.) was used to send the control signals to the DC motor controllers to drive the Peltier modules. Additionally, the microcontroller reads signals from thermistors (103JT-025, ATC Semitic, Ltd.), which were affixed to the surface of the Peltier modules using copper foil tape. A hot plate

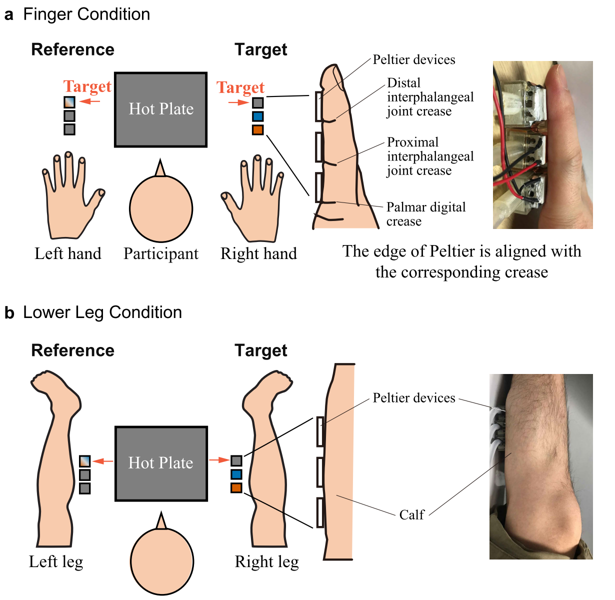

FIGURE 4. Study setup. We used the adaptive staircase method to measure the perceived temperature. In our setup, the right three Peltier modules were utilized for ETS stimulation, while the left three modules provided adaptive stimulation to match the two target locations. Throughout the experiment, participants touched the three Peltier modules with their right hand (leg) and another three modules with their left hand (leg). Participants touched the hot plate between each trial to regulate the skin temperature. We recorded their psychophysical responses for analysis.

(NHP-M30N, New Japan Chemical Co., Ltd.) was used to maintain the skin temperature to 30°C (Fig.4).

All analyses were performed using the R statistical software.

III. RESULTS

A. EXPERIMENT 1

In this study, we measured the perceived temperature of extrapolated skin area as a function of the thermal stimulation applied to other skin areas that varied thermally and spatially. Fig.5 illustrates the experimental results and corresponding conditions. The perceived temperatures at the same segmental distances were almost identical. Repeated-measures ANOVA revealed that the arrangement of stimulus pairs at the same segmental distance did not influence the perceived temperature. The perceived temperature in the $D_{sg} = 0$ condition was approximately 41°C, which was almost equal to the actual temperature of the warm stimulus. For every increase in segmental distance of 1, the perceived temperature decreased by approximately 5°C.

We performed a two-way repeated-measures ANOVA to investigate the thermal and segmental effects on ETS. The analysis indicated that the temperature combination had a significant effect on perceived temperature ($F(1, 12) = 53.00$, $p < 0.001$). This result shows that, ETS cannot be explained as a heat conduction phenomenon on the skin, providing evidence that ETS is an illusion caused by neural activity.

Additionally, the analysis indicated that segmental distance had a significant effect on the perceived temperature ($F(2, 24) = 44.69$, $p < 0.001$). A significant two-way interaction was observed between the temperature combination and segmental distance ($F(2, 24) = 48.14$, $p < 0.001$). For the $D_{sg} = 0$ and $D_{sg} = 1$ condition, the target location was perceived to be different from its perceived temperature in the control condition ($p < 0.001$ for the $D_{sg} = 0$ and $D_{sg} = 1$ conditions). In contrast, for $D_{sg} = 2$, no significant difference was found between ETS and control conditions ($p = 0.5$, n.s.). This result indicates that ETS on the fingers was induced within and across adjacent segments.

Moreover, we performed a one-way repeated-measures ANOVA to investigate the segmental effect on TGI. The analysis indicated that the segmental distance had a significant effect on the perceived temperature ($F(2, 24) = 102.88$, $p < 0.001$). Pairwise comparisons indicated that the perceived temperature in $D_{sg} = 2$ was significantly different from that in other conditions ($p < 0.001$). No significant difference was observed between the $D_{sg} = 0$ and $D_{sg} = 1$ condition ($p = 0.3$, n.s.). This analysis indicated that TGI was induced within and across adjacent segments. In summary, Experiment 1 showed that ETS and TGI on the fingers were induced within or across adjacent dermatomes.

B. EXPERIMENT 2

In Experiment 2, we investigated the ETS phenomenon while controlling for the interstimulus distance. Fig.6 illustrates the experimental results and the corresponding conditions. A repeated-measures ANOVA was performed with segmental distance and temperature combination as within-subject factors and perceived temperature as the dependent variable. The analysis indicated that the segmental distance and temperature combination significantly affected the perceived temperature ($F(1, 12) = 13.39$, $p < 0.001$ for segmental distance, and $F(3, 36) = 199.80$, $p < 0.001$ for temperature combination). There was a significant two-way interaction between segmental distance and temperature combination ($F(3, 36) = 3.30$, $p < 0.05$). Pairwise comparisons indicated that in the $D_{sg} = 0$ and $D_{sg} = 1$ conditions, there was a significant difference between ETS and other temperature combinations ($p < 0.001$ for ETS-warm, ETS-cold, and ETS-neutral combinations). In the ETS condition, there was a significant difference in perceived temperatures between the $D_{sg} = 0$ and $D_{sg} = 1$ conditions ($p < 0.001$). Therefore, we replicated the segmental effects of ETS in this experiment.

C. EXPERIMENT 3

In Experiment 3, we aimed to illustrate the perceptual distribution of the fingers. Fig.7 illustrates the experimental results and corresponding conditions. In the $D_{sg} = 0$ condition, warmth at D2 was not limited to the location of the neutral stimulator. The results for Participants 1 and 4 show that warmth was perceived in the air. Participant 4 reported that part of D1 was perceived as warm, demonstrating that warmth was induced in the dermatome, where there was no thermal

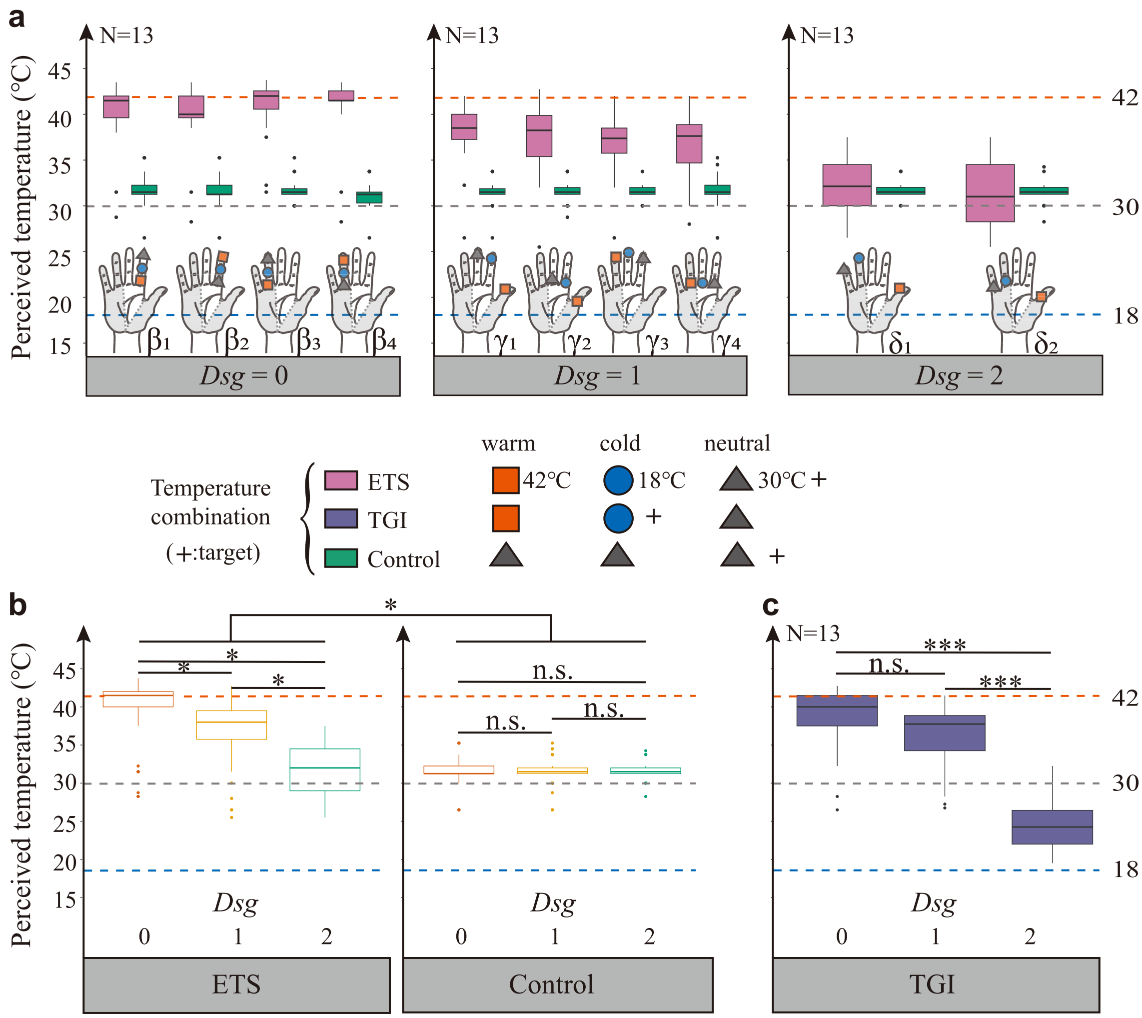

FIGURE 5. Results of Experiment 1. ETS and TGI were investigated on the fingers. + mark stands for the target location in each temperature combination condition. (a) Results of ETS. ETS varied in units of segmental distance. (b) Group mean of ETS under each segmental distance condition. (c) Results of TGI under each corresponding segmental distance condition. Both ETS and TGI on the fingers were induced within or across the adjacent dermatomes. n.s. $p > 0.05$; * $p < 0.05$; *** $p < 0.001$.

stimulus. In the $D_{sg} = 1$ condition, the warm area was larger than that in the $D_{sg} = 0$ condition. In general, we found that the resulting warmth was diffuse. Warmth was not limited to the skin surface. This can be extrapolated to the airy areas between the fingers. Generally, warmth was perceived in the dermatomes where warm and cold stimuli were applied. However, in some cases, a sense of warmth was perceived in adjacent dermatomes where no stimulus was applied. Participants sometimes volunteered comments about the sensation, such as "it feels like radiant heat," or "it feels warm, but I do not know where the heat is coming from." The sensation in air has also been reported in a study on the lateral inhibition of the sense of warmth, demonstrating that warmth can be perceived in the area between the fingers where no skin is exposed to thermal stimuli [35]. We initially observed that warmth could also occur in the air across the stimulus boundaries.

The sense of cold was only perceived in a limited area, specifically in the areas exposed to cold stimuli. There was no sensation of cold outside the skin. Perception was complex for the area subjected to cold stimuli and did not remain consistent within each participant. In the $D_{sg} = 0$ condition, a sense of warmth was frequently observed in the area exposed to cold stimuli (Participants 1, 2, and 4). On the other hand, in the $D_{sg} = 1$ condition, an overlap between the senses of warmth and cold appeared frequently (Participants 2 and 4). Such an overlap was observed with the cold or neutral stimulator rather than with the warm stimulator. This asymmetry suggests that warm stimuli play a dominant role in spatial-thermal integration. In addition, a side view of the thermal sensation showed that the resulting sensation was approximately axially symmetric to the finger.

D. EXPERIMENT 4

In Experiment 4, we investigated the segmental effects of the ETS on the lower leg. Fig.8 a illustrates the experimental results and corresponding conditions. A two-way repeated-measures ANOVA indicated that the temperature

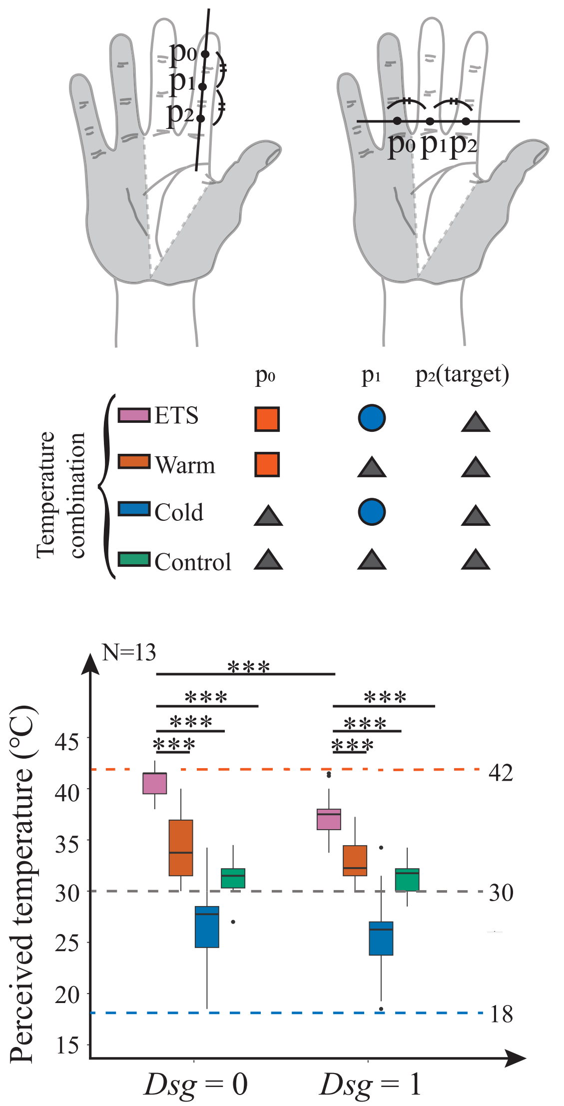

FIGURE 6. Results of Experiment 2. The generation of ETS was investigated under $D_{sg} = 0$ condition and $D_{sg} = 1$ condition while the physical distance between every two adjacent stimulators was 20 mm. The red squares, blue circles, and gray triangles represent the stimulus temperatures of 42°C, 18°C, and 30°C, respectively. We replicated the segmental effect of ETS in Experiment 1. *** p < 0.001.

combination and segmental distance had a significant effect on the perceived temperature of the neutral stimulator on the anterior lower leg ($F(1, 12) = 36.57$, $p < 0.001$ for temperature combination, and $F(1, 12) = 42.27$, $p < 0.001$ for segmental distance). A significant two-way interaction was observed between temperature combination and segmental distance ($F(1, 12) = 50.26$, $p < 0.001$). Pairwise comparisons indicated that, under the $D_{sg} = 0$ condition, there was a significant difference between the ETS and control conditions ($p < 0.001$). In contrast, no significant difference was observed under the $D_{sg} = 1$ condition ($p = 0.1$, n.s.). These results indicated that ETS on the anterior lower leg was induced only when the stimuli were within the dermatome. Similar results were obtained in the posterior lower leg. Under the $D_{sg} = 0$ condition, a significant difference was observed between the ETS and control conditions ($p < 0.001$). In contrast, no significant difference was observed under the $D_{sg} = 1$ condition ($p = 0.5$, n.s.). Therefore, these results indicate that ETS in the lower leg is induced within the dermatome.

Six participants could not satisfy the $D_{sg} = 2$ condition and the data of the remaining seven participants were analyzed. We performed a two-way repeated-measures ANOVA with the perceived temperature of the cold stimulator as the dependent variable to investigate the segmental effect on TGI. The analysis indicated that segmental distance had a significant effect on TGI ($F(2, 12) = 12.69$, $p < 0.05$). Pairwise comparisons indicated that the perceived temperature in the $D_{sg} = 2$ condition was significantly different from those in the $D_{sg} = 0$ condition ($p < 0.01$) and $D_{sg} = 1$ ($p < 0.05$) conditions. No significant difference was observed between the $D_{sg} = 0$ and $D_{sg} = 1$ conditions ($p = 0.2$, n.s.). These results indicate that TGI on the anterior lower leg was induced when the stimuli were within and across the adjacent dermatomes. Similar results were obtained in the posterior lower leg. Segmental distance had a significant effect on the perceived temperature ($F(2, 12) = 24.79$, $p < 0.001$). The perceived temperature in the $D_{sg} = 2$ condition was significantly different from those in the $D_{sg} = 0$ ($p < 0.001$) and $D_{sg} = 1$ conditions ($p < 0.01$). However, no significant difference was observed between the $D_{sg} = 0$ and $D_{sg} = 1$ condition ($p = 0.4$, n.s.). This analysis indicated that TGI in the posterior lower leg was induced within and across the adjacent dermatomes. Therefore, ETS and TGI had different segmental effects on the lower leg. ETS was not reproduced where TGI was reproduced.

We estimated the effect size of spinal integration on ETS and TGI. The confidence intervals and data probability densities of ETS and TGI are shown in Fig.8 b and Fig.8 d, respectively. The results reveal that the 95% confidence intervals for the ETS condition were half as small as those for the TGI condition. This result indicates that the illusion is more reproducible outside the stimulus area than just below it, which has a spatial temperature gradient on the lower leg, further characterizing the extrapolation phenomenon.

E. EXPERIMENT 5

In Experiment 5, we aimed to illustrate the perceptual distribution of the lower leg. Fig. S2 illustrates the experimental results and corresponding conditions. Generally, warmth was perceived in the dermatomes where warm and cold stimuli were located. In the $D_{sg} = 0$ condition, the sense of warmth was limited by the location of the three stimulators. In the $D_{sg} = 1$ condition, warmth was perceived by the warm and cold stimulators, while almost no warmth was perceived by the neutral stimulator. These results support the overestimation of cold and neutral stimuli in Experiment 4. In contrast, no sense of cold was almost not perceived. When

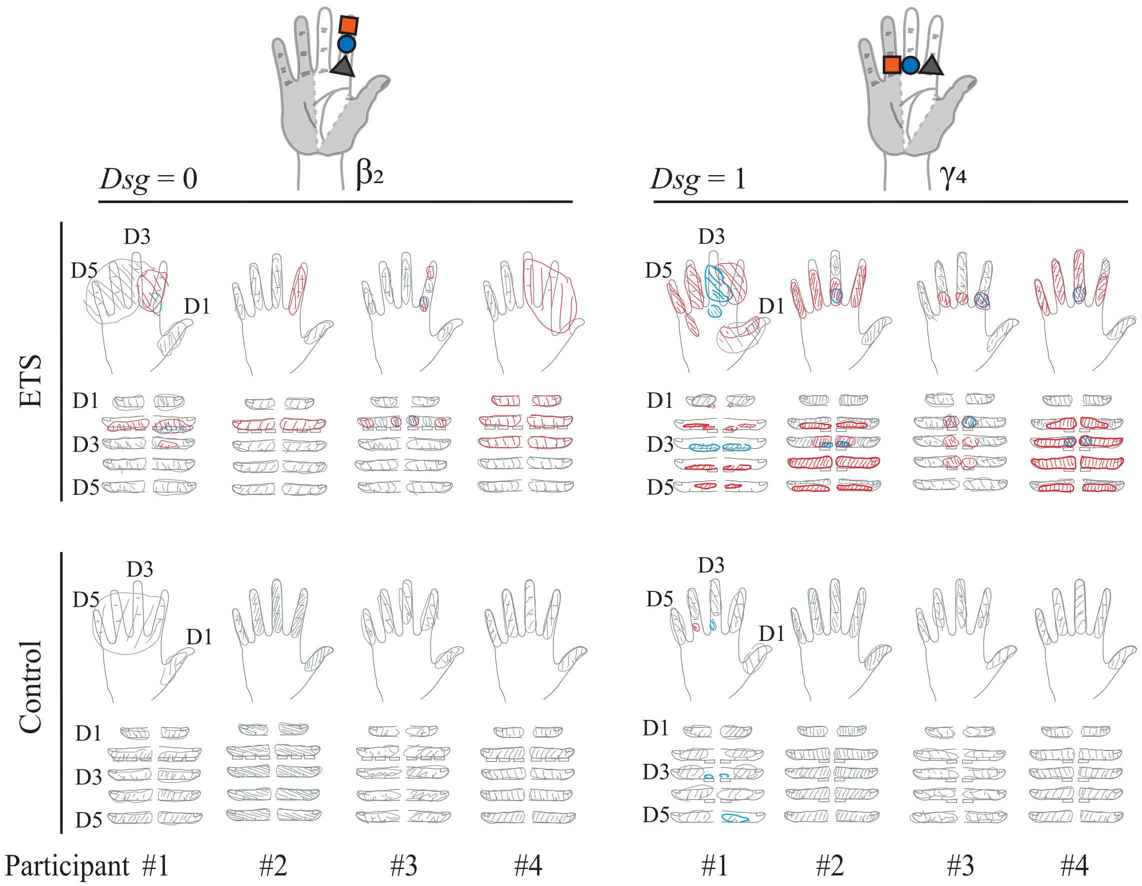

FIGURE 7. Results of Experiment 3. Participants drew the shape and field of warmth, cold, and neutral sense with a red, blue, and gray circle, respectively. Warmth was perceived at the neutral location. In some cases, warmth appeared to extend beyond the skin, into the air.

viewed from the side, the thermal sensation was only present in the area where the stimulator made contact with the skin.

IV. DISCUSSIONS

A. PRINCIPAL FINDINGS

The ETS phenomenon occurs when a neutral stimulus area feels warm in a sequence of warm, cold, and neutral stimuli. Comparative studies as well as our pilot study indicate that this phenomenon is not a physical phenomenon of heat conduction on the skin from warm stimulation to neutral stimulation [1], [48]. Instead, ETS results from neural activity that integrates spatially continuous warm and cold representations of the skin surface. The intensity of the ETS, as indexed by the degree of temperature overestimation, depends on the segmental distance between the warm and cold stimuli. Overestimation of ETS stimuli is greater when the number of dermatomes that the warm-cold pair crosses is small, whereas it is reduced when the warm-cold pair crosses more dermatomes. Furthermore, by comparing ETS and TGI, we observed that the bodily location of the stimulus affected ETS, but not TGI. When stimuli were applied across adjacent dermatomes on the lower leg, although warmth in the cold area (TGI) was reproduced, warmth in the neutral area (ETS) was not, indicating that the intersegmental lateral connection of the thermal stimuli was not uniform. Finally, by illustrating perceptual distribution, we found that warmth could be perceived in areas where there was no skin or stimulus, suggesting the involvement of suprasegmental spatial organization.

In Experiments 1 and 2, we confirmed that segmental distance influenced ETS. The ETS varied in units of segmental distance. Under the same segmental distance conditions, ETS did not vary with the arrangement of the stimulus pair. It was best captured within the dermatome. When warm and cold stimuli were within the dermatome, the perceived temperature of the neutral stimulator was almost equal to the actual temperature of the warm stimulus. For every increase in segmental distance of 1, the perceived temperature decreased by approximately 5°C. These results reveal that spatially discrete observations can be integrated through intersegmental lateral connections, which is consistent with the findings of the TGI study [27]. This spatial property allows us to observe the spatial property of the ETS phenomenon using a segmental distance paradigm.

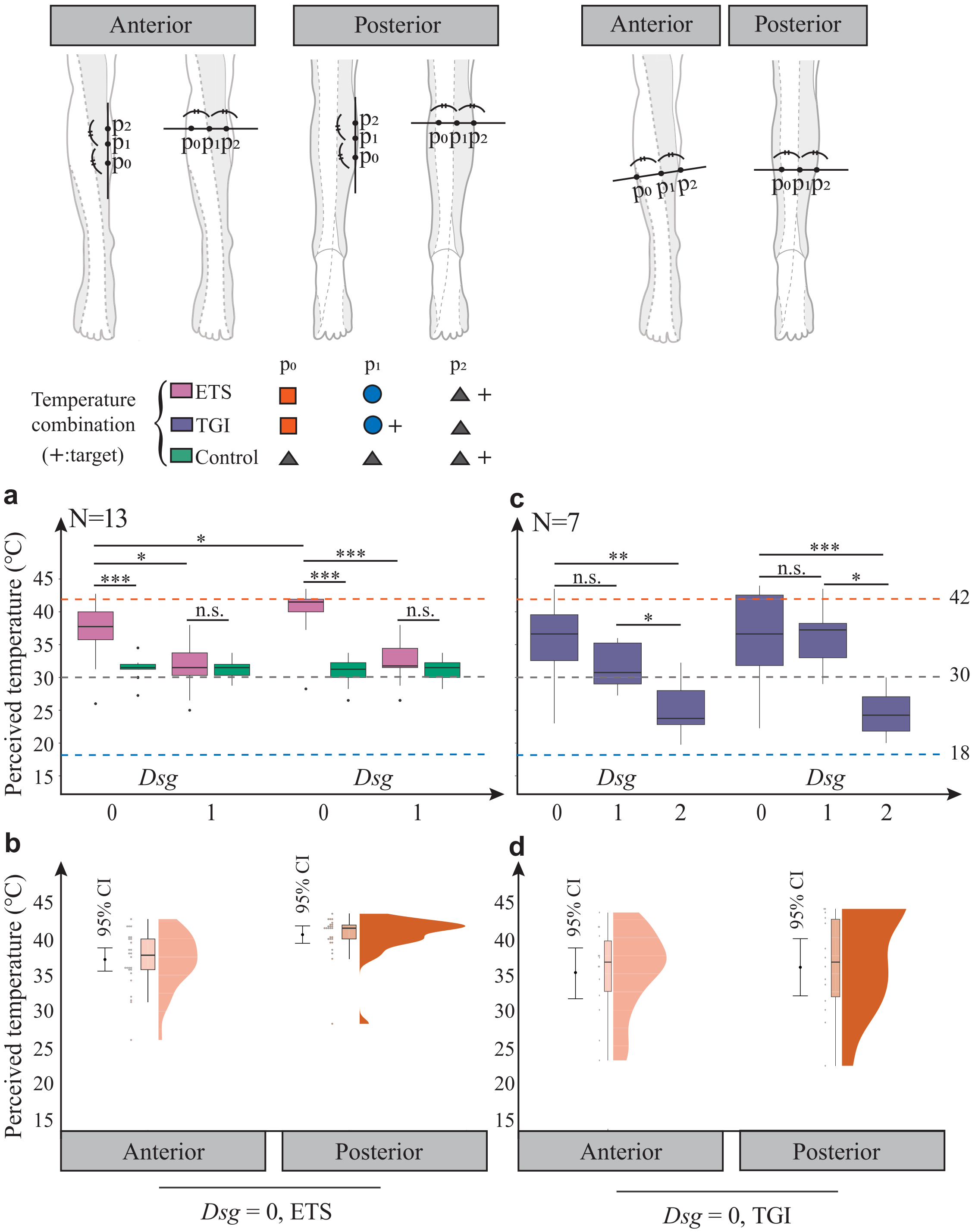

FIGURE 8. Results of Experiment 4. ETS and TGI were investigated on the anterior and posterior lower leg. The red squares, blue circles, and gray triangles represent the stimulus temperatures of 42°C, 18°C, and 30°C, respectively. + mark stands for the target location in each temperature combination condition. (a) Results of ETS. (b) The confidence intervals for the population mean of ETS results and the data probability density. (c) Results of TGI. (d) The confidence intervals for the population mean of TGI results and data probability density. On the lower leg, TGI was induced within or across adjacent dermatomes, whereas ETS was induced only within the dermatome. n.s. $p > 0.05$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

A previous psychophysical study on TGI demonstrated that its intensity is influenced by the distance between spinal segments receiving warm and cold stimuli, regardless of the bodily location [27]. The results of Experiments 1 and 4 aligned with this finding. However, our data indicated that the bodily location of the stimulus affected the ETS when warm and cold stimuli crossed the adjacent dermatomes. ETS was not reproduced where TGI was reproduced, indicating a reduced reproducibility of sensations in areas outside the stimulus, suggesting that when discrete spatial observations are integrated across dermatomes, the intersegmental lateral connection is not uniform. These results suggest that the segmental distance and the strength of lateral connections in the body play an important role in sensory processing.

Although the ETS is dominated by segmental distance, the involvement of suprasegmental organization in ETS generation has also been observed. Experiment 3 revealed that warmth sometimes extended beyond the skin, into the air. Some participants reported that warmth was induced in the dermatome in the absence of thermal stimulus. The perception in the area where there is no skin or stimulus strongly suggests the presence of suprasegmental spatial organization, because somatosensory experiences occurring in areas without direct bodily contact are thought to result from reorganization in the cerebral cortex, not the spinal cord [52], [53], [54], [55]. The involvement of the dorsal posterior insular cortex is probable, given the topographical projection of thermoreceptive neurons in lamina I to this region [44], [45]. It has been reported that the human posterior insular cortex is organized somatotopically, responding differently to cold stimuli on different body parts, such as the hand and neck. Further neurophysiological studies are necessary to accurately identify the cortical areas involved.

B. LATERAL CONNECTION IN DORSAL HORN

Our results reveal a marked influence of spinal segments on the ETS phenomenon. This suggests that the reproducibility of ETS is dominated by lateral connections between spinal segments and that lateral connections between spinal segments are not uniform across spinal segments.

Here, we first list possible models that explain the ETS phenomenon and then identify models that explain the ETS phenomenon by matching them with the experimental results. First, unmasking theory, a mechanistic model of the TGI phenomenon, makes it possible to interpret the ETS phenomenon. Second, because the ETS phenomenon requires warm and cold stimuli, we considered the contribution of Wide Dynamic Range (WDR) neurons, which are relay nuclei for warm, cold, and mechanical stimuli.

First, we consider the unmasking model proposed by Craig, a model of the TGI phenomenon. This model explains that burning sensation or pain is caused only by warm or cold stimulation without nociceptive stimulation [15] and is explained by the disinhibition of heat-pinch-cold (HPC) cell activity. This model assumes nociceptive HPC cell activity and argues that HPC cell activity is normally inhibited by COLD cells in the dorsal horn (lamina I). When COLD cells are inhibited by warm stimulation, the inhibition of HPC cell transmission by COLD cells is unmasked, resulting in the transmission of HPC cell activity to the central nervous system, causing a burning sensation and pain. Our qualitative observations of the perceptions produced by ETS indicate that there are few reports of burning sensations and none of pain [29]. Therefore, the classic unmasking model cannot explain ETS.

Fardo described the mechanism of "the unmasking (or disinhibition) of HPC cell activity as an overestimation phenomenon in which cold stimuli are mistakenly thought to be warmer than the physical temperature" as part of the TGI phenomenon [27]. Furthermore, Fardo has included "overestimation of cold stimuli" in the TGI phenomenon. Fardo reported that the phenomenon of cold stimulus overestimation decreased as the segmental distance between warm and cold stimulators increased, and concluded that the Lissauer Tract was the mechanism by which the integration of warm and cold stimuli across the dermatome occurred. However, Fardo did not argue that this was the result of unmasking the HPC cell activity.

Here, we discuss the contribution of the Lissauer tract to the "overestimation of cold stimuli, " as reported by Fardo. First, we assume that unmasking of HPC cells is the main cause of "overestimation of cold stimuli." In other words, the problem is set up such that the Lissauer tract can interpret the unmasking of the HPC cells. Next, neurophysiological findings indicate that excitatory coupling can travel long distances, whereas inhibitory coupling can only travel short distances. This implies that the assumption that HPC cells receive inhibitory coupling from COLD cells implies that HPC and COLD cells are nearby. This further suggests that only the WARM cells, which transmit warm stimuli across the spinal segment, are relatively distal and can couple with COLD cells. In this study, the position of HPC cells is used as the reference position. Assuming that COLD cells are located within the same spinal segment, the location of WARM cells that can inhibit COLD cells is logically shown to be in the same spinal segment, an adjacent spinal segment, or another spinal segment distal to the COLD cells. However, it is assumed that the inhibitory couplings from the WARM cells are established because the transmission pathway extends from the WARM cells to the Lissauer tract as an excitatory coupling and the inhibitory interneurons are located proximal to the COLD cells. This is a new finding in the mechanism of the TGI phenomenon, and we conclude that the Lissauer tract contributes to the overestimation of cold stimuli (TGI), due to the excitatory coupling of WARM cells at a distance from COLD cells that inhibit the activity of COLD cells.

The overestimation of cold stimuli was reproduced in our study, and furthermore, the above considerations could provide the insight that the ETS phenomenon was the result of the unmasking of HPC cells. According to the observations of the lower leg when warm and cold stimuli were across adjacent spinal segments, TGI was reproduced, whereas ETS was not. The unmasking of HPC cells may help explain the overestimation of cold stimuli. However, if ETS and TGI can be interpreted by the location of neutral and cold stimuli in the same segment, the overestimation of cold stimuli (TGI) and warmth at neutral stimuli (ETS) should be reproduced when

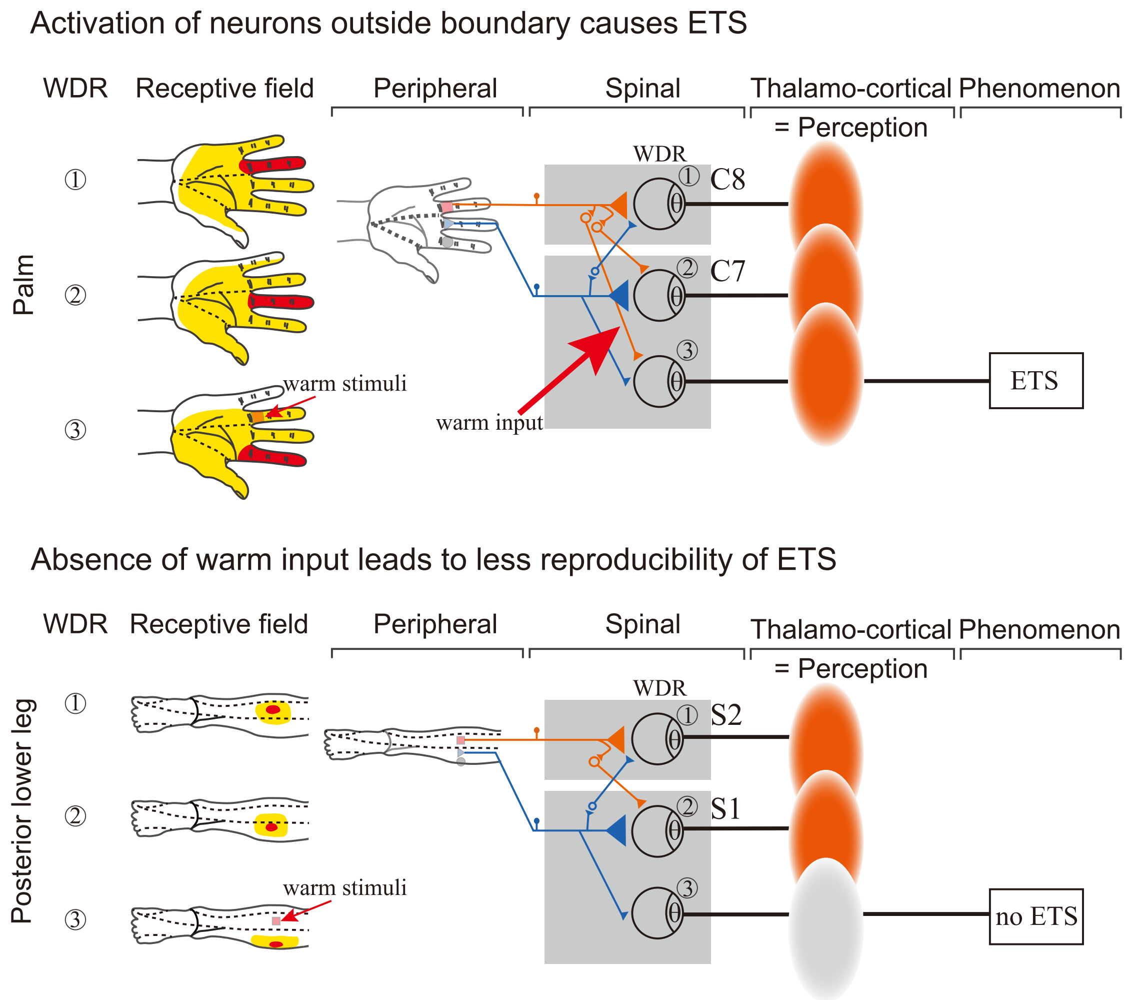

FIGURE 9. **A model involving spinal summation and thalamocortical combination of stimuli. Wide Dynamic Range (WDR) neurons in the spinal cord have a central/surround receptive field organization. The central receptive field zone (red) responds to mild and intense stimuli, while the surround receptive field (yellow) only responds to intense stimuli. Receptive field size is plotted from rat data. (a) The receptive field corresponding to the palm covers about 80-100% of the palm [40]. On the fingers, mildly warm and cold stimuli converge on WDR neurons, including the No.3 WDR neuron outside the boundary, increasing the stimulation to levels usually produced by more intense heating (the pathways that decide the perception are omitted for clarity). This thermal information from the spinal cord is projected to the thalamus cortex and further combined. Consequently, warmth is perceived within and across adjacent dermatomes. (b) The receptive field corresponding to the lower leg is about 4-12% of the lower leg [46]. On the lower leg, warm stimuli do not project to the No.3 WDR neuron in the neighboring spinal segment. The absence of warm input leads to an inability to activate this WDR neuron. Consequently, no ETS is induced across adjacent dermatomes.**

warm and cold stimuli cross adjacent segments, regardless of the stimulation site. However, our experimental results did not support this hypothesis. Therefore, the contribution of HPC cells alone do not explain the ETS phenomenon, and new considerations from a different perspective are required.

Alternatively, WDR neurons in the dorsal horn may contribute to the spatial integration of warm and cold stimuli. WDR neurons respond to warm and cold stimuli [5], [36]. It is considered that warm and cold stimuli converge on WDR neurons and that these neurons construct intensity paths parallel to the pathways that determine perception, eliciting a sense of heat [37], [39]. A recent study reported the necessity of cold-sensitive afferents for the sense of warmth [38]. This finding provides insights into how cold inputs interact with warm inputs to create a sense of warmth.

In addition, the stimuli intensity depending receptive field of the WDR neurons, shows that these neurons have lateral connections and a central or surrounding receptive field organization. The central receptive field is small and responds to mild and intense stimuli. The surrounding receptive field covers almost all the fingers (three dermatomes) and responds only to intense stimuli [40]. This configuration allows intense inputs to activate WDR neurons that are remote from the actual stimuli. Accordingly, mildly warm and cold stimuli converge on WDR neurons, whose central receptive field is outside the physical boundary (Fig.9 a), increasing stimulation to levels usually produced by more intense heating. This intensity information from the WDR neurons is projected onto the thalamus cortex and combined across multiple fingers to remap an ordered thermoreceptive intensity space. After spatial remapping, a continuous sense of warmth is perceived within and across adjacent dermatomes.

This finding can also explain the lower reproducibility of ETS in the lower leg when warm and cold stimuli cross adjacent dermatomes. Rat data show that the area of the receptive field corresponding to the palm is approximately 100 mm^2 [40],[1] because the receptive field almost covers the rat palm size [41]. The area of the receptive field corresponding to the lower leg is estimated to be approximately 20-60 mm^2 [46].[2] Body size data show that the area of the palm and lower leg of a human are approximately 90[3] and 48[4] times the corresponding areas of a rat, respectively [42], [43]. Accordingly, the area of the receptive field corresponding to the palm of humans is 1800-5400 mm^2; the area of the receptive field corresponding to the lower leg of humans is 4800 mm^2. Fig.9 shows the estimated area differences as the filled areas in yellow and red. These areas were calculated using the rat data applied to humans. Additionally, it is found that the WDR neurons corresponded to the palm, covering three dermatomes, whereas the neurons corresponding to the lower leg covered one to two dermatomes [46], [47]. The smaller receptive field and fewer covered dermatomes indicate that as a process of integration of spatially continuous warm or cold representations at the skin surface, spatially discrete peripheral inputs are significantly sparser in the lower leg than in the palms [40], [46]. A less overlapping receptive field indicates that distant stimuli in adjacent spinal segments may not activate all WDR neurons. The absence of warm input leads to an inability to activate WDR neurons. Consequently, ETS was not induced across adjacent dermatomes (Fig.9 b).

C. IMPLICATIONS, LIMITATIONS, AND FUTURE WORK

Exploring the spatial organization of perception is a critical step in understanding how the brain structures sensory experiences. Previous studies on thermal sensations have mainly focused on the organisms involved in thermal processing. In this study, we focused on the spatial organization of thermal sensations by observing ETS. We proposed a model involving spinal summation and a thalamocortical combination of stimuli based on WDR neurons. This model can provide insights into the lateral connections of neurons related to thermal sensation. The idea that spatial summation can lead to extrapolation highlights the complexity and sophistication of neural processes underlying sensory experiences. Through the integration process, basic somesthetic activity is disrupted, and warm-cold representations are distorted on the skin surface. Interestingly, the receptive fields surrounding WDR neurons exhibit sensitivity gradients [40]. Consequently, increasingly intense stimuli are necessary to progressively activate the peripheral regions of the surrounding receptive field. Increasingly intense warm and cold stimuli are expected to activate more WDR neurons, resulting in further extrapolation. Therefore, further investigations are required.

There have been no reports on thermal sensations outside the stimulation areas of warm and cold stimulators. We initially demonstrated that thermal sensations were induced across the boundaries that enveloped the physical stimuli. Our findings provide a knowledge base for the development of thermal displays, as they improve the ability to display temperature and support the development of VR or AR.

V. CONCLUSION

This study reports on the ETS observed on the fingers and lower leg. We found that a neutral stimulation area felt warm when stimuli with a spatial arrangement in the order of warm, cold, and neutral were received simultaneously. Comparative experiments indicated that this was not a physical phenomenon of heat conduction on the skin from warm to neutral stimulation. Instead, ETS is a perceptual phenomenon as an illusion created by the spatial integration of warm and cold stimuli through neural activity. Contrastingly, we showed that the intensity of ETS is related to the distance between warm and cold stimuli, with the phenomenon becoming less pronounced as the distance increases.

Additionally, we explored the relationship between ETS and TGI in Experiments 1 and 4. On the fingers, ETS and TGI can be triggered within and across adjacent dermatomes (Experiments 1 and 2). However, an interesting difference was observed in the lower leg; while TGI could occur across dermatomes, ETS was only induced within a single dermatome (Experiment 4). This suggests non-uniformity in neural connections across different body parts. We suggest that WDR neurons in the spinal cord contribute to this phenomenon. On the fingers, the large receptive fields of WDR neurons allow warm and cold stimuli to activate WDR neurons in the adjacent dermatomes [40]. In contrast, smaller receptive fields in the lower leg lead to a lack of activation of WDR neurons distant from the stimuli [46], preventing the occurrence of ETS across dermatomes.

[1] The manuscript mentions wrist width and forefoot length.

[2] The manuscript mentions lower rear leg length and knee width. The surface area is estimated with [41] in the same way on the palm receptive field.

[3] The manuscript mentions hand length and wrist breadth.

[4] The manuscript mentions crotch-knee distance, crotch-ankle distance, and ankle circumference.

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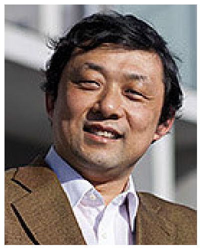

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