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Extrapolation of Thermal Sensation: Enlargement of Perceptual Boundary Induced by Spatiotemporal Integration of Thermal Stimulation

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ABSTRACT

Humans rely on their ability to perceive external temperatures to recognize material properties. Despite its significance, thermal sensation has not been well studied. While there have been physiological studies on temperature representation, the spatial organization of thermal sensation, particularly its perceptual boundary, remains unclear. This thesis investigates Extrapolation of Thermal Sensation (ETS). Classical thermal phenomena including Thermal Grill Illusion (TGI) are perceived only at the stimulus location or within the boundary formed by multiple stimuli. ETS, however, reports perception outside the physical boundary.

This thesis uses psychophysical methods to determine if classical models explaining TGI—such as unmasking and addition theories—can also explain ETS. The thesis explores whether the perceptual boundary extends beyond the physical stimulus under various spatiotemporal conditions. It was found that the temporal sequence of warm and cold stimuli applied to the fingertip and base of the middle finger influences perception. Warmth applied before a cold stimulus induced a reliable perception of warmth beyond the cold stimulus, demonstrating ETS.

The relationship between ETS and stimulus temperature was also explored. Gradually increasing warm and cold stimuli increased the percentage of hot judgment outside the physical boundary, indicating that the unmasking theory in TGI does not explain ETS. Instead, the addition theory explains

ETS. Warmth outside the physical boundary results from the addition of warm and cold stimuli.

Comparing the spatial characteristics of ETS to TGI, simultaneous warm, cold, and neutral stimulation of the fingers or lower leg revealed that both phenomena showed segmental-distance-dependent variations in perceived temperature. However, ETS did not occur in areas evoking TGI, suggesting distinct mechanisms for the two phenomena.

In conclusion, the thesis author found ETS for the first time and also revealed the phenomenon expands the perceptual boundary in human thermal sensation.

ABBREVIATIONS

TGI: Thermal grill illusion

PHS: Paradoxical heat sensation

TR: Thermal referral

ETS: Extrapolation of thermal sensation

HPC: Spinal cord neurons that respond to heat, pinch, and cold stimulation

WARM: Spinal cord neurons that convey warm sensation

COLD: Spinal cord neurons that convey cold sensation

WDR: Wide dynamic range in the spinal cord

PIP: Proximal interphalangeal

DIP: Distal interphalangeal

MCP: Metacarpophalangeal

CONTENTS

Chapter 1

DISCRETE in the SKIN, CONTINUOUS in the MIND

Somatic sensation has fascinated humankind for millennia.

- 2021 Nobel Prize in Physiology or Medicine

1.1 Summary

This chapter reviews the existing literature to understand how spatially discrete sensory spots react to thermal stimuli, creating a spatially continuous perception within the brain. Thermal stimulation applied to the human skin is spatially discretely detected within the skin by primary afferents. As a result of spatial interpolation of the thermal sensation within the spinal cord and projected to the primary somatosensory cortex, it is formed as a spatially continuous temperature perception. In this chapter, I will attempt to discuss the spatial extrapolation phenomenon of thermal sensation reported in this thesis using classical theories and to clarify the limitations. Two primary theoretical frameworks, the unmasking theory and the addition theory, propose mechanisms for integrating warm and cold signals. These frameworks attempt to explain how such integration can evoke a burning pain known as the Thermal Grill Illusion (TGI). The addition theory claims that "TGI is a mixture of simultaneous sensations of warmth and coldness." According to this theory, warm and cold inputs converge onto Wide Dynamic Range (WDR) neurons in the spinal cord, adding their excitatory effects. As a result, the burning pain (TGI) is generated. On the other hand, unmasking (aka disinhibition) theory claims that the "TGI is a result of unmasking of nociceptive cells." The unmasking theory posits that the sensation of burning pain is experienced due to the inhibition of cold-sensitive pathways by warm-sensitive pathways. This inhibition unmasks the normally inhibited nociceptive cells from the cold-sensitive pathways, leading to the perception of burning pain (TGI). However, neither theory adequately addresses the spatial characteristics of the resulting sensation. Finally, the chapter points out the possibility of change in perceptual boundaries of thermal sensation, suggesting that new insights in this area could significantly advance our understanding of sensory integration.

1.2 From Discrete Sensory inputs to Continuous Percept

Like other mammals, humans rely on their ability to perceive external temperatures to regulate their internal body temperature, a process known as thermoregulation (Mota-Rojas et al., 2021). This sensory perception is crucial because it triggers behavioral and physiological responses that help maintain a stable internal environment, which is essential for survival. When the body detects cold conditions, it can initiate mechanisms such as shivering and the constriction of blood vessels to conserve heat. In contrast, sweating and dilation of the blood vessels in hot environments facilitate heat loss. Thus, the precision and efficiency of these sensory and response systems play a vital role in protecting mammals from extreme temperatures, which can lead to fatal conditions such as hypothermia or heatstroke.

In fact, the ability to recognize temperature plays a crucial role beyond just maintaining intracellular homeostasis; it also improves our sensory perception, particularly in identifying the material properties of objects (Shuichi et al., 1994). The temperature difference from the normal skin temperature has been reported to be very important to recognize what kind of materials contact the skin surface (Shuichi et al., 1994). This capability is linked to the conductive properties of materials: Metals typically feel cooler than wood under the same conditions because metals have higher thermal conductivity and can rapidly draw heat away from the skin. Conversely, materials like wood or fabric, which have lower thermal conductivity, do not transfer heat as efficiently and thus feel warmer to the touch. This sensory information is vital for humans in making everyday decisions, such as choosing appropriate clothing or utensils, and even influences safety measures, such as determining whether an object is too hot to handle directly.

When we squeeze a coin in our hand, the distinct coolness we feel helps us determine its metallic nature. This sensation is due to the coin's high thermal conductivity, which allows it to absorb heat from our hand more quickly than materials with lower conductivity. The ability of the metal to conduct heat efficiently gives it a unique tactile signature that our sensory system interprets as "cool" or "metallic." This type of tactile feedback is integral to our understanding of objects around us, providing not only practical information on the properties of the material, but also enhancing our interactions with our environment in a meaningful way. Through such interactions, we gain a more nuanced appreciation of the objects we encounter daily.

Humans have specialized receptors known as thermoreceptors located under the skin, which play a crucial role in detecting and responding to changes in external temperature (Schepers & Ringkamp, 2010). These receptors are categorized into two main types: cold and warm receptors. At normal skin temperature, neither warm nor cold receptors are activated. Cold receptors are activated by decreasing temperatures, while warm receptors respond to increasing temperatures. The signals from these receptors travel through the peripheral nervous system to the brain, where they are processed to provide accurate perceptions of temperature. This intricate system allows humans to react to temperature changes swiftly, whether they seek warmth, move to a cooler environment, or adjust clothing to maintain comfort and safety. This sensory input is essential for physical well-being and enables humans to interact effectively with their environment, adapting behaviors based on thermal cues.

Although the thermoreceptors are spatially discrete, our overall perception of temperature is spatially continuous. Thermoreceptors are known to be clustered rather than randomly distributed. This leads to a huge blank space between two clusters (Ezquerra-Romano et al., 2023). However, according to our daily knowledge, we almost cannot feel such a blank. This phenomenon arises because the brain integrates the localized inputs from these receptors across the skin's surface to create a seamless and continuous perception of temperature. This integration allows us to perceive gradual temperature gradients rather than discrete points of cold or warmth.

The transition from discrete sensory input to a continuous perception of temperature involves a sophisticated neural process of interpolation. This neural mechanism effectively fills in the gaps between the points of sensory input, allowing for a smooth and continuous perception across the skin's surface. In the brain, specifically within the somatosensory cortex, there is a mapping of sensory information that receives and processes signals from various parts of the body. The brain integrates these discrete signals, smoothing out the sensory input to form a coherent and continuous representation of external conditions. This process is not only crucial for temperature perception but is also fundamental to other sensory systems, such as vision and touch, where similar mechanisms allow us to perceive a smooth visual field or a continuous tactile surface. This neural interpolation enables us to function effectively in our environment, ensuring that we can respond to external stimuli in a manner that is both precise and adapted to our surroundings.

Studying the process by which our brains interpolate discrete sensory inputs to form continuous perceptions is fundamental for several reasons, particularly in understanding the boundaries of sensation. These boundaries define where one sensation ends and another begins, which is crucial for accurately interpreting our environment. For example, being able to discern the boundary of a hot surface by feeling can prevent injury. In the next section, I will review the existing literature to understand the process by which spatially discrete sensory spots react to thermal stimuli to create a spatially continuous perception within the brain.

1.3 Peripheral Processing of Thermal Stimulus

Skin Structure

Thermal stimuli are first converted in the skin. Among the five human senses, touch (thermal sensation included) is the only sensory organ that is distributed throughout the body. The skin structure consists of the epidermis (Epidermis), dermis (Dermis), and subcutaneous tissue (Subcutis). The epidermis is about 0.7 mm thick on the palm. The dermis is 0.3 - 2.4 mm thick and consists of strong fibrous connective tissue. At the boundary between the epidermis and dermis, where the skin is subjected to considerable frictional forces, such as in the palm, downward protruding epidermal folds (epidermal ridges) and upward protruding dermal papillae interlock to strengthen the adhesion between the epidermis and dermis. The subcutaneous tissue is a reticulated, loosely connective tissue, the meshes of which are filled with adipose tissue. It is usually tightly bound to the dermis and the periosteum, fascia, and tendon membranes. Cutaneous sensations are external information received by receptors located in the skin, such as touch, pressure, pain, and temperature.

The heat transfer process within the skin during contact with thermal stimulation roughly follows the bioheat equation (Wilson & Spence, 1988). This equation accounts for the effects of blood perfusion and metabolic heat generation on the energy balance within the tissue.

$$\rho c \frac{\delta T}{\delta t} = k \frac{\partial^2 T}{\partial x^2} + \rho_b \omega_b c_b (T_a - T) + q \tag{1.1}$$

, where:

- ρ is the density of the tissue,
- c is the specific heat capacity of the tissue,
- $\frac{\partial T}{\partial t}$ is the time rate of change of temperature,
- $k \frac{\partial^2 T}{\partial x^2}$ represents the conduction term, with k being the thermal conductivity,
- ρ_b is the density of the blood,
- ω_b is the blood perfusion rate,
- c_b is the specific heat capacity of the blood,
- T_a is the arterial blood temperature,
- T is the local tissue temperature,
- q is the metabolic heat generation per unit volume.

The bioheat equation accounts for the contributions of thermal conduction, blood perfusion, and metabolic heat generation. The resting temperature of the skin on the hand ranges from 25 °C to 36 °C (Verrillo et al., 1998), which is generally higher than the temperature of objects encountered in the environment. When the hand is in contact with an object, the heat is transferred across the interface by conduction. During this process, the heat flux that is conducted out of the skin and the corresponding change in skin temperature are used to identify the object by touch.

On the other hand, chemical stimulation can also produce temperature signals in the skin instead of thermal stimulation. For example, the transient receptor potential cation channel subfamily V member 1 (TRPV1) can be activated by temperatures greater than 43 °C, and also by chemicals such as capsaicin (as in chili pepper). There are some other receptors that can respond to both thermal and chemical stimulation. Transient receptor potential cation channel subfamily M member 8 (TRPM8) is primarily found in sensory neurons and is activated by mild cool temperatures (typically below 26 °C) and chemical agents such as menthol (found in mint) (Pedersen et al., 2005). Thus, anomalous chemosensory activation could produce thermal sensations without thermal stimulation.

Thermosensitive Receptors

Thermosensitive receptors (thermoreceptors) respond to thermal stimuli through a well-coordinated process involving changes in their ion channel activities. Free nerve endings are widely distributed in the epidermis, dermis, and subcutaneous tissue. These free nerve endings respond to thermal stimulation. Thus, the thermoreceptors are considered as free nerve endings morphologically (see Table 1.1). Functionally, thermoreceptors can be divided into cold nociceptors (5 °C), cool receptors (25 °C), warm receptors (>35 °C), and heat nociceptors (>45 °C).

The specialized areas on the skin where thermosensitive receptors are concentrated are called sensory spots, including warm spots and cold spots. These sensory spots are particularly sensitive to changes in temperature and play key roles in the perception of warmth and coldness, respectively. These sensory spots can be found using psychophysical methods, such as scanning the skin with blunted aluminum wires (diameter: 1 mm). If sensory spots are being tested, they feel warm or cold; if there is no sensory spot, they feel nothing. Sensory spots have different spatiotemporal properties. In general, the density of cold spots far exceeds that of warm spots (Table 1.2). In many parts of

Table 1.1: Receptor Types Active in Somatic Sensation. Cite from Kandel (Kandel et al., 2021a).

Receptor type	**Fiber group**	**Fiber name**	**Modality**
Mechanoreceptors			**Touch**
Meissner corpuscle	$A\alpha, \beta$	RA1	Stroking, flutter
Merkel disk receptor	$A\alpha, \beta$	SA1	Pressure, texture
Pacinian corpuscle	$A\alpha, \beta$	RA2	Vibration
Ruffini ending	$A\alpha, \beta$	SA2	Skin stretch
Thermoreceptors			**Temperature**
Cool receptors	$A\delta$	III	Skin cooling ($< 25°C$)
Warm receptors	C	IV	Skin warming ($> 35°C$)
Heat nociceptors	$A\delta$	III	Hot temperature ($> 45°C$)
Cold nociceptors	C	IV	Cold temperature ($< 5°C$)
Nociceptors			**Pain**
Mechanical	$A\delta$	III	Sharp, pricking pain
Thermal-mechanical(heat)	$A\delta$	III	Burning pain
Thermal-mechanical(cold)	C	IV	Freezing pain
Polymodal	C	IV	Slow, burning pain

the body, the density of cold spots is more than ten times greater than the density of warm spots. The finger volar is the part with the smallest C/W ratio. The density of warm spots at human finger is 1.6/cm^2 and that of cold spots at human finger is 2.0 - 4.0/cm^2 (Arens & Zhang, 2006). Generally, warm and cold sensations reveal different properties because of the different densities. The cold sensation is more sensitive than the warm sensation and has a high spatial resolution. The warm sensation is more diffuse than the cold sensation.

The sensory spots are spatially discrete and not uniform. It is known that thermoreceptors are clustered rather than randomly distributed. This leads to a huge blank space between two clusters. On the forearm, it is found that almost 1/4 of the forearm is blank (Ezquerra-Romano et al., 2023). Although the density is found to be different among participants, this non-uniform distribution is common among participants (Ezquerra-Romano et al., 2023). Even on the body part with high density, e.g., fingers, space where there is no sen-

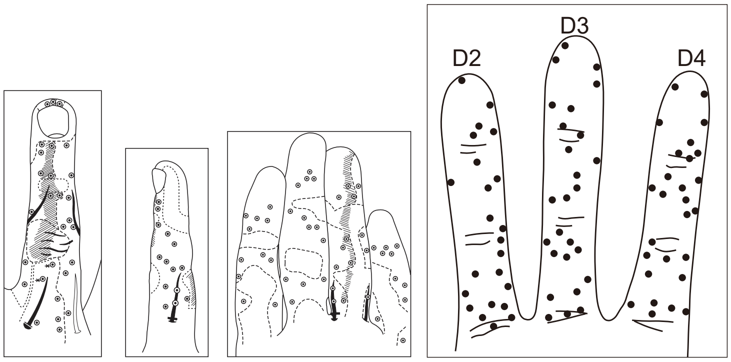
Table 1.2: Density of Warm and Cold Spots (/cm^2, cite from Arens (Arens & Zhang, 2006)).

Body Parts	**Cold Spots**	**Warm Spots**	**C/W Ratio**
Forehead	5.5 - 8		
Nose	8	1	8
Lips	16.0 - 19.0		
Chest	9.0 - 10.2	0.3	30 - 34
Upper Arm	5.0 - 6.5		
Forearm	6.0 - 7.5	0.3 - 0.4	15 - 25
Back of Hand	7.4	0.5	14.8
Palm of Hand	1.0 - 5.0	0.4	2.5 - 12.5
Finger Dorsal	7.0 - 9.0	1.7	4.1 - 5.3
Finger Volar	2.0 - 4.0	1.6	1.3 - 2.5
Thigh	4.5 - 5.2	0.4	11.3 - 13

sory spot can be found (for detail, see Figure 1.1). It has been discovered that the number of sensory points decreases with age. The reduction in number will undoubtedly cause the distribution of sensing points to become sparser.

Primary Afferents

Thermosensitive primary afferents transmit thermal information from cutaneous receptors to the central nervous system. Thermal signals generated from warm receptors are conducted through C fibers, while signals generated from cold receptors are conducted through Aδ fibers (see Table 1.1). Aδ fibers are small-diameter (1 - 6μm), myelinated primary afferent fibers; C fibers are smaller-diameter (1.0μm) unmyelinated primary afferents. Conduction velocity of Aδ afferents is 15 - 40 m/s while that of C afferents is 0.5 - 2 m/s (Darian-Smith et al., 1973; Duclaux & Dan, 1980). These primary afferent nerve fibers are the axons (nerve fibers) carried by a sensory nerve. The cell bodies of primary afferent sensory nerve fibers are located in the dorsal root ganglia (DRG). The neurons comprising the DRG cells are pseudo-unipolar, meaning they have a cell body with two branches that act as a single axon. Unlike the majority of neurons found in the central nervous



(a) warm spots on fingers (b) cold spots on fingers

Figure 1.1: Sensory spots on fingers. (a) warm spots on fingers (cite from (Arens & Zhang, 2006)). (b) cold spots on fingers. Data of cold spots was collected and drawn by the author according to a traditional measurement. A rubber stamp was placed on specific fingers. A bottle filled with cold water was placed on the stamp. The participant, blindfolded, reported if they feel cold. The reported sensations were marked on a corresponding diagram. Fingertip joint locations were recorded, and the sensations were mapped for analysis. D2, D3, and D4 stand for index, middle finger, and ring finger.

system, an action potential in posterior root ganglion neuron initiates in the distal process in the periphery, bypasses the cell body, and continues to propagate along the proximal process until reaching the synaptic terminal in the posterior horn of the spinal cord. In summary, thermal signals are generated at receptors (peripheral) and conducted to the spinal cord. The spinal cord is the first-order terminal of temperature signals. At there, temperature signals get processed primarily and then conducted to the high-order regions of the brain.

Because temperature-sensitive receptors are distributed throughout the body surface, the cell body is located in the spinal cord. Primary afferents are usually very long. The length of primary afferent nerve fibers from the fingertip to the spinal cord can vary significantly based on the individual's arm length and overall size. However, a general estimation can be provided by considering the anatomical path these fibers take from the fingertip, along the arm, and up to the spinal cord. From the fingertip to the wrist, the nerves travel approximately the length of the finger plus the length of the hand. This is usually about 20 cm in an average adult (Mirmohammadi et al., 2016). From the wrist to the shoulder, the nerves run along the forearm. This section typically measures around 75 cm (Mirmohammadi et al., 2016). The nerves enter the cervical region of the spinal cord. The distance is generally about 15 cm in an adult. Adding these segments together gives an estimated total length of about 110 cm from the fingertip to the spinal cord for an average adult.

Long-distance signal transmission results in a huge difference in the conduction time of warm and cold signals. According to the conduction velocity data provided previously (Arens & Zhang, 2006), it takes 0.5 - 2 s for the warm signal to conduct from the fingertips to the spinal cord, while for the cold signal, the conduction time only takes 0.025 - 0.07 s. This huge difference in conduction times makes it necessary to consider the time difference between warm and cold signals when considering their interaction.

1.4 Central Processing of Thermal Stimulus

Spinal Cord

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 (Kandel et al., 2021a). The segmental distribution of sensory skin in the human body is most evident in the neck and trunk, where the dermatomes are arranged one at a time, each forming a ring-like fasciculus surrounding the trunk and neck (Greenberg, 2003). 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 (Abraira & Ginty, 2013). This neurophysiological finding indicates that thermal sensation is a spatially continuous perceptual phenomenon based on spatially discrete observations.

Here, I focus on the dermatomes on the hand. As Figure 1.2 shows, D1 (thumb) finger belongs to C6; D2 (index), D3 (middle), and part of D4 (ring) finger belong to C7; part of D4 and D5 (little) finger belong to C8 dermatome. Fibers in the same dermatome conduct perception information to the same dorsal horn of the spinal cord. This kind of convergence of local perception information offers a probability of integrating the local spatial pattern.

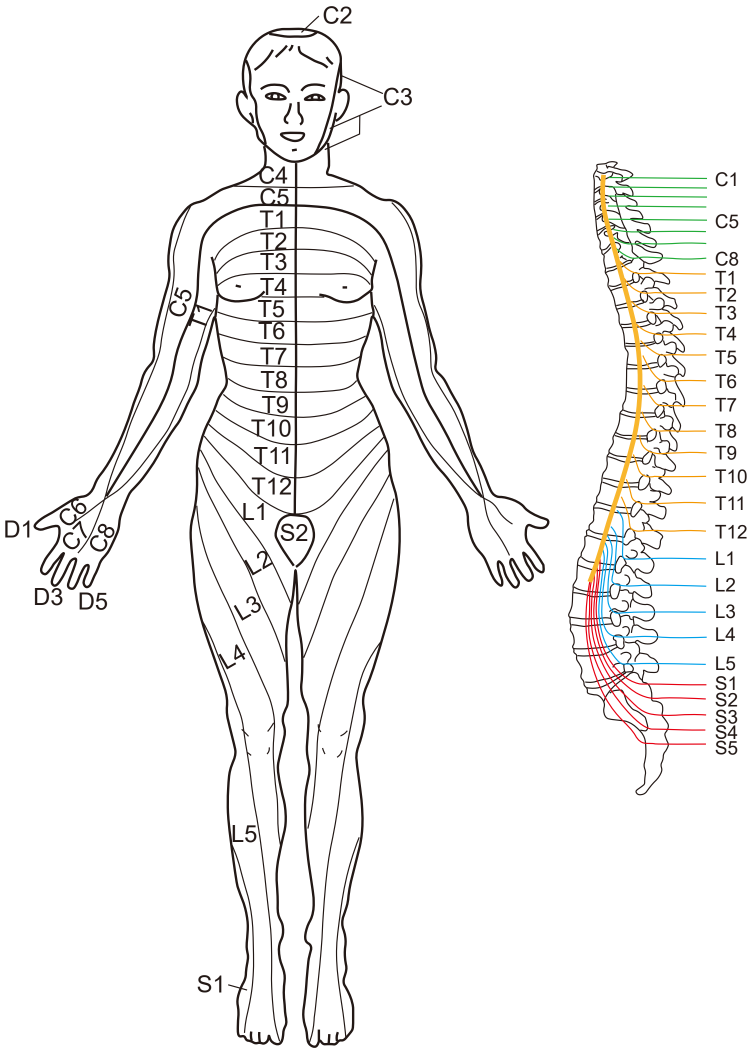


Figure 1.2: Dermatome. Changed from (Greenberg, 2003).

Thermosensitive fibers enter the corresponding spinal segment and synapse with neurons in lamina I, lamina II, and lamina V. Lamina I neurons selectively respond to warm and cold stimuli Figure 1.3. Neurons in lamina V respond to a wide range of stimuli, including noxious heat and cold. They receive inputs from both Aδ and C fibers and are involved in integrating these with other sensory inputs. Therefore, the spinal cord is a site of multimodal interactions and integrations.

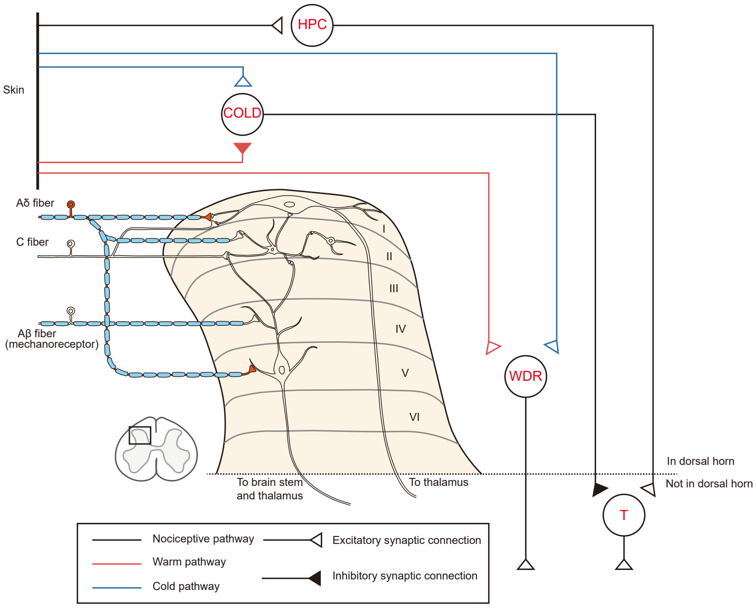


Figure 1.3: Spinal cord inputs. Quoted from Kandel (Kandel et al., 2021b) and revised by the author of the thesis. HPC = Heat-Pinch-Cold; WDR = Wide Dynamic Range.

Several types of neurons in the spinal cord respond to thermal stimulation applied to the skin (see Figure 1.4). Spinal cord neurons that convey cold sensation (COLD cells) are found in the monkeys' lamina I (Dostrovsky & Craig, 1996). These neurons have an ongoing discharge at approximately normal skin temperature (34 °C). Cooling the skin increases their firing rates linearly down to 15 °C, the threshold for cold pain, beyond which their response rate plateaus. Thermally neutral mechanical stimuli applied to the receptive fields do not excite them. The receptive fields of these COLD cells are "primarily on glabrous skin of the digits and foot and usually included a few digits and/or part of the sole of the foot." They may also contribute to the perception of warmth, as warming the skin inhibits their spontaneous firing (Dostrovsky & Craig, 1996).

Andrew found spinal cord neurons that convey warm sensation (WARM cells) that selectively respond to cutaneous warming in the lamina I (Andrew & Craig, 2001) of the cat. These neurons respond to slight increases in skin temperature, with firing rates increasing linearly up to approximately 40 °C, at which point their response plateaus. Warm cells are found to have moderately sized receptive fields. The unit with the smallest receptive field is activated over all of the glabrous pads of the hindlimb, whereas the cell with the largest field responds over all the glabrous and hairy skin of the plantar hindlimb. The conduction speed of peripheral inputs to WARM cells is 0.8 - 1.2 m/s. Thus, it has been thought that WARM cells receive inputs from unmyelinated C fibers.

Heat-Pinch-Cold (HPC) neurons are found in the lamina I of the cat (A. Craig et al., 2001). These polymodal nociceptive neurons respond to noxious heat above 43 °C. They do not respond to innocuous mechanical stimulation but respond to noxious pinchs. They are specific to unmyelinated fiber input and are associated with the experience of second pain, which can be described as dull, achy, or burning. The receptive field of the HPC cell is the entire central pad and the glabrous portion of two toes (A. Craig & Kniffki, 1985).

Wide dynamic range (WDR) neurons are found deep in the lamina V of the rat (Le Bars & Cadden, 2008). They are found to respond to both innocuous and noxious stimulation of the skin (Khasabov et al., 2001). WDR neurons almost do not respond to thermal stimulus from 28 °C to 35 °C. However, WDR firing rates increase linearly down to -12 °C and up to 51 °C. When accepting the warm input, the increasing rate of firing rate is much higher than the increasing rate when accepting the cold input. Accordingly, the response property of WDR neurons appears like a "✓." Other than thermal stimulation, WDR neurons are also found to respond to mechanical stimulation (Ma & Sluka, 2001). WDR neurons have complex central/peripheral receptive field organization and respond to noxious stimuli and light touch in spatially distinct parts of their receptive fields. Each neuron's central receptive field area responds to noxious and innocuous stimuli, while the peripheral surrounding areas respond only to noxious stimuli. Furthermore, the peripheral surrounding areas have a sensitivity gradient such that increasingly intense nociceptive stimuli are required to gradually activate peripheral areas of the surrounding excitatory receptive fields (Coghill, 2020).

The receptive field structure of WDR neurons has been thought to contribute to the heat-induced spatial radiation of painful sensations that human subjects report when skin temperatures exceed 45 °C (Price et al., 1978). First, WDR neurons whose receptive field's center lies directly under the Peltier would increase their activity. Second, more nociceptive neurons would be activated, including WDR neurons with very extensive receptive fields and whose most sensitive receptive-field regions are remote from the actual stimulus. As a result, a spatial spread of perceived heat pain is generated. Although this is a phenomenon of heat pain, it can be seen as a phenomenon of enlargement of the perceptual boundary.

The axons of neurons, which are responsible for carrying temperature information, enter the spinal cord through the dorsal horn. Once they reach the dorsal horn, these axons branch out into ascending and descending collaterals. These branches form the Lissauer tract (Purves et al., 2001), which travels up and down the spinal cord for one or two segments before making its way into the gray matter of the dorsal horn.

The Lissauer tract is crucial in integrating and transmitting thermal signals within the spinal cord. It allows for integrating thermal signals from multiple adjacent spinal cord segments. As axons ascend and descend within the tract, they can exchange information with neighboring neurons, enabling the nervous system to form a more comprehensive picture of the sensory environment. The Lissauer tract also serves as a site for modulating thermal signals. Inhibitory and excitatory interneurons within the tract can influence the activity of ascending nociceptive axons, thereby regulating the transmission of thermal signals to the brain. This modulation plays a critical role in controlling thermal sensation.

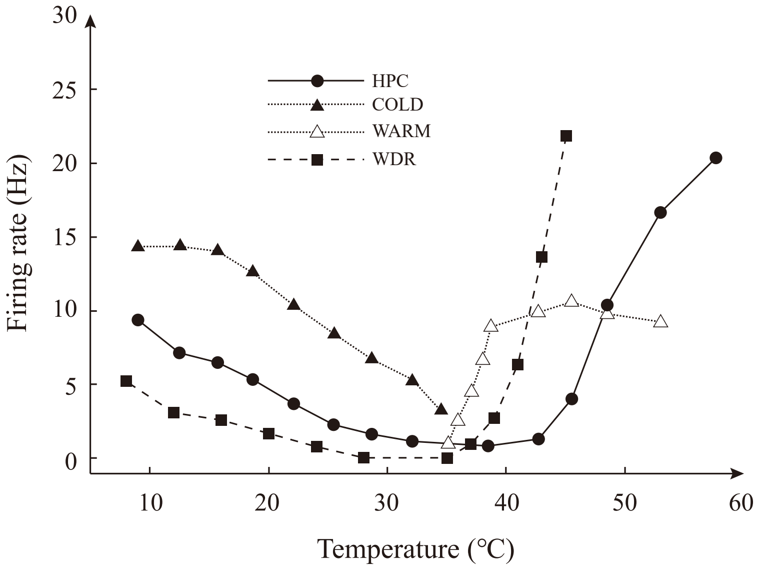


Figure 1.4: Response properties of second-order thermosensitive neurons. HPC = Heat-Pinch-Cold; WDR = Wide Dynamic Range. Data of COLD cells are obtained from the monkeys (Dostrovsky & Craig, 1996); data of WARM cells and HPC cells are obtained from the cats (Andrew & Craig, 2001; A. Craig & Kniffki, 1985); data of WDR neurons are obtained from the rats (Price et al., 1978). Quoted from Harper (Harper, 2014).

Brain

After initial detection and modulation in the spinal cord, thermal signals are relayed to the thalamus and the cerebral cortex (Figure 1.5), contributing to complex behaviors and responses. It has been thought that the thalamus only relays incoming and outgoing signals, which implies thermotactic signals do not interact and integrate at this stage (Sheridan & Tadi, 2019). A recent study revealed features of neuronal responses to temperature changes both in the primary somatosensory cortex (S1) and the insular cortex (IC), highlighting the central role of IC in thermal perception (Vestergaard et al., 2023). Interestingly, this study identified a small number of neurons responsive to warming stimuli in S1. These findings are supported by brain-wide mapping of thermosensory cortices (Bokiniec et al., 2023).

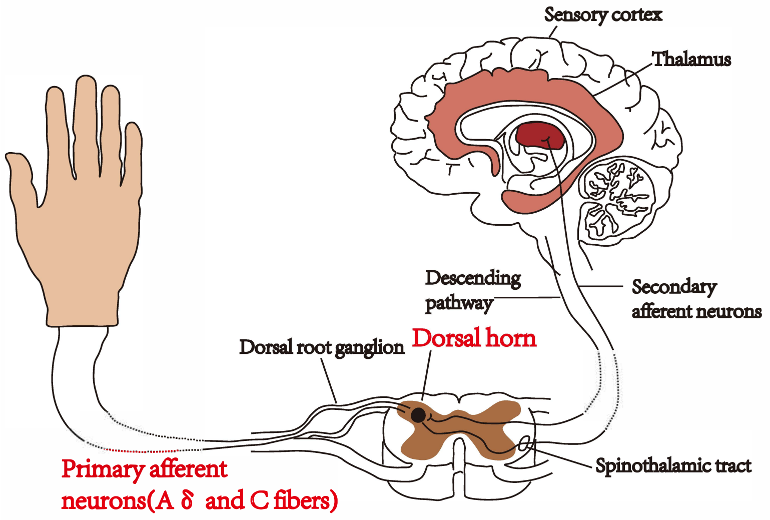


Figure 1.5: Ascending path. Quoted from Kandel (Kandel et al., 2021a) and revised by the thesis author.

The cerebral cortex is thought to be involved in the spatial organization of thermal sensation. Marotta investigated how our brain perceives TGI from temperature (Marotta et al., 2015). The experiment involved crossing fingers to see if burning pain depended on finger location or perceived location in space. Participants adjusted the temperature on one hand to match the perceived coldness on a specific finger on the other hand. She found a significant overestimation of the cold stimulus when it was central within the spatial configuration (warm-cold-warm) compared to when it was peripheral (cold-warm-warm). This effect depended on the spatial configuration of thermal inputs, but it was independent of the finger posture - the TGI for the middle finger was abolished when it was crossed over the index to adopt a spatiotopically peripheral position, while the same effect was newly generated for the index finger by the same postural change.

These psychophysical results suggest that the cerebral cortex perceives TGI based on the overall spatial pattern of temperature, not just individual finger location. She proposed a model involving additional thalamocortical summation of multiple warm stimuli and interaction with a cold pathway from the middle finger. In this model, warm activation is assumed to spread gradually across a neural representation of external space, inhibiting cold on the middle finger. The summation of warm inputs occurs after remapping somatotopic inputs into external spatial coordinates. Crossing the fingers, therefore, reduces the inhibition of cold on the now-peripheral middle finger because it is less affected by spreading warm activation. The stronger cold activation results in stronger inhibition of nociceptive afferents and a reduced TGI. TGI depends on the central spatiotopic position of the cold finger relative to the warm fingers and not on finger crossing. When cold stimulation is given to the index finger, the TGI sensation is reduced relative to the crossed posture in the uncrossed posture.

However, the cortical encoding of temperature has long been poorly understood, and few cortical neurons have been reported to respond to non-painful temperatures. It was not until 2023 that cortical neurons with different spatial and temporal response properties to cooling and/or warming were discovered (Vestergaard et al., 2023). Warm-sensitive, cold-sensitive, and polymodal neurons (sensitive to both warm and cold stimuli) were reported. The firing rate of warm-sensitive neurons increases monotonically from 32 °C. The firing rate of cold-sensitive neurons decreases with temperature starting from 32 °C, first increased, and then plateaus at approximately 25 °C. The firing rate of multimodal neurons is zero at 32 °C. When the temperature increases from 32 °C, the firing rate increases monotonically; when the temperature decreases from 32 °C, the firing rate first increases, and then plateaus at approximately 25 °C. The receptive field of these cortical neurons is still unclear.

1.5 Thermal Sensation and Neural Phenomena

Spatial Pattern Modulates Perception

In the previous sections, I have reviewed the knowledge of the neurobiology of thermal sensation from the skin to the brain. The previous sections did not consider how thermal stimuli might interact with each other to alter the resulting perception. This section will review studies of perceptual phenomena evoked by thermal interaction.

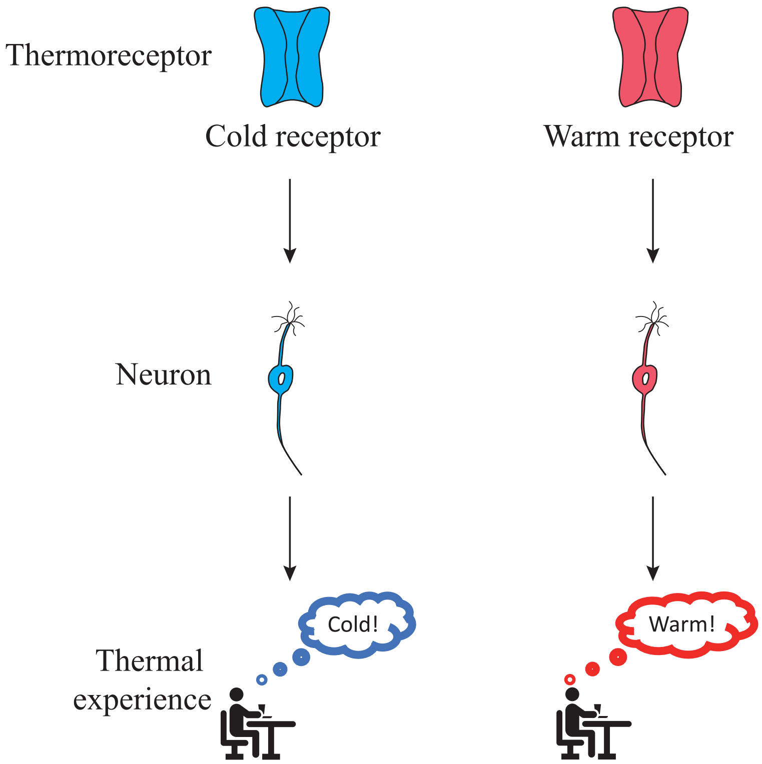


Figure 1.6: Labeled line theory.

It has been thought that thermal sensation is served by thermosensitive neurons sensitive to only one form of stimulation and encode only one perceptual quality (Green, 2004; Melzack, 1996). This theory is called the “labeled line” doctrine (Figure 1.6). Its central premise of neural specificity gained support as electrophysiological studies found evidence of neurons that were selectively sensitive to temperature. It is worth noting that the “labeled line” theory focuses on perceptual quality while lacking an explanation of perceptual boundary.

The discovery of Thermal Grill Illusion (TGI) challenges this classic theory’s “encode only one perceptual quality” point. TGI is a phenomenon in which simultaneous contact with a cold and a warm bar produces a thermal pain sensation (A. Craig & Bushnell, 1994; A. Craig et al., 1996; Defrin et al., 2008; Green, 2004; Harper & Hollins, 2014; Leung et al., 2005; Lindstedt et al., 2011; Marotta et al., 2015; Patwardhan et al., 2019; Saga et al., 2022; Shin & Chang, 2021; Susser et al., 1999; Watanabe et al., 2014) as if one were touching a hot stick (Figure 1.7). Two theories have been proposed for the mechanism of TGI, and both have been discussed as interactions between warm and cold pathways. On the other hand, the mechanism in terms of perceptual boundary has not been discussed. In this thesis, I first focus on the theories that warm stimuli interfere with cold perception and discuss its mechanism.

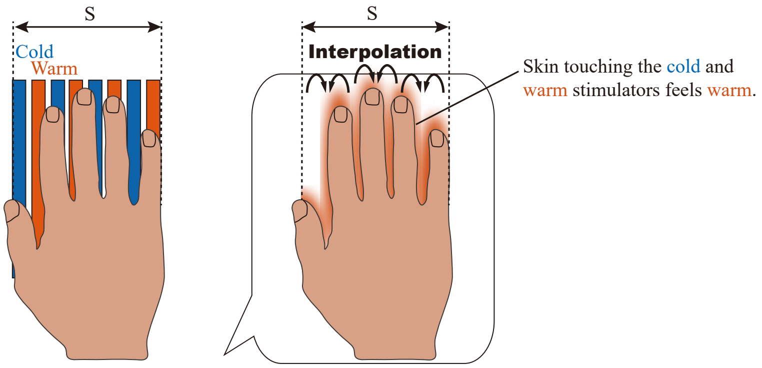


Figure 1.7: Schematic representations of Thermal grill illusion.

Addition Theory

Green investigated thermal sensation with the mild temperature pairs (Green, 2002, 2004). Data were collected on the quality of sensation as well as the intensity. Participants rated temperature and pain perception separately, selecting from a list (nothing, cool, cold, warm, hot, burn, sting, pain) the sensation representing the specific quality experienced on each trial. Using 33 °C as a baseline, cooling to 31 °C and warming from 35 °C to 40 °C resulted in a rating of “hot” on 40.6% of trials.

Furthermore, another group of participants evaluated the intensity of the sensations produced by these sensations. Gentle temperature differences were set up to measure the intensity of the sensory changes caused by the stimulus pairs. For the range of temperature pairs tested, simultaneously warm and cold stimuli were generally perceived with approximately twice the intensity of either stimulus alone. When the warm (e.g., 36 °C) and cold (e.g., 30 °C) stimuli were presented alone and rated as the same intensity, the perceived intensity was twice as high when the two were presented simultaneously.

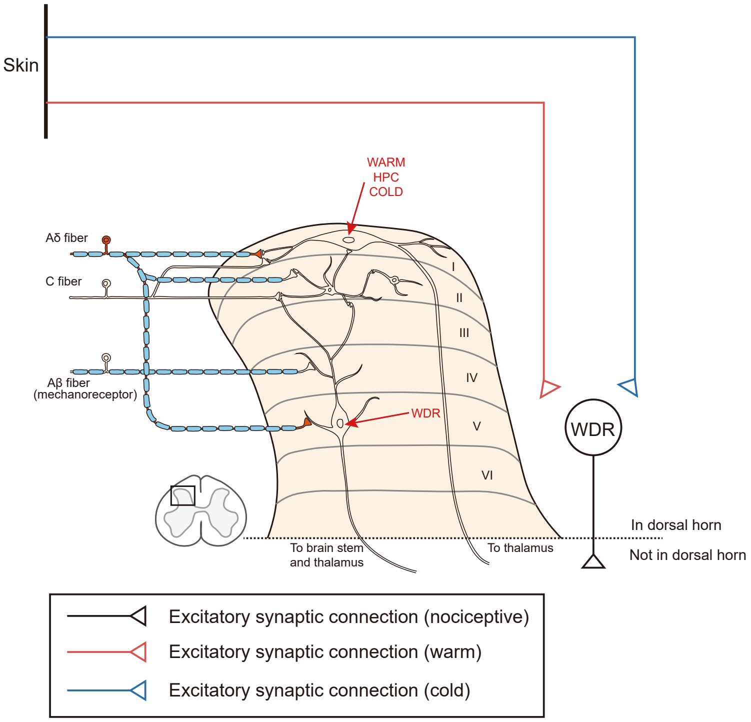


Figure 1.8: Addition theory.

On the other hand, Khasabov discovered wide dynamic range neurons in the dorsal horn of the spinal cord. WDR neurons respond to temperatures as low as 28 °C. They also respond to heating of the skin, but only slightly respond below 40 °C (Cain et al., 2001; Green, 2004). The majority of WDR neurons are located deep (in lamina V) of the dorsal horn, although some are positioned in the superficial layer (in lamina I and lamina II).

According to these observations, Green proposed the addition theory (Green, 2002). Addition theory claims that the “TGI is a mixture of simultaneous sensations of warmth and coldness" (see Figure 1.8). According to this theory, warm and cold signals elicited by the grill converge onto WDR neurons in the dorsal horn, adding their excitatory effects. WDR neurons integrate information from multiple modalities and respond in a graded fashion, spanning the transition from innocuous to noxious heat and cold. Thus, they appear capable of adding inputs, heightening the firing rate to a level normally reserved for noxious stimuli.

The addition theory predicts two psychological assumptions: 1. the greater the difference between the warm and cold stimuli, the warmer it feels; 2. the small difference between the cold and warm stimuli can produce painless heat.

Unmasking Theory

Craig identified specific neuronal responses in cats' spinothalamic tract that are crucial for understanding the Thermal Grill Illusion. He discovered that lamina I dorsal horn "COLD" cells respond selectively to cold stimuli at 20 °C and are inhibited by warmer stimuli at 40 °C (A. Craig & Bushnell, 1994). This differential response is central to the proposed mechanisms of thermal perception and pain.

Further extending his research to human subjects, Craig conducted psychophysical experiments that demonstrated similar patterns of thermal sensation. Subjects reported a "painful thermal sensation similar to a cold sore burn" when exposed to alternating 20 °C and 40 °C stimuli. This sensation was comparable to that produced by cooling to 10 °C, thus suggesting a complex interplay of thermal receptors and neural pathways (A. Craig et al., 1996).

Based on these observations, Craig proposed the unmasking or disinhibition theory, illustrated in Figure 1.9. According to this theory, heat is transmitted from C fibers through the spinothalamic tract to HPC (heat-pinch-cold) neurons in the thalamus via lamina I of the dorsal horn of the spinal cord. Concurrently, cold stimuli and their noxious components are conducted via both the C and Aδ fibers. However, the inhibitory interactions from Aδ fibers towards C fibers and COLD cells towards HPC cells result in selective recognition of cold stimuli, effectively unmasking the pain pathway (A. Craig & Bushnell, 1994; A. Craig et al., 1996). The neuron with a T mark in Figure 1.9 is thought as a transmission neuron. This neuron compares the activity between HPC cells and COLD cells. When the activity of COLD cells exceeds that of HPC cells, it does not generate pain signals; when the activity of HPC cells exceeds that of COLD cells, pain signals are generated and transmitted to the brain.

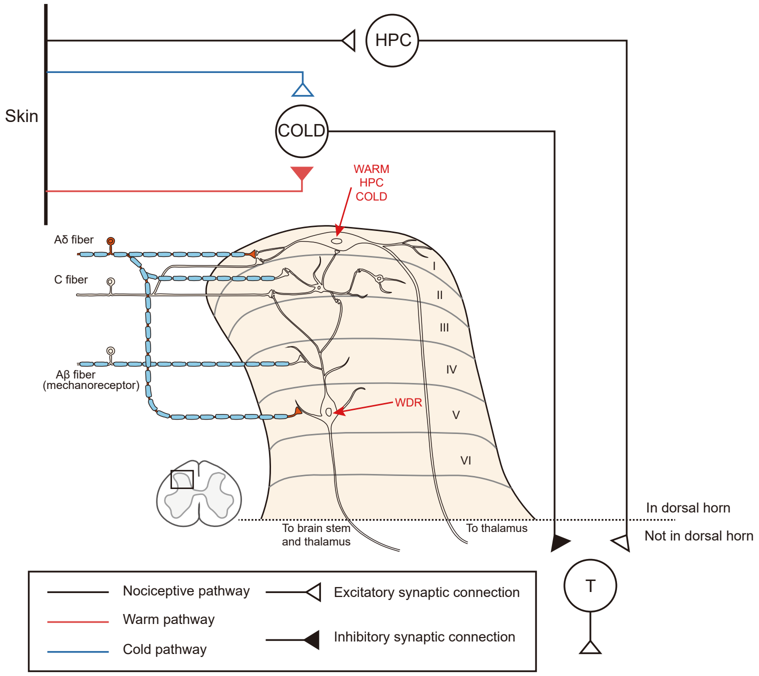


Figure 1.9: Unmasking theory.

However, there are also criticisms of the unmasking theory. Bouhassira analyzed from the viewpoint of whether the illusion increases when one of the two temperatures is made extreme, and the other is made constant (Bouhassira et al., 2005). According to the unmasking theory, if the temperature of the cold stimulus is kept constant and the temperature of the warm stimulus is raised, the inhibition of COLD cells becomes stronger, and the HPC-COLD difference should increase, so the illusion will be predicted to increase. On the other hand, in the unmasking theory, it is predicted that lowering the temperature of the cold bar does not affect the intensity of TGI because the signals of both HPC and COLD cells increase almost equally. Bouhassira found that increasing the temperature of the warm grill increased the TGI, as predicted by the unmasking theory but decreasing the temperature of the cold grill also found a significant increase, which is a contradictory result (Bouhassira et al., 2005).

Figure 1.3 illustrates the inputs of the spinal cord and the locations of the second-order neurons. Neurons in lamina I of the dorsal horn receive direct input from myelinated (Aδ) fibers, as well as direct and indirect input from unmyelinated C fibers through lamina II neurons. The unmasking theory claims the process that warm stimulus inhibits COLD cells in lamina I. Neurons in lamina V receive low-threshold input from large-diameter myelinated fibers ($A\beta$) from mechanoreceptors, as well as input from afferent fibers (Aδ and C fibers). The addition theory claims the addition of activity of warm and COLD cells occurs here. Lamina V neurons send dendrites to lamina IV, where they are contacted by the terminals of primary afferents of $A\beta$. Lamina III dendrites from cells in lamina V contact the axon terminals of lamina II neurons.

The addition theory and unmasking theory provide insights into the neural mechanisms that evoke painful heat or burning sensations. According to the addition theory, the perception of pain results from the additive effects of simultaneous warm and cold stimuli, leading to a burning sensation. The unmasking theory, on the other hand, suggests that normally inhibited nociceptive pathways become unmasked and active, resulting in a burning sensation. While these theories effectively explain the pathways involved in generating intense and painful thermal sensations, they do not account for the mechanisms underlying the perception of mild warmth.

Since the addition theory and unmasking theory do not explain every aspect of thermal sensation, there are some pathways unknown. Evidence can be found in the previous studies (A. Craig & Bushnell, 1994). Craig points out that "integration could be performed by cells in the thalamus or cortex that are excited by HPC activity and inhibited by COLD activity." This means the T neuron in Figure 1.9 can be found in the thalamus or cerebral cortex. The

T neuron in the thalamus or the cortex receives inhibition from the COLD cells in the lamina I of the dorsal horn. However, the inhibitory connection indeed cannot conduct far. Instead, the conduction from the spinal cord to the thalamus or the cortex suggests an excitatory connection pathway, which is not clear in the unmasking theory. The unknown pathways should generate the mild warm sensation.

Previous studies on TGI focus on the quality of the burning pain resulting from spatial configuration of warm and cold stimuli. The finding of TGI has indicated that the spatial pattern of stimuli modulates perception. However, TGI is not the only phenomenon that has been found to modulate the perception. Besides TGI, a sense of warmth has been reported to arise between spatially discrete warm stimuli. When three stimuli are touched simultaneously with the middle three fingers of one hand, but only the two outside stimuli are cooled or heated, the central (neutral) stimulus is also perceived as cold or hot (Figure 1.10). This phenomenon is known as TR (Arai et al., 2021; Cataldo et al., 2016; Green, 1977; Hashiguchi, 2021; Ho et al., 2019; Ho et al., 2010, 2011; Liu et al., 2021; Son et al., 2023).

Both TGI and TR are spatially interpolated phenomena of thermal sensation. Previous studies focus on the interesting quality of the resulting perception (the burning pain evoked by TGI and the heat or cold evoked by TR). Instead, the characteristic of the perceptual boundary lacks focus. TR is a phenomenon in which a sense of warmth arises between spatially discrete warm stimuli . Additionally, the TGI can be seen as a phenomenon in which multiple pairs of spatially distributed warm and cold stimuli induce a burning sensation or pain. From this perspective, both TR and TGI are evoked within the physical boundary formed by the physical stimuli.

Temporal Pattern Modulates Perception

In the previous section, I discussed the mechanism explained only in terms of spatial gradient. In this section, I will discuss the mechanism explained only in terms of temporal sequencing. Paradoxical Heat Sensation (PHS) is a temperature phenomenon that occurs when the skin is cooled (Susser et al.,

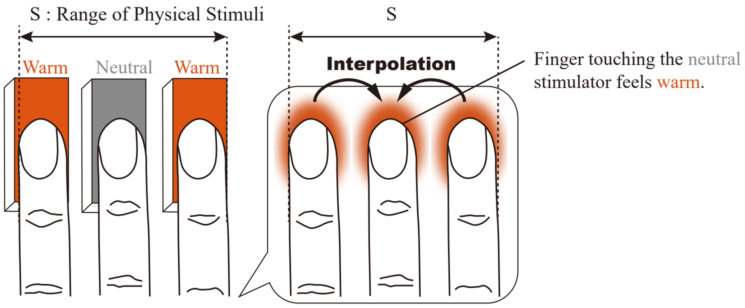


Figure 1.10: Schematic representations of Thermal referral.

1999). Even if the stimulation technique is improved to make it more strongly felt, the general public does not feel it very much. On the other hand, since it is often observed in patients with nerve damage, it has not been studied as a normal temperature phenomenon. This section is a case study of the theory that temperature stimulation interferes with cold perception.

PHS is a thermal phenomenon resulting from temporal integration of thermal stimulation (Susser et al., 1999). Goldsheider describes that the paradoxical sensation was warmth, not heat, and was caused by direct cooling of a warm area. Jenkins and Karr further show that paradoxical warmth occurs more frequently when the skin is heated before cooling. Thus, this phenomenon can be seen as a sense of warmth resulting from cold stimulation before warm stimulation (Hämäläinen et al., 1982).

Studies of PHS have been based on the knowledge gained from TGI, with the viewpoint that PHS is a type of TGI. Susser showed that the latency to respond to paradoxical heat coincided with the conduction velocity of C fibers (Susser et al., 1999). Considering that normal cold signals are conducted by Aδ fibers, this finding suggests that signals that produce heat sensation and are conducted by C fibers are generated. Accordingly, Susser suggests that the activation of COLD cells is inhibited by warm stimulation; the nociceptive HPC cells are, in turn, unmasked, transmitting signals that produce heat sensation to the brain. Although how warm and cold signals temporally integrate is still a problem, Susser's finding supports the perspective that PHS shares the same mechanism with TGI.

The different conduction speeds of C fibers and Aδ fibers might result in the special stimulation sequence when evoking PHS. As aforementioned, there is a time difference of about 1 s between C fiber and Aδ fiber when they conduct through the primary afferent of about 1 m into the spinal cord. The premise of integrating warm and cold stimulation is the co-existence of warm and cold signals in the spinal cord. Thus, it is impossible to evoke an integration if applying cold stimulation before warm stimulation. Instead, it is possible to integrate warm stimulation before cold stimulation. From this point of view, it is possible to create a new thermal illusion by cleverly designing it based on the spatiotemporal patterns of the warm and cold stimuli received by the spinal cord.

1.6 Elimination of Physical Constraints In the Use of Illusions

Currently, there is a physical limitation of heat in temperature presentation, and it is physically unfeasible to present temperatures that produce heat frequently while limiting heat as much as possible, which is why little progress has been made in temperature sensory research.

A commonly used method for generating temperature stimuli involves the use of Peltier elements. These devices function based on the Peltier effect, where an electric current is passed through the junction of two different types of conductors, causing heat to be absorbed at one junction and released at the other. This principle allows Peltier elements to create both heating and cooling effects. However, using Peltier elements to present temperatures that frequently generate heat requires a large electric current, which in turn produces a significant amount of heat. To manage this heat, high-capacity water cooling systems are necessary to dissipate it effectively. This requirement for substantial cooling infrastructure significantly limits the practical application of temperature stimulation schemes based on Peltier elements.

However, it is thought to be capable of presenting temperature even though it does not produce localized heat. To be precise, the above heat problem can be alleviated if it can be interpreted that humans “feel the temperature

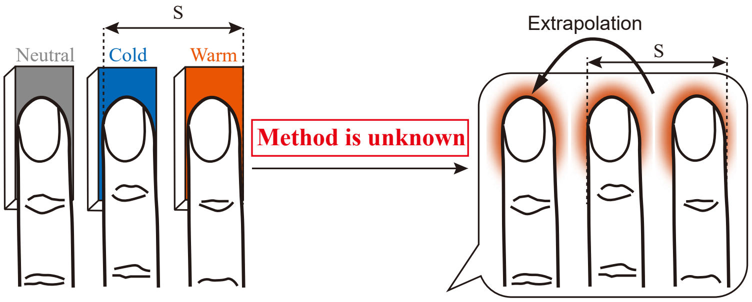


Figure 1.11: Problem in evoking perception outside boundary. Red circles stand for warm sensations.

there" at locations that do not receive a thermal stimulus. The environment that humans perceive is not the same as the physical stimuli of the external environment. Since physical phenomena and perceived phenomena do not coincide, physical constraints can be relaxed and eliminated. The temperature of the leftmost finger in the figure does not change because it receives neutral stimuli. However, it is perceived to be warm. If we use this difference between physical and perceptual phenomena, we can display temperature at the skin area without thermal stimulation. This method based on perceptual understanding can decrease the consumed energy when we display temperature using Peltier elements. However, the method of evoking a perception outside the physical boundary remains unclear (Figure 1.11).

Since it is possible to create the next generation of temperature presentation devices using engineering illusions only by understanding the human perception mechanism, understanding the human information processing mechanism to generate extrapolations of temperature sensation is the subject of this thesis.

1.7 A Functional View of Spatiotemporal Integration of Thermal Sensation

Functionally, thermal sensation provides information about the environment temperature and object temperature. When thermal sensation provides information from a radiant source, it is interoceptive because it takes part in the adjustment of body temperature through the circulatory system; on the other hand, when thermal sensation provides information about object temperature with touch, it is exteroceptive because it focuses on processing the thermal characteristic when touching the object. This means thermal sensation serves both thermoregulation (interoceptive) and haptic perception (exteroceptive). This duality of function in thermal sensation is different from vision and audition because thermal sensation is required to satisfy humans' most basic survival needs.

The duality of function in thermal sensation to serve both thermoregulation and haptic perception "requires a sensitive and flexible temperature-sensing system that can process thermal stimulation differently depending on its source and thermoregulatory importance." Such sensitivity and flexibility in thermal sensation require humans to make the most use of both spatial and temporal information in local areas. This offers the possibility of spatiotemporal integration of local thermal information. By using spatiotemporal integration, neurons that respond to thermal stimuli fire more frequently and thus make humans process local thermal signals when touching an object sensitively.

Evidence for one way to achieve this flexibility comes from a perceptual illusion known as the TR. In TR, the thermal sensation is transferred to an adjacent skin site with the same mechanical stimulus but is itself thermoneutral. Heat transfer even occurs between the fingers of the hand. This effect can be experienced by touching two cool (e.g., refrigerated) coins with the first and third fingers while touching a neutral coin (e.g., keep warm in hand) with the second (middle) finger. All three coins feel cool.

The change in perceptual boundary, especially the enlargement of perceptual boundary, also potentially achieves this flexibility in thermal sensation. Imagine holding a cup of hot water in the hand. The heat pain might make your entire hand feel hot, even though only a small portion is directly touching the cup. This enlargement of perceptual boundary helps us evaluate the overall temperature of the object and the potential danger.

1.8 Purpose of Thesis

In summary, influenced by the historical “labeled line” doctrine, past research on thermal sensation has often been limited to one perspective of thermal sensation—the quality of the perception. Although the addition theory and the unmasking theory have different claims, both the theories focus on the quality of the resulting perception, e.g., cold, cool, warm, cold, burning pain (Figure 1.12). For other characteristics of thermal sensation, such as perceptual boundary, past research has lacked sufficient understanding. The models proposed in the past have also been unable to adequately explain the formation of the perceptual boundary, let alone its changes.

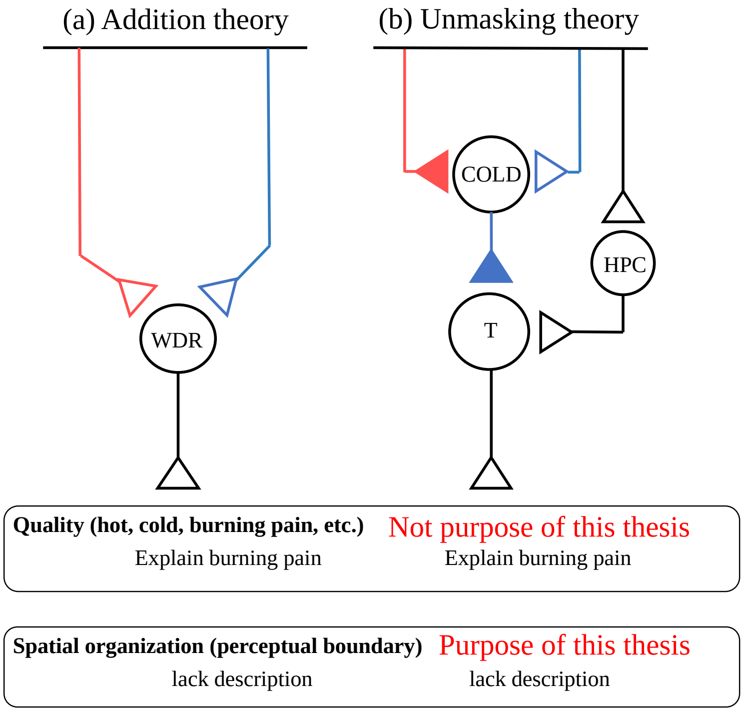


Figure 1.12: Summary of the known theories.

This thesis studies the phenomenon of the Extrapolation of Thermal Sensation (ETS), an enlargement of the perceptual boundary of thermal sensation beyond their physical boundary (Figure 1.13). In this thesis, I aim to investigate the thermal, spatial, and temporal characteristics of ETS and clarify the characteristics of this phenomenon using psychophysical methods. I will discuss the spatiotemporal relationship between ETS and the conditions for the generation of classic thermal illusions, TGI and PHS, and use the classic theory of TGI to explore insights into the perceptual boundary. The results of the discussion will help us understand the classic illusion of TGI at a deeper level. Based on the understanding of these characteristics, a spatiotemporal mechanism underlying the Extrapolation of Thermal Sensation is proposed.

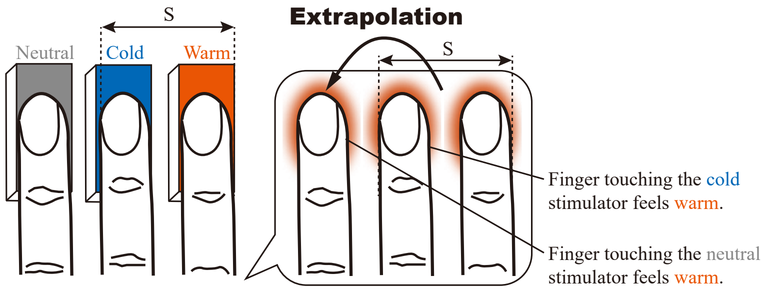


Figure 1.13: Schematic representations of Extrapolation of Thermal Sensation (ETS).

To achieve this, the thesis is structured around two main objectives:

- Proposal of Underlying Mechanisms: To identify and describe the neural and perceptual processes that enable the extrapolation of thermal sensation from discrete skin inputs to a continuous perceptual experience. This involves demonstrating how thermal stimuli are integrated over time and space to form a broader perceptual boundary.
- Demonstration of characteristics of ETS by comparing with Thermal Grill Illusion: To investigate the underlying mechanism of ETS, this thesis demonstrates the spatial and temporal characteristics of ETS by comparing with TGI.

This thesis employs a combination of experimental studies and theoretical analysis to achieve its objectives. Each chapter systematically builds upon the findings of the previous ones, using controlled experiments to isolate and examine different aspects of ETS:

Chapter 1 Discrete in the Skin, Continuous in the Mind

This chapter reviews the existing literature to understand how spatially discrete sensory spots react to thermal stimuli, creating a spatially continuous perception within the brain. The discussion follows the trajectory of the somatosensory pathway, starting from the receptors in the skin and extending to the formation of perceived objects. Then, this chapter will discuss the already-known interpolation phenomenon generated from thermal signal processing, including exploring prevailing theories. Two primary theoretical frameworks propose mechanisms for integrating warm and cold signals: the unmasking theory and the addition theory. These frameworks attempt to explain how such integration can evoke an interpolation phenomenon known as the Thermal Grill Illusion. From the question of perceptual boundary that these theories cannot answer, I point out the value of investigating the perceptual boundary of thermal sensation.

Chapter 2 Perceptual Boundary of Thermal Sensation Is Enlarged by Spatiotemporal Integration of Thermal Sensation

Thermal displays that use thermoelectric modules face a contradiction between high-speed display and cooling ability when displaying thermal sensation. Thermal illusions are expected to address this problem. However, research on thermal illusions remains inadequate, and unknown elements for inducing thermal illusions must be elucidated. Time may be one such element. Chapter 2 will report a phenomenon: the sensation at the middle finger's fingertip and root of the finger changes when receiving stimuli in different temporal sequences of thermal inputs, but the traditional model cannot explain this. I propose a model to describe the differences in spatially distributed perception induced by the temporal effect based on the distribution difference and interactions of thermoreceptors. In this model, warm and cold receptors are assumed to have different effective ranges owing to their different spatial distributions. In addition, receptors have an inhibitory and disinhibitory effect on the other receptors in the effective range. This model clarifies the temporal effect on thermal sensation and describes how receptors' effective range and interactions influence thermal sensation.

Chapter 3 Warmth Spatially Spreads With an Increase of Temperature Difference

Previous chapter reported that perception at the fingertip and base of the finger (middle finger) changed when receiving stimuli in different temporal sequences of thermal inputs. Warmth (far from fingertip) prior to cold stimulus (close to fingertip) induces a reliable warmth outside cold stimulus (Extrapolation of Thermal Sensation). A model based on inhibition and disinhibition of receptors is proposed. In this model, when ETS is evoked, TGI is also generated. However, it is unclear that ETS shares the same mechanism with TGI. Chapter 3 will claim a common mechanism based on the transition of the spatiotemporal conditions among ETS, PHS, and TGI. Accordingly, the unmasking theory or the addition theory that has been proposed to explain TGI should interpret ETS. Then, Chapter 3 will investigate the relationship between Extrapolation of Thermal Sensation and the temperature of warm and cold stimuli to test whether the addition or unmasking theory also works in ETS. This study will provide the first evidence of the relationship between ETS and TGI.

Chapter 4 Spinal Segments Dependently Interfere With ETS and TGI Differently

Chapter 3 investigated the relationship between ETS and the temperature of thermal stimulus to study whether ETS is supported by the unmasking theory or addition theory that interprets the phenomenon of TGI. Chapter 4 will investigate the spatial characteristics of ETS. I will 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. I will also investigate the ETS mechanism by comparing it with TGI and whether ETS has the same segmental effect on the fingers and lower leg.

Chapter 5 General Discussion

Chapter 5 will synthesize this thesis's findings, compare the model proposed in Chapter 2 and Chapter 4, and propose a model that explains the findings.

Chapter 6 Conclusion

The final chapter will conclude the findings in this thesis and outline future research avenues opened by this work.

Chapter 2

PERCEPTUAL BOUNDARY of THERMAL SENSATION IS ENLARGED by SPATIOTEMPORAL INTEGRATION of THERMAL STIMULATION

The question of how we sense the physical world through somatic sensation has fascinated humankind for millennia.

- 2021 Nobel Prize in Physiology or Medicine

2.1 Summary

In the previous chapter, I reviewed the generation process of spatially continuous temperature perception from thermal stimulation. Thermal stimulation applied to the human skin is sensed spatially discretely within the skin by primary afferents. As a result of spatial interpolation of the thermal sensation within the spinal cord and projection to the primary somatosensory cortex, it is formed as a spatially continuous temperature perception. In addition, I reviewed the classic thermal phenomena, e.g., TGI and TR. These phenomena occur when warmth or cold is perceived just at the location of the physical stimulus or within the physical boundary formed by multiple stimuli. Perception generated outside the physical boundary is not reported. This chapter investigates the enlargement phenomenon of the perceptual boundary of thermal sensation (ETS). The study investigated whether ETS could occur, particularly focusing on changes in perception at the fingertip and base of the finger (middle finger) when receiving stimuli in different sequences of thermal inputs. The results reveal that warmth (applied far from the fingertip) prior to a cold stimulus (applied close to the fingertip) induces a reliable sensation of warmth outside the area directly stimulated by cold. A similar phenomenon is induced at the base of the finger. It was observed that when participants experienced this phenomenon (perceived warmth), the temperature of the extrapolated part did not change, indicating that ETS is not a result of heat conduction. These findings suggest that the perceptual boundary of thermal sensation can be expanded, leading to a sense of warmth being induced outside the physical boundary when warmth is applied prior to a cold stimulus.

2.2 Introduction

The unmasking theory and addition theory have attempted to explain the interaction between WARM and COLD cells in the central nervous system (A. Craig & Bushnell, 1994; Green, 2002). It is important to first clarify that both of these theories can be considered non-causal models that primarily assume equilibrium states. This means that the final state after both stimuli have been applied for a long enough time is independent of the order of stimulus presentation. Consequently, these models address steady-state problems rather than transient response problems.

However, it remains unclear whether there are different resulting sensations under different time sequences of thermal inputs, suggesting a potential transient response issue. To investigate this, I will discuss the theoretical results using the unmasking theory and addition theory, while also considering the possibility of a model that is dependent on the stimulus order as a hypothesis for comparison.

I first discuss the results that the unmasking theory predicts. In the case that warm stimuli are applied first, then cold stimuli are applied as well. According to the unmasking theory, when warm stimuli are applied, the COLD cells are slightly inhibited (the spontaneous firing is inhibited), leading to a slight unmasking of HPC cells. The spontaneous firing rate of COLD cells and HPC cells is approximately 6 Hz and 1 Hz, respectively (for reference, see Figure 1.4). When the COLD cells are inhibited by warm stimuli, the firing rate of COLD cells possibly still exceeds that of HPC cells. Thus, only warmth is generated. When the cold stimuli are also applied, the COLD cells are excited but soon get inhibited by warm stimuli, leading to a huge unmasking of HPC cells. At this time, the firing rate of HPC cells exceeds that of COLD cells. Thus, TGI(burning pain) is generated.

In the case that cold stimuli are applied first, then warm stimuli are applied as well. According to the unmasking theory, when cold stimuli are applied, the COLD cells are activated. At this time, the firing rate of COLD cells exceeds that of HPC cells. Therefore, only cold is generated. When the warm stimuli are also applied, the COLD cells get inhibited by warm stimuli, leading to a huge unmasking of HPC cells. Because the firing rate of HPC cells exceeds that of COLD cells, TGI (burning pain) is generated.

Here, I discuss the results that the addition theory predicts. In the case that warm stimuli are applied first, then cold stimuli are applied as well, the WDR neurons receive only warm inputs. At this time, only warmth is generated. When the cold stimuli are also applied, the WDR neurons receive both warm and cold inputs, leading to a higher activation. Thus, TGI (burning pain) is generated.

In the case that cold stimuli are applied first, then warm stimuli are applied as well. According to the addition theory, the WDR neurons receive cold inputs when the cold stimuli are applied. Thus, only cold is generated. When the warm stimuli are also applied, the WDR neurons receive both warm and cold stimuli, leading to a higher activation. Thus, TGI (burning pain) is generated.

PHS, a phenomenon resulting from a particular sequence of stimuli, provides evidence that different thermal sensations are produced when thermal stimuli are applied in different time sequences (Susser et al., 1999). It is reported that PHS occurs frequently when the skin is heated before cooling. On the contrary, there is no report of PHS when the skin is cooled before heated. Thus, this phenomenon is a sense of warmth resulting from a particular "warm-cold" sequence (Hämäläinen et al., 1982).

In summary, both theories predict a change from a warm sensation to burning pain when applying warm stimuli prior to cold stimuli, and a change from a cold sensation to burning pain when applying cold stimuli prior to warm stimuli. Although the final perceptions are the same, the transient responses should differ. These results suggest that different qualities of transient response may be obtained under different time sequences of thermal inputs.

To further explore this, I propose to study whether thermal sensation can be perceived outside the physical boundary by applying different sequences of thermal inputs. This chapter will compare the predicted outcomes of the unmasking theory and addition theory with a hypothetical model that depends on the order of stimulus presentation, allowing for a comprehensive understanding of the transient responses in thermal perception.

2.3 Possibility of Change in Perceptual Boundary

In the previous section, I explore the spatially interpolated phenomena of thermal sensation. In these interpolations of Thermal Sensation, the perceptual boundary is limited to the physical boundary. It is still unclear whether the perceptual boundary can be changed, especially enlarged. This section will discuss the potential existence of Extrapolation of Thermal Sensation.

The concept of Extrapolation of Thermal Sensation posits that the perceptual boundary of thermal sensation may extend beyond the physical boundary of thermal stimuli. This hypothesis stems from the observation that the sensory perception of warmth, unlike other sensations, e.g., mechanical sensation, is characterized by a notably diffuse boundary. The fundamental reason for this difference can be attributed to the anatomical and physiological characteristics of the sensory systems involved in perceiving thermal stimuli.

The density of thermosensitive spots on the human skin is significantly lower than that of mechanical sensory spots. Research indicates that thermosensitive spots constitute only about 2-10% of the density of mechanical sensory spots (There are over 100 mechanical sensory spots per cm^2 on the fingertip. Still, there are only 3 - 15 cold spots and 1 - 4 warm spots (Arens & Zhang, 2006)). Spatially discrete sensitive spots (including mechanical sensory spots and thermosensitive spots) realize lateral interaction between neurons of the same layer through lateral inhibition (S.-I. Amari, 1980; Kohonen, 1982; Von der Malsburg, 1973). Lateral inhibition is a function of distance: an excitatory effect is applied to neurons that are closer and an inhibitory effect is applied to neurons that are farther away. Thus, assuming that there is a stimulus on the skin, neurons within a circle centered on that stimulus will be active, but neurons farther away from the point stimulus will be inhibited. In addition, lateral inhibition has been confirmed as a common mechanism in the central nervous system (including the spinal cord, thalamus, and cerebral cortex) that maintains the topology of perceptual signaling from the periphery to the cerebral cortex (Werner & Whitsel, 1968). The final result of this effect is that perception within a certain range centered on that stimulus presents a spatial continuity (Chorzempa, 1980). Lower-density sensory spots require a larger interaction range to maintain this lateral interaction between neurons in the same layer. This also leads to the perception of a larger area.

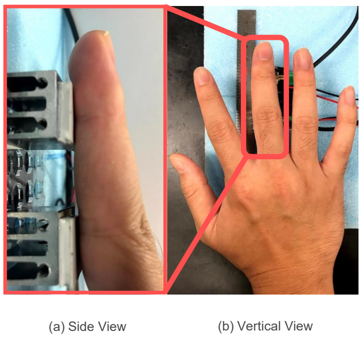
Another critical aspect in the conceptualization of Extrapolation of Thermal Sensation is the role of C fibers, the primary afferents responsible for transmitting warm signals from peripheral sensory receptors to the spinal cord. These fibers are unmyelinated and span considerable lengths—often exceeding one meter from fingertip to spinal cord. The unmyelinated nature of these fibers results in slower conduction speeds and potentially increases the temporal summation. In addition, it is known that warm stimulus conducted by C fibers inhibits cold stimulus (A. Craig & Bushnell, 1994). Warm signals might accumulate and result in the inhibition of adjacent cold signals, finally leading to an enlargement of warmth.

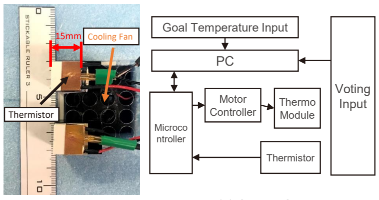
Moreover, second-order neurons in the sensory pathways of warmth detection are responsible for relaying information from primary afferents to higher brain centers. These neurons tend to integrate signals over a much larger area. Animal experiments show that COLD cells in the spinal cord have a receptive field that covers one to two fingers (Dostrovsky & Craig, 1996); the receptive field of HPC cells is the entire central pad and the glabrous portion of two toes (A. Craig & Kniffki, 1985); WDR neurons have a wide receptive field that covers over 80% of the hand (Menetrey et al., 1977). This integration process allows for a single neuron to respond to stimuli affecting extensive skin regions, which can lead to a perception of warmth that extends beyond the direct area of stimulus application.

2.4 Methods

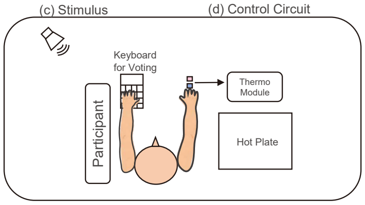
Experimental Setup

I created a thermal display to conduct all the experiments in this chapter (Figure 2.1). The thermal display consists of two 15 mm x 15 mm Peltier thermoelectric modules (TEC1-01705T125, Kaito Denshi Co., Ltd.), two heat sinks for thermoelectric modules, two thermistors (103JT-025, ATC Semitic, Ltd.), a dual-channel DC motor controller (DBH-12V, MiZOELEC), a 32-bit microcontroller (mbed NXP LPC1768, NXP Semiconductors Taiwan Ltd.),


(a) Side View (b) Vertical View



(c) Stimulus (d) Control Circuit



(e) Setup in the experiments

Figure 2.1: Experimental setup in Chapter 2.

and one cooling fan. Thermoelectric modules are fixed to the heat sinks, while thermistors are fixed to the surface of the thermoelectric module by copper foil tape with heat conduction. I prepared a 180 mm x 150 mm x 120 mm foam board with a 50 mm x 50 mm hole for the cooling fan. With the thermoelectric modules, the heat sinks were placed on a perforated plastic plate above the cooling fan. A downward wind from the cooling fan kept the heat transferred by modules away from the skin, so the heat generated by modules did not influence the observation spot. The microcontroller adjusts the temperature of the module in the PI control. To maintain the participants' skin temperature at a thermally neutral temperature, we prepared a warm plate consisting of a copper block immersed in a constant temperature heat sink (TMi-150, AS ONE Co.). By controlling the water temperature, the surface of the copper block can be held at 32 °C. Prior to the experiment and in the intertrial interval (ITI), participants were instructed to place their right hand on a copper block to maintain skin temperature as 32 °C. I prepared a keyboard for voting. A beep was set up to instruct all the experiments.

Experiment 2.1: Temporal Effect Under Near-Cold, Far-Warm Configuration

Data in this experiment were obtained from 15 participants (11 males and 4 females; average 26.5 years). Their finger-length data were recorded. The distances between fingertip and distal interphalangeal joint (DIP), DIP and proximal interphalangeal joint (PIP), PIP and metacarpophalangeal (MCP) joints were 24.73±2.11 mm, 24.13±2.06 mm and 27.20±3.41 mm, respectively. Participants suffering from pain, diseases causing potential neural damage (e.g., diabetes), systemic illnesses, and mental disorders were excluded. The experimental procedures were approved by the Research Ethics Committee of Osaka University and were conducted by the guidelines outlined in the Declaration of Helsinki.

Prior to the experiment and in the intertrial interval, participants were instructed to place the right hand on a warm plate to adjust the skin temperature to 32 °C. The room temperature was maintained at 25 °C. In this experiment, we assessed the cues associated with perceived thermal sensation by comparing experimental conditions. Percentages of hot judgments in light of temporal sequences and stimulus patterns were assessed while keeping the warm stimulator at 43 °C and the cold stimulator at 15 °C. The temporal sequences factor was divided into five states when receiving thermal stimuli (see Figure 2.2):

- Far to Near: The spot far from the observation spot receives stimulus first, after which the spot close to the observation spot receives stimulus as well.
- Near to Far: The spot close to the observation spot receives stimulus first, after which the spot far from the observation spot receives stimulus as well.
- Simultaneous: Spot far from observation spot and spot close to observation spot receive stimulus simultaneously.
- Near: Only spot close to observation spot receives stimulus.

- Far: Only spot far from observation spot receives stimulus.

In this experiment, I investigated the perception under Near-Cold, Far-Warm configuration: The spot close to the observation spot receives a cold stimulus, while the spot far from the observation spot receives a warm stimulus. I set the base of the finger and the fingertip as the observation spot. I set the distal interphalangeal joint (DIP) and the proximal interphalangeal joint (PIP) as two stimulation spots. Thus, when the fingertip was the observation spot, DIP and PIP were the close and the remote stimulation spot; when the base of the finger was the observation spot, PIP and DIP were the close and the remote stimulation spot. Prior to each trial, participants were instructed to place their right hand on the warm plate for at least 30 s. They were then instructed to place the middle finger of the right hand several millimeters above the thermal display. The stimulus onset asynchrony (SOA) period was set to 5 s. As mentioned in Chapter 1, warm and cold signals spend about 1 s and 0.1 s conducting through the primary afferent into the spinal cord, respectively. This setting ensures that the first signal has been processed in the central nervous system before the second signal starts to conduct. When hearing the first beep, they placed the first joint on the display, followed by another (5 s after the first beep) when hearing the second beep. They were asked to respond to the sensation at the fingertip immediately after completing the motion. A two-alternative forced choice (2AFC) standard psychophysical protocol was used. Participants were instructed to answer HOT or COLD. Ten trials were performed under each experimental condition. Stimuli were applied randomly.

Experiment 2.2: Temporal Effect Under Near-Warm, Far-Cold Configuration

In Experiment 2.1, we observed thermal sensation under Near-Cold, Far-Warm configuration. However, thermal sensation under the reversed configuration remains unknown. In this experiment, I investigated the perception under Near-Warm, Far-Cold configuration: The spot close to the observation spot receives a warm stimulus, while the spot far from the observation spot re-

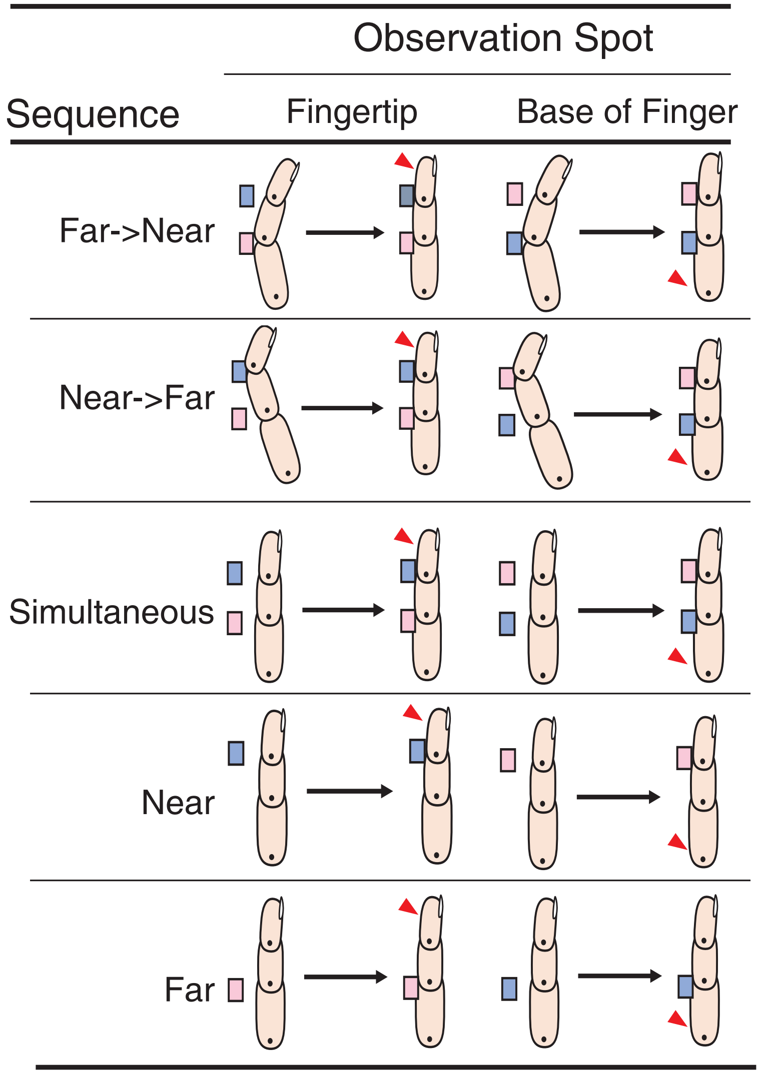


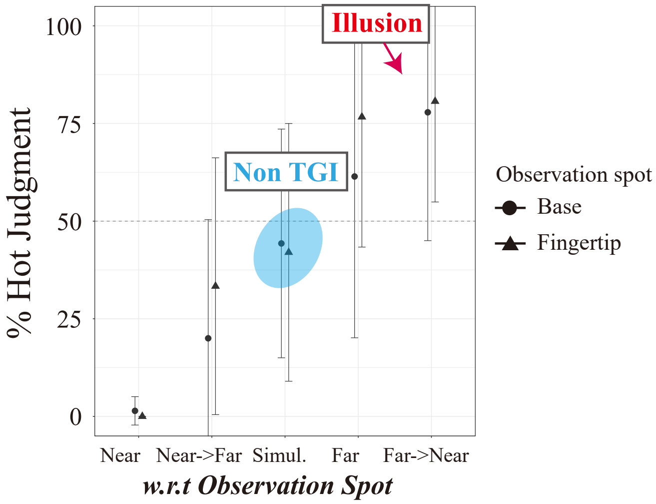
Figure 2.2: Experimental conditions in Chapter 2. The blue and pink squares stand for the cold and warm stimuli, respectively. The red triangles point to the observation spot in the experiments. Participants were instructed to answer HOT or COLD at the observation spot immediately after completing the temporal sequence.

ceives a cold stimulus. Fourteen participants (10 males and 4 females; average 26.7 years) were recruited. The distances between the fingertip and DIP, DIP and PIP, PIP and MCP joints were 25.05±1.75 mm, 24.57±1.59 mm, and 27.57±3.09 mm, respectively. One male and one female were new to the task; the remaining nine males and three females had served in Experiment 2.1 or knew thermal sensation. None knew the results of Experiment 2.1, nor did any know the purpose of the present experiment. The methodology was the same as Experiment 2.1, except that participants were asked to describe the sensation at the finger's base right after completing the motion (see Figure 2.2).

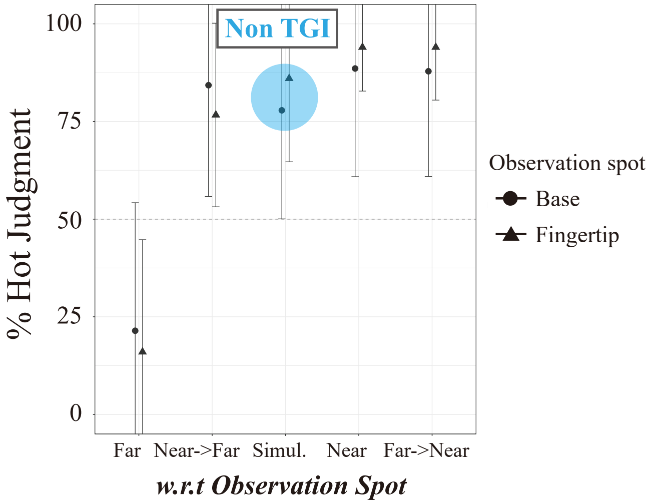
2.5 Results

Figure 2.3. (a) represents the results under Near-Cold, Far-Warm configuration. The horizontal axis stands for the temporal sequence of stimuli and the vertical axis stands for the percentage hot judgment. Results for each temporal sequence at the fingertip were based on 150 trials (15 participants x 10 trials). The corresponding results at the base of the finger were based on 140 trials (14 participants x 10 trials). 0% means that cold was felt in all the trials and 100% means that heat was felt in all the trials. Percentage hot judgment increases from 0% to about 80% as the temporal sequence is, in order, near, near to far, simultaneous, far, and far to near both for fingertip and base of the finger. It is thought that TGI (burning pain) will be generated when applying warm and cold stimuli simultaneously, i.e., a high hot judgment should be obtained under the simultaneous condition. However, in this experiment, the result under the simultaneous condition (the blue circle in Figure 2.3. (a)) was 50%, suggesting that no TGI was evoked in this experiment. In addition, warmth was observed under the far to near sequence. Since there was no warm stimulus applied at the fingertip or the base of the finger, this result indicated that an illusionary warmth was perceived outside the cold stimulator when applying a warm stimulus (far from the observation spot) prior to the cold stimulus (close to the observation spot).

In contrast, Figure 2.3. (b) represents the results under Near-Warm, Far-Cold configuration. Percentage hot judgment keeps a high level (over 75%)



(a) NearCold & FarWarm



(b) NearWarm & FarCold

Figure 2.3: Experimental results in Chapter 2.

except for “far” for both fingertip and base of the finger. Even in this case, the result under the simultaneous condition (the blue circle in Figure 2.3. (b)) was not the highest. Thus, it is difficult to claim that TGI was evoked in this experiment.

The results first demonstrated that the temporal sequence of stimuli influences thermal sensation. More interestingly, I found a paradoxical heat sensation at both the fingertip and base in the “Far to Near” condition. Indeed, about 85% of the participants in Experiment 2.1 reported this illusion at the fingertip, and approximately 70% of the participants in Experiment 2.2 reported this illusion at the base of the finger. Thirteen participants who took part in Experiment 2.1 (11 of them reported the illusion) also took part in Experiment 2.2. Among the 11 participants, 7 reported the illusion at the base of a finger. On the other hand, 13 participants who took part in Experiment 2.2 (9 of them reported the illusion) also participated in Experiment 2.1. Among the nine participants, seven people reported an illusion at their fingertips. These results indicated that the generation of warmth outside the physical boundary was not influenced by the local spatial configuration of thermal stimulation.

2.6 Evidence 1: Does it Result From Heat Conduction?

I conducted the skin temperature change simulation based on the bio-heat equation to clarify whether the illusion results from heat conduction or the central nervous system. Supposing that when human skin receives thermal stimuli, the thermal structure of the superficial skin can be used as a basis for calculating skin temperature and for determining responses to transient changes in surface conditions (Wilson & Spence, 1988). The superficial skin is assumed to consist of infinite sheets of layers and the one-dimensional bio-heat transfer equation

$$\rho c \frac{\delta T}{\delta t} = k \frac{\partial^2 T}{\partial x^2} + \rho_b \omega_b c_b (T_a - T) + q \tag{2.1}$$

can be used to derive the temperature distributions at superficial skin where thermal conductivity, specific heat, specific heat of blood, density of skin

Table 2.1: Thermal properties of skin tissue.

Thermal properties of skin	**Variable**	**Value**	**Unit**
Thermal conductivity	k	5.0×10^{-1}	$Wm^{-1}K^{-1}$
Density	ρ	1.0×10^{3}	kgm^{-3}
Specific heat	c	4.2×10^{3}	$Jkg^{-1}K^{-1}$
Blood perfusion rate	ω_b	0.5×10^{-3}	$m^3s^{-1}kg^{-1}$
Density of blood	ρ_b	1.0×10^{3}	kgm^{-3}
Specific heat of blood	c_b	4.2×10^{3}	$Jkg^{-1}K^{-1}$
Metabolic heat	q	4.2×10^{3}	Wm^{-3}
Arterial temperature	T_a	3.7×10^{1}	°C

tissue, density of blood, blood perfusion, arterial temperature are denoted $k, c, c_b, \rho, \rho_b, \omega_b, T_a$ and q respectively. The term on the left-hand side of the equation is the rate of change of thermal energy contained in a unit volume per unit time. On the right-hand side, the three terms represent the rate at which thermal energy enters or leaves the unit volume in unit time by conduction, perfusion, and metabolism, respectively. According to the equation above, skin temperature changes dynamically during thermal stimulation.

Parameters were set, as shown in Table 2.1 (Zhang, 2015). I modeled the finger as a 80 mm×15 mm rectangle area. Original skin temperature was held at 32 °C. A 43 °C hot stimulus (15 mm ×15 mm area) was set at first at PIP joint (30 mm from the bottom). After 5 s, a 15 °C cold stimulus (15 mm×15 mm area) was set at the DIP joint (25 mm from the top) for 1 s. The simulation result in Figure 2.4 shows the skin temperature of the fingertip remains unchanged during this process.

This process was confirmed using thermography. Figure 2.4 shows the thermography of the fingertip before and after a PIP→DIP trial, which is taken by a 80×60 thermal camera module (PureThermal 2 Smart I/O Module, Switch Science, Inc.). In detail, we placed the thermal camera 50 mm below a subject's fingertip. Two foam balls were pasted on the fingertip with a distance of 5 mm in electrostatic adsorption. The subject was instructed to place the PIP joint on a hot stimulator for 5 s first and then place the DIP joint on a cold stimulator. Thermography was taken before and after the trial. The

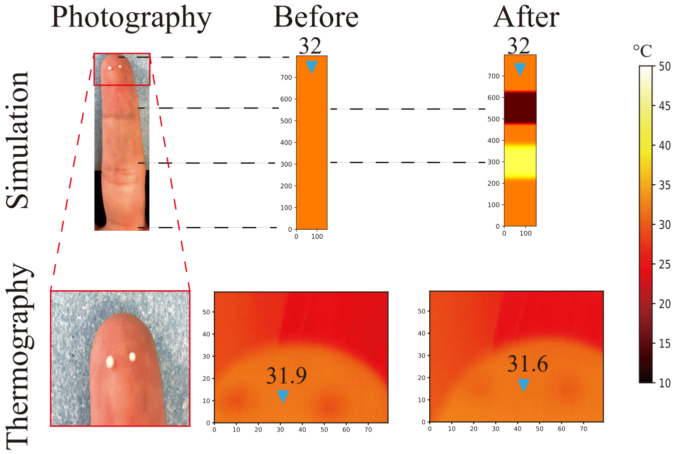


Figure 2.4: (Upper left) Photography of finger. (Upper center) Modeling of the finger before receiving thermal stimuli. (Upper right) Simulation result of finger after receiving thermal stimuli according to the bio-heat equation. (Lower left) Zoom in on the fingertip of the photography (Lower center). Thermography of the fingertip before receiving thermal stimuli. (Lower right) Thermography of fingertip after receiving thermal stimuli.

thermal camera's raw data was read using Python and Lepton Windows SDK and figured out with color bar as Figure 2.4 shows. I observed that the skin temperature had insignificant changes during the process. This result rules out the possibility that this phenomenon results from heat conduction. Instead, this result indicates a phenomenon resulting from the neural processing of warm and cold integration.

2.7 Discussion

In this chapter, I first showed a significant temporal sequence effect on thermal sensation outside physical boundary. The experiments were conducted in five temporal sequences, considering only the temporal sequence of receiving thermal stimuli. The results show different perception qualities at the observation spot (outside the physical boundary) under different temporal sequences of receiving thermal stimuli. Especially, a phenomenon of warmth outside the physical boundary was reported in this chapter. Warmth was observed under the far to near sequence regardless of the observation spot. Since there was no warm stimulus applied at the fingertip or the base of the finger, this result ruled out the possibility that ETS results from activating TRP ion channels outside the physical boundary (Lamas et al., 2019; Moparthi et al., 2016; Okazawa et al., 2004). Instead, these results indicated that an illusionary warmth was perceived outside the cold stimulator when applying a warm stimulus (far from the observation spot) prior to a cold stimulus (close to the observation spot). In contrast, the result under the simultaneous condition (the blue circle in Figure 2.3. (a)) was 50%, suggesting that no TGI was evoked when receiving warm and cold stimuli simultaneously for a short time. Because participants were instructed to answer immediately after completing the sequence, the only difference between the far to near condition and the simultaneous condition was the 5-second warm stimulation. Accordingly, the warm stimulation prior to the cold stimulation was significant for the generation of the warmth outside the cold stimulator. All the already-known thermal sensations are induced inside the stimulation area, while the thermal sensation we reported in this chapter is induced outside. I call this phenomenon Extrapolation of Thermal Sensation.

Proposed Model

ETS cannot be explained by the classical model that is based on the lateral inhibition theory (S.-i. Amari, 1977; Chorzempa, 1980). First, the classical model based on lateral inhibition cannot explain a phenomenon evoked by the interaction between two types of neurons. ETS is an illusionary warm perception when applying a warm stimulus (far) prior to a cold stimulus (close), which is a phenomenon based on the interaction between warm and cold signals. As aforementioned, lateral inhibition is a process of creating a suppressive effect by surrounding stimuli (S.-I. Amari, 1980; Kohonen, 1982; Von der Malsburg, 1973). It emphasizes the lateral interaction effect among the homologous neurons in the same layer. However, it lacks a description of heterologous neurons, e.g., interaction between WARM and COLD cells. Second, because of the first point, the classical model based on lateral inhibition cannot explain the different observations under different temporal sequences.

In addition, the classical theories of TGI, i.e., the unmasking theory and the addition theory cannot explain the warm perception evoked outside the perceptual boundary (A. Craig & Bushnell, 1994; Green, 2002). Both the unmasking theory and the addition theory focus on the quality of perception - the burning pain generated because of the interaction between warm and cold stimuli. The two theories lack a description on a spatial scale and cannot explain the spatial continuous perception. Additionally, the unmasking theory and the addition theory cannot explain the different observations under different temporal sequences. However, the two theories might be used to explain the generated warmth.

The different densities of warm and cold receptors might contribute to the warm sensation outside the physical boundary. Cold receptors have a higher density than warm receptors (Arens & Zhang, 2006). The density of warm spots at the human finger is $1.6/\text{cm}^2$ and that of cold spots at human finger is 2.0 - $4.0/\text{cm}^2$ (Arens & Zhang, 2006). Lower-density sensory spots require a larger interaction range to maintain this lateral interaction between neurons in the same layer. This also leads to the perception of a larger area. When the warm receptor located outside the physical boundary is activated because of some interaction, the warm receptor might be located far from the physical boundary. Thus, a warm sensation will be perceived outside the physical boundary. In contrast, the cold receptor has higher density, meaning a small average distance between two adjacent cold receptors. Even when the cold receptor located outside the physical boundary is activated, this receptor is close to the boundary. As a result, it is difficult to perceive cold outside the boundary.

Thus, I propose a model that explains the different perceptions induced by the temporal sequences under the premise of evenly-distribution among homologous receptors, but different distributions among heterologous receptors, as shown in Figure 2.5.

The effective range is assumed to be equal to the distance of two adjacent homologous receptors. The first layer is based on the lateral inhibition process, which has been confirmed as a common mechanism in the central nervous system: thermoreceptors have a lateral inhibition effect on all homologous receptors within their effective range. Warm and cold receptors work independently.

The second layer is based on the inhibition process of heterologous receptors. The warm receptors for heat dissipation and the cold receptors for heat production inhibit each other (Bligh, 1984), indicating a mutual inhibition relationship. On the other hand, I assume that: For a receptor A within the effective range of a heterologous receptor B, the pre-inhibited receptor A may be disinhibited by the post-inhibited receptor B. Additionally, the pre-excited receptor A may be inhibited by the post-excited receptor B.

The third layer describes the spatial summation process as follows: thermoreceptors have a lateral summation effect on all the homologous receptors within their effective range. Warm and cold receptors work independently. Spatial summation has been confirmed in thermal sensation (Jones & Ho, 2008).

Simulations based on the equations defined as such can explain thermal sensations. In detail, it is assumed that thermoreceptors are evenly distributed in the 50 mm x 20 mm area; the density for modeling was set to $1.6\,\mathrm{cm}^{-2}$ and $4.0\,\mathrm{cm}^{-2}$ for warm receptors and cold receptors, respectively. To simplify the problem, I transform it into a one-dimensional problem. It is estimated that there are $\sqrt{1.6} * 5 \approx 6.32$ warm receptors and $\sqrt{4} * 5 = 10$ cold receptors in a slice of the 50mm-length area, ignoring the width of the finger, as shown in Figure 2.6. The horizontal axis represents a one-dimensional location. The rightmost part represents the observation spot. Figure 2.6 illustrates the difference in perception distribution when a cold stimulus is close to the observation spot and a warm stimulus is far from the observation spot.

In the simultaneous condition, no disinhibition process occurs. As a result, the percentage hot judgment at the observation spot is close to the chance level.

In the "Near to Far" condition, the decrease in warm receptor #4 (from left) induces the disinhibition of cold #7. However, this change is limited because no additional cold receptors can be disinhibited. As a result, although the disinhibition process occurred, the effect remained limited, and there was

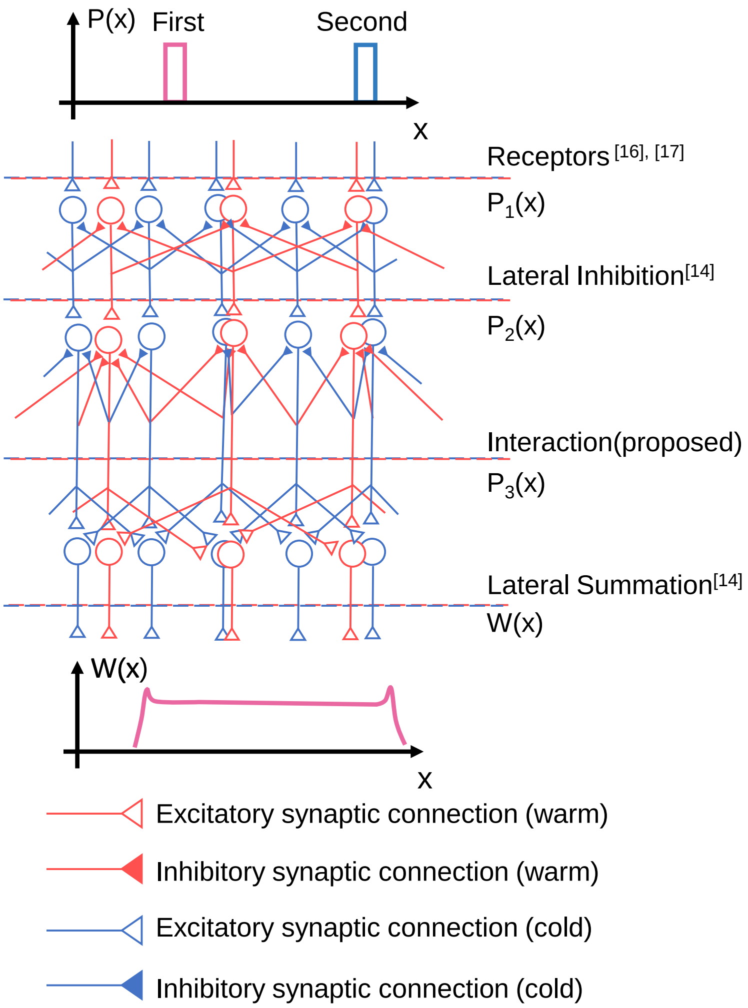


Figure 2.5: Structure of the proposed model. The red line shows the warm stimulus and the blue line shows the cold stimulus. The first layer describes the lateral inhibition among homologous receptors. The second layer describes the mutual inhibition relationship among heterologous receptors. The third layer describes lateral summation that works on homologous receptors.

no heat sensation at the observation spot.

In the “Far to Near” condition, when applying the warm stimulus first, warm #2, 3 are activated and warm #1, 4 are inhibited because of lateral

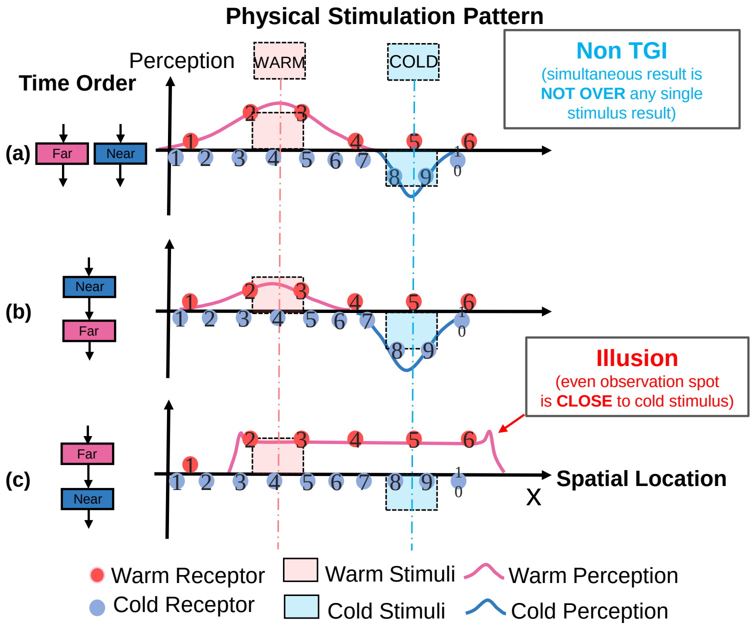


Figure 2.6: Simulation results based on the proposed model.

inhibition. The nearby cold receptors are inhibited by the warm stimulus. When the cold stimulus is also applied, cold #8, 9 are activated, and cold #7, 10 are inhibited because of lateral inhibition. The decrease in cold #7 induces the disinhibition of warm #4. The activity of warm #4 inhibits the excited cold #4, 5, 6. Furthermore, the decreased activity of cold #4, 5, 6 induces the disinhibition of warm #2, 3 (“chain reaction”). As a result, all the warm receptors involved are excited, and all the cold receptors are inhibited. Thus, the percentage hot judgment is very high at the observation spot.

Here, I discuss the influence of the density of receptors. Figure 2.7 shows the different simulation results under different receptor densities. Figure 2.7. (a) is the result based on the assumption above. The density of cold receptors is higher than that of warm receptors. Figure 2.7. (b) is the result based on the same density of warm and cold receptors. In the “Far to Near” condition, when applying the warm stimulus first, warm #2, 3 is activated and warm #1, 4 is inhibited because of lateral inhibition. The nearby cold receptors are

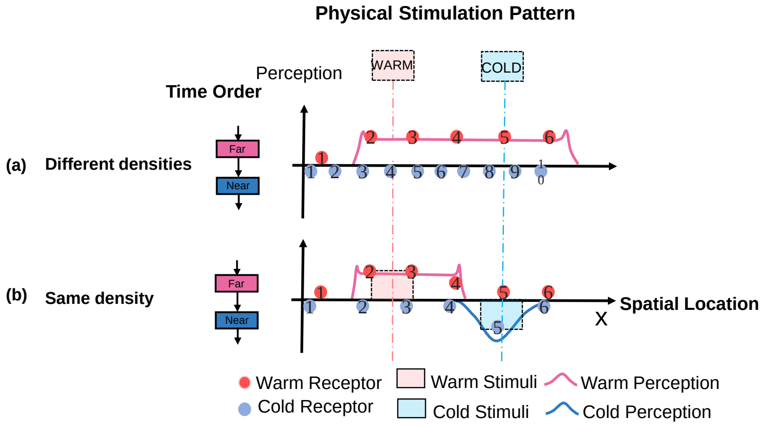


Figure 2.7: Simulation results under different densities.

inhibited by the warm stimulus. When the cold stimulus is also applied, cold #5 is activated and cold #4, 6 is inhibited because of lateral inhibition. Warm #4 also receives inhibition from cold #5. The decrease in cold #4 induces the disinhibition of warm #4. At this time, warm #4 is activated by cold #4 while inhibited by cold #5. Thus, cold #5 is only inhibited a bit. As a result, warm #5, 6 is not disinhibited. Accordingly, there is no warmth perceived outside the cold stimulator. These results indicated that densities of receptors are significant in evoking ETS.

Next, I discuss the influence of the spatial distribution of receptors. Figure 2.8 shows the different simulation results under different receptor densities. Figure 2.8. (a) is the result based on the assumption above. The density of cold receptors is higher than that of warm receptors. Figure 2.8. (b) is the result based on the same density of warm and cold receptors. The density at the joint is set to be twice the density at the area between joints. In the "Far to Near" condition, when applying the warm stimulus first, warm #2, 3 is activated and warm #1, 4 is inhibited because of lateral inhibition. The nearby cold receptors are inhibited by the warm stimulus. When the cold stimulus is also applied, cold #9, 10, 11, 12 are activated, and cold #8, 13 are inhibited because of lateral inhibition. At this time, warm #4 does not receive inhibition from cold #9. As a result, warm #5, 6 is not disinhibited.

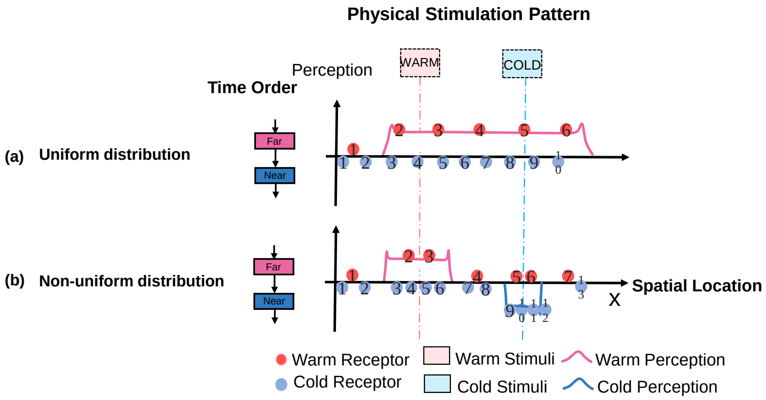
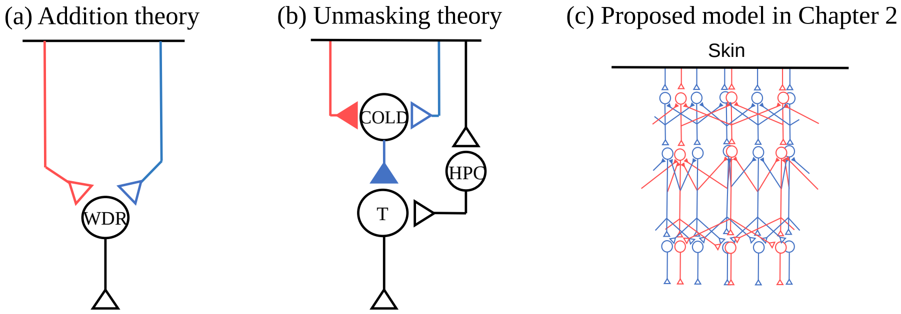


Figure 2.8: Simulation results under different distributions.

Accordingly, there is no warmth perceived outside the cold stimulator. These results indicated that the distribution of receptors is significant in evoking ETS. In this model, the state of the warm receptor in the middle (warm #4 in this figure) is very important. This is related to the effective range of the receptors. In this model, the effective range is assumed to be equal to the distance of two adjacent homologous receptors. Although the real effective range usually is larger than the model so that it can ensure the interaction, this simulation result shows the vulnerability of the model.

In summary, I discussed the limitations of classical theories (unmasking and addition theory) in explaining the ETS. These theories focus on the quality of perception arising from the interaction of warm and cold stimuli, while fail to consider the spatial aspect of the perception. They cannot explain how the perceptual boundary enlarges, nor how the perception changes with different sequences of warm and cold stimuli (Figure 2.9). However, they might be useful in understanding the generated warmth itself. I will investigate this problem in the next chapter.

This chapter proposed a model based on the lateral inhibition among homologous receptors and the inhibition of heterologous receptors. This model can explain how the perceptual boundary enlarges and the different perceptions with different temporal sequences (Figure 2.9). As the basis of this


(a) Addition theory
(b) Unmasking theory
(c) Proposed model in Chapter 2

Resulting warmth	unknown	unknown	can explain
Enlargement of perceptual boundary	lack description (this model explains burning pain)	lack description (this model explains burning pain)	can explain
Different results under sequences	lack description (this model explains burning pain)	lack description (this model explains burning pain)	explain different transient responses under sequences

Figure 2.9: Comparison based on knowledge in Chapter 2.

model, lateral inhibition among homologous receptors and mutual inhibition among heterologous receptors have been confirmed in the nervous system. Whereas, this model assumes that warm receptors are disinhibited by inhibited cold receptors, and cold receptors are disinhibited by inhibited warm receptors.

Notice that the thermal stimulus applied in this experiment requires contact with the Peltier element; mechanical stimulation induced by tactile contact with the Peltier may also contribute to thermal sensation. The tactile factor should also be considered, which requires further study.

In conclusion, this chapter reported an enlargement of the perceptual boundary. Specifically, when a warm stimulus is applied far from the observation spot first and then a cold stimulus is applied close to the observation spot, warmth is perceived outside the physical boundary immediately after the application of the cold stimulus. This phenomenon shows the integration of warm and cold inputs both spatially and temporally. These findings contribute to our understanding of thermal sensation. However, further perceptual and neurophysiological studies are required to confirm the nature of this phenomenon and describe its neural mechanism.

Chapter 3

WARMTH SPATIALLY SPREADS WITH an INCREASE of TEMPERATURE DIFFERENCE

> *The ability to sense and adapt to the environment is essential for survival in all organisms.*
>
> **- 2021 Nobel Prize in Physiology or Medicine**

3.1 Summary

The previous chapter reported that perception at the fingertip and base of the finger (middle finger) changed when receiving stimuli in different temporal sequences. Warmth (far from fingertip) prior to cold stimulus (close to fingertip) induces a reliable warmth outside cold stimulus (Extrapolation of Thermal Sensation). This phenomenon shows an integration of warm and cold inputs both spatially and temporally. On the other hand, the transition of the spatiotemporal conditions among ETS, PHS, and TGI suggests a common mechanism. This chapter investigates the relationship between ETS and the temperature of thermal stimuli, T_{warm} and T_{cold}, to study whether the addition and unmasking theory in TGI also works in ETS. I found that gradually increasing warm and cold stimuli increased the percentage hot judgment at the observation spot outside the physical boundary. This means that with the greater temperature difference of the thermal inputs, T_{warm}-T_{cold}, there is a more intense sensation of warmth outside the physical boundary. Thus, the unmasking theory in TGI does not explain ETS. Instead, the addition theory in TGI explains ETS. Additionally, the illustration of perceptual boundary indicated that the sense of warmth spatially spread outside gradually with a gradual increase of warm and cold stimuli. These results suggest that warm and cold inputs converge on the Wide Dynamic Range neurons, leading to an enlargement of warm sensation.

3.2 Introduction

One type of thermosensitive neuron is considered sensitive to one form of stimulation and encodes one perceptual quality. However, the discovery of TGI, PHS, and extrapolation of thermal sensation challenge this perspective (A. Craig & Bushnell, 1994; Green, 2004; J. Hua et al., 2021; Prescott et al., 2014; Susser et al., 1999). In TGI, a sensation of burning pain is felt by touching interlaced warm and cool bars simultaneously to the skin. In PHS, a sensation of heat occurs if the skin is heated immediately prior to cooling. In ETS, heat is felt outside the cold stimulator if given a single warm stimulus for 5 s and then both warm and cold stimuli for 0.5 s.

Interestingly, these three illusions present temporal and spatial transition characteristics. I summarized the temporal pattern of three thermal illusions by separating thermal stimuli and the spatial pattern by area of thermal stimuli. As shown in Table 3.1, in the aspect of time, the cold and warm stimuli are separate in PHS (because of the pre-heating) while converging in TGI (because of simultaneous touch). In ETS, the cold and warm stimuli are partly separate from each other. On the other hand, in the aspect of space, the cold and warm stimuli are convergent in PHS (because of the same stimulation site) and separate in TGI (usually over 3 pairs, area over $100\,\mathrm{cm}^2$). ETS is between PHS and TGI (one pair, $4.5\,\mathrm{cm}^2$). Thus, we can see the spatiotemporal transition when inducing thermal illusion, and the extrapolation of thermal sensation looks like a transitional form between PHS and TGI, suggesting a common mechanism among the three illusions.

Studies of PHS support the common mechanism hypothesis (Green, 2004; Prescott et al., 2014). It is found that PHS is conducted peripherally through C afferents while not $A\delta$ afferents (Susser et al., 1999). Green described it as a "paradoxical discharge of warm afferents in a field of cooling would produce a mixture of cold and warm afferent stimulation no different than that produced by TGI."

If we hold the perspective that there is a common mechanism in TGI, PHS, and ETS, the two central theories that explain TGI—"addition theory" or "unmasking theory"—should also explain ETS. This chapter will investigate the relationship between ETS and the temperature of the thermal stimulus to study whether one of the TGI theories interprets ETS.

3.3 Methods

Participants

In Experiment 3.1, 15 participants (12 males and 3 females) aged between 23 and 30 participated, and four men participated in Experiment 3.2. Participants suffering from pain, diseases causing potential neural damage (e.g., diabetes), systemic illnesses, and mental disorders were excluded. All reported being right-hand dominant. 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.

Experiment 3.1: Physical Stimulus on Thermal Sensation

This experiment aimed to clarify which theory works for the “extrapolation” phenomenon by observing hot judgment outside the cold stimulus using various temperature pairs. The addition theory predicts that both warm and cold stimuli positively affect the hot judgment. In contrast, the unmasking theory predicts that warm and cold stimuli positively and negatively affect hot judgment.

Prior to the experiment, participants were instructed to put their right hand on the hot plate to adjust skin temperature to 32 °C (baseline temperature). The experiment was conducted in a room with a constant temperature at 25 °C. The physical intensities, ΔT, applied were -5, -9, -13, or -17 °C for cooling and 2, 5, 8, or 11 °C for warming (relative to the baseline temperature).

Perception of the fingertip was observed. The warm stimulus was always given at the distal interphalangeal (DIP) joint. In contrast, the cold stimulus was always given at the proximal interphalangeal (PIP) joint[1]. Between every

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[1] In the pilot experiment, ETS occurred most frequently when the two stimuli were applied at the DIP and PIP joint

Table 3.1: Summary of Spatiotemporal Characteristic of Thermal Illusion.

Illusionary Thermal Sensation	**Temporal (separation)**	**Spatial (area)**
Paradoxical Heat Sensation (Greenspan et al., 1993; Hansen et al., 1996; Susser et al., 1999)	Totally separate	Small
Extrapolation of Thermal Sensation (J. Hua et al., 2021)	In between	Medium
Thermal Grill Illusion (Green, 1977, 2002)	Totally convergent	Large

two trials, participants were instructed to place their right hand on the hot plate for at least 30 s.

Before each trial, they were instructed to place the D3 (middle) finger of the right hand several millimeters above the device. They touched the hot stimulator with the PIP joint first for 5 s and then also touched the cold stimulator with the DIP joint for 0.5 s according to the sound cue. Then, they answered the sensation at the fingertip. A two-alternative forced choice (2AFC) standard psychophysical protocol was employed. They answered hot or cold at the observation spot. Five trials were performed under each condition, and the stimuli were applied randomly. In total, each participant was given 80 trials.

Experiment 3.2: Physical Stimulus on Perceived Boundary

Experiment 3.1 tested the percentage hot judgment at the observation spot outside the physical boundary under different stimuli temperatures. Experiment 3.2 aimed to confirm the spatial characteristics of the sensation resulting under different stimuli temperatures by examining the perceptual distribution on the fingers. Considering that the sensation induced by ETS was nonverbal, I instructed the participants to sketch their thermal sensations. They sketched the sensation on the palm side from the top side.

Three stimulators were applied to bases of D4, D3, and D2. A neutral stimulator was held at the base of D4. The touching edge of the Peltier module was aligned with the corresponding crease. The experiment was conducted in a room with a constant temperature at 25 °C. The physical intensities, ΔT, applied were -6 °C or -12 °C for cooling and 6 °C or 12 °C for warming (relative to the baseline temperature). The stimulus presentation time was 15 s to ensure 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.

3.4 Results

Experiment 3.1

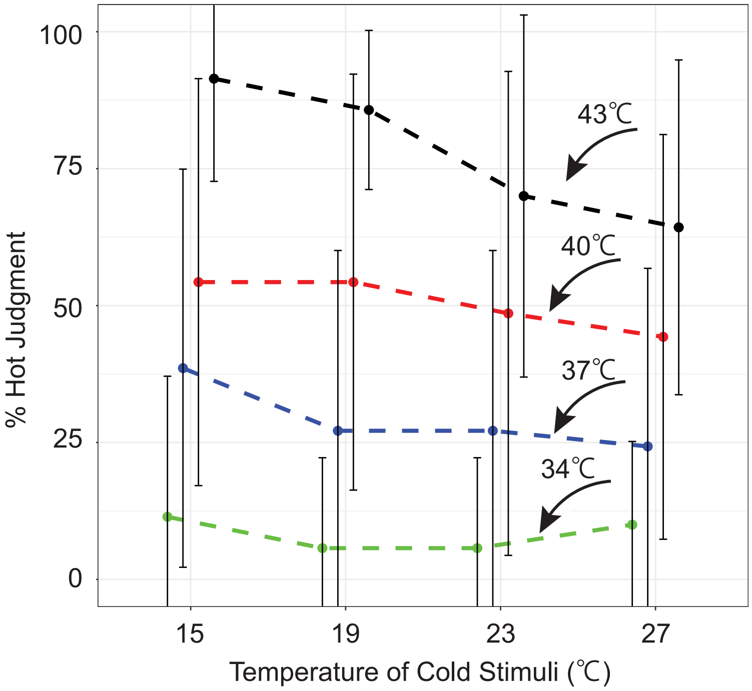


Figure 3.1: Percentage hot judgment at the D3 (middle) finger as a function of cold stimulator temperature.

Geometric means of percentage hot judgment at the fingertip of the D3 finger in Figure 3.1 as a function of cold stimulator temperature. Each point is based on 75 observations. The empty circles stood for the percentage hot judgment at the fingertip when the temperature of the cold stimulator at the DIP joint and that of the warm stimulator at the PIP joint varied. The green, blue, red, and black dashed lines stand for the temperature of warm stimulus as 34 °C, 37 °C, 40 °C and 43 °C, respectively.

In general, if the intensity of the warm stimulus is held, the percentage hot judgment increases when the intensity of the cold stimulus increases, indicating a positive effect of the cold stimulus on the illusion. On the other

Table 3.2: Comments from Participants.

Comment	Age	Gender
I felt a burn at my fingertip.	29	Male
A cold sensation at first, followed immediately by an intense hot sensation.	25	Male
I felt a burn at one point on my fingertip, but not at the entire tip.	22	Female
Not only is the finger pulp but also the back of the finger is hot.	28	Male
Difficult to judge. I can feel both heat and coldness.	27	Male
Sting, but cannot feel heat or coldness.	29	Male
I do not know how to answer.	23	Male

hand, if the intensity of the cold stimulus is held, the percentage hot judgment also increases when the intensity of the warm stimulus increases, indicating that there is a positive effect of the warm stimulus on the illusion. Percentage hot judgment reached the maximum when the temperature difference reached the maximum. This result suggests that the addition of the warm and cold stimulus occurs. Adding warm and cold stimuli causes a hot sensation outside the cold stimulus by the direct stimulation at DIP and PIP joints when the physical stimuli are intense enough. Indeed, participants sometimes volunteered comments that "I felt burn at the fingertip" (see Table 3.2). Also, notice that participants did not touch anything with the D3 fingertip while an illusion is evoked there. The phenomenon of "extrapolation without touching" is different from TR and was never reported (Green, 1977; Ho et al., 2011).

Experiment 3.2

Experiment 3.2 aimed to illustrate the perceptual distribution of the fingers. Figure 3.2, Figure 3.3, Figure 3.4, and Figure 3.5 illustrate the experimental results and corresponding conditions. Although a warm stimulus was applied to D2, the resulting warmth was not limited to D2. The resulting warmth spatially spreads outside with the increased intensity of warm and cold stimuli. When the warm and cold stimuli were intense enough, warmth was reported on D4, although this finger was applied with a neutral stimulus.

In addition, the results for Participant 1 showed that warmth was perceived in the air when the warm and cold stimuli were intense enough (the temperature difference was large enough). In general, the resulting warmth was diffuse. Warmth spatially spread outside with the increased temperature difference of stimuli and was not limited to the skin surface.

The sense of cold was generally 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. This asymmetry suggests that warm stimuli play a dominant role in spatial-thermal integration.

3.5 Discussion

This chapter investigated the relationship between Extrapolation of Thermal Sensation and the temperature of warm and cold stimuli. Gradually increasing warm and cold stimuli increased the percentage hot judgment at the observation spot outside the physical boundary. Additionally, the illustration of perceptual boundary indicated that the sense of warmth spatially spread outside gradually with a gradual increase of warm and cold stimuli. These results indicated that ETS is the result of an addition of warm and cold stimuli.

Experiment 3.1 found that the resulting sensation outside the physical boundary is influenced by the temperature of thermal stimuli. The model proposed in Chapter 2 fails to explain the experimental results in the next chapters (Figure 3.6). Chapter 3 reports the relation between ETS and the temperature difference of the thermal stimuli. With the greater temperature difference of the thermal inputs, T_{warm}-T_{cold}, there is a more intense sensation of warmth outside the physical boundary. This result indicates that with a more intense warm input, the resulting ETS should be more intense. On the other hand, in this model, the activity of the warm cell in the middle

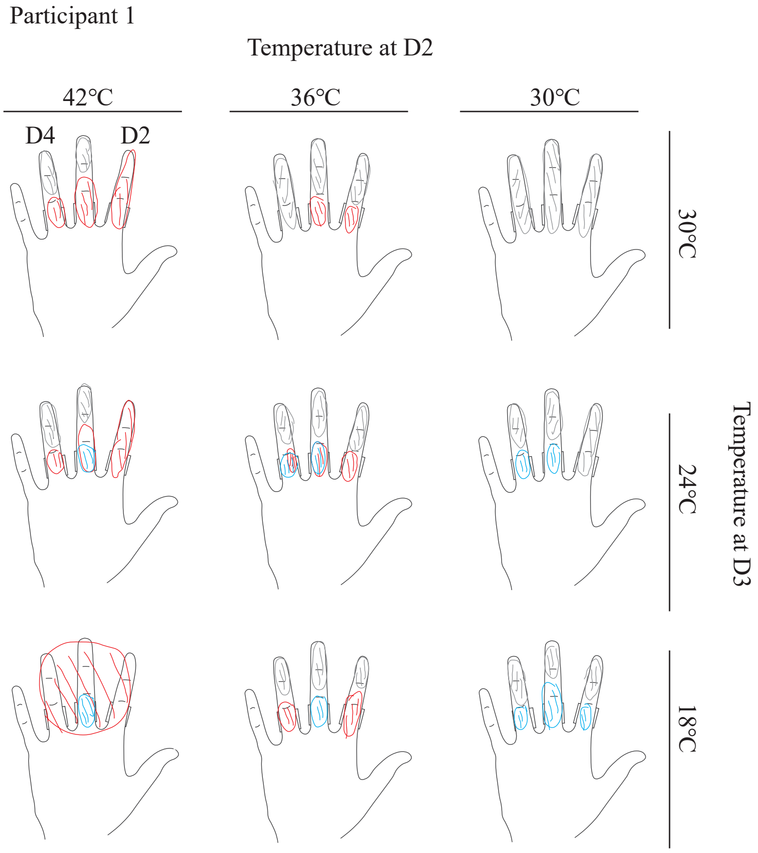


Figure 3.2: Results of Experiment 3.2 (Participant 1). Participants drew the shape and field of warmth, cold, and neutral sense with a red, blue, and gray circle, respectively. Warmth was perceived at the neutral location. In some cases, warmth extended beyond the skin into the air.

(warm #4 in Figure 2.6) is significant. With a more intense warm input, warm #4 becomes more inhibited, hence it is more difficult for warm #4 to be disinhibited. Unable to be disinhibited makes it more difficult to evoke ETS. Therefore, the receptor interaction model cannot explain the findings in Chapter 3.

These findings cannot be explained by the unmasking theory of TGI. The unmasking theory posits that the intensity of the illusion is influenced by the

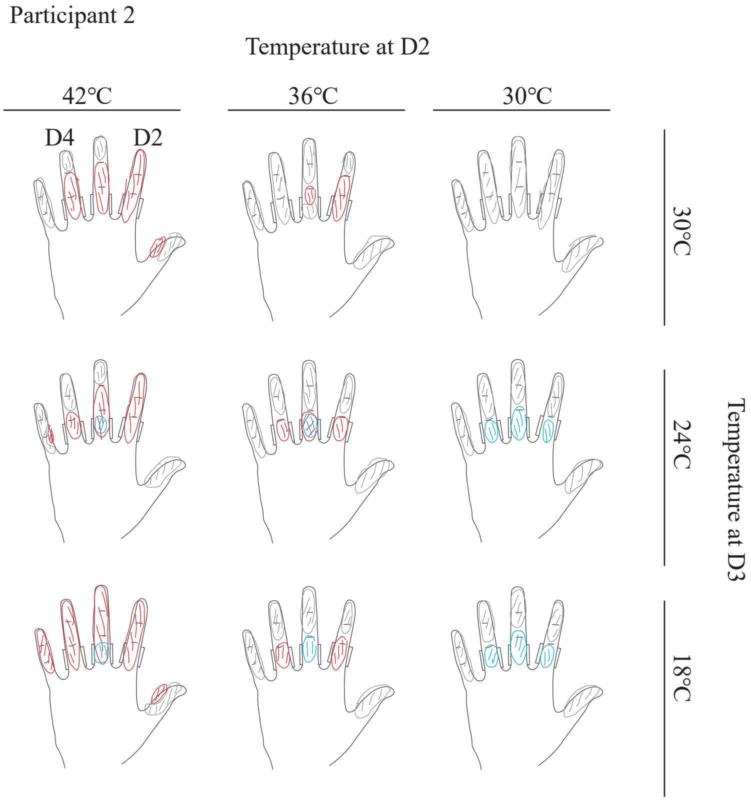


Figure 3.3: Results of Experiment 3.2 (Participant 2). Participants drew the shape and field of warmth, cold, and neutral sense with a red, blue, and gray circle, respectively. Warmth was perceived at the neutral location. In some cases, warmth extended beyond the skin into the air.

relative intensities of the warm and cold stimuli. Specifically, it predicts that a stronger warm stimulus and a weaker cold stimulus will result in a warmer experience. However, the findings in Experiment 3.1 differ from the prediction based on the unmasking theory, indicating that ETS is not the result of the unmasking of the nociceptive pathway.

Instead, the findings in this chapter can be explained by the addition theory of TGI. The addition theory predicts a sense of warmth resulting from the mixture of warm and cold stimuli. WDR neurons are found to be involved in the integration of information from multiple modalities in the dorsal horn

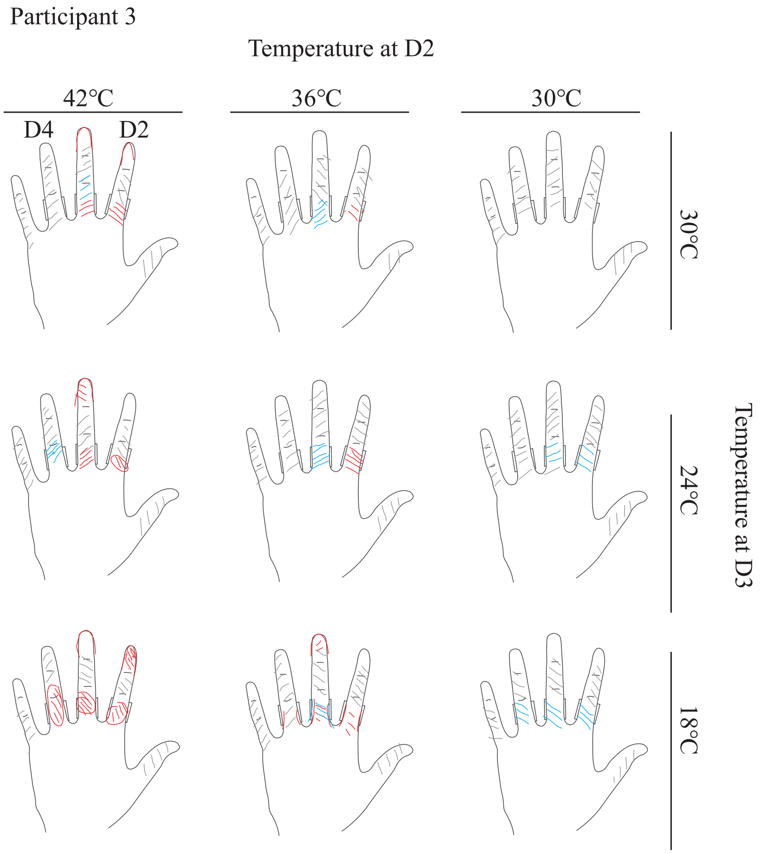


Figure 3.4: Results of Experiment 3.2 (Participant 3). Participants drew the shape and field of warmth, cold, and neutral sense with a red, blue, and gray circle, respectively. Warmth was perceived at the neutral location. In some cases, warmth extended beyond the skin into the air.

of the spinal cord, and they respond in a graded manner during the transition from non-noxious warm or cool to noxious heat or cold. Thus, warm and cold signals might converge on the WDR neurons in the spinal cord, leading to a sense of warmth outside the physical boundary (Khasabov et al., 2001).

The illustration in Experiment 3.2 indicated that the sense of warmth spatially spread outside gradually with a gradual increase of warm and cold stimuli. As mentioned above, the model proposed in Chapter 2 predicts that ETS weakens as the thermal stimulus is enhanced. Thus, this model cannot

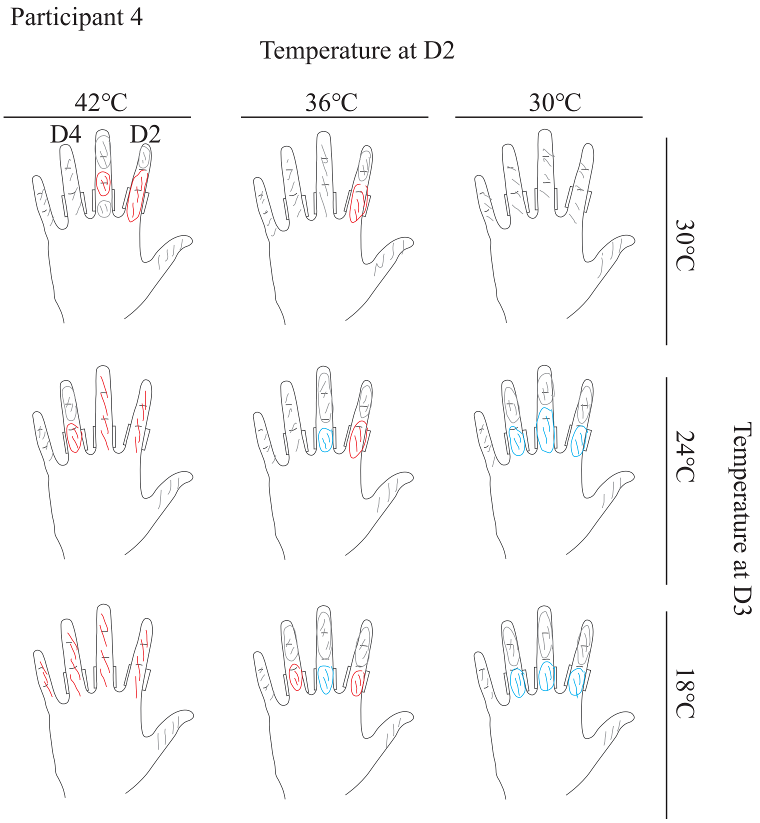
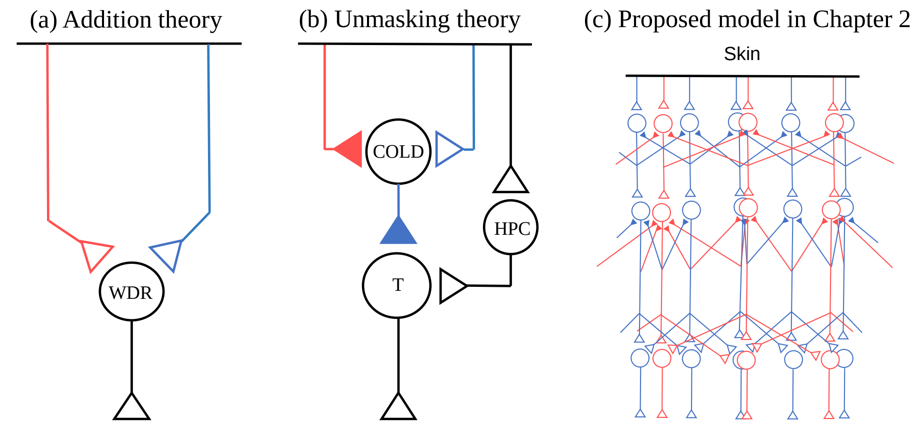


Figure 3.5: Results of Experiment 3.2 (Participant 4). Participants drew the shape and field of warmth, cold, and neutral sense with a red, blue, and gray circle, respectively. Warmth was perceived at the neutral location. In some cases, warmth extended beyond the skin into the air.

explain the gradual enlargement of warm sensation. On the other hand, classical models including addition theory and unmasking theory lack description of perceptual boundary. Hence, the two classical models cannot explain the results in Experiment 3.2.

The illustration of perceptual boundary in Experiment 3.2 indicated that ETS and heat pain have a similar spatial spread effect. It is found that heat pain spatially spreads when skin temperature exceeds 45 °C (Price et al., 1978). The receptive field structure of WDR neurons has been thought to contribute



Results in Exp. 3.1:	match	not match	not match
Results in Exp. 3.2:	lack description (this model explains burning pain)	cannot explain	cannot explain

Figure 3.6: Comparison based on knowledge in Chapter 3.

to this heat-induced spatial spread. First, WDR neurons whose receptive field's center lies directly under the Peltier would increase their activity. Second, more nociceptive neurons would be activated, including WDR neurons with extensive receptive fields and whose most sensitive receptive-field regions are remote from the actual stimulus. As a result, a spatial spread of perceived heat pain is generated. Although this is a phenomenon of heat pain, it can be seen as a phenomenon of enlargement of perceptual boundary.

Results in Experiment 3.2 indicated a spatial spread of warm sensation with a gradual increase of warm and cold stimuli. Warm and cold signals may converge on WDR neurons, leading to a higher activation of WDR neurons that is usually generated by heat pain. As a result, a similar spatial spread effect with heat pain is evoked.

Although results in Experiments 3.1 and 3.2 indicated the role of WDR neurons, the involvement of suprasegmental organization in ETS generation has also been observed. One participant in Experiment 3.2 reported that warmth can be perceived in the airy area. The perception in the area where there is no skin or stimulus strongly suggests the presence of organization in the cerebral cortex, because somatosensory experiences occurring in areas without direct bodily contact are thought to result from reorganization in the cerebral cortex (Bolognini et al., 2013; Flor & Birbaumer, 2000; Mercier et al., 2006; Nardone et al., 2019). In detail, the human posterior insular cortex in the cerebral cortex is found to be organized somatotopically, responding differently to cold stimuli on different body parts, such as the hand and neck. Further study has reported neurons representing cold and warm in the posterior insular cortex (Vestergaard et al., 2023). The representation of thermal information in the posterior insular cortex is robust and somatotopically arranged. Further neurophysiological studies are necessary to accurately identify the cortical areas involved.

In conclusion, my psychophysical observations regarding physical stimulus suggest an interaction of warm and cold inputs. Warm and cold inputs might converge on Wide Dynamic Range neurons, leading to an enlargement of warm sensation. In the following chapter, I will further investigate the spatial characteristics to study the relationship between TGI and ETS.

Chapter 4

SPINAL SEGMENTS DEPENDENTLY INTERFERE WITH ETS and TGI DIFFERENTLY

> *Apart from providing conscious awareness about our body and its surroundings, the somatosensory system is also essential for tasks that I perform effortlessly and without much thought.*
>
> **- 2021 Nobel Prize in Physiology or Medicine**

4.1 Summary

Chapter 2 investigated the temporal characteristic of thermal sensation. I reported that perception at the fingertip and base of the finger (middle finger) changed when receiving stimuli in different temporal sequences. Warmth (far from fingertip) prior to cold stimulus (close to fingertip) induces a reliable warmth outside cold stimulus (Extrapolation of Thermal Sensation). Chapter 3 investigated the thermal characteristics of ETS and found a relationship between ETS and the temperature difference between warm and cold stimuli. In Chapter 4, I will investigate the spatial characteristics of ETS. Although the ETS shares similarities with the 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. This chapter 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, the segmental distance between warm and cold stimuli was manipulated, and the resulting perceived temperatures of the neutral and cold stimulators were observed. 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, this chapter concludes 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.

4.2 Introduction

Chapter 2 investigated the temporal characteristic of thermal sensation and reported that perception at the fingertip and base of the finger (middle finger) changed when receiving stimuli in different temporal sequences. Warmth (far from fingertip) prior to cold stimulus (close to fingertip) induces a reliable warmth outside cold stimulus (Extrapolation of Thermal Sensation). Chapter 3 investigated the thermal characteristics of ETS and found a relationship between ETS and the temperature difference between warm and cold stimuli. I found that gradually increasing warm and cold stimuli increased the percentage hot judgment at the observation spot outside the physical boundary. This means that with the greater temperature difference of the thermal inputs, T_{warm}-T_{cold}, there is a more intense sensation of warmth outside the physical boundary. These results indicates that although the addition theory cannot explain the spatial organization of thermal sensation, i.e., how the perceptual boundary is decided and enlarged, the addition theory can provide insights about the warmth evoked by ETS.

The close connection between the addition theory of TGI and the warmth generated by ETS, along with the inapplicability of the unmasking theory to ETS, brings up an important question: Do ETS and TGI share the same mechanism? If ETS and TGI do not share the same mechanism, then ETS is governed by the addition theory, while TGI is governed by the unmasking theory. This implies that the addition theory and unmasking theory are responsible for different aspects of thermal sensation. If this possibility is true, then the addition theory might be responsible for explaining the formation of the perceptual boundary of thermal sensation, while the unmasking theory actually explains the formation of the quality of thermal sensation.

In Chapter 4, I will investigate whether ETS and TGI share the same mechanism through investigation of the spatial characteristics of ETS. Using a warm-cold stimulus pair, Fardo found that cold stimulation reproduced an overestimation as if it were a more neutral stimulus (Fardo et al., 2018). 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 (Fardo et al., 2018). However, ETS has not been observed in dermatomes. This chapter compares 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. I 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 (Lamotte, 1977). In contrast, in the lumbosacral segments, the distribution of nerve fibers may remain relatively uniform (Lamotte, 1977). Considering the varying strengths of lateral connections across spinal segments, I 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 (Fardo et al., 2018). However, 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 chapter describes the role of these lateral connections in thermal integration, based on the findings of previous research (Fardo et al., 2018). Moreover, this chapter explores the effect of the Lissauer tract on the lateral connection strength and density of connections to second order neurons in neighboring segments. Therefore, this chapter elucidates the role of lateral connections in thermal integration, thereby advancing our understanding of sensory perception mechanisms based on prior research (Fardo et al., 2018).

4.3 Methods

Participants

A total of 47 healthy volunteers participated in Experiment 4.1 (n = 13, all men), Experiment 4.2 (n = 13, 11 men), Experiment 4.3 (n = 4, all men), Experiment 4.4 (n = 13, all men), and Experiment 4.5 (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.

Experiment 4.1

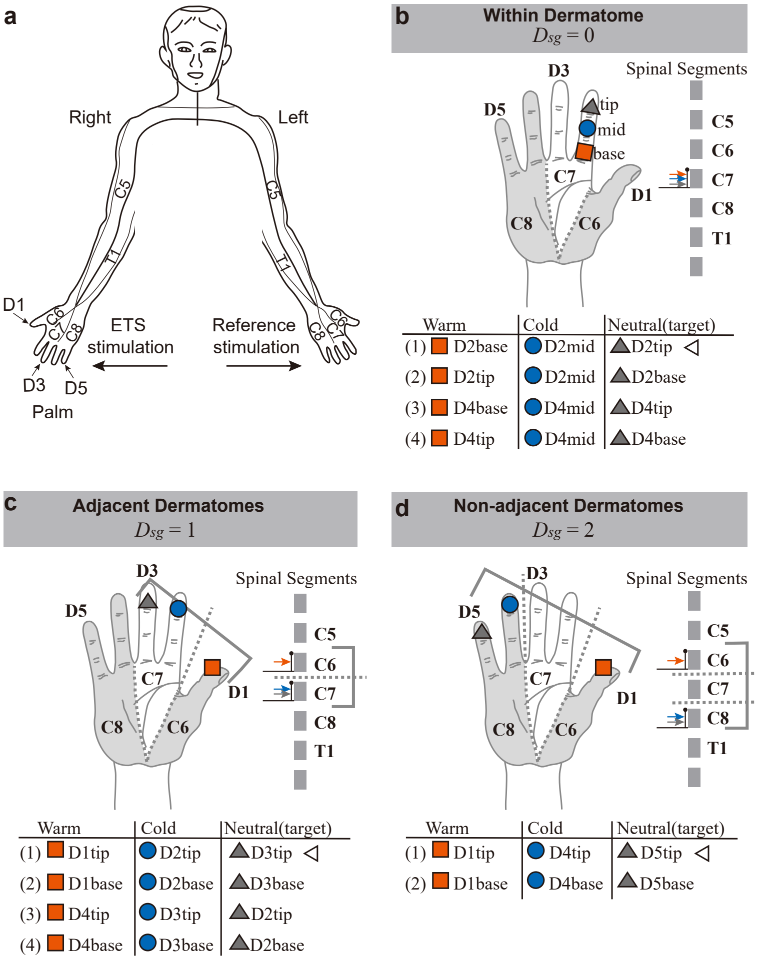
First, this chapter confirmed that ETS varied in units of segmental distance. This phenomenon was initially reported based on the reproducibility of the sense of warmth, which did not quantify the perceived temperature resulting from ETS. To address these limitations, I adopted the adaptive staircase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

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.

Segmental distance

I 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.



(b)

	Warm	Cold	Neutral(target)
(1)	🟥 D2base	🔵 D2mid	▲ D2tip ◁
(2)	🟥 D2tip	🔵 D2mid	▲ D2base
(3)	🟥 D4base	🔵 D4mid	▲ D4tip
(4)	🟥 D4tip	🔵 D4mid	▲ D4base

(c)

	Warm	Cold	Neutral(target)
(1)	🟥 D1tip	🔵 D2tip	▲ D3tip ◁
(2)	🟥 D1base	🔵 D2base	▲ D3base
(3)	🟥 D4tip	🔵 D3tip	▲ D2tip
(4)	🟥 D4base	🔵 D3base	▲ D2base

(d)

	Warm	Cold	Neutral(target)
(1)	🟥 D1tip	🔵 D4tip	▲ D5tip ◁
(2)	🟥 D1base	🔵 D4base	▲ D5base

Figure 4.1: Experimental conditions in Experiment 4.1. (a) Dermatomes are sketched based on the work of Keegan (Keegan & Garrett, 1948). 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.

Arrangement

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

To investigate the segmental hypothesis, the spatial arrangement of the three stimulators was varied 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 (Keegan & Garrett, 1948; Ladak et al., 2014; M. Lee et al., 2008). The detailed layout of the dermatomes is depicted in Figure 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 the experiment, I placed the cold and neutral stimulators in the same dermatome.

I 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. Experiments were conducted 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 Figure 4.1 b-d.

To further validate earlier research on TGI (Fardo et al., 2018), I examined how the participants perceived the temperature of the cold stimulator. The study adopted a factorial within-subject design comprising the following:

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.

Segmental distance

I 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 b(1), c(1), and d(1) conditions (Figure 4.1 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.

Experiment 4.2

Experiment 4.1 confirmed that ETS varied in units of segmental distance. However, this did not rule out the possible role of physical distance in ETS. Thus, I investigated ETS under a controlled inter-stimulus distance. This procedure was based on the method described in Experiment 4.1. 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 stimulator. I followed a 4×2 full-factorial within-subjects design.

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.

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 chapter.

Experiment 4.3

Experiment 4.2 quantified the perceived temperature of the neutral area resulting from ETS on the fingers. Experiment 4.3 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, I 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 4.3. In the $D_{sg} = 0$ condition, a warm-cold-neutral stimulus pair was applied to the fingertip, middle, and base of D2, respectively (Figure 4.1 b(2)). In the $D_{sg} = 1$ condition, three stimulators were applied to bases of D4, D3, and D2 (Figure 4.1 c(4)). 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.

Experiment 4.4

Experiments 4.1-4.3 investigated the perceptual characteristics of ETS on the fingers. In experiments 4.4 and 4.5, I explored these characteristics in the lower leg to investigate whether the segmental effect of ETS is independent of body parts. A factorial within-subjects design was followed.

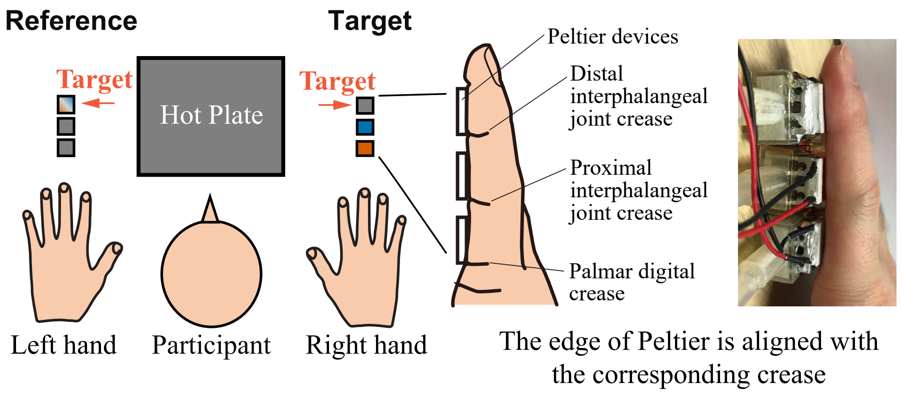
Temperature combination

“control” and “ETS” conditions were tested.

Segmental distance

Based on the work of Keegan (Keegan & Garrett, 1948; Ladak et al., 2014; M. Lee et al., 2008), the stimulators were arranged in a way that allowed the delivery of two warm and cold stimuli either within the dermatome or across dermatomes.

a Finger Condition



b Lower Leg Condition

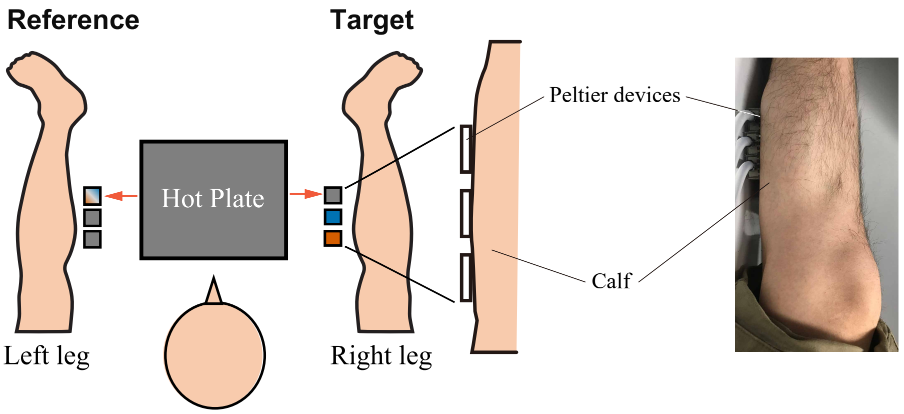


Figure 4.2: Study setup. The adaptive staircase method was used to measure the perceived temperature. In the setup, the right three Peltier modules were utilized for ETS stimulation, while the left three modules provided adaptive stimulation to match the two target locations. Throughout the experiment, 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. I recorded their psychophysical responses for analysis.

Arrangement

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

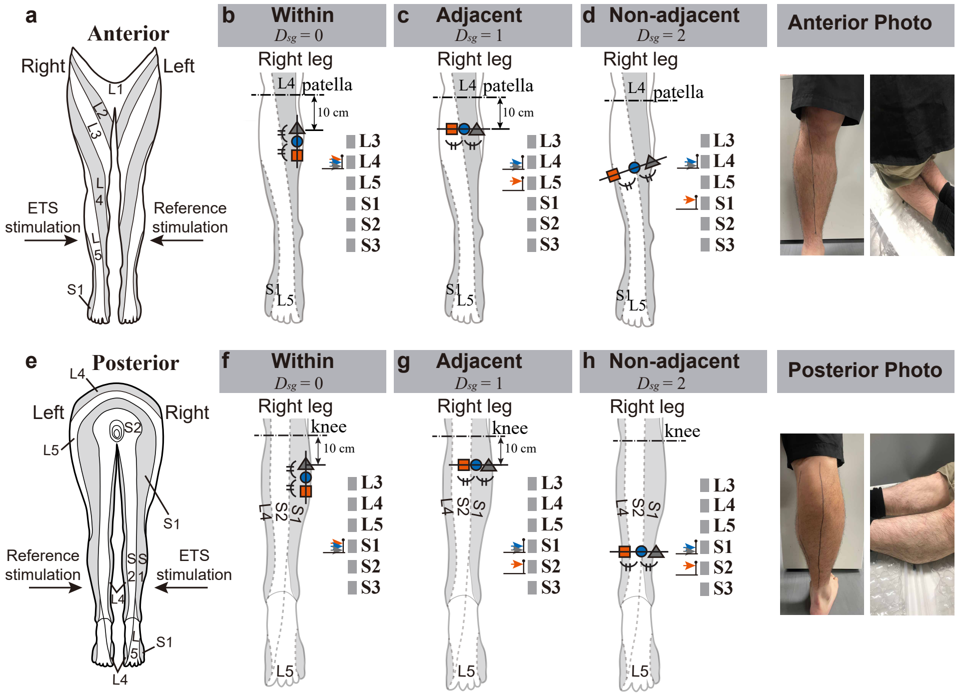


Figure 4.3: Experimental conditions in Experiment 4.4. Dermatomes are sketched based on the work of Keegan (Keegan & Garrett, 1948). The generation of ETS was investigated at both the anterior and posterior lower leg, while the physical distance between every two adjacent stimulators was equidistant. (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.

The dermatomal boundary of the anterior lower leg descends from the medial femoral condyle above the knee to the medial malleolus (Figure 4.3 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. A factorial within-subjects design was followed.

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.

Segmental distance

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

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 4.1. 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.

Experiment 4.5

I 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 4.3. $D_{sg} = 0$ 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.

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, I 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. The cooling surface area was 2400 mm^2. I 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 (NHP-M30N, New Japan Chemical Co., Ltd.) was used to maintain the skin temperature to 30°C (Figure 4.2).

All analyses were performed using the R statistical software.

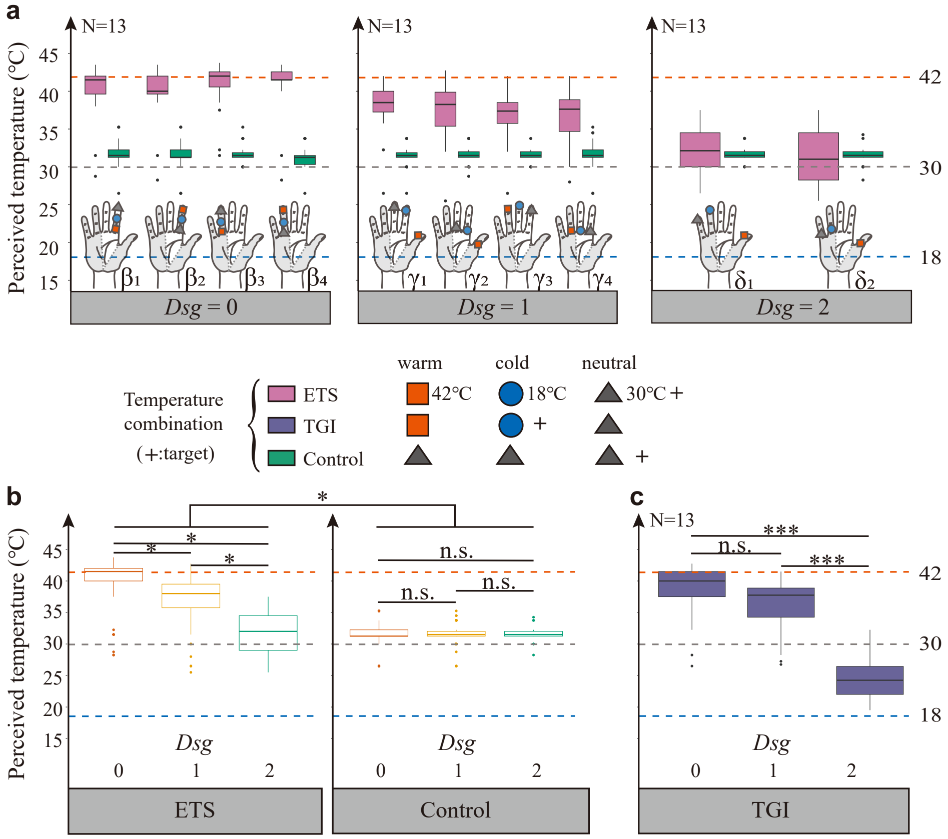


Figure 4.4: Results of Experiment 4.1. ETS and TGI were investigated on the fingers. + mark stands for the target location in each temperature combination condition. (a) Results of ETS. ETS varied in units of segmental distance. (b) Group mean of ETS under each segmental distance condition. (c) Results 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. $p > 0.05$; * $p < 0.05$; *** $p < 0.001$.

4.4 Results

Experiment 4.1

In this study, I 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. Figure 4.4 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.

I 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, a one-way repeated-measures ANOVA was performed 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 4.1 showed that ETS and TGI on the fingers were induced within or across adjacent dermatomes.

Experiment 4.2

Experiment 4.2 investigated the ETS phenomenon while controlling for the interstimulus distance. Figure 4.5 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, the segmental effects of ETS was replicated in this experiment.

Experiment 4.3

Experiment 4.3 aimed to illustrate the perceptual distribution of the fingers. Figure 4.6 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 stimulus. In the $D_{sg} = 1$ condition, the warm area was larger than that in the $D_{sg} = 0$ condition. In general, 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

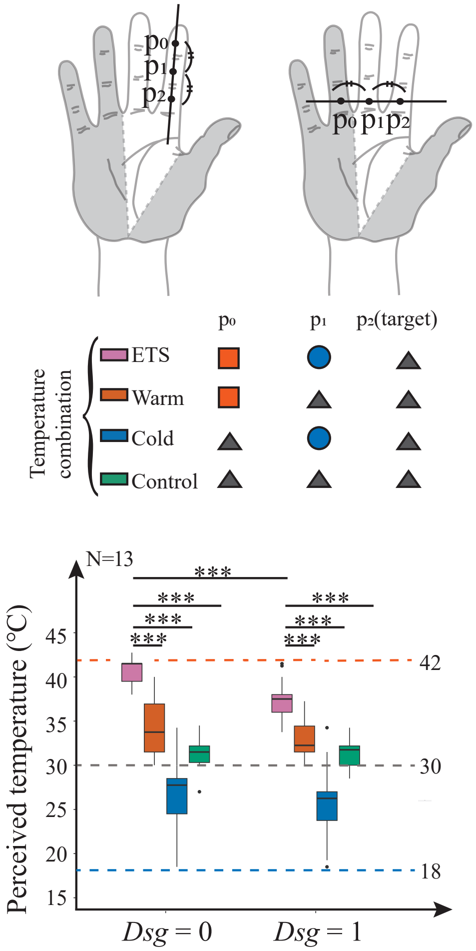


Figure 4.5: Results of Experiment 4.2. The generation of ETS was investigated under $D_{sg} = 0$ condition and $D_{sg} = 1$ condition while the physical distance between every two adjacent stimulators was 20 mm. The red squares, blue circles, and gray triangles represent the stimulus temperatures of 42°C, 18°C, and 30°C, respectively. The segmental effect of ETS in Experiment 4.1 was replicated. *** $p < 0.001$.

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 the air has

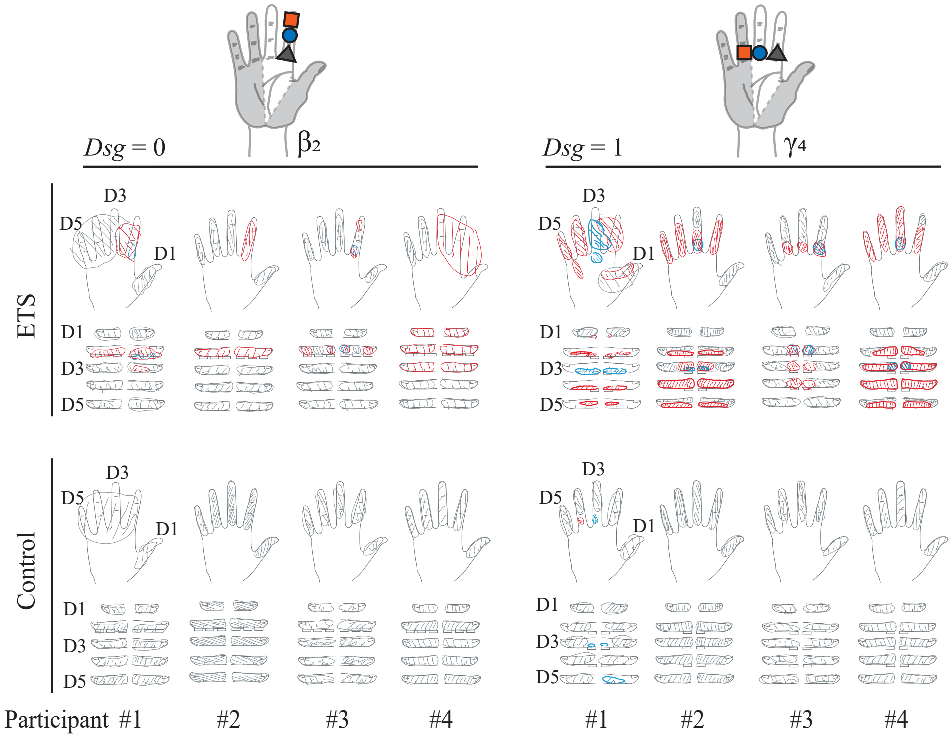


Figure 4.6: Results of Experiment 4.3. Participants drew the shape and field of warmth, cold, and neutral sense with a red, blue, and gray circle, respectively. Warmth was perceived at the neutral location. In some cases, warmth appeared to extend beyond the skin, into the air.

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 (Bekesy, 1962). It is the first report 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.

Experiment 4.4

Experiment 4.4 investigated the segmental effects of the ETS on the lower leg. Figure 4.7 a illustrates the experimental results and corresponding conditions. A two-way repeated-measures ANOVA indicated that the temperature 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. A two-way repeated-measures ANOVA was performed 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

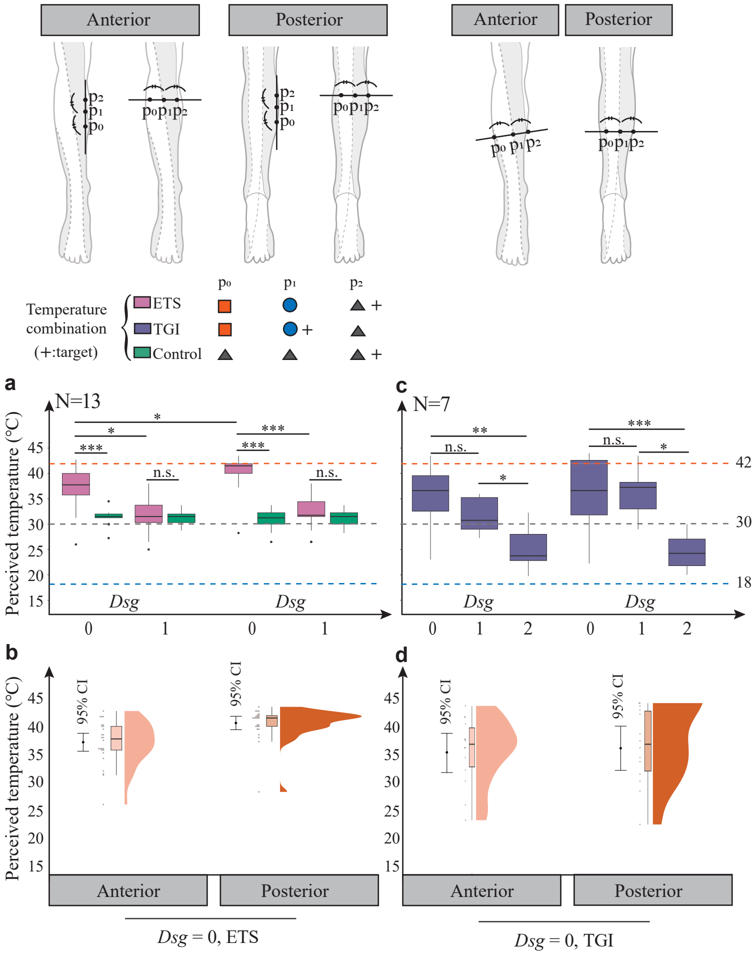


Figure 4.7: Results of Experiment 4.4. ETS and TGI were investigated on the anterior and posterior lower leg. The red squares, blue circles, and gray triangles represent the stimulus temperatures of 42°C, 18°C, and 30°C, respectively. + mark stands for the target location in each temperature combination 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. $p > 0.05$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

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.

I 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 Figure 4.7 b and Figure 4.7 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.

Experiment 4.5

Experiment 4.5 aimed to illustrate the perceptual distribution of the lower leg. Figure 4.8 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

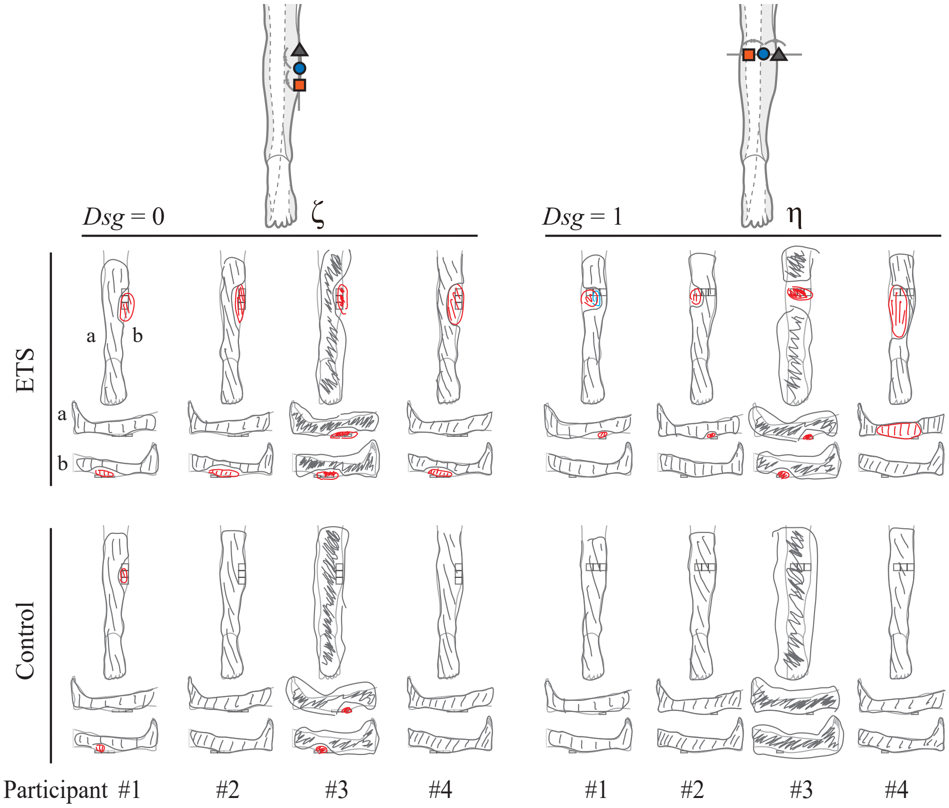


Figure 4.8: Results of Experiment 4.5. Participants drew the shape and field of warmth, cold, and neutral sense with a red, blue, and gray circle, respectively. Warmth was perceived at the neutral location. In some cases, warmth appeared to extend beyond the skin, into the air.

sense of cold was almost not perceived. When viewed from the side, the thermal sensation was only present in the area where the stimulator made contact with the skin.

4.5 Discussion

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 my pilot study indicate that this phenomenon is not a physical phenomenon of heat conduction on the skin from warm stimulation to neutral stimulation (Ho & Jones, 2006; Jones & Ho, 2008). 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, I 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. The difference between the palm and the lower leg does not result from the conduction distance. The length of the lower leg is approximately 45 cm (Nor et al., 2013). The length of the thigh is approximately 40 cm (Nor et al., 2013). The distance from the pelvic cavity (where the sciatic nerve enters the pelvis) to the sacral spinal cord is about 15 cm. Therefore, the total distance for thermal signals to conduct from the lower leg to the spinal cord is approximately 100 cm. Since a total length from the fingertip to the spinal cord is about 110 cm, the distance of conduction from the fingertips is similar to that from the lower leg, ruling out the possibility that different conduction distance leads to the different observation results. These results indicated that the intersegmental lateral connection of the thermal stimuli was not uniform. Finally, by illustrating perceptual distribution, I found that warmth could be perceived in areas where there was no skin or stimulus, suggesting the involvement of suprasegmental spatial organization.

Experiments 4.1 and 4.2 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 (Fardo et al., 2018). This spatial property allows us to observe the spatial property of the ETS phenomenon using a segmental distance paradigm.

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 (Fardo et al., 2018). The results of Experiments 4.1 and 4.4 aligned with this finding. However, my 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 4.3 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 (Bolognini et al., 2013; Flor & Birbaumer, 2000; Mercier et al., 2006; Nardone et al., 2019). The involvement of the dorsal posterior insular cortex is probable, given the topographical projection of thermoreceptive neurons in lamina I to this region (A. D. Craig et al., 2000; L. H. Hua et al., 2005). 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.

Lateral Connection in Dorsal Horn

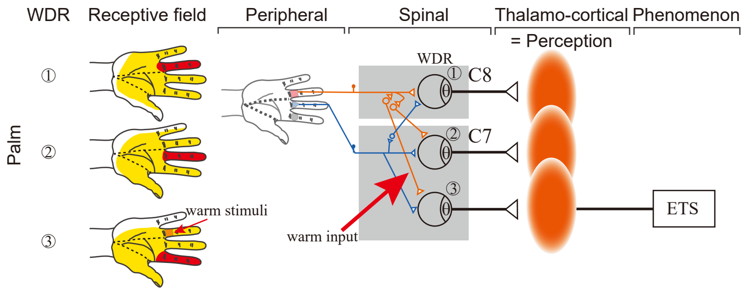
The results reveal a marked influence of spinal segments on the ETS phenomenon. This suggests that the reproducibility of ETS is dominated by lateral connections between spinal segments and that lateral connections between spinal segments are not uniform across spinal segments.

Here, I 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, I considered the contribution of Wide Dynamic Range neurons, which are relay nuclei for warm, cold, and mechanical stimuli.

First, I 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 (A. Craig & Bushnell, 1994) 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. The qualitative observations of the perceptions produced by ETS indicate that there are few reports of burning sensations and none of pain (J. Hua et al., 2022). Therefore, the classic unmasking model cannot explain ETS.

Fardo described the mechanism of “the unmasking (or disinhibition) of

a Activation of neurons outside boundary causes ETS



b Absence of warm input leads to less reproducibility of ETS

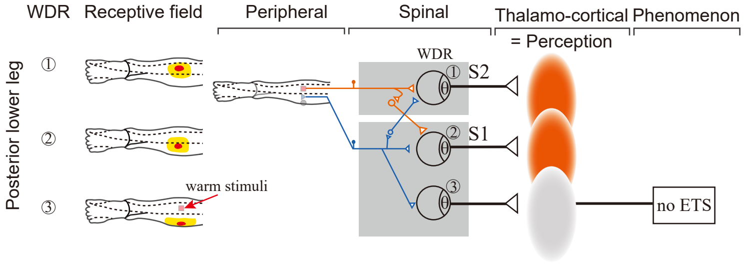


Figure 4.9: A model involving spinal summation and thalamocortical combination of stimuli. Wide Dynamic Range neurons in the spinal cord have a central/surround receptive field organization. The central receptive field zone (red) responds to mild and intense stimuli, while the surround receptive field (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 (Coghill, 2020). 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 (Tan et al., 2012). 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.

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 (Fardo et al., 2018). 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, I discuss the contribution of the Lissauer tract to the "overestimation of cold stimuli, " as reported by Fardo. First, I 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 chapter, 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 I 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 this chapter, and the above considerations could provide 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 warm and cold stimuli cross adjacent segments, regardless of the stimulation site. However, the experimental results did not support this hypothesis. Therefore, the contribution of HPC cells alone does 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 (Green, 2004; Le Bars & Cadden, 2008). 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 (Bouhassira et al., 2005; Green, 2002). A recent study reported the necessity of cold-sensitive afferents for the sense of warmth (Paricio-Montesinos et al., 2020). 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 (Coghill, 2020). 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 (Figure 4.9 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 (Coghill, 2020) [1], because the receptive field almost covers the rat palm size (Watson & Broadhurst, 1976). The area of the receptive field corresponding to the lower leg is estimated to be approximately 20 - 60 mm^2 (Tan et al., 2012) [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 (Cakit et al., 2014; Hyncik et al., 2021). 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. Figure 4.9 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 (Takahashi & Nakajima, 1996; Tan et al., 2012). 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 (Coghill, 2020; Tan et al., 2012). 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 (Figure 4.9 b).

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[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 (Watson & Broadhurst, 1976) 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.

Chapter 5

GENERAL DISCUSSION

I have not touched the outline of a star nor the glory of the moon, but I believe that God has set two lights in mind, the greater to rule by day and the lesser by night, and by them I know that I am able to navigate my life-bark, as certain of reaching the haven as he who steers by the North Star.

- Helen Keller

5.1 General Discussion of Findings

Influenced by the "labeled line" doctrine (Green, 2004; Melzack, 1996), previous studies of thermal sensation primarily focused on the quality of thermal sensations, such as cool, cold, warm, hot, and burning pain (A. Craig & Bushnell, 1994; Green, 2004; Yarnitsky & Ochoa, 1990). However, another critical aspect of thermal sensation—the perceptual boundary—remains relatively unexplored. This thesis addresses this gap by investigating the perceptual boundary characteristics of thermal sensation, emphasizing an enlargement phenomenon of the perceptual boundary known as Extrapolation of Thermal Sensation (ETS). The thesis author examined several key research questions to deepen our understanding of this phenomenon and its implications for thermal sensation (Table 5.1).

The findings in Chapter 2 indicate that the temporal sequence of thermal stimuli significantly affects the perception outside the boundaries of the stimulator regardless of the spatial configuration of the thermal stimuli. Specifically, a warm stimulus followed by a cold stimulus leads to the perception of warmth beyond the area of the cold stimulator. The warmth outside the cold stimulator was observed at the fingertip and the base of the finger, indicating that the spatial configuration does not influence ETS. The results in Chapter 4 further confirmed this spatial characteristic. Chapter 4 reported that there is no significant difference in the perceived temperature while the segmental distance between the warm and cold stimuli is maintained. This result highlights the robustness of ETS, allowing us to ignore the potential influence of spatial configuration (e.g., the direction of thermal stimuli) when explaining the mechanism underlying ETS. The fact that thermal sensation is relatively less susceptible to the influence of spatial configuration has also been verified in TGI-related research. Defrin found that TGI on the forearm existed up to 30 cm separation between the warm and cold stimulator (Defrin et al., 2008). These results show that warm and cold inputs integrate in a large space.

The unmasking theory, which posits that the perception of warmth arises from the unmasking of inhibition on HPC cells (A. Craig & Bushnell, 1994), was tested against the observations of ETS. The results demonstrated that the unmasking theory does not adequately explain the warmth evoked by ETS. This finding suggested that alternative mechanisms must be considered to account for the observed phenomenon. Conversely, the addition theory, which proposes that the combined intensity of warm and cold stimuli leads to the perception of warmth (Bouhassira et al., 2005), was supported by the findings. The thesis author observed that the perception of warmth increased with the intensity of both warm and cold stimuli. This supports the idea that ETS may result from an additive process where the thermal inputs are integrated to produce a sensation of warmth. Although the addition theory proposed by Green can only explain the quality of ETS while cannot explain the enlargement of the boundary of warmth, this theory provides a basic framework for understanding ETS.

The thesis also sought to clarify whether ETS and TGI represent the same phenomenon. The results in Chapter 4 indicated that although the perceived temperatures of the ETS and TGI varied in units of segmental distance, the ETS was not reproduced where the TGI was, suggesting they are distinct perceptual experiences. The perceived temperature of the ETS was observed to vary in the units of the segmental distance, indicating that the mechanism of ETS involves the process in the spinal cord. The same for the mechanism of TGI. Therefore, although both ETS and TGI involve spinal cord processes, they are determined by different spinal cord processes.

Although the ETS is dominated by segmental distance, the involvement of suprasegmental organization in ETS generation has also been observed. Experiments in Chapter 3 and Chapter 4 revealed that warmth sometimes extended beyond the skin, into the air. The perception in the air suggested the presence of cortical organization (the related discussion can be found in Chapter 4). Thus, the mechanism underlying ETS involves the cortical process.

In addition, the segmental condition where warmth is perceived in the air appeared to have some similarities. Chapter 3 reported the warmth in the air when the warm and cold stimuli were within the same dermatome (the warm and cold stimuli were applied to D2 and D3, respectively). Chapter 4 reported an obvious warmth in the air when within the dermatome as well. This sim-

Table 5.1: Summary.

Research question	**Answer**
Does the sequence of input affect perception outside boundary?	Yes. Warmth is perceived outside cold stimulator if given a warm stimulus prior to a cold stimulus.
Does unmasking theory explain warmth evoked by ETS?	No.
Does addition theory explain warmth evoked by ETS?	Yes. Warmth is perceived with increase of warm and cold intensity.
Is ETS equivalent to TGI?	No. ETS and TGI have different reproducibilities.

ilarity might indicate that when the warm and cold stimuli are projected to the same spinal segment, it is more likely to evoke warmth in the air.

5.2 Comparison of Proposed Models

This thesis investigated the integration of spatiotemporal warm and cold stimulation in evoking Extrapolation of Thermal Sensation. In this phenomenon, the perceptual boundary of thermal sensation extends beyond the physical boundary of the stimulus. Here, I used Peltier elements to study how warm and cold stimuli integrate spatiotemporally to alter the perceptual boundary, evoking the ETS. In this section, we compare two proposed models that elucidate the underlying mechanisms of ETS based on findings from temporal, thermal, and spatial characteristics studies. The comparative analysis will highlight the strengths and limitations of each model, ultimately leading to a synthesis that aims to offer a comprehensive explanation of ETS.

Chapter 2 reports the temporal characteristics of ETS and introduces a Receptor Interaction Model, which focuses on the temporal sequence of warm and cold stimuli and their effects on thermal perception. In this chapter, I found that warm stimuli (far from the extrapolation part) prior to cold stimuli (close to the extrapolation part) induce a sensation of warmth outside the cold stimulus. However, in the opposite temporal sequence, cold stimuli prior to warm stimuli do not induce a similar warm sensation. Based on these observations regarding the temporal characteristic of ETS, a model was proposed based on the interaction among thermoreceptors.

First, thermoreceptors exhibit lateral inhibition, where activation of a receptor inhibits adjacent homologous receptors (those of the same type) (S.-I. Amari, 1980; Kohonen, 1982; Von der Malsburg, 1973). lateral inhibition has been confirmed as a common mechanism in the central nervous system (including the spinal cord, thalamus, and cerebral cortex) that maintains the topology of perceptual signaling from the periphery to the cerebral cortex (Werner & Whitsel, 1968).

Second, warm and cold receptors inhibit each other within their effective ranges. Here, I made an assumption that pre-inhibited receptors by one type (warm or cold) may become disinhibited by subsequent inhibition of the heterologous type; pre-excited receptors can be inhibited by subsequent excitation of heterologous receptors.

This receptor interaction model explains the different observation results under different temporal sequences. In addition, as the first model that explains the ETS, this model explains how receptors mutually interact to change the result of the lateral inhibition process—as a result, the perceptual boundary is enlarged. However, there are limitations to this model. In the part of mutual inhibition, this model is constructed on the disinhibition of WARM cells, which is based on assumption. According to the knowledge of neurophysiology experiments, after the decrease in activity of cold cells, the disinhibited (or unmasked) cell is a nociceptive HPC cell, rather than a WARM cell. Accordingly, this model lacks neurophysiological evidence.

Besides the lack of neurophysiological evidence, the receptor interaction model fails to explain the experimental results in the next chapters. Chapter 3 reports the relation between ETS and the temperature difference of the thermal stimuli. With the greater temperature difference of the thermal inputs, T_{warm}-T_{cold}, there is a more intense sensation of warmth outside the physical boundary. This result indicates that with a more intense warm input, the resulting ETS should be more intense. On the other hand, in this model, the activity of the warm cell in the middle (warm #4 in Figure 2.6) is significant.

With a more intense warm input, warm #4 becomes more inhibited, hence it is more difficult for warm #4 to be disinhibited. Unable to be disinhibited makes it more difficult to evoke ETS. Therefore, the receptor interaction model cannot explain the findings in Chapter 3.

Additionally, the receptor interaction model cannot interpret the segmental effect found in Chapter 4. There are several layers in this model, however, it is unclear whether the neurons in each layer are supported by physiology evidence. Thus, the receptor interaction model lacks a description of the location of neurons in each layer. Accordingly, it is difficult to interpret the segmental effect with the current version of the receptor interaction model.

Chapters 3 and 4 reported the thermal and spatial characteristics of ETS, respectively. This warmth is intense when the intensity of warm and cold inputs are intense. With an increase in temperature difference between the two inputs, the sense of warmth spatially spreads and extends beyond the physical boundary. In response to these results, a model was proposed involving spinal summation and a thalamocortical combination of stimuli. Here, I call it spinal-thalamocortical integration model. In this model, WDR neurons in the spinal cord have a central/surround receptive field organization. The central receptive field zone responds to mild and intense stimuli, while the surround receptive field only responds to intense stimuli. Mildly warm and cold stimuli converge on WDR neurons, including the WDR neuron outside the boundary, increasing the stimulation to levels usually produced by more intense heating. 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.

There are also limitations in the spinal-thalamocortical integration model. First of all, this model cannot explain the different results under different temporal sequences found in Chapter 2. In addition, while this model explains the perception outside the physical boundary, it does not answer the different qualities of the resulting thermal sensations. As the basis of this model, the polymodal WDR neurons, are found to be responsive to warm, cold, and mechanical stimulation because of physiology evidence. Because only the firing rate of WDR neurons changes with an increase in the modality number of inputs, it is difficult to believe that this type of neuron contributes to the quality of thermal sensation.

Moreover, this model emphasizes the core role of neurons in the spinal cord while some of the more essential interactions between neurons are ignored. First, as Figure 1.3 shows, WDR neurons are found deep in the lamina V of the rat (Le Bars & Cadden, 2008). The C fibers and Aδ fibers contact directly or indirectly to WDR neurons. When these fibers indirectly contact the WDR neurons, they first contact the cells in the lamina I or lamina II, where WARM cells, COLD cells, and HPC cells are located. The superficial layers of the dorsal horn are dominated by inhibitory connections, while the deep layers are dominated by excitatory connections. This means that the excitatory connections of WDR neurons located in the deep layers may be formed by inhibitory connections between superficial layers such as WARM cells and COLD cells through complex interactions. However, this model ignores these more essential interactions. Second, it is important to note that the cortical neurons and spinal neurons possibly work together to generate the ETS. The cortical encoding of temperature is not clear until 2023 (Vestergaard et al., 2023). Although the recently discovered cortical neurons cannot explain ETS, as the understanding of cortical neurons deepens, more and more cortical neurons will be discovered. The findings in Chapter 4 cannot rule out that cortical neurons also play the role of WDR neurons.

In summary, while the receptor interaction model provides a detailed and mechanistic explanation for the temporal characteristics of ETS, it has limitations when applied to the findings in Chapters 3 and 4. The model can partially explain the increased intensity of warmth with higher stimulus intensity and the role of spatial summation. However, it does not fully account for the extensive spatial extension of warmth beyond the physical boundaries of the stimuli.

To comprehensively explain the thermal and spatial characteristics of ETS, it is necessary to integrate neural mechanisms, as proposed in spinal-thalamocortical integration model. The next section will propose a new model closer to the essence based on the interaction of warm and cold cells to describe the generation of ETS.

5.3 A Model for Extrapolation of Thermal Sensation

Based on the findings from Chapters 2, 3, and 4, as well as the comparative analysis of the receptor interaction model and the spinal-thalamocortical integration model, the thesis author propose a new, integrated model to comprehensively explain the phenomenon of ETS. This model synthesizes the already known neural processes, providing a comprehensive understanding of ETS.

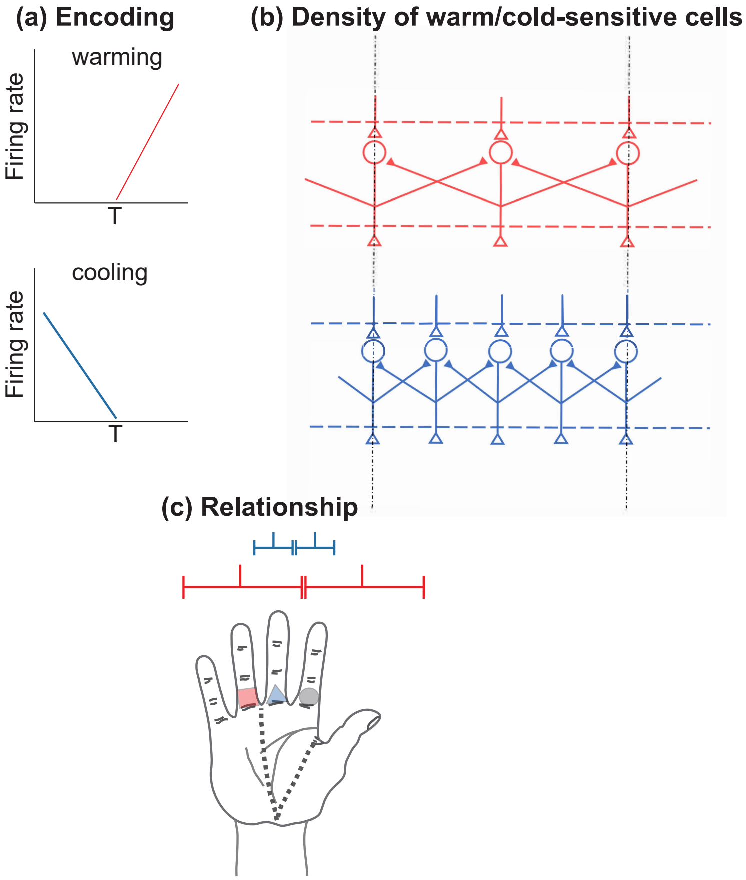
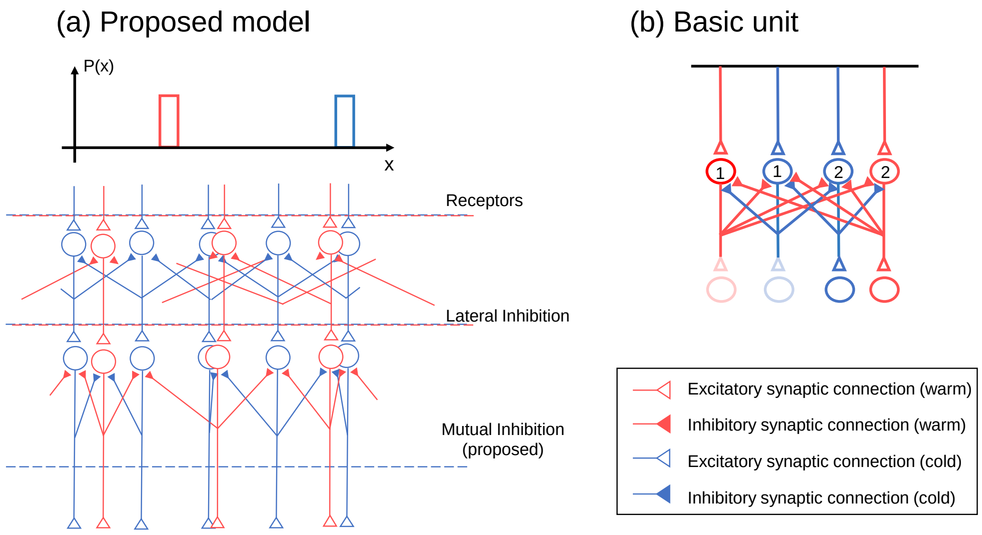


Figure 5.1: Set ups of proposed model.

Figure 5.1 shows the set ups of the proposed model. Figure 5.1.(a) illustrates a model of encoding of warming and cooling by warm and cold cell. “T” stands for the neutral temperature. For the warm cell, it is activated when the stimulation temperature is above neutral temperature “T”; for the cold cell, however, it is activated when the stimulation temperature is below the neutral temperature “T”.

Figure 5.1.(b) illustrates the the different densities of warm- and cold-sensitive cells. Cold-sensitive cells have a higher density than warm-sensitive cells. At peripheral, the density of cold spots at human finger is about 4/cm^2 while that of warm spots is about 1.5/cm^2 (Arens & Zhang, 2006). Since the topology of perceptual signaling, at least the topology within the same dermatome is maintained from the periphery to the cerebral cortex (Werner & Whitsel, 1968), the quantitative relationship between warm-sensitive cells and cold-sensitive cells also remains roughly the same during conduction.

Figure 5.1.(c) shows the relationship between the stimuli and the corresponding thermosensitive cells.


(a) Proposed model

(b) Basic unit

Figure 5.2: Model of Extrapolation of Thermal Sensation based on the interaction of warm- and cold-sensitive cells.

Figure 5.2.(a) illustrates the proposed model. When thermal stimuli are applied, the warm- and cold-sensitive cells engage in lateral inhibition and mutual inhibition processes. Lateral inhibition, a common mechanism in the central nervous system, involves the suppression of adjacent homologous re-

ceptors (receptors of the same type), enhancing the contrast of the thermal signal (S.-I. Amari, 1980; Kohonen, 1982; Von der Malsburg, 1973). For instance, when warm receptors are activated, they inhibit nearby warm receptors, increasing the perceived intensity of warmth in the stimulated area.

Mutual inhibition occurs between heterologous thermosensitive cells (warm- and cold-sensitive cells). When warm-sensitive cells are activated, they inhibit nearby cold-sensitive cells, and vice versa. Such mutual inhibition has been shown in the spinal cord through animal work (McCoy et al., 2013; Zheng et al., 2010). Among the mutual inhibition, the inhibition of cold-sensitive cells forms the basis of the unmasking theory (A. Craig & Bushnell, 1994) and has been recognized in human through psychophysical experiments. On the other hand, the inhibition of warm-sensitive cells has not been considered in the previous study. In this model, the inhibition of the warm-sensitive cells and the inhibition of the cold-sensitive cells form the basis for the initial perception of thermal stimuli.

In this model, the output of the warm- and cold-sensitive cells decide the local quality of the sensation. This proposal has been partly supported by the findings of mice. It has been found that the loss of the cool-sensitive ion channel TRPM8 in mice leads to an inability to perceive warmth (Paricio-Montesinos et al., 2020). This finding indicates that the local quality of the warm sensation is not only decided by the warm-sensitive cells but also decided by the cold-sensitive cells. Similar integration that two types of cells decide the local sensation has been found in the cerebral cortex.

Figure 5.2.(b) illustrates a basic unit that explains ETS. Suppose that warm and cold stimuli are applied to the area where warm #1 and cold #1 are, and the area of cold #2 is the goal area. Now analyze the interaction effect that each thermosensitive cell receives. For warm #1, it receives lateral inhibition from warm #2 and mutual inhibition from cold #1. It is not influenced by cold #2 because it exceeds the interaction range of cold #2. For warm #2, it receives lateral inhibition from warm #1 and mutual inhibition from cold #2. For the same reason, warm #2 is not influenced by cold #1. For cold #1, it receives lateral inhibition from #2 and mutual inhibition from warm #1 and #2. The same situation for cold #2. For cold #2, it receives lateral

inhibition from cold #1 and mutual inhibition from warm #1 and #2. Now consider the situation in which warm and cold stimuli are applied to warm #1 and cold #1, respectively. Warm #1 is activated by the warm stimulus. Accordingly, warm #2, cold #1, and cold #2 are inhibited. On the other hand, cold #1 is activated by the cold stimulus. Accordingly, warm #1 and cold #2 are inhibited. The activation of warm #1 and warm #2 exceeds cold #2, indicating that the balance at cold #2 is broken and warmth exceeds cold. As a result, warmth is perceived at cold #2.

This basic unit functionally has the ability of the WDR neurons mentioned in Chapter 4 that respond to warm and cold stimuli. When the warm stimulus becomes more intense, the extrapolation area, cold #2 receives more mutual inhibition from warm #1. On the other hand, cold #2 receives more lateral inhibition from cold #1 when the cold stimulus becomes more intense. No matter whether the warm or cold stimulus becomes more intense, the imbalance at cold #2 is increased, leading to a stronger warmth perceived at cold #2.

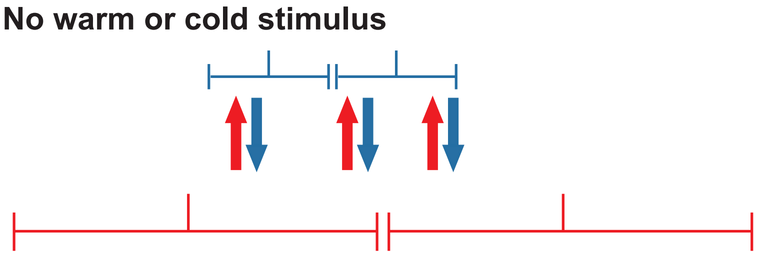


Figure 5.3: Explanation of results (no warm or cold stimulus).

Figure 5.3 shows the case that no warm or cold stimulus is applied. In this case, warm and cold cells fire autonomously. A balanced situation is maintained (for simplicity, only mutual inhibition is illustrated). As a result. there is no thermal sensation.

Figure 5.4 shows the case that a single warm stimulus is applied. The left warm cell is activated by the warm stimulus while the the right warm cell is not. Thus, the part on the right side of the left warm cell is the extrapolation part. The left warm cell has a strong mutual inhibition effect on the two

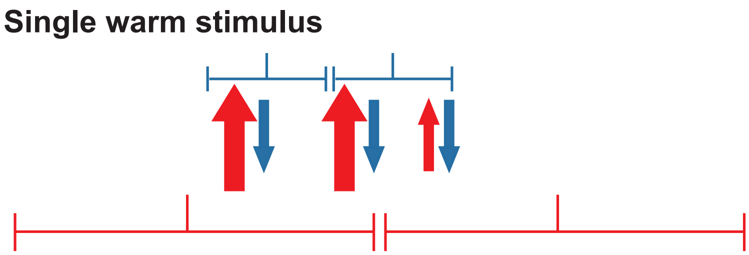


Figure 5.4: Explanation of results (single warm stimulus).

cold cells. Thus, the two cold cells are inhibited. On the other hand, the right warm cell is also inhibited because of lateral inhibition. As a result, a balanced situation between the right warm cell and the right cold cell is generated. As a result, there is no thermal sensation at the part on the right side of the left warm cell.

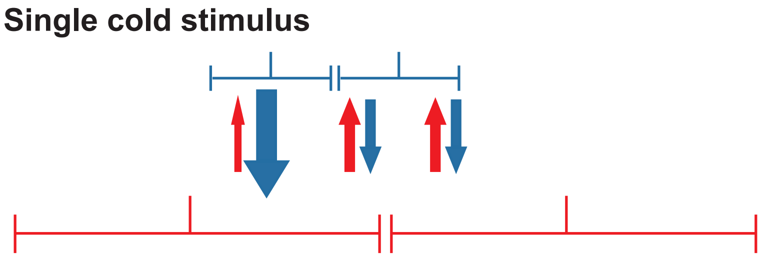


Figure 5.5: Explanation of results (single cold stimulus).

Figure 5.5 shows the case in which a single cold stimulus is applied. The left cold cell is activated by the cold stimulus while the the right cold cell is not. Thus, the part on the right side of the left cold cell is the extrapolation part. The left cold cell has a strong mutual inhibition effect on the left warm cell while does not inhibit the right warm cell. Thus, the left warm cell is inhibited. On the other hand, the right cold cell is also inhibited because of lateral inhibition. As a result, a balanced situation between the right warm cell and the right cold cell is generated. As a result, there is no thermal sensation at the extrapolation part.

Figure 5.6 shows the case in which warm and cold stimuli are applied.

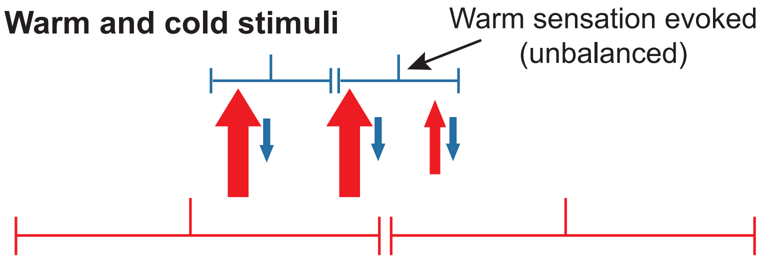


Figure 5.6: Explanation of results (warm and cold stimuli).

The left warm cell is activated by the warm stimulus and the left cold cell is activated by the cold stimulus. Hence, the right cell is the extrapolated area. The left warm cell has a mutual inhibition effect on the two cold cells because the cold cells are located in their interaction field. However, the left cold cell has a mutual effect only on the left warm cell. On the other hand, the right warm cell is laterally inhibited by the left warm cell. The right cold cell is lateral inhibited by the left cold cell. Thus, the right cold cell is strongly inhibited. As a result, the activation of the right warm cell exceeds that of the right cold cell, leading to a warm sensation at the extrapolation area.

Since there is no cold stimulus applied on the left side of the left warm cell, there is no cold cell being inhibited by the left warm cell on the left part because of mutual inhibition. As a result, there is no similar ETS generated on the left part. This explains the observations that warmth is perceived outside the cold stimulus.

The proposed model anticipates a steady-state response rather than a transient one when interpreting thermal stimuli. This steady-state expectation is crucial for understanding how the model aligns with the experimental outcomes presented in this thesis. The results discussed in Chapter 2 are transient responses. These transient responses are probably attributed to the different conduction speeds of warm and cold signals. When applying the cold stimulus first and then both warm and cold stimuli for a short duration (0.5 s), since the warm signals are conducted at a slow speed (over 1 s to conduct to the cerebral cortex), there is no enough time to integrate warm and cold signals. As a result, there is no warm sensation outside the cold stimulator.

On the other hand, however, when applying the warm stimulus first and then both warm and cold stimuli for a short duration, since the cold signals are conducted at a fast speed, there is enough time for integration. Thus, a warm sensation is evoked outside the cold stimulator. Despite these transient responses, the proposed model predicts that the final perceptual state remains consistent irrespective of the sequence in which the stimuli are applied. This is a key feature of the model, emphasizing that the eventual sensory perception reaches an equilibrium that is independent of the initial order of thermal input.

Appendix data supports the proposed model by demonstrating perceptual changes when stimuli are applied simultaneously (for detail, see Figure A.1). Participants were applied warm and cold stimuli simultaneously for 1.8 s, 3.6 s, 5.4 s, 7.2 s, 9.0 s, 10.8 s, and 12.6 s and they were asked to answer hot or cold at each time point. I found that the percentage hot judgment was as low as 25 at first, then it increased and could be maintained when the duration of warm stimulus increased. In detail, the percentage hot judgment exceeded 50 when the duration of warm stimulus exceeded 3.6 s, suggesting the balanced point be 3.6 s. The result also indicated that the warm sensation can be maintained for at least 12.6 s. These results show a change in perception from cold to warmth. This data provides support for the model's prediction: when warm and cold stimuli are delivered, the final perception is warmth.

Chapter 6

CONCLUSION

The best and most beautiful things in the world cannot be seen or even touched - they must be felt with the heart.

- Helen Keller

6.1 Summary

Humans rely on their ability to perceive external temperatures to recognize material properties. Despite its significance, thermal sensation has not been well studied. While there have been physiological studies on temperature representation, the spatial organization of thermal sensation, particularly its perceptual boundary, remains unclear. This thesis investigates Extrapolation of Thermal Sensation (ETS). Classical thermal phenomena including Thermal Grill Illusion (TGI) are perceived only at the stimulus location or within the boundary formed by multiple stimuli. ETS, however, reports perception outside the physical boundary. This thesis explores the spatiotemporal and thermal characteristics of ETS and clarifies the mechanism underlying this enlargement phenomenon of perceptual boundary of thermal sensation.

Regarding the question "Whether thermal sensation can be evoked outside physical boundary," this thesis demonstrates for the first time an enlargement phenomenon of the perceptual boundary, indicating that thermal sensations can indeed be evoked outside the physical boundaries of the stimuli.

Regarding the question "How is sensation outside boundary evoked," this thesis explores the conditions for evoking ETS from the factor of space, time, and temperature of configuration of thermal stimuli. Temporally, the thesis found that the sequence in which thermal stimuli are applied significantly affects the perception of warmth. Specifically, warmth is evoked more effectively when a warm stimulus precedes a cold stimulus. Spatially, this thesis showed segmental-distance-dependent variations in perceived temperature. From the factor of temperature, this thesis showed that gradually increasing warm and cold stimuli increased the warm sensation outside the cold stimulator. Based on the results of a series of experiments conducted, it has been argued that the model based on lateral inhibition and mutual inhibition proposed in this thesis is the most appropriate theory to explain the spatial, temporal, and thermal characteristics of ETS. The model proposed in this thesis identified neural processes, including lateral inhibition and mutual inhibition among thermosensitive cells, which play crucial roles in enlarging perceptual boundary.

In conclusion, the research objectives set out in Chapter 1 have been comprehensively addressed and achieved through a series of detailed experiments and analyses. The proposed integrated model provides a robust framework for understanding the neural mechanisms underlying ETS, offering new insights into how thermal stimuli are integrated over time and space to form the perceptual boundary, which is a perspective that has not been focused enough. Additionally, the comparative analysis with TGI has further clarified the distinct characteristics and mechanisms of ETS, advancing the overall understanding of thermal sensation. This work not only contributes to the field of sensory neuroscience but also sheds the light for future research exploring various characteristics of thermal sensation.

6.2 Limitations

The methods in this thesis have limitations that should be addressed in future research. In this thesis, I used Peltier elements to investigate the Extrapolation of Thermal Sensation. The use of Peltier elements relies on contact with skin, resulting in the activation of mechanosensitive fibers. This means the thermal inputs in this thesis accompany mechanical inputs, and the observations were obtained under the coexistence of thermal and mechanical inputs. Although it has been reported that tactile does not influence TR (Cataldo et al., 2016) or TGI (A. Craig & Bushnell, 1994). However, the model proposed in Chapter 4 is based on WDR neurons, which respond to thermal and mechanical stimulation. Thus, mechanical stimulation may influence the resulting ETS. Developing a contactless method, e.g., radiation and chemical stimulation, would strengthen the conclusions that can be drawn from the results and further understand the interactions between warm and cold signals.

Exploring the spatial organization of perception is a critical step in understanding how the brain organizes sensory experiences. Previous studies on thermal sensations have mainly focused on the organisms involved in thermal processing. In this thesis, the thesis author focused on the spatial organization of thermal sensations by observing ETS. The spatial organization of perception has been thought to occur in the cerebral cortex. However, in Chapter

4, the thesis author strengthed the core role of WDR neurons while did not construct a model based on cortical organization. This was because the cortical neurons that encode temperature has not been found. Whereas, with the discovery of thermosensitive cortical neurons, the core role of cortical neurons in the spatial organization needs to be confirmed.

6.3 Future Directions

There have been no reports of thermal sensations outside the stimulation areas of warm and cold stimulators. I initially demonstrated that thermal sensations were induced across the boundaries that enveloped the physical stimuli. My 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.

As mentioned in Chapter 1, a classical method to display temperature on human skin is to use Peltier elements. When using Peltier elements to display temperatures in a VR or AR environment, frequently switching temperature for displaying requires a large electric current, which in turn produces a significant amount of heat. To manage this heat, high-capacity water cooling systems are necessary to dissipate it effectively. This requirement for substantial cooling infrastructure significantly limits the practical application of Peltier-based thermal displays in the VR/AR environment. The ETS phenomenon has the potential to be used to alleviate this problem. The larger perceptual boundary than the physical boundary indicates that we can display temperature at the skin area without thermal stimulation. Accordingly, the application of ETS provides a potential solution to the heat problem resulting from the Peltier elements.

Moreover, in the illustrations of perceptual boundaries, some participants reported a warm sensation in the air, suggesting the involvement of the cortex neurons. However, we still know too little about cortex neurons. The first cortex neurons were not discovered until last year (2023). In addition, we lack knowledge about the interaction of cortex neurons. More research should be conducted to investigate the organization of thermal signals in the cortex.

Previous studies regarding thermal sensation are generally based on unimodal thermosensitive neurons (A. Craig & Bushnell, 1994). On the other hand, there is little research on polymodal neurons. In this thesis, I point out a potential involvement of polymodal WDR neurons in organizing perceptual boundaries. More studies should be conducted to investigate the role of polymodal neurons.

Appendix A

TEMPORAL SUMMATION LEADS TO THE TEMPORAL CHARACTERISTIC OF ETS

Methods

The aim was to determine how the duration of warm stimulus affects ETS. What is the balanced point of duration? Is ETS maintained under the prolonged warm stimulus? The present experiment sought to answer these questions.

This experiment's data were obtained from 11 participants (9 males and 2 females) aged between 23 and 29. Participants suffering from pain, diseases causing potential neural damage (e.g., diabetes), systemic illnesses, and mental disorders were excluded. All reported being right-hand dominant.

The procedure included seven duration conditions (1.8 s, 3.6 s, 5.4 s, 7.2 s, 9.0 s, 10.8 s and 12.6 s). I applied warm and cold stimuli simultaneously in this experiment. All the trials were run in random order. Four observations were recorded at each duration condition for a total of 44 observations per point across all subjects.

Results

Figure A.1 illustrates the experimental result. In general, the percentage hot judgment is as low as 25 at first, then it increases and can be maintained when the duration of warm stimulus increases. In detail, percentage hot judgment exceeds 50 when the duration of warm stimulus exceeds 3.6 s, suggesting the balanced point be 3.6 s. The result also reveals that the illusion can be maintained for at least 12.6 s. In addition, the standard deviation is large when the duration of the warm stimulus is short and becomes small when it exceeds 5.4 s. This result reveals that the sensation is paradoxical, and individual differences are great when the temporal integration is in progress.

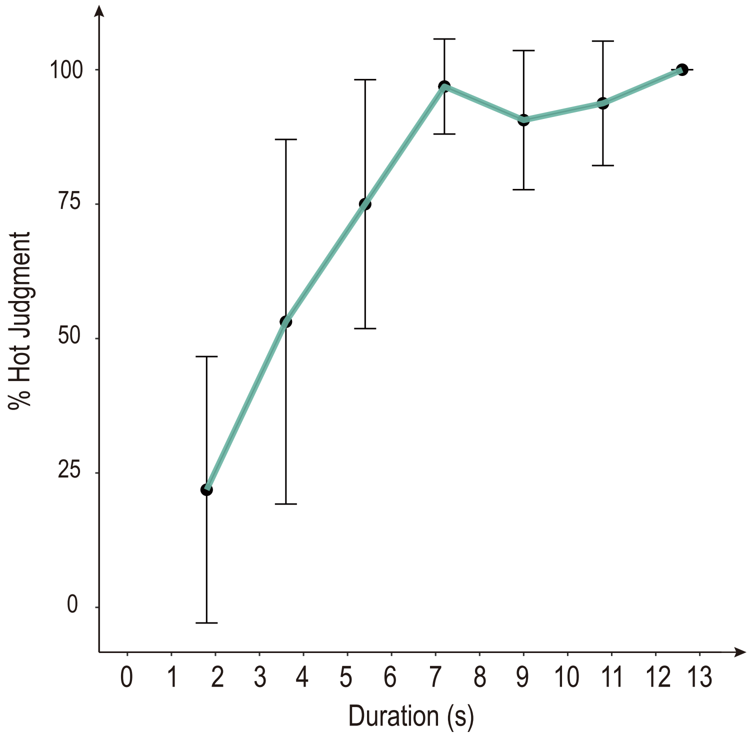


Figure A.1: Results of Experiment B.1. Percentage hot judgment at D3 finger as a function of duration of warm stimulus.

Once this process is done, the participants can perceive an intense and stable illusion.

Discussion

The results support this process of change in the quality of perception. When applying warm and cold stimuli simultaneously, a sense of cold is perceived at first. Then it becomes ambiguous (percentage hot judgment was 50 when the duration of warm stimulus was 3.6 s). Then, a stable sense of warmth is perceived. The temporal summation hypothesis may interpret findings in other thermal illusions. In the study of TGI, Green reported that some participants felt heat if a cold stimulus at D3 was bracketed by warm stimuli at D2 and D4. He also wrote the comment from these participants as “first feeling cold, then turning very warm or hot” (Green, 1977). A similar change of perception was reported in other thermal illusions. Studies in PHS show that when the skin is heated immediately before cooling, “there is a loss of heat pain, a brief period of infatuation, followed by a slow buildup of warmth, and then heat again” (Hämäläinen et al., 1982). Alrutz described contacting a warm object with a large surface skin area that stimulated the warm spots and cold spots on the skin simultaneously, and “the initial coldness was followed by a feeling of heat, and then painful heat” (Harper, 2014).

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