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Characteristics of brain functional networks specific for different types of tactile perception

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Abstract Tactile perception is a fundamental sensory system, playing a pivotal role in our understanding of the surrounding environment and aiding in motor control. In this study, we investigated the distinct neural underpinnings of discriminative touch, affective touch (specifically the C tactile system), and knismesis. We developed a paradigm of EEG experiment consisted of three types of touch tuned in terms of their force and velocity for different submodalities: discriminative touch (haptics or fast touch), affective touch (C-tactile or slow touch), and knismesis (alerting tickle or ultralight touch). Touch was delivered with a special high-precision robotic rotary touch stimulation device. Thirty nine healthy individuals participated in the study. Utilizing functional brain networks derived from EEG data, we examined the patterns of brain connectivity associated with fast, slow, and ultralight touches. Our findings revealed significant differences in functional connectivity patterns between these touch conditions, with the majority of variations occurring in the theta frequency range. Notably, connections in frontal, frontal-central, frontal-parietal, and occipitotemporal regions exhibited distinct activation strengths. Pairwise statistical comparisons further highlighted the unique characteristics of each touch modality. The theta band, in particular, played a prominent role in distinguishing ultralight from slow touches. These results shed light on the interplay between different touch submodalities and their distinctive processing in the brain, contributing to a comprehensive understanding of tactile perception. This research bridges a critical gap in our knowledge of the neural mechanisms underlying tactile perception and its role in shaping our perception of the world.

1 Introduction

Tactile perception has long been the subject of scientific inquiry, serving as a sensory system responsible for conveying information about objects and surfaces that come into contact with the skin, a phenomenon known as mechanoreception. This plays an essential role in the shaping our overall perception of the surrounding environment and aiding in motor control. Central to this process are low-threshold mechanoreceptors (LTMRs), specialized sensors distributed throughout the skin. These receptors respond to various forms of skin deformation and are

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innervated by fast-conducting $A\beta$-type myelinated nerve fibers, allowing for rapid transmission and central processing [1].

Yet, within the realm of tactile perception, there exists a lesser-known class of touch receptors known as C-LTMRs [2]. Unlike their fast-conducting counterparts, C-LTMRs are innervated by slow-conducting C-type unmyelinated fibers, establishing a distinct tactile perception subsystem referred to as the C tactile (CT) system. This subsystem selectively responds to slow and gentle touches, often associated with caressing and pleasant sensations. What sets the CT system apart from the discriminative touch system is its unique projection not only to the somatosensory cortex but also to the posterior insular cortex, a brain region heavily involved in affective processing [3]. The CT system is primarily regarded as a system that reinforces prosocial tactile communication [4]. This notion is supported by the results linking autistic traits to abnormalities in tactile processing [5].

The CT system is not the sole player in affective mechanoreception. Knismesis, another tactile submodality, elicits an alerting and ticklish sensation in response to ultra-light, fleeting touches. Individuals often describe this sensation as annoying and aversive [6]. Knismesis is believed to have evolved as a defense mechanism against parasitic insects [7]. However, it remains the least studied tactile submodality, and there is still uncertainty regarding the receptors involved, as well as the spinal and cortical processing pathways. Some suggest that knismesis is innervated by fast myelinated fibers.

Remarkably, two seemingly similar stimuli—slow and light strokes—can evoke two contrasting emotional responses: a desire to make contact and aversion to contact. The factors contributing to these distinct responses remain elusive, whether it is due to receptor specificity, top-down context-dependent cortical influence, central nervous system inhibition, or other factors. Prior studies have predominantly examined these tactile systems separately or in comparison to the discriminative touch system. The current study aims to shed light on the interplay between different touch submodalities and the distinctive characteristics of their processing.

The central hypothesis of this study posits that various submodalities—discriminative touch, affective touch, and knismesis—have distinct neural underpinnings, and an investigation of brain activity represents the optimal approach to reveal common features and distinctions in their processing.

To test this hypothesis, we employ the concept of functional brain networks, a promising approach to explore brain activity [8]. This approach views the brain as a cohesive system comprising interconnected areas. The unique functional connectivity patterns captured through this approach provide insights into brain activity during cognitive task performance and reveal its normal and pathological states [9–12]. Notably, this approach is particularly effective at detecting disruptions in the collective dynamics of the brain rather than individual brain regions [13–15]. Therefore, it is well-suited to studying differences in brain activity patterns among different touch submodalities.

In this work, we undertake a comparative analysis of the neural mechanisms underlying fast, slow, and ultra-light touches by examining functional brain networks derived from EEG data on the sensor level.

This study seeks to bridge the gap in our understanding of tactile perception, offering a comprehensive exploration of how various touch submodalities are processed in the brain, and thus contributing to a deeper understanding of this fundamental sensory system.

2 Materials and methods

2.1 Subjects

The study comprised 39 subjects (33 women) aged 18–32 years, with a mean age of 21.7 ± 8.52 (mean ± standard deviation). None of the subjects had a previous psychiatric or neurological history. The study received approval from the Institutional Ethics Committee of the Pushkin State Russian Language Institute (protocol code 17-3-24-118, date of approval 15 July 2022) and was conducted in accordance with the Declaration of Helsinki. The participants signed a written informed consent document, and were informed that they had the option to withdraw from the experiment at any point. Most members of the study took part at no cost, out of personal interest, while some were given minor monetary compensation for participating.

2.2 Experimental design

The experimental procedure encompassed a structured sequence of activities, which can be delineated as follows: briefing, recording, and debriefing. In the initial briefing phase, each participant was comfortably seated in an ergonomic office chair. The positioning entailed placing their left hand upon a specialized pillow mount, while their right hand was rested upon a table surface. Positioned directly in front of the participant was a 21-inch computer display, which served as a central focal point for the experiment.

The purpose of the pillow mount was twofold: first, it provided comfort to the participants, and second, it served to restrict inadvertent arm movements. Furthermore, it compensated for the anatomical conical shape of

the human forearm, ensuring that the dorsal forearm remained parallel to the table surface. Above the pillow mount, a custom-designed Rotary Tactile Stimulation (RTS) system (Dancer Design) was carefully positioned. This RTS system featured two brushes that played a pivotal role in the tactile stimulation process.

To maintain participant blindness to the RTS, a folding screen was employed to conceal the device and the left hand of the participant. After seating a participant, laboratory personnel provided comprehensive briefings. These briefings encompassed an elucidation of the experimental procedure and the overarching objectives of the study, thereby facilitating a clear understanding of the task at hand. Any queries posed by the participants were addressed during this phase.

Following the briefing, an electroencephalography (EEG) cap, equipped with 32 active AgCl electrodes, was expertly fitted on the participant's head. Once the EEG cap was securely in place and prepared for recording, the RTS underwent a calibration process. This calibration phase was crucial, as it determined the optimal operating parameters required to achieve the desired tactile force delivery.

Subsequent to the calibration process, participants were explicitly instructed to refrain from moving their left hand for the duration of the experiment. To mitigate auditory interference from the RTS servomotors, participants were provided with earplugs. All further instructions and cues were presented via the computer display. In instances when the display did not convey specific instructions, a fixation cross was displayed.

Throughout the experiment, participants were instructed to maintain a stationary posture without succumbing to drowsiness and to concentrate their attention on the tactile sensations elicited by the touch stimuli.

The tactile stimulation regimen consisted of a total of 153 stimuli, categorized into three distinct types: fast, slow, and ultralight. The fast stimuli were administered using a synthetic squirrel fur brush with a force of 0.8 N and a velocity of 30 cm/s. The slow stimuli employed the same synthetic squirrel fur brush with identical force but a reduced velocity of 4 cm/s. The ultralight stimuli were administered with a synthetic peacock feather brush, featuring a force magnitude less than 0.1 N and a velocity of 4 cm/s.

It should be noted that we analyzed 144 of these stimuli, which were presented without any accompanying feedback. These stimuli were delivered in a pseudorandom sequence, and the interstimulus intervals were randomized within a range of 4.5–5.5 s. This deliberate variation in interstimulus intervals served to prevent the synchronization of EEG rhythms with the timing of the tactile stimuli, ensuring the integrity of the experimental data.

2.3 EEG acquisition

In our study, we employed the LiveAmp system (Brain Products GmbH) in conjunction with the ActiCap active electrode system. Electrode placement adhered to the international 10–20 system, albeit with a noteworthy modification. Specifically, electrodes TP9 and TP10, typically situated on the mastoids, were relocated to the respective earlobes using adhesive bandages. Prior to electrode application, meticulous cleansing of the earlobes and forehead was undertaken using alcohol wipes, serving a dual purpose of disinfection and enhancing electrical conductivity.

Stringent impedance control measures were implemented, ensuring that all electrodes maintained impedance levels at or below 10 kOhms. The EEG data acquisition transpired at a sampling rate of 500 Hz.

2.4 EEG preprocessing and epoching

Subsequently, data preprocessing procedures were executed utilizing Brain Vision Analyzer 2 (Brain Products GmbH). EEG recordings underwent re-referencing, with reference electrodes placed on the average earlobe location. To mitigate potential noise and artifacts, a bandpass filter ranging from 0.1 to 90 Hz was applied, further supplemented by a narrow 49.5−50.5 Hz notch filter employing Butterworth filters with a steepness of 48 decibels per octave.

Artifact contamination in the EEG recordings, such as those originating from participant movement, eye movements, blinking, neck muscle strain, and cardiovascular artifacts, were diligently addressed through the application of Independent Component Analysis (ICA), facilitating their systematic removal.

The EEG data were subsequently divided into discrete epochs, temporally aligned with the initiation of the sensory stimulation events. These epochs were uniformly set at a duration of 0.45 s, a temporal window standardized across all types of sensory stimuli for the sake of consistency and comparability in subsequent analyses.

2.5 Reconstruction of functional brain network

We undertook the reconstruction of sensor-level functional brain networks, a pivotal step in elucidating the neural connectivity patterns, using FieldTrip Toolbox [16]. To establish connectivity between all pairs of EEG channels, we employed the coherence coefficient as our chosen measure [17]. We used imaginary part of the coherence because it allows to exclude more effectively false connections that are caused by the effect of field spread. This coefficient served as an effective quantification of the functional relationships between the EEG signals recorded from the different electrode sites.

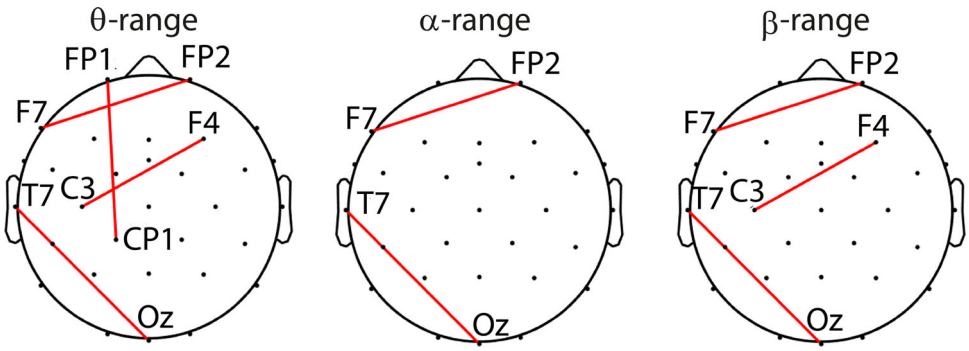

Fig. 1 Connections in brain functional networks that significantly differ between the slow, fast, and ultralight types of touches; $p < 0.05$. Results are shown for the following frequency ranges: θ, α, and β

For each subject, across all epochs corresponding to each type of sensory stimuli, we computed averaged connectivity matrices. To enhance the robustness of our analyses and ensure consistency, we performed an absolute baseline correction of all connectivity values. This correction utilized a 2 s interval positioned 1 s prior to the onset of the stimulus.

To discern statistically significant differences in the connections across various types of sensory stimulation, we applied the false discovery rate (FDR) method [18] within the framework of the network-based statistic approach using NBS software [19]. Specifically, we assessed significance at the $p = 0.05$ level using the F test for comparisons involving the three distinct stimulation types. For paired comparisons, we adopted a more stringent significance level of $p = 0.025$ in the paired t tests. These statistical procedures allowed us to robustly identify and quantify differential connectivity patterns in our EEG-derived functional brain networks. To overcome the field spreading effect, we ignored the close connections between neighboring channels.

We carried out the described analysis in the following frequency ranges: θ (4–8 Hz), α (8–14 Hz), and β (14–30 Hz).

3 Results

We determined connections that are significantly differed concurrently between three conditions: between the slow, fast, and ultralight types of touches (see Fig. 1). Most of the connections are repeated in different frequency ranges. The majority of significantly different connections are in the θ-range. The following connections can be distinguished: frontal (F7-FP2), frontal-central (F4-C3), frontal-parietal (FP1-CP1), and occipitotemporal (T7-Oz).

To detail the results of the F test, we performed pairwise statistical comparisons between touches types. Figure 2 shows the results of pairwise statistical testing of functional networks between different combinations of conditions. Most of the connections are repeated in different frequency ranges. The greatest number of significantly different connections in the theta band when comparing slow and ultralight types of touches. In the vast majority of cases, the following inequality for connections activation strength is true: $F > S > U$. In the θ-band, one compound "long connectivity" F3-T7-Oz was detected when comparing U vs. S.

4 Discussion and conclusion

Our findings indicate that there are significantly different functional connectivity patterns in the brain when experiencing slow, fast, and ultra-light touches. This aligns with the notion that distinct neural pathways are involved in processing these different tactile sensations. As previously suggested by McGlone et al. [2], the brain processes discriminative and affective touch differently. Slow touches, often associated with affective touch, appear to engage unique neural networks that distinguish them from fast and ultra-light touches. This is consistent with the idea that affective touch, mediated by C-LTMRs, has a specialized role in processing pleasant sensations [2].

Our results show that the majority of significantly different connections are found in the theta frequency band. This is particularly interesting, as it may suggest that theta oscillations play a crucial role in differentiating between touch modalities. While not directly related to tactile perception, it is known that the theta band is associated with memory and emotional processing. This finding may imply a link between emotional aspects of touch and the

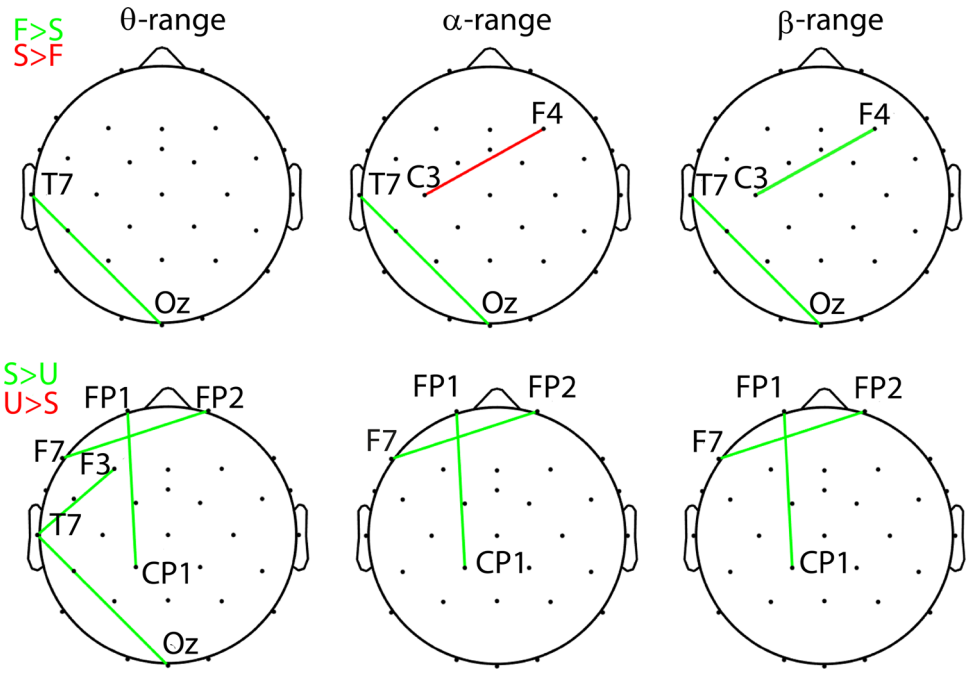

Fig. 2 Connections in brain functional networks that significantly differ between (upper row) slow (S) and fast (F) types of touches and (lower row) slow (S) and ultralight (U) types of touches; $p < 0.025$. Results are shown for the following frequency ranges: θ, α, and β. Color denotes direction of effect

theta band, potentially shedding light on the role of the posterior insular cortex, which is known to be involved in affective processing [3].

The consistent pattern where the activation strength follows the order $F > S > U$ (fast > slow > ultra-light) is intriguing. It suggests that fast touches result in the strongest activation of these connections, followed by slow and ultra-light touches. This pattern could be indicative of the brain's prioritization of processing faster and potentially more critical tactile information while giving less emphasis to ultra-light touches. This aligns with the idea that the brain must respond rapidly to certain touch sensations, such as those associated with fast-moving parasites [20].

The identification of the compound "long connectivity" F3-T7-Oz when comparing ultra-light and slow touches in the theta band could represent a specific neural circuit involved in distinguishing between these two contrasting touch sensations. The involvement of the frontal region (F3) in this connectivity may be linked to higher-order cognitive processing and emotional evaluation, given its role in affective touch processing [2].

In summary, our results contribute to understanding the neural underpinnings of tactile perception and the differentiation of touch modalities. They support previous research indicating that the brain processes affective and discriminative touch differently, highlighting the importance of the posterior insular cortex and the role of different frequency bands in this process. The distinct connectivity patterns and activation strength differences between touch modalities further emphasize the complex and dynamic nature of tactile perception, suggesting that the brain adapts its processing based on the specific nature of the tactile stimulus.

These findings also open up opportunities for future research to delve deeper into the neural mechanisms that underlie these touch modalities, potentially providing insights into tactile perception disorders and sensory processing in individuals with conditions such as autism [5].

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Data Availability Data are available from Ivan Skorokhodov under request iskor@live.com.

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