



Establishing the relationship between subjective perception and neural responses: Insights from correlation analysis and representational similarity analysis

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ABSTRACT

Exploring the relationship between sensory perception and brain responses holds important theoretical and clinical implications. However, commonly used methodologies like correlation analysis performed either intra- or inter- individually often yield inconsistent results across studies, limiting their generalizability. Representational similarity analysis (RSA), a method that assesses the perception-response relationship by calculating the correlation between behavioral and neural patterns, may offer a fresh perspective to reveal novel findings. Here, we delivered a series of graded sensory stimuli of four modalities (i.e., nociceptive somatosensory, non-nociceptive somatosensory, visual, and auditory) to/near the left or right hand of 107 healthy subjects and collected their single-trial perceptual ratings and electroencephalographic (EEG) responses. We examined the relationship between sensory perception and brain responses using within- and between-subject correlation analysis and RSA, and assessed their stability across different numbers of subjects and trials. We found that within-subject and between-subject correlations yielded distinct results: within-subject correlation revealed strong and reliable correlations between perceptual ratings and most brain responses, while between-subject correlation showed weak correlations that were vulnerable to the change of subject number. In addition to verifying the correlation results, RSA revealed some novel findings, i.e., correlations between behavioral and neural patterns were observed in some additional neural responses, such as “ γ -ERS” in the visual modality. RSA results were sensitive to the trial number, but not to the subject number, suggesting that consistent results could be obtained for studies with relatively small sample sizes. In conclusion, our study provides a novel perspective on establishing the relationship between behavior and brain activity, emphasizing that RSA holds promise as a method for exploring this pattern relationship in future research.

1. Introduction

The capacity to perceive the external environment is vital for our survival. Consequently, identifying stable and reliable perceptual neural indicators hold important theoretical and clinical implications. For instance, it can provide objective evaluation for pain assessment, serving as a critical benchmark to replace verbal reports in pain management (van der Miesen et al., 2019). Moreover, apart from directly assessing neural activity triggered by sensory stimuli, establishing the link between brain activity and perceptual behavior offers another essential avenue to comprehend the neural basis that underlies these behaviors. However, commonly used methodologies, such as between-subject

correlation analysis, to explore the connections between perceptual behaviors and brain activities, often yield inconsistent results across studies (Hu et al., 2014a; Hu and Iannetti, 2016, 2019; Ray and Maunsell, 2011; Schulz et al., 2011), which poses challenges in applying them to clinical practice. Therefore, to better characterize the relationship between behavior and brain activity, it is crucial to investigate the neural correlates of perception through various analytical approaches and identify the factors that influence the outcomes.

Between-subject correlation analysis and within-subject correlation analysis have been widely employed to evaluate the link between behavior and brain activity, each offering a unique perspective. Notably, between-subject correlation analysis stands as the most prevalent

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statistical method, aiming to uncover the neural underpinnings of inter-individual variability in perceptual behavior. However, this approach is heavily influenced by individual differences, and requires a large number of subjects to obtain reliable results. With limited samples, it often yields inconsistent findings across different studies (Hu and Iannetti, 2019; Schulz et al., 2011). The within-subject correlation analysis, on the other hand, has primarily been employed to elucidate the neural mechanisms underpinning intra-individual variability in perceptual behavior (Hu et al., 2014a). While normally yielding relatively stable outcomes across studies (Gross et al., 2007; Hu and Iannetti, 2019), this approach cannot assess inter-individual variability in perceptual behavior, limiting its generalizability in various applications (Hanslmayr et al., 2007), such as instances where the patient's sensory perception is recorded only once in clinical settings. Additionally, representational similarity analysis (RSA) provides a means to assess the relationship between behavior and brain activity by quantitatively linking behavioral and brain patterns to derive the neural representation of perception (Kriegeskorte et al., 2008). While RSA has been extensively applied to reveal the neural representation of cognitive processes such as memories, face processing, and object recognition in the human brain (Cichy et al., 2014, 2016; Dobs et al., 2019; Muukkonen et al., 2020), the neural representations of sensory perception (e.g., nociceptive somatosensory, non-nociceptive somatosensory, and auditory) assessed using RSA were rarely reported. The use of RSA may provide a novel perspective and offer new information to uncover the relationship between sensory perception and brain activity.

To test this research hypothesis, we delivered a number of graded sensory stimuli belonging to four different sensory modalities (i.e., nociceptive somatosensory, non-nociceptive somatosensory, visual, and auditory) to/near the left or right hand of 107 healthy subjects and collected their single-trial subjective perceptual ratings. Then, within-subject correlation analysis, between-subject correlation analysis, and RSA were used to explore the relationship between sensory perception and brain activity in each sensory modality from different perspectives. Furthermore, we evaluated the stability and reproducibility of the obtained results under different numbers of subjects and trials.

2. Methods

2.1. Subjects

107 healthy right-handed participants (66 females; $M_{\text{age}} = 21.60$ years, $SD_{\text{age}} = 1.82$ years) with normal audition and normal or corrected-to-normal vision were enrolled in this study. Subjects were excluded if they had any history of neurological or psychological impairments, chronic pain, and alcohol or drug abuse. The experiment was approved by the Institutional Review Board of the Institute of Psychology, Chinese Academy of Sciences. All procedures were performed in accordance with the Declaration of Helsinki. All participants provided written informed consent and were paid for their participation.

2.2. Sensory stimulation

Nociceptive somatosensory stimuli were pulses of radiant heat generated by an infrared neodymium yttrium aluminum garnet (Nd: YAP) laser with a wavelength of 1.34 μm and a pulse duration of 4 ms (Electronical Engineering, Italy). A He-Ne laser pointed to the area to be stimulated, and the laser beam was transmitted via an optical fiber and focused by lenses to a spot with a diameter of approximately 7 mm. Laser pulses were delivered to a squared area ($5 \times 5 \text{ cm}^2$) on the dorsum of the subject's left or right hand. To prevent fatigue or sensitization of the nociceptors, the laser beam target was manually shifted by at least 1 cm in a random direction after each stimulus. The ascending method of limits was adopted for each subject to determine the laser energies: the four laser energies that evoked subjective ratings of ~ 2 , 4, 6, and 8 on the 0–10 numerical rating scale (NRS) were determined by increasing

the laser energy in steps of 0.25 J until the target score was obtained. Please note that, for each subject, the ascending method of limits was repeated three times for each hand, and the average energy was used for the following procedures of the experiment. Across subjects, four laser energies were as follows: E1, $2.16 \pm 0.22 \text{ J}$; E2, $2.72 \pm 0.25 \text{ J}$; E3, $3.45 \pm 0.31 \text{ J}$; and E4, $4.12 \pm 0.39 \text{ J}$.

Non-nociceptive somatosensory stimuli were constant current square-wave electrical pulses generated by an electrical stimulator (pulse duration: 1 ms; DS7A, Digitimer, UK). The electrical pulses were delivered via a pair of surface round electrodes (diameter: 1.6 cm; inter-electrode distance: 1 cm) placed at the wrist of the subject's left or right hand. The stimulus intensities used in the experiment were identical for all subjects and were determined based on a preliminary psychophysical experiment performed on 10 age- and sex-matched subjects, to ensure that subjective ratings were ~ 2 , 4, 6, and 8 on the 0–10 NRS for E1 to E4, respectively. All subjects were asked to assess the intensity of the electrical stimulation, and none reported painful sensations. The stimulus intensities were as follows: E1, 2 mA; E2, 3 mA; E3, 5 mA; and E4, 7 mA.

Auditory stimuli were brief 800 Hz pure tones (duration: 50 ms; 5-ms rise and fall time) delivered by a speaker placed in front of the subject's left or right hand. The stimulus intensities were identical for all subjects and were determined based on the preliminary experiment. The stimulus intensities were as follows: E1, 65 dB; E2, 69 dB; E3, 75.5 dB; and E4, 80 dB.

Visual stimuli were brief flashes (duration: 5 ms) delivered through a white light emitting diode placed on top of the speaker, which was close to the subject's left or right hand and pointed toward the subject's eye. The stimulus intensities were identical for all subjects and were also determined based on the preliminary experiment (E1, 0.3 lx; E2, 1.3 lx; E3, 40.5 lx; and E4, 53.9 lx).

2.3. Experimental design

The experiment consisted of four successive blocks with a 5-min interval: for two blocks, sensory stimuli were applied to the subjects' left side, while for the other two blocks, sensory stimuli were applied to their right side. For each sensory modality and each stimulated side (Fig. 1A), we delivered 10 trials at each of the four stimulus intensities (E1–E4), for a total of 320 trials ($4 \text{ sensory modalities} \times 2 \text{ stimulus sides} \times 4 \text{ stimulus intensities} \times 10 \text{ trials} = 320 \text{ trials}$), using a random and variable interstimulus interval between 11 and 15 s (rectangular distribution). The orders of sensory modalities and stimulus intensities were in a pseudo-random sequence, and the order of stimulated sides (left and right) was counterbalanced across subjects. An auditory tone delivered between 3 and 5 s after each sensory stimulation (rectangular distribution) prompted the subjects to rate the perceived stimulus intensity using NRS ranging from 0 ("no sensation") to 10 ("the most intense sensation imaginable").

During the experiment, subjects were asked to focus their gaze on a cross placed centrally in front of them at a distance of $\sim 1 \text{ m}$, 30° below eye level, and were instructed to place their both hands on the table about 60 cm apart. The distance between the source of stimulations and the subjects' heads was approximately 60 cm. All sensory stimuli were delivered on or near the dorsum of the subjects' left or right hand. To prevent the subject from generating the expectancy effect for the upcoming stimulus, a baffle was used to cover the subject's hands when the stimulus was presented.

2.4. EEG data recording and processing

2.4.1. EEG data recording

Subjects sat in a comfortable chair in a silent, temperature-controlled room and were asked to relax their muscles and focus their attention on the stimulation. Electroencephalographic (EEG) data were recorded using 64 Ag-AgCl scalp electrodes placed according to the International

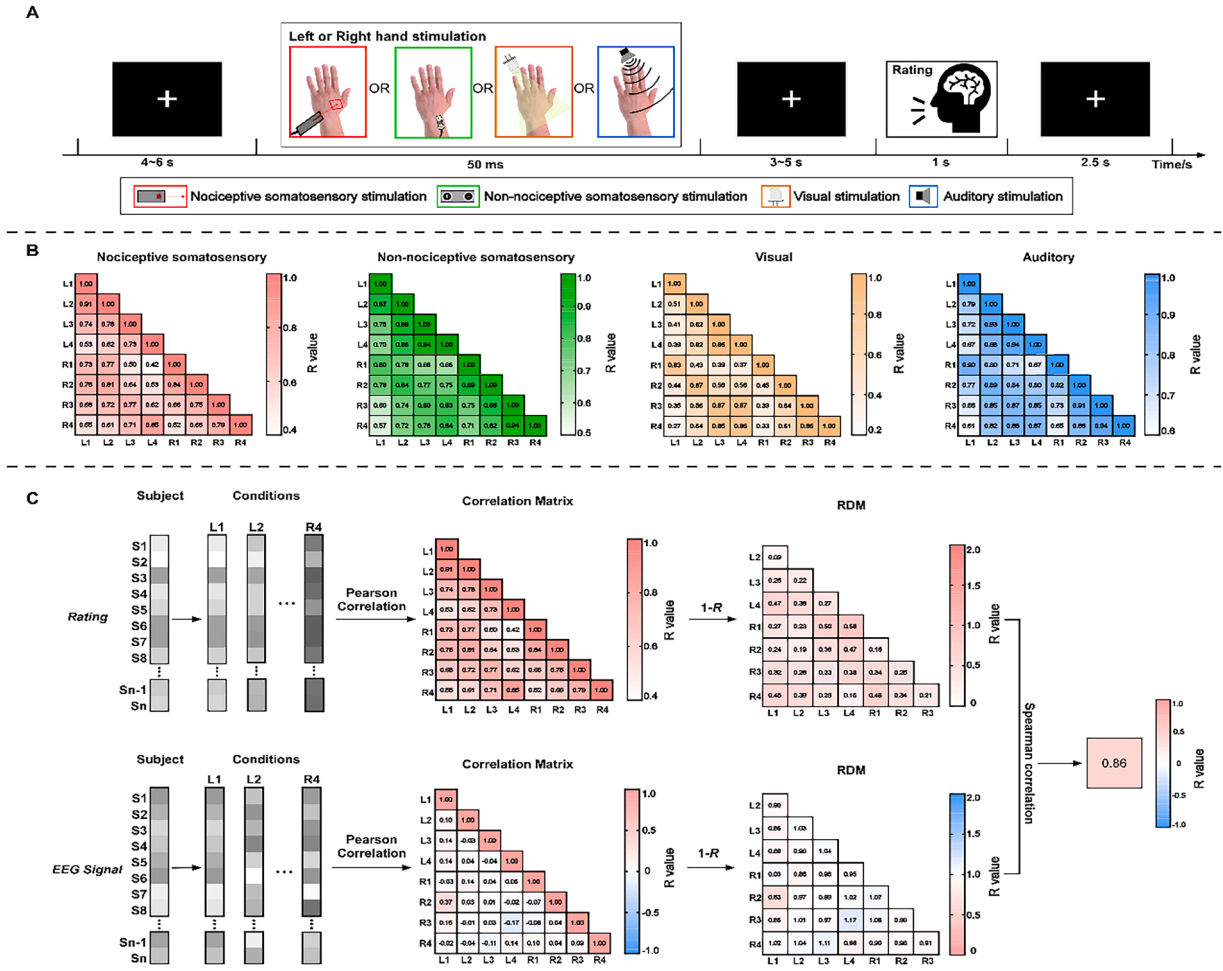


Fig. 1. Experimental design and representational similarity analysis (RSA). (A) Experimental design. A series of graded sensory stimuli belonging to four different modalities (i.e., nociceptive somatosensory, non-nociceptive somatosensory, visual, and auditory) were delivered to the participant's left or right side, and their single-trial perceptual ratings were collected. (B) Correlation matrices of perceptual ratings. For each sensory modality, Pearson correlation coefficients of perceptual ratings between each pair of conditions were assessed across all subjects. (C) RSA. For each subject, we averaged the behavioral variables (i.e., perceptual ratings) or EEG variables (i.e., amplitudes/magnitudes of EEG responses at each time point or at each time-frequency pixel) across trials for eight conditions (i.e., four stimulus intensities for left and right hands) within each sensory modality, respectively. Then, Pearson correlation analyses were performed on each variable between each pair of conditions across all subjects for each sensory modality, respectively. Correlation distance (1-correlation coefficient) was measured to create the representational dissimilarity matrix (RDM) which contains an 8×8 cell reflecting the dissimilarity between the behavioral patterns or between the EEG activity patterns associated with each pair of conditions. Finally, numbers in the upper (or equivalently the lower) triangle of the matrices were used to perform the Spearman correlation (partial rank coefficient) between the behavioral RDM and EEG RDM.

10–20 system (Brain Products GmbH, Germany; bandpass: 0.01–100 Hz; sampling rate: 1000 Hz), using the nose as reference. Electrode impedances were kept below 10 k Ω . To monitor ocular movements and eye blinks, electrooculographic (EOG) signals were simultaneously recorded using two surface electrodes: one placed over the lower eyelids and the other placed ~ 1 cm lateral to the outer corner of the orbit.

2.4.2. EEG data preprocessing

EEG data were preprocessed using EEGLAB (Delorme and Makeig, 2004). Continuous EEG data were band-pass filtered between 1 Hz and 100 Hz and segmented into epochs using a time window of 1500 ms (500 ms pre-stimulus and 1000 ms post-stimulus). EEG trials were baseline corrected in the time domain using the pre-stimulus interval (–500 to 0 ms). Trials contaminated by eye blinks and movements were corrected using an independent component analysis algorithm (runica) (Delorme and Makeig, 2004). Please note that, after preprocessing, the EEG data of each electrode acquired during stimulation applied to the subjects' right side was swapped into its mirrored electrode in the opposite hemisphere along the central axis to reduce the possible laterality effects on EEG activity (Zhang et al., 2021).

2.4.3. Time-frequency decomposition

For each sensory modality, time-frequency distributions (TFDs) of EEG epochs were obtained using a windowed Fourier transform (WFT) with a fixed 250 ms Hanning window. The WFT yielded, for each EEG epoch, a complex time-frequency estimate $F(t, f)$ at each time-frequency point (t, f), extending from –500 to 1000 ms (in steps of 1 ms) in the time domain, and from 1 to 100 Hz (in steps of 1 Hz) in the frequency domain. The resulting spectrogram, $p(t, f) = |F(t, f)|^2$, represented the signal power as a joint function of time and frequency at each time-frequency point. The spectrograms were baseline-corrected (reference interval: –400 to –100 ms relative to stimulus onset) at each frequency f using the subtraction approach (Hu et al., 2014b). This reference interval was chosen to reduce the adverse influence of spectral estimates biased by windowing post-stimulus activity and padding values.

2.5. Correlation analyses

2.5.1. Within-subject correlation

To identify time intervals or time-frequency regions whose amplitudes/magnitudes reflected the within-subject variability of perceptual

ratings for each sensory modality, we performed a point-by-point linear correlation analysis between the amplitudes/magnitudes of stimulus-elicited brain responses and the corresponding perceived ratings at single trial level for each sensory modality and each subject. The obtained correlation coefficients were transformed to z values using the Fisher r -to- z transformation. Finally, z -values from all subjects were compared with zero using one-sample t -test at each time point or each time-frequency pixel.

2.5.2. Between-subject correlation

To identify time intervals or time-frequency regions whose amplitudes/magnitudes reflected the between-subject variability of perceptual ratings for each sensory modality, we performed a point-by-point linear correlation analysis between single-subject average amplitudes/magnitudes and the corresponding single-subject average perceptual ratings for each sensory modality.

2.5.3. Representational similarity analysis

To identify the time intervals or time-frequency regions whose response patterns represented perceptual ratings for each sensory modality, we also performed the RSA (Fig. 1C). Specifically, for each subject, we averaged the behavioral variables (i.e., perceptual ratings) or EEG variables (i.e., amplitudes/magnitudes of EEG responses at each time point and at each time-frequency pixel) across trials for eight conditions (i.e., four stimulus intensities for both hands) within each sensory modality, respectively. Then, Person correlation analyses were performed on each variable between each pair of conditions across all subjects for each sensory modality. Correlation distance (1-correlation coefficient) was calculated to create the representational dissimilarity matrix (RDM), which contains an 8×8 cell reflecting the dissimilarity between the behavioral patterns or between the EEG activity patterns associated with each pair of conditions. Finally, numbers in the upper (or equivalently the lower) triangle of the matrices were used to perform the Spearman correlation analysis (partial rank coefficient) between the behavioral RDM (Fig. 1B) and EEG RDM, which yielded the RSA results.

2.6. Statistical analysis

To test the effect of stimulus intensity on the electrophysiological response elicited by sensory stimuli, we performed a one-way repeated measures analysis of variance (ANOVA) at each time point or at each time-frequency pixel. To account for multiple comparisons, the significance level was corrected using an false discovery rate (FDR) procedure ($p < 0.05$) (Benjamini and Hochberg, 1995).

For within-subject correlation analysis, permutation-based non-parametric testing with 5000 random permutations was performed on the averaged z values in each cluster to assess the significance of the correlation at cluster level (Maris and Oostenveld, 2007). Please note that the cluster was defined as the adjacent time points or the adjacent time-frequency pixels exhibiting a significance threshold of $p < 0.05$ after FDR correction in the one-sample t -test.

For both between-subject correlation analysis and RSA, permutation-based non-parametric testing with 5000 random permutations was conducted on the correlation coefficients to assess the significance of the correlation at each time point or at each time-frequency pixel. The resulting statistical maps were thresholded at $p = 0.05$ and corrected for the multiple comparisons using the FDR. Please note that one-tailed tests were used in the RSA permutation test because negative values are typically uninterpretable in RSA.

2.7. Stability assessment

To examine the impact of the number of subjects and trials on the results obtained from three analytical methods (i.e., within-subject correlation analysis, between-subject correlation analysis, and RSA), we performed a subsampling analysis. Specifically, we randomly

selected subsets corresponding to 80 %, 60 %, and 40 % of the original subjects (i.e., 85, 64, and 42 subjects) or trials (i.e., 8, 6, and 4 trials) and then re-performed the aforementioned analyses. Each of these random selection procedures was repeated 100 times. A time point or time-frequency pixel was considered statistically significant if it reached a significance threshold of $p < 0.05$ in 80 or more of the 100 iterations.

To evaluate and compare the robustness of the results obtained from three analytical methods, we calculated the proportion of significant data points within the time frame of 0 to 500 ms in the time domain as well as the proportion of significant time-frequency pixels within the pre-defined region of interest (ROI) in the time-frequency domain. Please note that the ROI was defined based on the findings obtained from three analytical methods, with a special focus on “event-related potentials” (ERP), “alpha-band event-related desynchronization” (α -ERD), and “gamma-band event-related synchronization” (γ -ERS). Additionally, we employed the Intraclass Correlation Coefficient (ICC) to assess the consistency between the time series (ranging from 0 to 1000 ms) obtained from all subjects or all trials and the time series derived from the subsets (i.e., 85, 64, and 42 subjects or 8, 6, and 4 trials) in the time domain. The same ICC analyses were also conducted in the time-frequency domain. In detail, ICC was calculated using SPSS statistical package version 26 (SPSS Inc, Chicago, IL) based on a single measure, absolute-agreement, 2-way mixed-effects model.

3. Results

3.1. The influence of stimulus intensity on EEG responses elicited by sensory stimuli

In the time domain (Fig. 2), scalp topographies of the N2 wave were maximal at the vertex and extended bilaterally towards temporal regions, and scalp topographies of the P2 wave were more centrally distributed for all four sensory modalities. The peak latencies of the N2 wave evoked by stimuli of different sensory modalities were 198.50 ± 65.55 ms (nociceptive somatosensory), 130 ± 65.51 ms (non-nociceptive somatosensory), 143.30 ± 53.88 ms (visual), and 132.50 ± 40.61 ms (auditory), respectively. The peak latencies of the P2 wave evoked by stimuli of different sensory modalities were 347.97 ± 36.78 ms (nociceptive somatosensory), 280 ± 29.77 ms (non-nociceptive somatosensory), 369.90 ± 39.64 ms (visual), and 213.30 ± 48.05 ms (auditory), respectively. One-way repeated-measures ANOVA showed a significant main effect of “stimulus intensity” for both N2 and P2 amplitudes in all four sensory modalities (FDR corrected, $p < 0.05$, Fig. 2).

In the time-frequency domain (Fig. 3), one-way repeated-measures ANOVA revealed a significant main effect of “stimulus intensity” for the “ERP”, “ α -ERD”, and “ γ -ERS” magnitudes in the nociceptive somatosensory modality. In the non-nociceptive somatosensory modality, one-way repeated-measures ANOVA revealed a significant main effect of “stimulus intensity” for the “ERP” and “ γ -ERS” magnitudes. In the visual and auditory modalities, one-way repeated-measures ANOVA revealed a significant main effect of “stimulus intensity” for the “ERP” magnitudes.

3.2. Neural indicators for within-subject sensory perception

In the time domain (Fig. 4A), the amplitudes of all main EEG waves were significantly correlated with the subjective perceptual ratings to nociceptive somatosensory (i.e., N2 wave, 48–269 ms; P2 wave, 280–463 ms), non-nociceptive somatosensory (i.e., N2 wave, 57–205 ms; P2 wave, 215–375 ms), visual (i.e., N2 wave, 10–173 ms; P2 wave, 260–426 ms), and auditory (i.e., N2 wave, 95–158 ms; P2 wave, 170–336 ms) stimuli.

In the time-frequency domain (Fig. 5A), the magnitudes of stimulus-induced modulations of most EEG responses also reflected within-subject variability of perceptual ratings to nociceptive somatosensory (i.e., “ERP”, 50 to 450 ms, 1 to 10 Hz; “ α -ERD”, 550 to 980 ms, 7 to 13 Hz; “ γ -ERS”, 95 to 450 ms, 40 to 98 Hz), non-nociceptive somatosensory

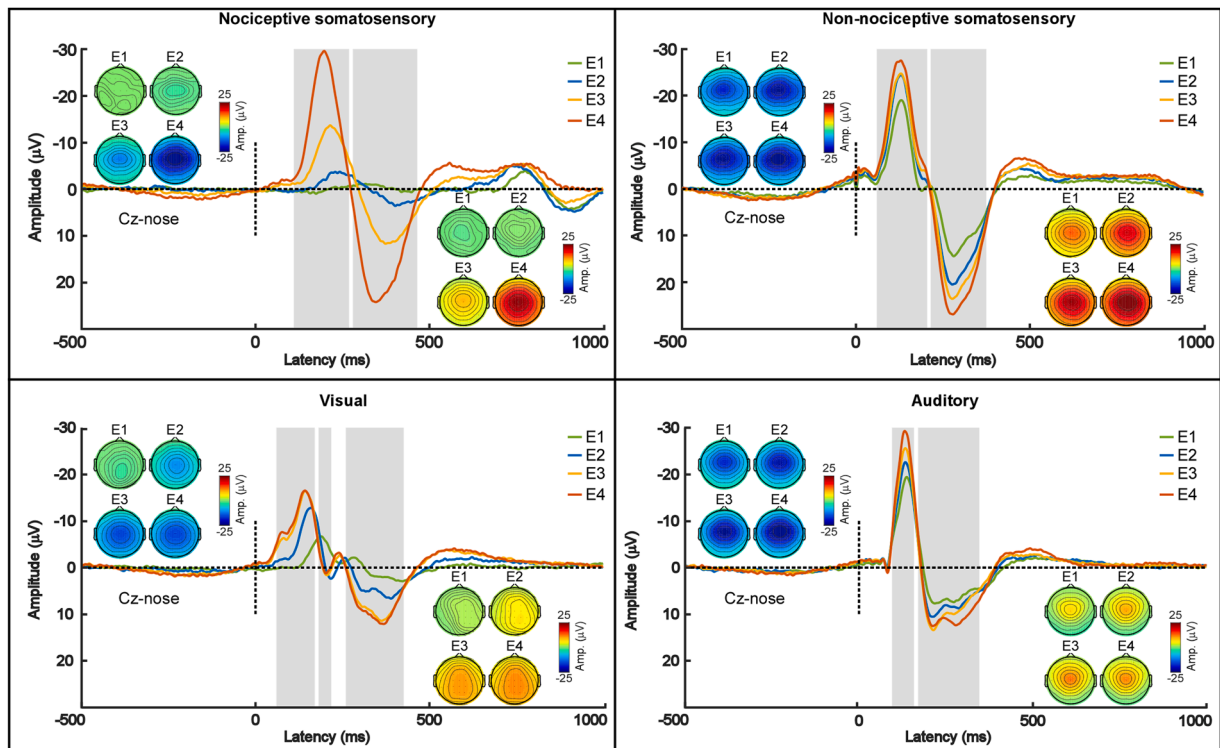


Fig. 2. Group-level ERP waveforms and scalp topographies of N2 and P2 vertex potentials elicited by nociceptive somatosensory, non-nociceptive somatosensory, visual, and auditory stimuli. For each sensory modality, the effect of stimulus intensity (i.e., E1 to E4) on electrophysiological responses at each time point elicited by sensory stimuli was evaluated. Significant main effects of stimulus intensity are shaded in gray ($p < 0.05$, False Discovery Rate correction). Larger N2 and P2 waves are induced when the stimulus intensity increases for all sensory modalities.

(i.e., “ERP”, 50 to 450 ms, 1 to 10 Hz; “ γ -ERS”, 80 to 450 ms, 40 to 98 Hz), visual (i.e., “ERP”, 50 to 405 ms, 1 to 10 Hz), and auditory (i.e., “ERP”, 50 to 350 ms, 1 to 10 Hz; “ γ -ERS”, 80 to 220 ms, 84 to 96 Hz) stimuli.

3.3. Neural indicators for between-subject sensory perception

In the time domain (Fig. 4B), the amplitudes of vertex EEG responses were only significantly correlated with subjective perceptual ratings to non-nociceptive somatosensory stimuli across subjects (i.e., N2 wave, 83–144 ms; P2 wave, 215–266 ms). No other significant results were detected.

In the time-frequency domain (Fig. 5B), the magnitudes of stimulus-induced modulations of EEG responses (i.e., “ERP”, 170 to 450 ms, 1 to 10 Hz; “ γ -ERS”, 250 to 450 ms, 40 to 98 Hz) were also significantly correlated with subjective perceptual ratings to nociceptive somatosensory stimuli across subjects. However, for the other three modalities, aside from the magnitudes of “ERP” (95 to 165 ms, 1 to 7 Hz) in the non-nociceptive somatosensory modality, no other significant correlations were observed across subjects.

3.4. Neural indicators for sensory perception patterns as explored using RSA

In the time domain (Fig. 4C), the amplitude patterns of all main EEG waves were significantly correlated with the subjective perceptual rating patterns to nociceptive somatosensory (i.e., 170–554 ms), non-nociceptive somatosensory (i.e., 58–551 ms), visual (i.e., 35–956 ms), and auditory (i.e., 163–243 ms and 337–421 ms) stimuli.

In the time-frequency domain (Fig. 5C), the magnitude patterns of stimulus-induced modulations of most EEG responses also reflected subjective perceptual rating patterns to nociceptive somatosensory (i.e., “ERP”, 50 to 450 ms, 1 to 10 Hz; “ α -ERD”, 550 to 980 ms, 7 to 13 Hz;

“ γ -ERS”, 160 to 450 ms, 40 to 98 Hz), non-nociceptive somatosensory (i.e., “ERP”, 85 to 450 ms, 1 to 10 Hz; “ α -ERD”, 550 to 890 ms, 7 to 13 Hz; “ γ -ERS”, 80 to 450 ms, 40 to 70 Hz), visual (i.e., “ERP”, 75 to 450 ms, 1 to 10 Hz; “ γ -ERS”, 80 to 180 ms, 43 to 85 Hz), and auditory (i.e., “ERP”, 180 to 430 ms, 1 to 10 Hz; “ α -ERD”, 550 to 596 ms, 7 to 13 Hz; “ γ -ERS”, 110 to 165 ms, 75 to 84 Hz) stimuli.

3.5. Stability results

For within-subject correlation, the proportions of significant time points within the 0 to 500 ms interval (Fig. 6A and Supplementary Figure 1A) and the proportions of significant time-frequency pixels within the selected ROI (ERP: 50–450 ms, 1 to 10 Hz; α -ERD: 550–980 ms, 7–13 Hz; γ -ERS, 80–450 ms, 40–98 Hz; Fig. 6D and Supplementary Figure 2) in all modalities remained stable, regardless of the varying number of subjects and trials (Supplementary Table 1). The ICCs analyses revealed good to excellent reliability (all coefficient values > 0.85) between the time series obtained from all subjects or all trials and the time series derived from the subsets both in the time domain (Fig. 6A) and the time-frequency domain (Fig. 6D) in all modalities (Supplementary Table 2). These findings suggest that the within-subject correlations exhibit a high degree of stability.

For between-subject correlation, regardless of the varying number of subjects or trials, no significant between-subject correlations were observed in either the time domain for nociceptive somatosensory, visual, and auditory modalities (Supplementary Table 1, Fig. 6B, and Supplementary Figure 1B) or in the time-frequency domain for visual and auditory modalities (Supplementary Table 1, Fig. 6E, and Supplementary Figure 3). When the number of subjects reduces to 80 % (i.e., 85 subjects), no significant between-subject correlations were observed in the time domain for non-nociceptive somatosensory modality (Supplementary Table 1, Fig. 6B, and Supplementary Figure 1B). When the number of subjects reduces to 60 % (i.e., 64 subjects), no significant

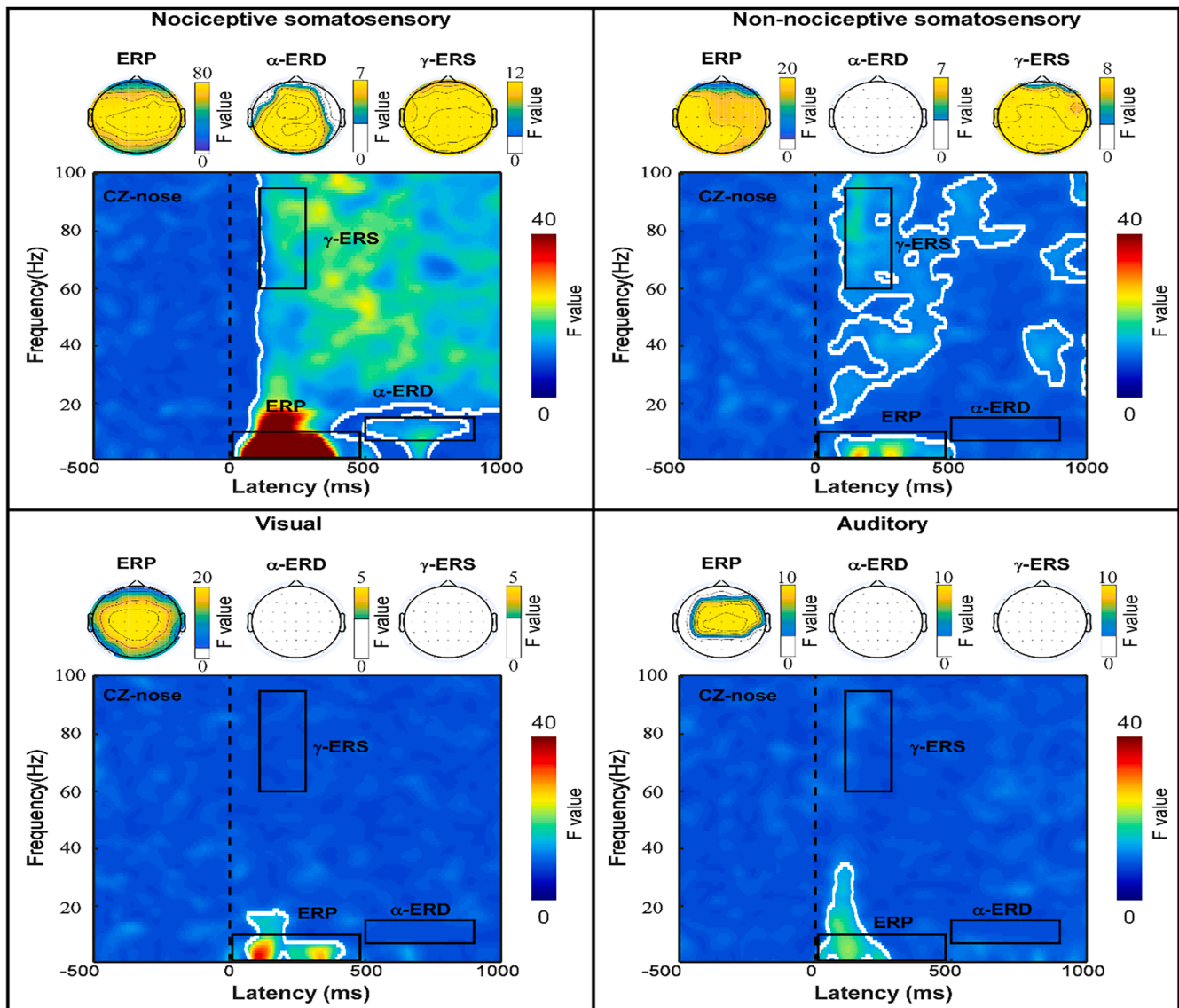


Fig. 3. Group-level time-frequency distributions and scalp topographies of “ERP”, “ α -ERD”, and “ γ -ERS” responses elicited by nociceptive somatosensory, non-nociceptive somatosensory, visual, and auditory stimuli. In the nociceptive modality, significant main effect of stimulus intensity (i.e., E1 to E4) on “ERP”, “ α -ERD”, and “ γ -ERS” was detected. In the non-nociceptive somatosensory modality, significant main effect of stimulus intensity on “ERP” and “ γ -ERS” was detected. In the visual and auditory modalities, significant main effect of stimulus intensity on “ERP” was detected. White contour lines indicate significant main effect of stimulus intensity ($p < 0.05$, False Discovery Rate correction).

between-subject correlations were observed in the time-frequency domain for both nociceptive and non-nociceptive somatosensory modalities (Supplementary Table 1, Fig. 6E, and Supplementary Figure 3). However, the ICCs analyses revealed moderate to excellent reliability (all coefficient values > 0.50) between the responses obtained from all subjects and those obtained from a subset of subjects in the time-frequency domain for all modalities (Supplementary Table 2 and Fig. 6E). This stability was not observed in the time domain (Supplementary Table 2 and Fig. 6B). Furthermore, as the number of trials decreases, between-subject correlations detected in the time (Supplementary Figure 1B) and time-frequency domains (Supplementary Figure 3) remained stable. This stability was evident when examining the proportions of significant time points/time-frequency pixels (Supplementary Table 1, Fig. 6B and 6E) as well as the ICC between the responses obtained from all trials and those obtained from a subset of trials in the time (all coefficient values > 0.85) and time-frequency domains (coefficient values: 0.165–0.996) for all modalities (Supplementary Table 2, Fig. 6B and 6E). These findings suggest that the

between-subject correlation outcomes are primarily influenced by the number of subjects, with a lesser impact from the number of trials.

For RSA, although the proportions of significant time points/time-frequency pixels decreased with the reduction of subject number for all modalities (Supplementary Table 1, Fig. 6C and 6F, Supplementary Figure 1C and 4), the ICC analyses reveal good to excellent reliability (all coefficient values > 0.85) between the responses obtained from all subjects and those obtained from a subset of subjects in the time (Fig. 6C) and time-frequency domains (Fig. 6F) for all modalities (Supplementary Table 2). In contrast, when the number of trials decreased (i.e., 6 and 4 trials), both the proportions of significant time points/time-frequency pixels (Supplementary Table 1, Fig. 6C and 6F, Supplementary Figure 1C and 4) and the ICC (Supplementary Table 2) remarkably decreased in all modalities. These findings suggest that reducing the number of subjects has a minor impact of the RSA results, while reducing the number of trials has a significant impact on the RSA results.

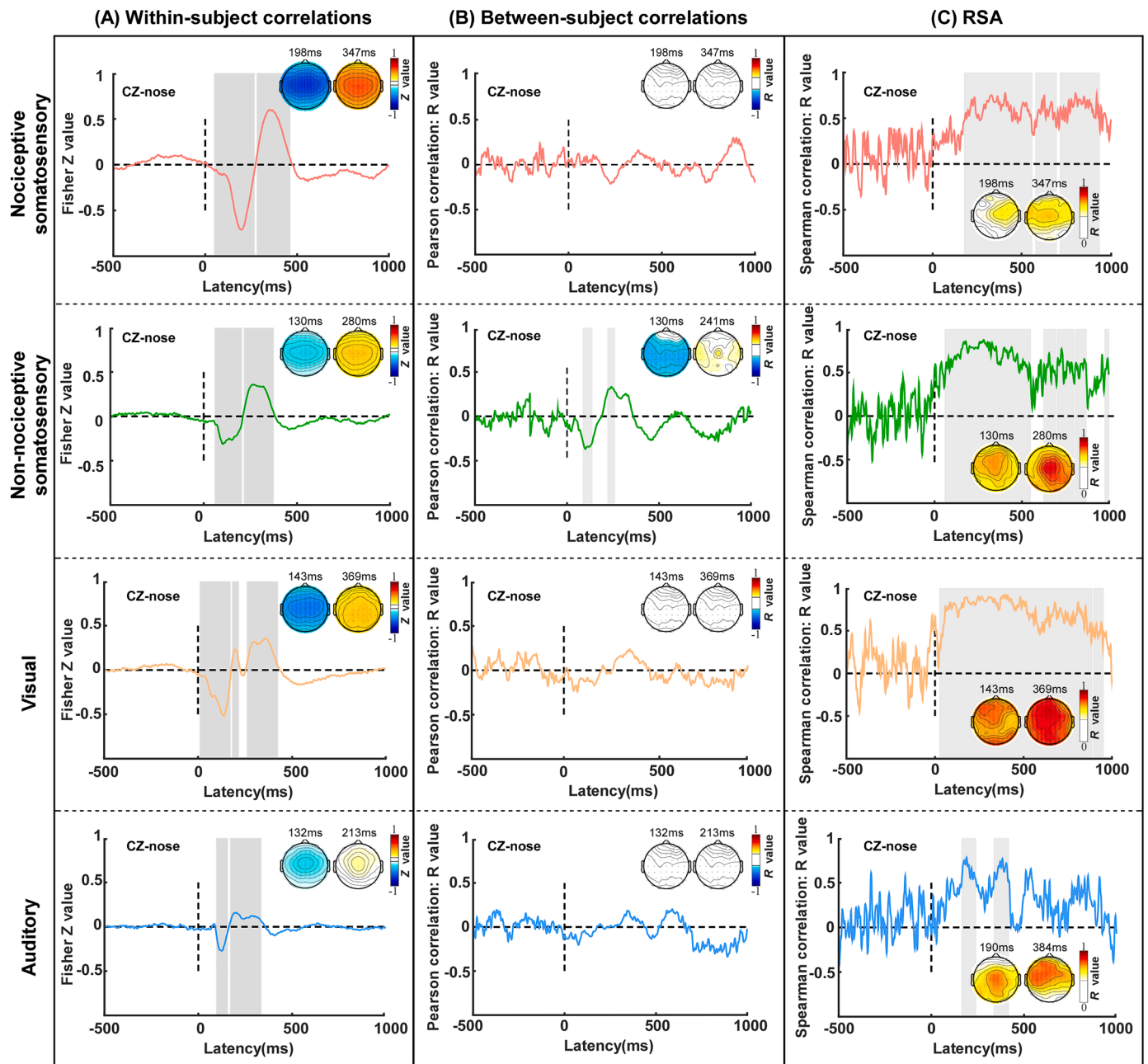


Fig. 4. Neural correlates or representations of nociceptive somatosensory, non-nociceptive somatosensory, visual, and auditory perceptions in the time domain. (A) Within-subject correlation analysis. For each sensory modality, the amplitudes of N2 and P2 waves were significantly correlated with their respective subjective ratings. (B) Between-subject correlation analysis. The amplitudes of N2 and P2 waves were only significantly correlated with subjective ratings to non-nociceptive somatosensory stimuli across subjects. (C) RSA. For each sensory modality, the amplitude patterns of N2 and P2 waves can reflect the patterns of perceptual ratings across subjects. Significant results are shaded in gray ($p < 0.05$, False Discovery Rate Correction). The time point with the highest correlation coefficient for N2 and P2 was selected as the time point for extracting topographical maps.

4. Discussion

In the current study, we examined the relationship between sensory perceptions (i.e., nociceptive somatosensory, non-nociceptive somatosensory, visual, and auditory) and EEG responses in a cohort of 107 healthy subjects using three distinct analysis methods: within-subject correlation analysis, between-subject correlation analysis, and RSA. Additionally, we assessed the stability of each analysis method across various numbers of subjects and trials. We obtained three main findings. First, within-subject and between-subject correlations yielded distinct results: within-subject correlation revealed strong and reliable correlations between perceptual ratings and most brain responses, while

between-subject correlation showed weak correlations that were vulnerable to the change of subject number. Second, beyond verifying the correlation results, RSA also revealed some novel findings, i.e., correlations between behavioral and neural patterns were observed in some additional neural responses, such as “ γ -ERS” in the visual modality. Finally, RSA results were sensitive to the trial number, but not to the subject number, suggesting that consistent results could be obtained for studies with relatively small sample sizes. Overall, these findings provide new insights into the relationship between sensory perception and brain activity, underscoring the potential utility of RSA as a valuable tool for assessing this pattern relationship.

In addition to extracting stimulus-induced brain responses, previous

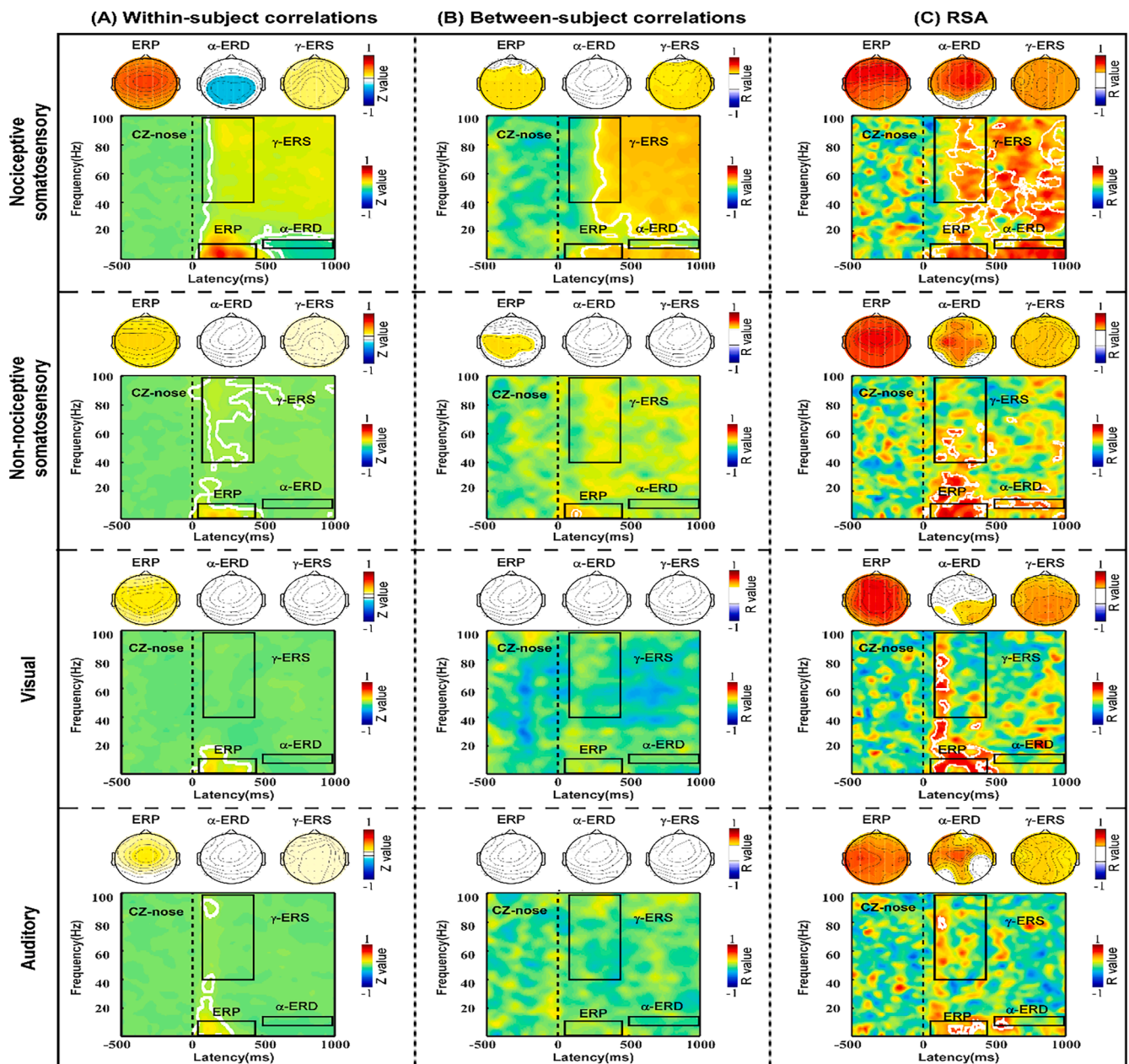
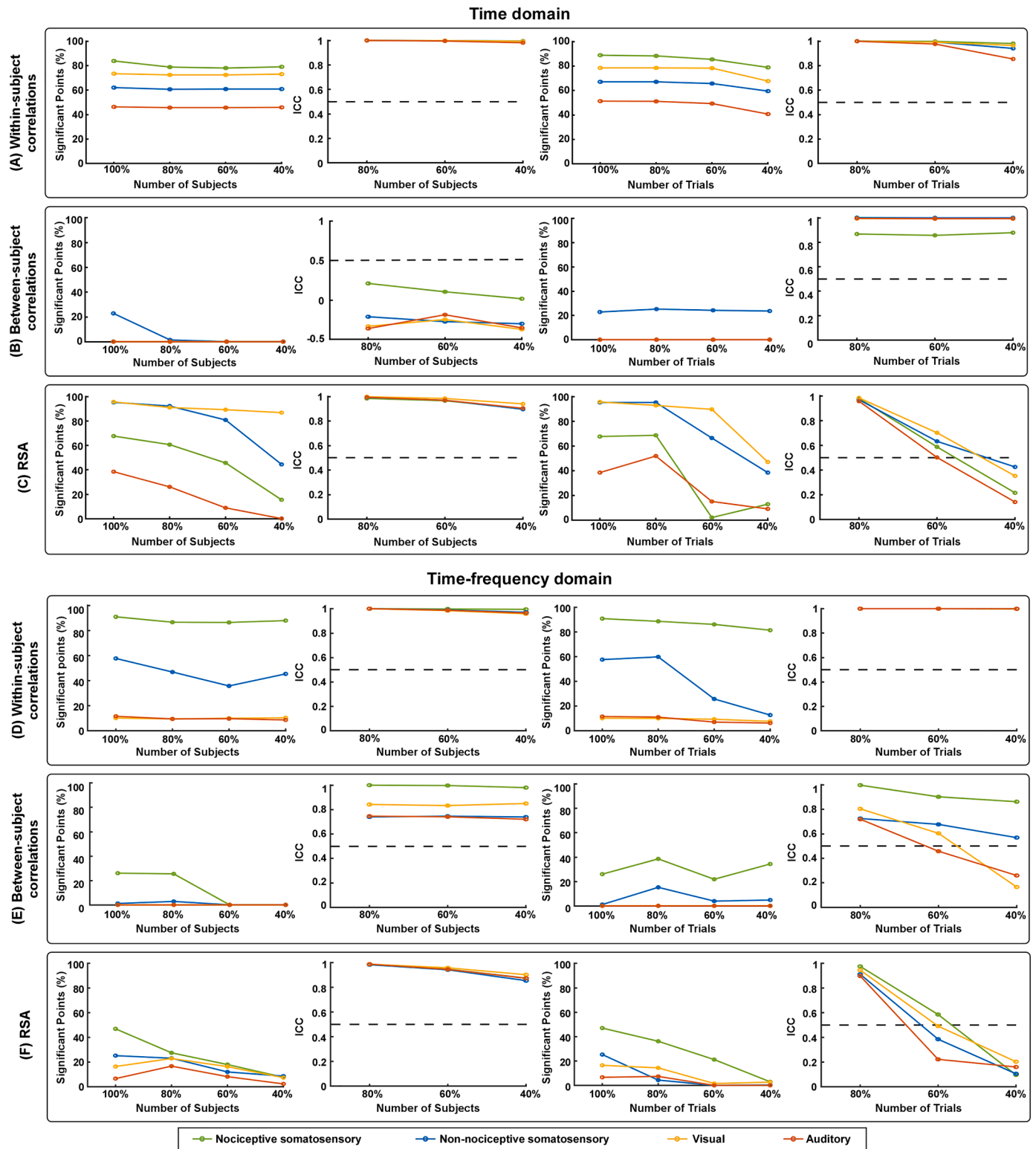


Fig. 5. Neural correlates or representations of nociceptive somatosensory, non-nociceptive somatosensory, visual, and auditory perceptions in the time-frequency domain. (A) Within-subject correlation analysis. For each sensory modality, the magnitudes of most EEG responses were significantly correlated with their respective subjective ratings. (B) Between-subject correlation analysis. The magnitudes of EEG responses (i.e., “ERP”, “ γ -ERS”) was significantly correlated with subjective ratings to nociceptive stimuli across subjects. The magnitudes of EEG responses (i.e., “ERP”) was significantly correlated with subjective ratings to non-nociceptive somatosensory stimuli across subjects. (C) RSA. For each sensory modality, the patterns of most EEG response magnitudes can reflect the patterns of perceptual ratings across subjects. Besides, the “ γ -ERS” magnitude patterns can reflect the visual perception patterns. White contour lines indicate significant results ($p < 0.05$, False Discovery Rate Correction).

studies often employed correlation analysis to establish the association of behavioral and electrophysiological data to deeply investigate the neural mechanism (Hanslmayr et al., 2007; Mouraux et al., 2011; Ribeiro et al., 2016; Su et al., 2020). In line with findings from the majority of previous studies (Hu and Iannetti, 2019; Iannetti et al., 2008; Peng et al., 2015; Ploner et al., 2017; Schulz et al., 2015; Zhang et al., 2012), our study revealed significant correlations between neural responses (i.e., N2 and P2 in the time domain, “ERP”, “ α -ERD”, and “ γ -ERS” in the time-frequency domain) that reflect the stimulus intensity and sensory perception at within-subject level. Notably, even as the number of subjects and trials decreased, the within-subject correlation results remained robust and consistent. These findings suggest that the

within-subject correlations exhibit a high degree of stability. This stability likely arises from the close coupling between perceptual ratings and brain responses within the same subject. In other words, the observed brain responses would reflect neural processing closely associated with perceptual ratings. This stability assessment provides evidence for the observed consistency of within-subject correlation results across different studies (Hu et al., 2014a; Hu and Iannetti, 2019).

Between-subject correlation is widely used to explore the neural responses that reflect individual differences of behavioral outcomes (Erpelding et al., 2012; Furman et al., 2020; Ta Dinh et al., 2019; Zhang et al., 2022). However, the replicability of these studies is often challenged, potentially due to the small sample size in many studies (Genon



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et al., 2022; Grady et al., 2021; Marek et al., 2022). Our between-subject correlation analysis also indicated weaker correlations under different numbers of subjects. This inconsistency between studies and weak correlations can be attributed to two factors. Firstly, sensory perception is highly subjective and exhibits considerable variation among individuals (Deco and Romo, 2008). Different individuals may have distinct anchors

when rating their sensory perception on a scale, influenced by factors such as previous experience of pain and psychosomatic conditions. Secondly, neural responses also vary considerably among different individuals, influenced by factors such as skull thickness and cortical structures. For these reasons, one subject may exhibit higher brain responses accompanying the same perceptual rating, while another may

Fig. 6. Effect of the number of subjects and trials on the results obtained from three analytical analyses in the time (A-C) and time-frequency (D-F) domains. (A) Within-subject correlation analysis. Regardless of the varying number of subjects or trials, the proportions of significant data points remained consistently stable. The intraclass correlation coefficient (ICC) analyses revealed good to excellent reliability for all modalities. (B) Between-subject correlation analysis. As the number of subjects decreases, no significant correlations were observed, and ICC analyses indicated a poor reliability for all sensory modalities. When the number of trials decreases, the correlations remained stable, and the ICC analyses revealed good to excellent reliability for all modalities. (C) RSA. When the number of subjects decreases, although the proportions of significant time points decrease for all modalities, the ICC analyses reveal good to excellent reliability. In contrast, when the number of trials decreases, both the proportions of significant time points and the ICC decrease for all modalities. (D) Within-subject correlation analysis. Regardless of the varying number of subjects or trials, the proportions of significant time-frequency pixels within the selected ROI remained stable, and the ICC analyses revealed an excellent reliability in all modalities. (E) Between-subject correlation analysis. When the number of subjects reduces to 60 %, no significant correlations were observed for nociceptive and non-nociceptive somatosensory modalities. For all numbers of subjects, no significant correlations were observed for visual and auditory modalities. The ICC analyses revealed moderate to excellent reliability in all modalities. When the number of trials decreases, the proportions of significant time-frequency pixels within the selected ROI remained relatively stable, and the ICC decreased in all modalities. (F) RSA. When the number of subjects decreases, although the proportions of significant time points decrease, the ICC analyses reveal good to excellent reliability for all modalities. In contrast, when the number of trials decreases, both the proportions of significant time points and the ICC decrease in all modalities.

show lower brain responses. These variations in the correspondence between perceptual ratings and stimulus-evoked brain responses across subjects can lead to instability in between-subject correlation results. Changes in the number of subjects, especially in small sample sizes or when sample homogeneity is low, can significantly influence correlation outcomes. This point was supported by the stability assessment of between-subject correlation results, which were markedly influenced by the number of subjects, especially when the sample size is relatively small (e.g., less than 64 subjects, 60 % of our total samples). Given our limited sample size ($n = 107$), it would be difficult to determine the sample size that will yield stable results in the current study.

Unlike correlation analysis, which directly evaluates the correlation between sensory perception and brain activity, RSA evaluates this correlation between perceptual patterns and brain patterns. The significance of RSA results is obtained when the perceptual patterns closely align with the corresponding brain patterns. Therefore, this approach holds the potential to provide new insights into the relationship between sensory perception and brain activity by establishing associations between perceptual patterns and neural patterns. Notably, RSA has been commonly employed to assess the neural representations of cognitive processes, such as memories, face processing, and object recognition (Cichy et al., 2014, 2016; Dobs et al., 2019; Muukkonen et al., 2020). However, its use in evaluating the neural representations of sensory perceptions, especially in somatosensory perception, has been relatively rare. This scarcity might be attributed to the limited variety of sensory stimuli (i.e., experimental conditions), both in terms of intensity and type, employed in most sensory research. In the present study, we observed that RSA can detect almost all correlations identified through traditional within- and between-subject correlation analyses. Furthermore, RSA revealed additional neural indicators that couldn't be detected through correlation analyses. One noteworthy example is the presence of “ γ -ERS” in the visual modality - a neural response consistently observed during visual stimulation, as evidenced by magnetoencephalographic recordings in humans (Hoogenboom et al., 2006) and intracranial EEG in animals (Han et al., 2021; Jia et al., 2013; Ray and Maunsell, 2011). This component seems to correlate with more intricate visual features, including spatial frequency (Han et al., 2021), bars (Singer and Gray, 1995), and illusory contours (Stroganova et al., 2012). In the present study, although we observed the role of gamma oscillations in visual perception using a visual stimulus consisting merely of a brief flash from a simple white light-emitting diode, we cannot ascertain whether these gamma oscillations were specifically related to certain visual processing mechanisms.

Importantly, the results of stability verification indicated that RSA remains largely unaffected by variations in the number of subjects, which suggests that replicable RSA results could be obtained in studies with small sample sizes. RSA involves computing the RDMS for perceptual ratings or brain responses across all conditions (i.e., four stimulus intensities for both hands) and then assessing their pattern correlations. The stability of patterns heavily relied on the stability of perceptual ratings across different conditions, which in turn depends on

the number of trials but not the number of subjects. Previous RSA-related studies also demonstrated that the number of trials and conditions significantly influenced the results (Kriegeskorte et al., 2008). Generally, a higher number of trials and conditions leads to greater stability and reliability of the analysis results. Therefore, to obtain robust results in RSA, it is often recommended to increase the number of trials and conditions to enhance statistical power and result stability. Altogether, our findings suggest that establishing the connection between stimuli-induced behavioral patterns and neural patterns via RSA could be an important avenue for unveiling the relationship between brain responses and sensory perception.

Several limitations of the present study should be noted. Firstly, although the analysis performed in the current study somewhat mitigated the influence of stimulus side on the EEG results, it may not completely rule out the impact of stimulus laterality on the outcomes. Secondly, RSA usually requires a diverse array of conditions, while the number of conditions in the present study was relatively small ($n = 8$). It is imperative that future studies consider employing a more extensive array of conditions. Thirdly, the sample size in the present study, both in terms of subjects ($n = 107$) and trials ($n = 10$ in each condition), was relatively limited. Consequently, we cannot determine the minimum sample size required for stable results, especially for between-subject correlation analysis. Lastly, while all three analytical methods revealed neural indicators associated with sensory perception, it is important to note that this study does not assert progress in establishing an objective neural marker for sensory perception in each sensory modality.

5. Conclusions

In summary, our study provides an important perspective on establishing the relationship between behavioral and electrophysiological data in perceptual studies. While within-subject correlation demonstrates notable stability in unveiling the neural mechanisms underpinning intra-individual variability in sensory perception, between-subject correlation can uncover the neural underpinnings of inter-individual variability in sensory perception. Importantly, we introduce an innovative use of RSA by establishing the link between behavioral and electrophysiological patterns. This approach exhibits good stability to variable subject numbers and has the capacity to identify some novel findings. Therefore, it holds promise as a method to explore the pattern relationship between sensory perception and brain activity and could be adopted in various studies with a diverse array of conditions.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

All data analyzed in the current study including the analysis code are available to researchers from the corresponding author upon reasonable request.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.neuroimage.2024.120650](https://doi.org/10.1016/j.neuroimage.2024.120650).

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