Sense of self in mind and body: an eLORETA-EEG study

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Abstract

The human brain engages the sense of self through both semantic and somatic self-referential processing (SRP). Alpha and theta oscillations have been found to underlie SRP but have not been compared with respect to semantic and somatic SRP. We recorded electroencephalography (EEG) from 50 participants during focused internal attention on life roles (e.g. “friend”) and outer body (e.g. “arms”) compared to resting state and an external attention memory task and localized the sources of on-scalp alpha (8–12 Hz) and theta (4–8 Hz) EEG signals with exact low-resolution tomography. Logarithm of F-ratios was calculated to compare differences in alpha and theta power between SRP conditions, resting state, and external attention. Results indicated that compared to resting state, semantic SRP induced lower theta in the frontal cortex and higher theta in the parietal cortex, whereas somatic SRP induced lower alpha in the frontal and insula cortex and higher alpha in the parietal cortex. Furthermore, results indicated that compared to external attention, both semantic and somatic SRP induced higher alpha in the dorsolateral prefrontal cortex with lateralized patterns based on task condition. Finally, an analysis directly comparing semantic and somatic SRP indicated frontal–parietal and left–right lateralization of alpha and theta oscillations in the frontal, parietal, and the insula cortex may play crucial roles in semantic and somatic SRP.

Keywords: sense of self; self-referential processing; eLORETA; neural oscillation

Introduction

It has long been known from phenomenological inquiry that self-referential processing (SRP) can occur via “introspection” upon semantic references (e.g. “Who am I?”) as well as via “interoception” upon somatic references (e.g. “How do I feel?”) (e.g. James 1890). However, it was not until only recently that neuroimaging studies contributed to our understanding of the brain bases of our semantic vs. somatic senses of self (Frewen et al. 2020, Qin et al. 2020), the latter often termed “bodily self-consciousness” in recent literature (e.g. Park and Blanke 2019). Introspective SRP of semantic content is associated with responses within the frontal hub of the default mode network (DMN), particularly the medial prefrontal cortex (MPFC), the orbitofrontal cortex, and the anterior cingulate cortex (ACC), whereas interoceptive SRP of somatic content is associated with the premotor cortex, the inferior parietal sulcus, the ventrolateral prefrontal cortex (VLPFC, including the inferior frontal gyrus, IFG), the temporoparietal junction (TPJ), and the insula (Araujo et al. 2015; Davey et al. 2016; Lutz et al. 2016; Salvato et al. 2020). Additionally, a meta-analysis using the Neurosynth database (Yarkoni et al. 2011) of 166 semantic and 81 somatic SRP studies found that semantic SRP may also be associated with the posterior cingulate cortex (PCC), the ventral precuneus, bilateral posterior TPJ, and temporal poles, while somatic SRP may also be associated with the ventral MPFC and frontal operculum (Frewen et al. 2020). This suggests that while semantic and somatic forms of SRP were associated with different sub-networks of the DMN (van Buuren et al. 2010), there may also be considerable degrees of overlap between the two forms of SRP. Another recent meta-analytic review comparing semantic and somatic SRP proposed a three-layer model that placed the insula as the core layer of the self, playing a part in introspection, interoception, and exteroception (Qin et al. 2020).

Most of the neuroimaging of SRP literature comes from analysis of the BOLD signal using fMRI, while comparably little is known about the underlying neuroelectrophysiology involved in SRP such as can be assessed by electroencephalography (EEG), which affords a direct measurement of the electrophysiological activity of the brain from scalp recordings. Only a few EEG studies have investigated semantic SRP during structured periods when participants are explicitly instructed to perform “on-task” SRP such as during self-referential encoding tasks (SRETs, e.g. Mu and Han 2013) or SRP that occurs spontaneously during unstructured periods of
“resting state” (Knyazev et al. 2012; Bocharov et al. 2019). Although resting-state EEG studies found the involvement of all EEG bands, among the existing SRP studies, different results in SRP compared to non-SRP conditions were most frequently observed in the alpha and theta bands. For example, Bocharov et al. (2019) found that frontal alpha and theta band power exhibited “decreases” while participants were experiencing spontaneously arising self-referential thoughts as compared to when they were experiencing non-self-referential thoughts during resting state. Comparably, Knyazev et al. (2012) asked participants to complete the Spontaneous Thought Questionnaire after recordings of resting-state EEG that were analyzed with the exact low-resolution electromagnetic tomography (eLORETA) and found that the frequency of self-reported self-referential thoughts during resting state was best predicted by “higher” alpha activity within the DMN, followed by “lower” theta activity in the frontal cortex. Finally, in a topographical on-task EEG study, participants were asked to complete a SRET requiring them to evaluate whether trait adjectives (e.g. “extroverted”) described themselves, on certain trials, or to evaluate the font of the adjective (bold vs. light) during other trials (Mu and Han 2010) and found that, compared to font-judgment, trait-judgment (semantic SRP) induced “decreased” theta over the posterior-occipital electrodes and “increased” theta over the left frontal–central electrodes, and further that trait-judgment induced decreases in alpha band over the frontocentral and posterior electrodes (Mu and Han 2010). Taken together, the few EEG studies of SRP that have so far been conducted have yielded heterogeneous findings suggesting that frontal alpha and theta oscillations play a particularly crucial role in semantic SRP, although the directionality of effects remains unclear.

Unfortunately, studies directly comparing the EEG correlates of semantic to somatic SRP are even scarcer. In interoceptive tasks, participants are typically instructed to focus attention on their momentary bodily sensations, similar to the practice of body scan meditation. For example, Fingelkurts et al. (2020) induced somatic SRP by asking eight experienced meditators to focus on “sensing yourself centered in the body from which you are experiencing the world” (p.6). Fingelkurts et al. (2020) showed when experienced meditators “up-regulate” the somatic self, alpha band synchrony within right posterior cortex exhibited significant increases compared to the “down-regulated” state (Fingelkurts et al. 2020). Comparably, Rodriguez-Larios et al. (2020) found that, compared to mind-wandering, attention toward breathing was associated with “higher” alpha and “lower” theta band power across the whole brain. Overall, previous EEG studies comparing semantic and somatic SRP implicate alpha and theta oscillations, albeit that the directionality of responses has varied across studies.

The current literature comparing the alpha and theta EEG correlates of semantic vs. somatic SRP exhibits several limitations. First, most studies only analyzed the scalp topographic EEG activity or used dipole source localization, thus limited by assumptions such as the perpendicularity of cortical pyramidal neurons and the fixed number of dipoles (Grech et al. 2008). As a result, EEG studies of SRP tend to report the activity of EEG bands across large surface areas on the scalp instead of making observations on specific regions of the brain, and future studies might be better to implement EEG analytics utilizing distributed source localization methods that do not make assumptions on the orientation of pyramidal neurons and number of dipoles, such as eLORETA used in Knyazev et al. (2012). Second, discrepancies in the choice of control conditions may contribute to the heterogeneity of results. While some studies chose to control for the effect of referential target by comparing SRP with other-referential processing (e.g. assigning traits to a friend; Mu and Han 2013), other studies used resting state as the control condition (Bocharov et al. 2019; Rodriguez-Larios et al. 2020). Third, emotional valence is an important aspect of SRP with implications regarding self-esteem and mental health, but few existing SRP tasks measured emotional valence with some exceptions (e.g. Mu and Han 2010; Frewen et al. 2013). For example, Mu and Han (2010) found that positively valenced SRP exhibited significantly less theta power than negative SRP. Nevertheless, existing studies only measured SRP valence with self-reports of emotional states and not psychophysiological responses that provide objective indicators of arousal. Finally, past task-based studies typically have small sample sizes, therefore limiting the sensitivity of statistical analyses.

Given the paucity and diversity of results regarding existing EEG studies investigating SRP, the current study investigates the oscillatory patterns of alpha and theta frequencies with a larger sample of participants during semantic and somatic SRP using eLORETA. We designed an SRP task similar to Simmons et al. (2013) and Lutz et al. (2016), where participants are asked to focus on semantic and somatic stimuli in different trials, controlling for both internal and external attention using resting state and a simple letter-counting task, respectively. To assess emotional valence and arousal in response to these tasks, participants provided self-reported ratings of feelings of pleasantness in response to task conditions, and we compared both mood ratings before vs. after the task and included secondary measures of arousal throughout the task [skin conductance level (SCL) and photoplethysmography (PPG)]. Based on the few fMRI studies that directly compared response to semantic and somatic SRP (Simmons et al. 2013; Araujo et al. 2015; Lutz et al. 2016) and the prior EEG literature, we predicted that compared to the resting state and external attention control conditions, both semantic and somatic SRP would induce lower alpha and either lower or higher theta in the frontal lobe (Mu and Han 2013; Bocharov et al. 2019; Rodriguez-Larios et al. 2020), while increased alpha oscillations were expected in the left and right parietal cortex for semantic and somatic SRP, respectively (Fingelkurts et al. 2020). Additionally, we directly compare the EEG correlates of semantic and somatic SRP in an exploratory fashion.

Methods
Participants
Fifty undergraduate students were recruited from the SONA research participation system at (Institution omitted for blind review). Age ranged between 18 and 22 with 52% female. In addition to being students, 73% indicated that they were employed part-time. Participants identified as White (31%), Chinese (22%), South Asian (19%), or “Other” (28%).

Procedures and materials
Upon entering the experiment and providing informed consent, participants completed a 30-item questionnaire on their current mood state, including the 20-item Modified Differential Emotions Scale (mDES; Fredrickson et al. 2003) and the 10-item Buddhist Affective State Scale (BASS; Zhu et al. 2019). The mDES consists of 10 positive affect items such as “Grateful, appreciative, thankful” and 10 negative affect items such as “Sad, downhearted, unhappy.” The BASS assesses affective states associated with Buddhist psychology such as “Oneness, unity, connectedness” and “Sacredness, reverence, spiritual.” All items were rated on an 11-point scale with increments of 10 (0 = “Not at all” and 100 = “Very much more than usual”).
Then, participants practiced one run of the SRP task before EEG data collection was initiated in order to ensure task familiarity and reduce novelty at the time of EEG recordings. Briefly, the SRP task required participants to evaluate how they feel about themselves in different life roles (student, child, friend, employee, consumer, and citizen) during the semantic SRP condition and to evaluate how they feel in different parts of their outer body (head, arms, shoulders, hands, legs, and feet) during the somatic SRP condition. Comparably, during an external attention condition, participants were asked to count the number of times they heard the letter “X” in a string of six letters, designed to be simple and thus of comparable cognitive load to the SRP tasks. Furthermore, during a resting state condition, participants were instructed simply to wait until further instructed, thus allowing their attention to wander during the intervening period (Fig. 1).

At the end of each block, participants were asked to rate their level of attentiveness on a 1–5 scale, with 1 referring to “very inattentive” and 5 “very attentive.” Additionally, following the semantic and somatic SRP tasks, participants were asked to rate how pleasantly they experienced the tasks on a 1–5 scale with 1 referring to “very unpleasant” and 5 “very pleasant.” Pleasantness was not rated in response to the external attention (letter counting) task, after which participants were instead asked to report the number of “X”s they heard from 1 to 5 to assess accuracy. Each individual stimulus (word or letter) was presented for 5 s, making each experimental block last 30 s, while the resting state condition [i.e. inter-block interval (IBI)] was also 30 s. Participants were presented with three blocks of each task condition (cumulatively 90 s), while the cumulative resting state acquired was 270 s (3 x 3 x 30 s). Between each run of SRP tasks, for 5 min, participants completed a brief meditation involving focusing their attention on the sensations of breathing and to bring their attention back from mind-wandering to breathing when they noticed mind-wandering. During the 5-min meditation, participants heard three bell sounds at 1-min intervals as reminders to bring their attention back to breathing. These 5-min meditations essentially acted as structured resting state sessions, since the degree of mind-wandering does not differ appreciably between resting state and breath-focusing meditation among novice meditators (Rodriguez-Larios and Alaerts 2021). The SRP task and the experimental procedure are described in Fig. 1. After the SRP task, participants completed the same 30-item mood state questionnaire once again before exiting the study. The study was approved by the institutional research ethics board of Western University, Canada.

**EEG data acquisition and peripherals**

EEG data were recorded with the Nexus-32 system (www.mindmedia.com) and the Biotrace+ software at 512 Hz sampling rate with standard 19-channel (Fp1, Fp2, F3, F4, Fz, F7, F8, C3, C4, Cz, T3, T4, T5, T6, P3, P4, Pz, O1, and O2) caps under the international 10–20 system. We also measured PPG (128 Hz) and SCL (32 Hz) from fingers of the non-dominant hand.

**EEG and peripheral data preprocessing**

EEG data was preprocessed using custom-made EEGLAB code (Delorme and Makeig 2004) under the MATLAB environment. EEG preprocessing steps in sequence included: (i) import raw data and events; (ii) bandpass filter between 1 and 50 Hz; (iii) reconstruct artifacts with the Riemannian method of Artifact Subspace Reconstruction (Blum et al. 2019); (iv) interpolate rejected data channels; (v) decompose data using Picard independent component analysis (ICA), chosen based on its balance in accuracy and processing speed (Ablin et al. 2018); (vi) accept ICA components using IClabel (Pion-Tonachini et al. 2019) based on at least 70% probability
on the "brain" category; and (vii) epoch data and export for the subsequent eLORETA (Pascual-Marqui 2007).

Preprocessing of PPG data in millivolts was conducted with the Kubios Premium Software (Tarvainen et al. 2013), which automatically rejects noisy data segments and calculates heart rate (HR) variability metrics. We included HR, standard deviation of the NN intervals, and root mean square of successive RR interval differences as time-domain metrics and normalized low (LF) and high-frequency (HF) power as well as LF-HF ratio (LF/HF) as frequency-domain metrics. SCL data in microsiemens were preprocessed using a fourth-order Butterworth bandpass filter of [0.05, 0.3] Hz and normalized with log-transformation for the subsequent analysis (Cacioppo et al. 2007).

Statistical Analyses

We used the LORETA-KEY software package for EEG source localization (www.uzh.ch/keyinst/loreta, Pascual-Marqui et al. 1999). First, electrode names were converted to Talairach coordinates to create eLORETA transformation matrices. The cross-spectra for each subject were then computed and tapered with the Hann window function (mean-corrected) for both alpha (8–12 Hz) and theta (4–8 Hz) bands. Given the cross-spectra, eLORETA was used to estimate the current density, reported on the MNI152 template (Maintz and Viergever 1998). For reporting results, the MNI coordinates were converted to Talairach space (Brett et al. 2002) and labeled by the Talairach Daemon (Lancaster et al. 1997). Only gray matter voxels that were unambiguously within the brain compartment were retained in the process. Albeit not the focus of this study, we analyzed other EEG bands (delta, beta, and gamma) and included their results in the Supplementary Materials.

Statistical analyses were also performed within the LORETA-KEY package (http://www.uzh.ch/keyinst/loreta). Subject-wise normalizations were performed on the processed data to correct for global source of variability. Two-tailed paired groups comparisons on the logarithm of \( F \)-ratios were conducted with the Statistical non-Parametric Mapping (SnPM) methodology, which corrects for multiple comparisons with 5000 non-parametric randomizations using maximum statistics, without assuming normality (Nichols and Holmes 2001). Results of the exceedance proportions test (Friston et al. 1990, 1991) indicating statistically significant supra-threshold clusters with \( p \leq 0.05 \) were accepted and reported herein. When a choice of multiple significant thresholds was yielded by the SnPM analysis, the lowest threshold was selected to maximize specificity. Brain structures with log of \( F \)-ratio > 0.1 are reported in the text, while all statistically significant results are reported in tables.

We also conducted statistical analysis on participants’ mood ratings, attentiveness (across three conditions), pleasantness (across two conditions), PPG metrics, and SCL signals using \( t \)-tests with the Holm-Bonferroni method to adjust for multiple comparisons. Outliers above \( [Q_1 + 1.5 \times (Q_3 - Q_1)] \) and below \( [Q_1 - 1.5 \times (Q_3 - Q_1)] \) were removed and replaced with the group median prior to analysis. We detected one outlier in the life roles condition for pleasantness rating and one outlier in both the outer body and letter-counting conditions for attentiveness rating. Additionally, we conducted regression analyses to determine the mediating effects of attentiveness and pleasantness on EEG spectral power using the LORETA-KEY program.

Results

Ratings of mood states, pleasantness and attentiveness

Supplementary Fig. 1 describes the changes in participants’ mood states reported before vs. after the SRP task. After the experiment, participants reported statistically significant increases in joy [\( \Delta M = 6.4, t(50) = 3.47, P_{adj} = 0.03 \)], awe [\( \Delta M = 9.6, t(50) = 3.31, P_{adj} = 0.05 \)], gratefulness [\( \Delta M = 9.0, t(50) = 3.93, P_{adj} = 0.007 \)], serenity [\( \Delta M = 16.6, t(50) = 5.25, P_{adj} < 0.001 \)], insightfulness [\( \Delta M = 9.2, t(50) = 5.23, P_{adj} < 0.001 \)], and oneness [\( \Delta M = 12.0, t(50) = 5.72, P_{adj} < 0.0001 \)]. Participants also reported decreased sadness [\( \Delta M = 5.6, t(50) = 3.35, P_{adj} = 0.05 \)], confusion [\( \Delta M = 8.2, t(50) = -3.21, P_{adj} = 0.05 \)], embarrassment [\( \Delta M = 8.0, t(50) = -3.40, P_{adj} = 0.03 \)], and stress [\( \Delta M = 10.4, t(50) = -4.66, P_{adj} < 0.001 \)].

Participants rated their levels of pleasantness during the SRP task to be slightly positive overall on the 1–5 rating scale and significantly different between life roles and outer body with \( t(49) = 2.84, P_{adj} = 0.007 \), Cohen’s \( d = 0.40 \). Descriptive statistics were, for life roles, \( M = 3.65, SD = 0.54, \min/\max = 2.7/4.7 \), and for outer body, \( M = 3.83, SD = 0.56, \min/\max = 3.00/5.00 \).

Given that the mean occurrences of the letter “X” was objectively accurate at 3, participants made very few mistakes in the letters counting task (before outlier removal: \( M = 3.00, SD = 0.16, \min/\max = 2.33/3.50 \)). Participants’ self-reported levels of attentiveness were also qualitatively high in response to the letter-counting task with \( M = 4.66, SD = 0.50, \min/\max = 3.35/5.00 \). Self-reported attention was also qualitatively high in response to the life roles task, \( M = 4.19, SD = 0.66, \min/\max = 2.33/5.00 \), and the outer body task, \( M = 4.29, SD = 0.53, \min/\max = 3.00/5.00 \). Nevertheless, participants reported that they paid significantly more attention during the letter-counting task when compared to both the life roles condition, \( t(49) = 3.58, P_{adj} < 0.001 \), Cohen’s \( d = 0.51 \), and the outer body condition, \( t(49) = 3.41, P_{adj} = 0.001 \). Cohen’s \( d = 0.48 \); self-rated attentiveness was not significantly different between the two SRP conditions with \( t(49) = 1.23, \text{ns} \).

Skin Conductance Levels and Photoplethysmography

No statistically significant differences were found between conditions from the PPG metrics indicative of average HR or its variability. Analysis of SCL signals revealed that SCL was lower during resting state (\( M = 0.81, SD = 0.85, \min/\max = -1.01/2.44 \)) than during semantic SRP (evaluation of life roles) (\( M = 0.90, SD = 0.86, \min/\max = -0.76/2.46, P_{adj} = 0.002 \)), or somatic SRP (attention to outer body) (\( M = 0.90, SD = 0.85, \min/\max = -0.90/2.44, P_{adj} = 0.006 \)), or the external attention control task (counting letters) (\( M = 0.92, SD = 0.85, \min/\max = -1.1/2.44, P_{adj} = 0.002 \)).

eLORETA results

Figures 2–4 and Supplementary Tables S1–S3 show the eLORETA contrasts in the alpha and theta bands between semantic SRP (life roles) and somatic SRP (outer body) in comparison to the external attention (letter counting) task and the resting state IBI.

SRP and resting state vs. external attention

Semantic SRP vs. external attention

The exceedance proportion tests comparing semantic SRP and external attention showed significance in the alpha band with two-tailed log of \( F \)-threshold = 0.017 (\( P = 0.006 \)). Semantic SRP induced higher alpha in the bilateral insula, and the frontal and the ACC, with the maximum activation in the left IFG.
Figure 2. Significant eLORETA maps comparing internal attention conditions (SRP and resting state) with external attention in the alpha band. Note. The log of F-ratio thresholds for significance: semantic SRP = 0.017, P = 0.006; somatic SRP = 0.017, P = 0.026; resting state = 0.019, P < 0.001

Figure 3. Significant eLORETA maps comparing SRP with resting state in the theta and alpha bands. Note: the log of F-ratio thresholds for significance: semantic SRP (theta) = 0.006, P = 0.008; somatic SRP (alpha) = 0.010, P = 0.002

(Supplementary Table S1, Fig. S2). Brain structures with log of F-ratio higher than 0.1 include the bilateral IFG, the bilateral precentral gyrus, the bilateral cingulate gyrus, the bilateral ACC, and the left middle frontal gyrus (MFG). Additionally, semantic SRP induced lower alpha in a posterior cluster with maximum deactivation in the precuneus (Supplementary Table S1, Fig. S2).

Somatic SRP vs. external attention
Our results also showed significant two-tailed contrasts between somatic SRP and external attention with log of F-threshold = 0.017 (P = 0.026) in the alpha band. Somatic SRP also induced higher alpha in the bilateral insula and the right frontotemporal cortex with the maximum activation in the right insula and the right IFG (Supplementary Table S1, Fig. S2). Brain structures with log of F-ratio higher than 0.1 include the right IFG, the right insula, the bilateral precentral gyrus, the bilateral MFG, and the left ACC. Additionally, somatic SRP induced lower alpha activity in a temporoparietal cluster with maximum deactivation in the temporal gyri and the parahippocampal gyrus (Supplementary Table S1, Fig. S2).
**Resting state vs. external attention**

The exceedance proportion tests comparing resting state and external attention showed significance in the alpha band with two-tailed log of F-threshold = 0.019 (P < 0.001). Resting state induced higher alpha in the bilateral insula and the frontal cortex with maximum activation in the right IFG and right insula (Supplementary Table S1, Fig. S2). Brain structures with log of F-ratio higher than 0.1 include the bilateral IFG, the bilateral precentral gyrus, the bilateral ACC, the bilateral MFG, the bilateral superior temporal gyrus, and the right cingulate gyrus. Additionally, resting state induced lower alpha in the parietal and occipital lobes with maximum deactivation in the right PCC (Supplementary Table S1, Fig. S2).

**SRP vs. resting state**

**Semantic SRP vs. resting state**

The exceedance proportion tests comparing semantic SRP and resting state showed significance in the theta but not alpha band with two-tailed log of F-threshold = 0.006 (P = 0.008). Semantic SRP induced lower theta in the bilateral insula and a frontal cluster with maximum deactivation in the ACC and MPFC (Supplementary Table S2, Fig. S3). Semantic SRP also induced higher theta in a posterior cluster with maximum activation in the right supramarginal gyrus and the temporal gyri (Supplementary Table S2, Fig. S3).

**Somatic SRP vs. resting state**

In comparison, our results showed significant two-tailed contrasts between somatic SRP and resting state with log of F-threshold = 0.010 (P = 0.002) in the alpha but not theta band. Somatic SRP induced lower alpha activity in the left insula but higher alpha activity in the right insula. Additionally, somatic SRP induced lower activity in the left frontotemporal cortex with maximum deactivation in the IFG and the superior temporal gyrus (Supplementary Table S2, Fig. S3). Finally, somatic SRP induced higher alpha activity in the right temporal–parietal–occipital (TPO) cortex with maximum activation in the lingual gyrus, the posterior cingulate, the fusiform gyrus, and the cuneus (Supplementary Table S2, Fig. S3).

**Semantic vs. somatic SRP**

The exceedance proportion tests comparing semantic SRP and somatic SRP showed significance in the alpha band with two-tailed log of F-threshold = 0.007 (P = 0.016). Semantic SRP induced higher alpha in the left cingulate gyrus, the left precentral gyrus, the left insula, the left superior temporal gyrus, the bilateral ACC, the left middle temporal gyrus, the left inferior temporal gyrus, the left IFG, the left postcentral gyrus, the left parahippocampal gyrus, the left MFG, the right frontal pole, the right superior frontal gyrus, the bilateral medial frontal gyrus, the middle occipital gyrus, the left PCC, and the left lingual gyrus (Supplementary Table S3, Fig. S4).
In contrast, somatic SRP induced higher alpha in the right IFG, the bilateral precentral gyrus; the right precuneus; the right insula; the right MFG, the right inferior parietal lobule; the right PCC, the right cuneus; the right postcentral gyrus; the right superior, middle, and inferior temporal gyrus; the right parahippocampal gyrus; and the left paracentral lobule (Supplementary Table S3, Fig S4).

The follow-up regression analysis investigating the potential mediating effect of attentiveness and pleasantness in the EEG results indicated that no cluster or single voxel was a significant predictor of the difference in ratings between experimental conditions.

**Discussion**

To our knowledge, this EEG study was the largest to investigate response to a structured SRP task when it comes to participant sample size and the first to compare the EEG alpha and theta oscillatory correlates of semantic SRP with somatic SRP as well as to both an internal (resting state) and external attention control condition utilizing eLORETA. Our study yielded several findings. First, compared to a simple external attention task (letter counting), conditions that involved internal attention (SRP and resting state) induced increasing alpha activity in the bilateral insula, the MFG (i.e. dorsolateral prefrontal cortex, DLPFC), the VLPFC (i.e. IFG), and the ACC, while decreasing alpha activity in the precuneus (Fig. 2). Second, within the internal attention tasks, when compared with the passive and unstructured resting state, active and structured SRP induced increasing alpha and theta activity in the right TPO cortex but decreasing alpha and theta activity in the left TPO cortex, the bilateral insula, the ACC, the VLPFC, and DLPFC (Fig. 3). Third, within the active and structured SRP conditions, direct comparison between semantic and somatic SRP suggested differential alpha activities in the anterior vs. posterior cortex and the left vs. right hemisphere, including notably the insula and the dorsal ACC (Fig. 4). Such findings were observed over the course of completing an SRP task that was generally found to be pleasant and associated with improved mood and that was also sensitive to certain measures of psychophysiological arousal. These self-reported findings may suggest that brief sessions of semantic and somatic SRP interspersed with breath-focused meditations might have stress-reduction and mood-enhancing effects, albeit requiring further investigation with control conditions. We discuss each set of findings in turn.

**Internal attention compared to external attention**

During the SRP task and resting state, participants were asked to focus their attention internally on their character (semantic SRP), bodily sensations (somatic SRP), or spontaneous thoughts (resting state) that are likely generated by the DMN and BSC system (Davey et al. 2016; Park and Blanke 2019). In our study, these internal attention task conditions induced increases in alpha activity in the DLPFC, the VLPFC, the ACC, and the anterior insula when compared to external attention, in agreement with several fMRI studies on SRP.

Regarding the VLPFC, fMRI studies have suggested that the right VLPFC may play a role in cognitive control during self-face processing as part of somatic SRP (Hu et al. 2016) while the left VLPFC may play a role in internal speech production as part of semantic SRP (Morin and Hamper 2012). Regarding the ACC and the insula, in addition to the insula’s role in interception, several studies found that both the dorsal ACC and the anterior insula are involved in the salience of the self during emotional SRP, such as during negative self-attribution, self-face recognition, and social rejection tasks (Cabani et al. 2013; Morita et al. 2014; Perini et al. 2018). Our results appear consistent with the meta-analysis of Hu et al. (2016) who suggested that the VLPFC/insula region and the ACC are consistently found in both semantic and somatic SRP studies, suggesting a “core self-representation” that integrates multimodal self-relevant stimuli underlying SRP.

Interestingly, compared to external attention, we also found that internal attention toward the self induced increased alpha activity in the DLPFC bilaterally (Supplementary Table S1). Although the DLPFC is known to play a role in executive control during negatively valanced SRP, such as during rumination and major depression (Renner et al. 2015; Delaveau et al. 2016; Baeken et al. 2017), few studies investigated the DLPFC in the context of internal and emotionally neutral SRP among healthy participants. In our study, we found the involvement of the alpha band in the DLPFC when participants were engaged in SRP that they rated, on average, to be emotionally neutral to slightly positive. Given the DLPFC’s role in executive control and our results, the DLPFC may be involved in attentional control of internal focus toward the self and coupling with the self-relevance of stimuli. In summary, the internal component of SRP induced alpha and theta activities that may be involved in cognitive control, internal speech, interception, and affective regulation.

Finally, we found that, compared to external attention, internal attention during resting state also induced higher alpha activity in the previously mentioned brain areas such as the bilateral VLPFC, bilateral insula, bilateral DLPFC, and the ACC. We know from fMRI evidence that the resting brain overlaps with the self-referential brain and that sub-networks of the DMN may be associated with different aspects of SRP (Gusnard et al. 2001; van Baaren et al. 2010; Wen et al. 2020). Furthermore, evidence suggests that internal attention that is not goal-directed may encompass numerous processes, including both semantic and somatic SRP (Welsh et al. 2020). Therefore, our findings may support these previous findings that various unprompted forms of SRP may occur during passive, unstructured periods of resting state.

**SRP compared to resting state**

Despite both usually being associated with an internal focus, SRP tasks differ from the resting state in their increased structure and goal-directedness, contrasting the task-free nature of the resting state. Therefore, our SRP vs. resting state contrasts reflect the active “on-task” component of SRP, such as attending to task-relevant stimuli and inhibition of task-irrelevant stimuli. We found large areas across the right TPO cortex exhibiting higher alpha and theta activities during task-related SRP as compared to rest. In fMRI studies, activations in the PCC and the right inferior parietal lobule were consistently found to be both semantic and somatic SRP exhibiting DMN-wide connections with the primary visual cortex, the posterior parietal cortex, and the fusiform cortex may be interpreted as multisensory integration required during SRP. However, it remains unclear why these processes during SRP were heavily lateralized to the right hemisphere in our study.

In the opposite direction, comparing resting state with SRP yields the background “at-rest” component that is less involved during active SRP. We found that higher activities in the VLPFC, the bilateral insula, and the ACC were observed during the resting state in both the alpha and theta bands. These findings are
consistent with the "core self-representation" mentioned previously and suggest that activities in the VLPFC/insula and ACC may be SRP-specific and cannot be accounted for only by internal attention in general. Again, this finding is consistent with Hu et al. (2016) who found that both semantic and somatic SRP share these common regions. Our findings thus suggest that such a "core self-representation" may be an endogenous background activity occurring during rest and that such resting-state SRP exceeds that occurring even during structured SRP tasks. An important note is that even though our results indicate that endogenous SRP during rest may be different from goal-oriented SRP, evidence suggests that both at-rest and on-task SRPs share substantial anatomical and functional similarities (Kim, 2012). Interestingly, more recent literature suggested that brain activities during resting state may be a “foundation” for semantic SRP. For example, Bai et al. (2016) found that high glutamate concentration in the perigenual ACC predicted higher alpha band activity before presentations of semantic SRP stimuli and higher subjective ratings of self-relevance. Additionally, Meyer and Lieberman (2018) demonstrated that BOLD activities in the MPFC/Brodmann Area 10 during the resting state predicted faster response times to semantic SRP stimuli in a SRET. Although our experimental design cannot address the direction of causality between resting state and SRP, our findings may contribute to the three-level processing model of the self (Qin et al. 2020) that on-task SRP may be an extension of at-rest SRP when we direct attention to exogenous self-related stimuli.

Semantic SRP compared to somatic SRP

We observed a clear dissociation between anterior vs. posterior and left vs. right hemisphere response when comparing semantic vs. somatic SRP, respectively. Semantic SRP involved the left frontal brain, while somatic SRP involved the right posterior brain. Differences were also seen in some of the cortical midline structures, specifically, the dorsal ACC, PCC, and precuneus.

In the frontal lobe, we found peak alpha activity in the dorsal ACC during semantic SRP compared to somatic SRP. Evidence suggests that dorsal ACC is involved in several self-related processes such as self–other face discrimination (Hu et al. 2016), processing emotional responses in autobiographical memory retrieval (Yang et al. 2012), and salience to self-related stimuli (Murray et al. 2012). Therefore, increases in alpha activity in the dorsal ACC may indicate that semantic SRP is associated with a higher salience and emotional processing than somatic SRP. The difference between semantic and somatic SRP in emotional processing is also supported by participants’ lower levels of experienced pleasantness during semantic SRP. In this regard, Yang et al. (2012) found that BOLD activity in the dorsal ACC exhibited a negative association with state-level self-esteem. Our results may imply that alpha activity in the dorsal ACC relates to the potentially greater emotional salience of semantic SRP when compared to somatic SRP in our task.

In the parietal lobe, somatic SRP induced higher alpha activity in the precuneus/PCC region, which is consistently found to be associated with SRP. However, the directionality of our findings is different from existing fMRI literature. For example, Araujo et al. (2015) found that participants undergoing SRETs exhibited higher BOLD response in responding to their traits (semantic SRP) compared to facts about their body (somatic SRP), and in the meta-analytical review conducted by Qin et al. (2020), semantic SRP was associated with higher BOLD responses in the precuneus/PCC region compared to somatic SRP. Although one may argue that such differences may be accounted for by the anticorrelation between the alpha wave and BOLD responses (Fang and Robinson 2018), more studies are needed before making solid conclusions.

In addition to the dissociation between frontal and parietal responses in semantic vs. somatic SRP, we also observed differential responses to semantic vs. somatic SRP in the left vs. right hemisphere, respectively. First, somatic SRP induced higher alpha activity in the right insula. Ample evidence supports the roles of the right insula in somatic SRP, including processing interoceptive signals and body ownership (Craig 2002; Simmons et al. 2013; Salvato et al. 2020). A meta-analysis of fMRI studies of SRP suggested that semantic SRP is located on higher layers of the self (i.e. requiring more integration) compared to somatic SRP and that the right insula serves an integrative role over all domains of SRP (Qin et al. 2020). Moreover, Scalabrini et al. (2021) showed that the right insula exhibits a wider autocorrelation window than the left insula during a face-morphing task. Given the link between autocorrelation and information integration (Honey et al. 2012), these results support that response within the right insula may reflect a more fundamental layer aspect of SRP when compared to the left.

Comparably, the role of the left insula in semantic SRP is less clear. Here, we report a novel finding where semantic SRP induced higher alpha activity in the left insula compared to somatic SRP. As a possible interpretation, such differences might reflect the different levels of sensory integration involved in semantic vs. somatic SRP. The life roles task would appear to require little sensory processing when switching from self-evaluating oneself in the roles of ‘student’ vs. ‘friend,’ for example, implying that BSC may be processed holistically in each life role, if at all. In contrast, differentially attending to one area of one’s outer body (e.g. arms) vs. another (e.g. legs) may require more sensory processing, implemented within the right insula.

We also observed higher alpha activity in the left VLPFC/superior temporal cortex during semantic vs. somatic SRP. Self-related inner speech production may be more salient in semantic SRP than somatic SRP, supporting the findings of a meta-analysis on left VLPFC (Morin and Hamper 2012) and consistent with the proposal that semantic SRP is more linguistic in nature than is somatic SRP (Frewen et al. 2020). The right VLPFC–DLPFC area, on the other hand, exhibited higher alpha activity during somatic SRP. These results contrast with those of Araujo et al. (2015) who found that somatic SRP was associated with higher BOLD signals in the bilateral VLPFC. Particularly given the role of the right VLPFC in attending to self-relevant stimuli and cognitive and emotional inhibition within the frontoparietal attention network, Hu et al. (2016) suggested that the right VLPFC may reflect high demands of cognitive control during SRP. However, our tasks did not explicitly require cognitive inhibition, and participants in our study did not report differential levels of attentiveness during somatic and semantic SRP. Our results, therefore, imply that right VLPFC involvement during somatic SRP may subserve a more general function than specifically cognitive inhibition.

Finally, we reported as a novel finding that alpha activity increased in the left vs. right DLPFC corresponding with semantic vs. somatic SRP, respectively. Regarding the observed lateralization in semantic vs. somatic SRP, our findings in the insula, VLPFC, and the DLPFC may suggest that distinct neural processes associated with semantic and somatic SRP exist in the left vs. right hemisphere in addition to the involvement of cortical midline structures, extending the findings of Fingelkurts et al. (2020) for the parietal cortex. The laterality of the results implies a possible fundamental distinction within the brain in processing SRP in semantic vs. somatic domains.
Study limitations, future directions, and conclusions

Our study is not without limitations. First, we did not include self-reported measures of the self and self-consciousness out of considerations of the length of study sessions, but recommend future SRP studies to include questionnaire measures of self-esteem and body self-awareness to be compared with task-related ratings of semantic and somatic SRP. Moreover, our task blocks were 30-s long, requiring sustained attention and potential depth of introspection and interoception beyond that facilitated by responding to discrete stimuli as in most prior studies utilizing the SRET, albeit less than that used in other studies that have used lengthy meditations. Future studies should consider the depth of SRP provoked by their tasks as a relevant design feature. Second, our homogenous sample consists of only undergraduate students aged 18–22, while studies have suggested that SRP may vary based on factors such as culture (Knyazev et al. 2012) and age (Moses-Payne et al. 2022). Future studies may investigate both semantic SRP and somatic SRP across different demographic groups. Third, while our EEG study was aimed at discovering some of the electrophysiological correlates of different forms of SRP, causal conclusions regarding the role of various brain regions in SRP would be stronger following the direct manipulation of oscillations in these brain regions, such as might be accomplished by non-invasive brain stimulation (Bao et al. 2021). In the same vein, future EEG studies may use an electrode-driven approach to investigate differences in autocorrelation window (ACW) between the SRP conditions, given the close relationship between ACW and self-specificity (Smith et al. 2022). Fourth, we used eLORETA with only a small number of channels, resulting in low spatial resolution. Given the positive correlation between electrode density and source localization accuracy, future studies may investigate SRP with high-density montages. Fifth, although we decided against analyzing the involvement of high gamma (>50 Hz) due to the few numbers of prior studies on which to base hypotheses and the impact on multiple comparisons, future studies may nevertheless be interested to investigate the high gamma band’s role in SRP, especially given the results of Dastjerdi et al. (2011). Finally, in our study, we investigated the differences between SRP conditions and the resting state, but did not address the direct correlation between SRP and the resting state. Given the close relationship between the brain functions involved during resting state and SRP (Bai et al. 2016, Northoff 2016; Meyer and Lieberman 2018), future studies may directly investigate the correlation between semantic and somatic SRP and resting state. Despite our study limitations, our study suggests that SRP in the brain is primarily associated with alpha oscillation, and source localization suggested that different elements of SRP (internal attention, somatic, and semantic) are associated with distinct spatial patterns in theinsula, the frontal cortex, the parietal cortex, and the cingulate cortices.

Supplementary data

Supplementary data are available at NCONSC online.

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Conflict of interest statement

None declared.

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