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RESEARCH PAPER



## Culture shapes spontaneous brain dynamics – Shared versus idiosyncratic neural features among Chinese versus Canadian subjects

Jiawei Xu<sup>a\*</sup>, Soren Wainio-Theberge<sup>b\*</sup>, Annemarie Wolff<sup>b</sup>, Pengmin Qin<sup>c</sup>, Yihui Zhang<sup>c</sup>, Xuan She<sup>c</sup>, Yingying Wang<sup>d</sup>, Angelika Wolman<sup>b</sup>, David Smith<sup>b</sup>, Julia Ignaszewski<sup>b</sup>, Joelle Choueiry<sup>e,f,g</sup>, Verner Knott<sup>e,f,g</sup>, Andrea Scalabrini<sup>h</sup> and Georg Northoff<sup>b,i,j\*</sup>

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### ABSTRACT

Environmental factors, such as culture, are known to shape individual variation in brain activity including spontaneous activity, but less is known about their population-level effects. Eastern and Western cultures differ strongly in their cultural norms about relationships between individuals. For example, the collectivism, interdependence and tightness of Eastern cultures relative to the individualism, independence and looseness of Western cultures, promote interpersonal connectedness and coordination. Do such cultural contexts therefore influence the group-level variability of their cultural members' spontaneous brain activity? Using novel methods adapted from studies of inter-subject neural synchrony, we compare the group-level variability of resting state EEG dynamics in Chinese and Canadian samples. We observe that Chinese subjects show significantly higher inter-subject correlation and lower inter-subject distance in their EEG power spectra than Canadian subjects, as well as lower variability in theta power and alpha peak frequency. We demonstrate, for the first time, different relationships among subjects' resting state brain dynamics in Chinese and Canadian samples. These results point to more idiosyncratic neural dynamics among Canadian participants, compared with more shared neural features in Chinese participants.

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Culture; EEG; resting state activity; inter-subject variability;; spectral dynamics

## Introduction


The brain's spontaneous activity has gained increasing attention in neuroscience. Rather than being considered merely a control state for measuring stimulus- or task-induced activity, it exhibits its own intrinsic spatial and temporal features (Fox et al., 2005; Northoff, 2012, 2013a, 2013b, 2018; Northoff et al., 2020; Raichle, 2015). Spatial features include functional connectivity between different brain areas (Ding et al., 2011; Mantini et al., 2007; Menon, 2011; Zhang et al., 2020) while temporal features include the structure of neural oscillations (Buzsáki, 2006). Spontaneous activity is characterized by oscillations in different frequency bands ranging from delta (1-4 Hz), theta (4-8 Hz), alpha (8-12 Hz), beta (12-30 Hz) to gamma (30-80 Hz) (Buzsáki, 2006; Buzsáki et al., 2013).

These temporal dynamics, as measured in resting state recordings, modulate a variety of different cognitive functions like self (Bai et al., 2016; Huang et al., 2016; Kolvoort et al., 2020; Sugimura et al., 2021; Wolff et al., 2019), consciousness (Benwell et al., 2017, 2021; Northoff & Zilio, 2022; Zilio et al., 2021), working memory (Maguire & Schneider, 2019; Van Dam et al., 2015), deliberate cognitive processes (Pei et al., 2023), processing speed (Ouyang et al., 2020), and social cognition (Spreng & Andrews-Hanna, 2015). However, the ways in which the intrinsic dynamics of the brain's spontaneous activity are shaped by the respective environment remain not fully clear.

While much attention has been paid to genetic factors underlying spontaneous brain activity (Cui et al.,

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2016; Foo et al., 2020; Richiardi et al., 2015; Sarkar et al., 2016; Wang et al., 2015), it is clear that environmental factors also shape spontaneous neural dynamics (also referred to as “resting-state dynamics”): recent estimates suggest that up to 33% of variability in functional connectivity is attributable to shared environmental inputs (Teeuw et al., 2019). Several environmental factors have been identified which may play such a role: these include childhood trauma (Chernyak et al., 2013; Duncan et al., 2015; Lu et al., 2017), socioeconomic status (Chan et al., 2018; Maguire & Schneider, 2019; Ramphal et al., 2020; Tooley et al., 2020), environmental enrichment (Sampedro-Piquero et al., 2018), and culture (Alahmadi et al., 2016; Knyazev et al., 2012, 2018; Kraus et al., 2021; Luo et al., 2020; Wang et al., 2013; Zhang et al., 2022).

The above findings demonstrate that environmental factors can shape individual differences in the spatio-temporal dynamics of spontaneous activity, providing an important source of variation in neural phenotypes. Additionally, environmental factors can constrain spontaneous activity also in other ways. Beyond increasing or decreasing the value of individual neural traits (e.g., power and functional connectivity), environmental factors can also constrain the population-level variability of neural phenotypes. An environment rich in different resources and ecological niches may encourage greater phenotypic diversity (Tilman, 2000). Such population-level variability remains to be investigated on the neural level with respect to inter-subject or inter-member relationships among different cultures. In the present work, we hypothesize that the sociocultural context may play such a role, with cultural norms promoting variability or encouraging more common neural phenotypes.

A variety of cultural differences have been found in previous cross-cultural studies. For example, compared to Western cultures (e.g., North America and Europe), Eastern cultures (e.g., East Asia) are more collectivistic (and less individualistic) – people shaped by Eastern cultures value their connectedness with other group members, aim to maintain group harmony, and are strongly motivated by collective goals (Hook et al., 2009; Triandis, 1988). Accordingly, people raised in Eastern cultures tend to perceive and process their selves in a more interdependent way than people raised in Western cultures, that is, in relation to others rather than in distinction from others (Han & Ma, 2014; Henrich et al., 2010; Kitayama et al., 2020; Kraus et al., 2021; Markus & Kitayama, 1991). More specifically, compared to people from Western cultures, East Asians are more inclined to adjust themselves to their environment and to conform to others’ opinions to maintain interpersonal harmony, rather than emphasizing their personal

uniqueness and stable individual traits (Chang et al., 2011; Heine, 2001; Ishii et al., 2014; Kim & Markus, 1999; Kitayama et al., 2009; Torelli, 2006); they thus show more of “a same self” rather than “a different self” (Triandis, 1993). In terms of adaptive strategies, there is evidence that East Asian people (e.g., people in mainland China) show more social learning (i.e., imitation of others) than Westerners (Chang et al., 2011; Mesoudi et al., 2015). In addition, East Asian countries generally score high on tightness, meaning they have strong norms and low tolerance for deviant behavior to promote coordination among members, a phenomenon referred to as being a tight (as opposed to loose) society (Gelfand et al., 2011).

The above-mentioned cultural differences may constrain or promote variability among members of cultural groups. Greater emphasis on social connectedness and collective goals, greater preference for harmony with others, higher frequency of social learning, stronger norms and lower tolerance for deviant behavior, etc., in Eastern cultures than in Western cultures, together lead us to reasonably predict that lower inter-individual variability of spontaneous neural activity would be observed in participants from Eastern cultures rather than those from Western cultures. This assumption of cultural influences on spontaneous neural activity is supported by initial observations on the influence of these cultural differences (especially collectivism vs. individualism, and interdependence vs. independence) on individual-level traits (Knyazev et al., 2012, 2018; Kraus et al., 2021; Luo et al., 2020; Wang et al., 2013).

Moreover, there is a growing body of evidence suggests that inter-subject neural synchrony during exposure to natural stimuli or cognitive tasks is closely related to inter-subject similarity of personality (Liu et al., 2019; Matz et al., 2022), shared understanding of narratives and ideology (De Bruin et al., 2023; Nguyen et al., 2019), as well as predicts collective performance (Reinero et al., 2021), popularity of musical performance (Hou et al., 2020), marital satisfaction (Li et al., 2022), and friendship (Parkinson et al., 2018). In short, similar neural responses may be the neural basis or result of shared understanding of personality and the world, social coordination, and close social relationships. Although the similarity between individuals in spontaneous brain activity (relative to stimulus- or task-induced activity) remains to be investigated, it has been proposed that in social interaction our default mode network (DMN) dynamically shapes and is shaped by others’ brains to achieve neural alignment, thus enabling shared understanding and social communication (Yeshurun et al., 2021). This also supports our hypothesis of lower inter-

individual variability (i.e., higher inter-individual similarity) in spontaneous activity in Eastern cultures which emphasize and promote social connectedness and coordination.

Methodologically, the influence of environmental factors on brain activity is traditionally operationalized on an individual level by, for instance, correlating neural traits (e.g., alpha power) in individual subjects with their individual values on a psychological variable (e.g., independent self-construal; see Kraus et al., 2021). Group-level investigation requires more methodological innovation to assess inter-subject variability. Inter-subject correlation (ISC), a method assessing the between-subject consistency, has been used in analyses of stimulus- or task-induced activity, for investigating common neural responses related to specific naturalistic stimulation or cognitive processes (Hasson et al., 2004; Nastase et al., 2019; Nguyen et al., 2019; Saha & Baumert, 2020; Seghier & Price, 2018). It has recently also been employed in resting state conditions, where it was used to explore the variability of resting state networks in magnetoencephalography (Wens et al., 2014). These studies suggest the potential utility of this method to compare different groups in the level of inter-subject correlation or variability. That makes it suitable for our main goal.

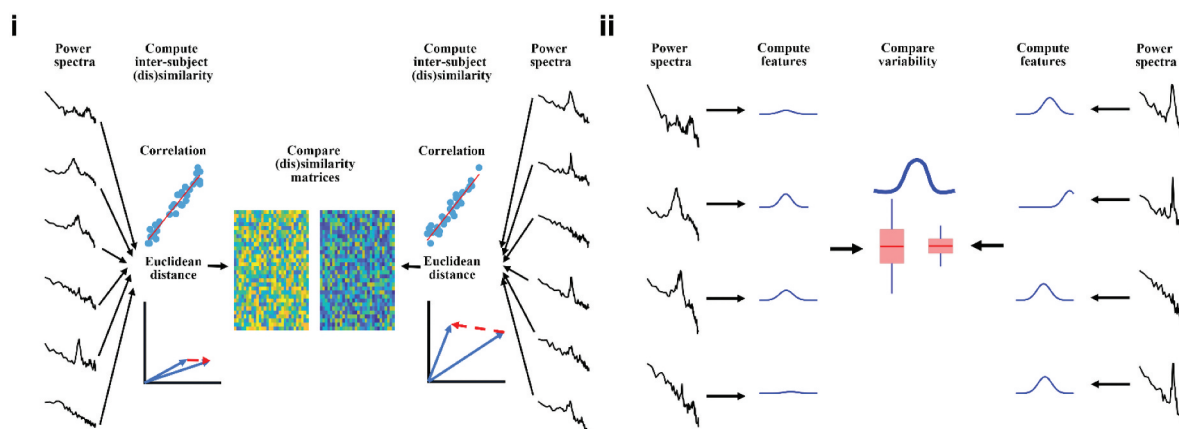
The main goal of our study was to examine group-level differences in the inter-individual variability of resting state dynamics between Eastern (China) and Western (Canada) samples. Our first specific aim was to compare the inter-individual variability of the resting state power spectrum between Chinese and Canadian samples. We hypothesized greater commonality, i.e., higher inter-subject correlation and lower inter-subject

variability, in the power spectrum among Chinese subjects, compared to Canadian subjects.

Our second specific aim is the investigation of alpha peak frequency as second marker of the resting state dynamics. Alpha peak frequency is well known to exhibit high inter-individual differences (Klimesch, 2012; Ouyang et al., 2020; Ramsay et al., 2021; Wolff et al., 2019). This makes it a likely candidate in which to observe group-level differences in variability. We hypothesized that Chinese subjects will show lower inter-subject variance in their alpha peak frequency than Canadian subjects.

To test our hypotheses, we employed a novel methodology, combining three distinct measures of inter-subject variability and similarity (see Figure 1, and Methods). Firstly, we employed inter-subject correlation (ISC) (Hasson et al., 2004; Nastase et al., 2019) to measure commonality between subjects in multivariate patterns such as neural power spectra. Secondly, we complemented the ISC by Euclidean distance, a metric commonly used in machine learning as a measure of similarity or dissimilarity (Dokmanic et al., 2015; Yu et al., 2020); we termed this measure inter-subject distance (ISD). Thirdly, we derived relevant metrics from the power spectra (including frequency band power and alpha peak frequency), and then compared these between groups based on their coefficient of variation (CV, generally defined as the sample standard deviation divided by the sample mean).

In brief, we find greater commonality in neural measures of resting state dynamics among subjects from China, when compared with subjects from Canada. More specifically, Canadian subjects showed more heterogeneity in features of their eyes-closed



**Figure 1.** Schematic of the methodological procedure of the study. The study procedure involves comparing inter-subject similarity of neural data, using two different procedures. In the first procedure, the raw data (power spectra) are used, and inter-subject correlation or distance is used to create a similarity/dissimilarity matrix; these matrices are then compared between groups. In the second procedure, various summary indices (frequency band power and alpha peak frequency) of the raw data are computed, and these are compared between groups with respect to their variability.

EEG power spectra, as well as higher variability in theta band power and alpha peak frequency, relative to Chinese subjects. These neural findings were replicated in independent datasets, and they also hold across various control analyses (see Results and Supplementary Materials).

## Methods

### Samples

We recruited four datasets from China and Canada to study cultural differences in population-level variability of eyes-closed resting state EEG temporal dynamics (Table 1). All data were collected from healthy participants.

Our main datasets include the Canada 1 (CA1) and the China 1 (CN1). CA1 was originally collected to investigate the relationship between individual resting state dynamics and self-consciousness (Wolff et al., 2019). Here it was used to study cultural differences in the inter-individual variability of resting state dynamics. For this purpose, three Asian or Asian-Canadian subjects were excluded from the original 34 subjects in CA1. CN1 was originally used as a baseline for the study of stimulus-induced activity.

The pairing of the other two datasets, the Canada 2 (CA2) and the China 2 (CN2) (Cai et al., 2020; Wolff et al., 2019), as well as their cross pairings with the main datasets (i.e., CA2 vs. CN1, and CA1 vs. CN2), were used as replications. The China 2 (CN2) is an open dataset from Gansu Provincial Key Laboratory of Wearable Computing, Lanzhou University, China (Cai et al., 2020).

### Ethics approval

Written informed consent was obtained from all participants before the studies. All procedures for obtaining the datasets were approved by the ethics committees, including the ethics committees of the University of

Ottawa Institute of Mental Health Research, the School of Psychology at the South China Normal University, and the Lanzhou University Second Hospital.

### Electroencephalography acquisition and preprocessing

All recordings were carried out in subjects seated comfortably with their eyes closed, for varying durations. The equipment (company), online reference, sampling rate, electrode impedance and resting state recording duration of each EEG dataset are shown in Table 1.

To compare inter-subject heterogeneity of resting state EEG features, we standardized the preprocessing pipelines for each dataset. All EEG data were preprocessed in EEGLAB (Delorme & Makeig, 2004), and down-sampled to 250 Hz. EEG data for CA1 and CN1 were cut to 2 minutes in length, and data for CA2 and CN2 were cut to 3 minutes. For each pair of datasets, electrodes which were not common to both caps were removed: this resulted in 57 electrodes for CA1 and CN1, and 31 electrodes for CA2 and CN2. Next, recordings were band-pass filtered from 1 to 30 Hz using an FIR filter, in order to avoid line-noise artifacts. High-amplitude artifacts were then cleaned and reconstructed using Artefact Subspace Reconstruction (Kothe & Jung, 2016). Data were then re-referenced to a common average reference. Finally, ICA decomposition was performed using the Infomax algorithm in EEGLAB, and artefactual components were automatically identified and removed using MARA (Winkler et al., 2011).

### Calculation of EEG power spectra and power-spectrum-derived features

To assess the inter-subject variability of EEG dynamics, we computed power spectra and various power-spectrum-derived features. Power spectra were computed separately for each channel using Welch's method

**Table 1.** The main and replication datasets with eyes-closed resting state EEG data.

Dataset	Subject	Number (Female)	Age (Mdn; M; SD)	Equipment (Company)	Online Reference; Sampling Rate; Electrode Impedance	Resting State Duration
CA1	Canadian	31 (17)	25; 30.58; 10.74	Neuroscan SynAmps amplifier with a 64-channel cap (Compumedics Neuroscan, Charlotte, NC, USA)	Right mastoid; 1000Hz; Under 5 k $\Omega$	5 minutes
CN1	Chinese	26 (8)	24; 27.15; 8.25	BrainAmp amplifier with a 64-channel cap (Brain Products GmbH, Munich, Germany)	FCz; 1000Hz; Under 5 k $\Omega$	2 minutes
CA2	Canadian	25 (14)	46; 45.88; 15.79	Brain Vision EasyCap with 32 Ag/AgCl electrodes (Brain Products GmbH, Munich, Germany)	Nose; 500 Hz; Under 5 k $\Omega$	3 minutes
CN2	Chinese	29 (9)	29; 31.45; 9.15	Net Amps Amplifier with a 128-channel HydroCel Geodesic Sensor Net (Electrical Geodesics Inc., Oregon Eugene, USA)	Cz; 250Hz; Under 50 k $\Omega$	5 minutes



(Welch, 1967), as implemented in MATLAB R2016a. Power spectra were subsequently log-transformed (Smulders et al., 2018), and then averaged over all channels.

Each subject's alpha peak frequency and individual alpha width were calculated using Corcoran et al.'s methods (Corcoran et al., 2018). Power in each frequency band was then calculated from the Welch power spectra using the individualized alpha band definitions. Delta was defined as 1–4 Hz. The theta band was defined as 4 Hz to the lower bound of the subject's alpha peak width, while the beta band was defined as the upper bound of the subject's alpha peak width to 30 Hz. Power values were then log-transformed and averaged over all channels.

### Calculation of eLORETA source time series

To determine if there were differences between regions with respect to the inter-subject variability of EEG spectra and spectral features, we computed source-level time series using eLORETA (Pascual-Marqui et al., 2011), as implemented in Fieldtrip (Oostenveld et al., 2011). The standard boundary-element method headmodel included with Fieldtrip was used as a headmodel, and the Conte69 template (Van Essen et al., 2012) was used as a template sourcemodel. Regions of interest were defined using Brodmann areas, taken from the surface-based atlas (Van Essen et al., 2012).

Source-level time series ("virtual channels") were first estimated at each vertex by multiplying the channel-level data by the eLORETA spatial filter. To get a single time series at each vertex, the three-time series estimated (for the x, y, and z dipoles) were projected along the axis that explained the greatest variance using a singular value decomposition. Time series were subsequently averaged within each Brodmann area. We then computed power spectra and spectral features on each ROI time series using the same methods as described above.

### Assessment of inter-subject variability of EEG dynamics

We assessed the inter-subject variability of EEG signals with two primary approaches. The first approach compared inter-subject correlation (ISC) and inter-subject Euclidean distance (ISD) between each subject's power spectrum. We treated each subject's EEG power spectrum as a vector, and computed a) Pearson correlation coefficient and b) Euclidean distance between each subject's power spectrum and

each other subject's power spectrum. These calculations resulted in a symmetric  $N \times N$  inter-subject correlation matrix and an inter-subject Euclidean distance matrix. Significant differences between cultural groups were assessed using a permutation test (Nastase et al., 2019). First, an observed test statistic for the difference between groups was calculated; this was the difference in the median inter-subject distance. To compute statistical significance, the assignment of subjects into cultural groups was randomly shuffled 10,000 times, and the observed test statistics were compared with the permutation distribution. The  $p$  value for the difference between the groups is the percentile of the observed test statistic within the permutation distribution. It is worth mentioning that the correlation coefficients were transformed to z-scores before the comparisons between groups, using Fisher's transformation (Nastase et al., 2019).

Next, we compared inter-subject variability of the EEG power spectrum metrics. For the alpha peak frequency, we used the coefficient of variation (CV) to compare relative variability. Statistical significance was assessed using the asymptotic test developed by Feltz and Miller (1996), as implemented in the CV-equality package in R (Marwick & Krishnamoorthy, 2019). The CV was chosen as it reflects a measure's relative variability, irrespective of multiplicative differences in the means of the samples; it is defined as the standard deviation divided by the mean. This measure is commonly used in organizational psychology for comparing different groups (Carroll & Harrison, 1998); it has also recently seen use in EEG as a measure of relative variability (Wolff et al., 2019).

However, testing the CV was an invalid approach for log-transformed frequency-band power, as the log-transformed power included negative values (Salkind, 2010). Therefore, we compared the CVs of the original (i.e., exponentiated) power values using a non-parametric permutation procedure. CV in this case was estimated using the formula from Koopmans et al. (1964), which is accurate for log-normal distributions:

$$\hat{cv} = \sqrt{e^{s_m^2} - 1} \quad (1)$$

We also tested for differences between cultures in the means of the power spectral features using Student's  $t$  tests.

For topographical analyses, the steps above were repeated at each individual electrode: multiple comparisons were corrected for using false discovery rate correction (Benjamini & Yekutieli, 2001).

### Assessment of representational similarity between EEG power spectra and responses to the Self-Consciousness Scale items

Our main datasets (CA1 and CN1) also had psychological data from the Self-Consciousness Scale (SCS) available (Fenigstein et al., 1975; Scheier & Carver, 1985), and thus they were also employed to investigate whether inter-subject variability in resting state dynamics and inter-subject variability in self-reported personality are correlated. As mentioned above, with respect to stimulus- or task-induced activity, there is evidence that neural similarity between individuals is associated with their personality similarity. Here the SCS was used as an example of self-reported personality. In previous studies, the SCS has been related to resting state dynamics on an individual level (Huang et al., 2016; Kolvoort et al., 2020; Wolff et al., 2019).

Subjects' original responses to the SCS items were normalized by being expressed on a scale from 0 to 1, and each subject's 22-item responses were treated as a vector to compute the Euclidean distance between subjects' responses (see Supplementary Materials for details).

To investigate the relationship between the variability of resting state EEG dynamics and the variability of responses to the SCS items, we employed inter-subject representational similarity analysis (Nguyen et al., 2019). In this procedure, similarity matrices are constructed for each of the two modalities (EEG power spectra and SCS item responses). Because the strongest group differences in variability were observed using Pearson correlation in the EEG power spectra and Euclidean distance for the SCS item responses (see Supplementary Materials for the results of the inter-subject distance analyses of responses to the SCS), these metrics were used to construct the similarity (or dissimilarity) matrices. Note that here Euclidean distance was log-transformed in order to ensure that the correlations with the power spectra similarity matrix were not outlier-driven. Representational similarity was then assessed by correlating the vector of the below-diagonal elements of these similarity matrices. Significance was computed by randomly shuffling the participants of one modality 10,000 times and recomputing the correlation: the  $p$ -value was computed relative to this permutation distribution. This procedure was done once for the concatenated whole dataset (i.e., CA1 and CN1 together), and once for each of the datasets independently.

### Control analyses for demographics

Since our samples were not matched with respect to demographics, we attempted to control for the influence of demographic variables on our analyses. Demographic factors could affect inter-subject variability both due to their mean values (e.g., if women are more collectivistic and interdependent than men) and due to their homogeneity (e.g., samples which are highly similar in age may show lower inter-subject variability than samples with a large age range). In order to control for these two factors in our tests of relative variability (CV), we used a statistical framework based on the Levene's test for equal variances of which the Brown-Forsythe test (Brown & Forsythe, 1974) is a variant. The  $p$ -value for the Brown-Forsythe test comes from an ANOVA on the absolute deviations of each subject's value from the median value:

$$z_{ij} = |y_{ij} - \tilde{y}_j| \quad (2)$$

Where  $z_{ij}$  is the transformed response variable,  $y_{ij}$  is the original data point  $i$  from group  $j$ , and  $\tilde{y}_j$  is the median of group  $j$ . Schultz (1985) proposed a modified version of this test for comparing relative variability (CV); and in that case, the transformed response variable is:

$$z_{ij} = \frac{|y_{ij} - \tilde{y}_j|}{\tilde{y}_j} \quad (3)$$

Since ANOVA is a special case of the general linear model (GLM), we controlled for demographic confounders by entering these as covariates into a general linear model on the transformed responses proposed by Schultz (1985). We entered both age and sex as covariates into these GLMs. Further, we transformed age according to Equation 3, and transformed sex by treating sex as a binary variable (0 or 1) and computing the absolute deviation from the mean within each sample. This gave us estimates of age and sex homogeneity, which we also entered as covariates. We computed  $p$ -values for each parameter in the model using a permutation test with 10,000 permutations, as implemented in the `permuco` package in R (Frossard & Renaud, 2019).

In order to control for demographic and noise-related factors in our ISC and ISD results, we used a mixed-effects modeling procedure which is recommended for testing ISC with covariates (Chen et al., 2017; Nastase et al., 2019). The details of this procedure are described in G. Chen and colleagues' study (Chen et al., 2017). Briefly, subject-related variance is accounted for in this model by including subjects as crossed random effects. In order to ensure normality, Euclidean distance values

were square-root-transformed for normality prior to this procedure. Pearson's  $r$  values were transformed using Fisher's  $z$ -transformation as described previously. This procedure allowed us to enter sex and age as covariates. We also considered age homogeneity by creating two variables for age: one reflecting the sum of ages between a participant pair, and the other reflecting the absolute value of their difference. We did not conduct the same procedure for sex, as this is already accounted for when considering the Male-Female subject-pair category.

### **Control analyses for signal-to-noise ratio**

Differences in inter-subject variability in EEG could conceivably be due to differences in signal-to-noise ratio between the groups, due either to different EEG amplifiers, different recording conditions, or differences in brain or skull conductivity. To investigate this possibility, we assessed signal-to-noise ratio in our EEG data in several ways.

The first method was to consider within-subject variability as "noise". While it is known that spontaneous fluctuations in neural activity are not entirely noise but contain functionally meaningful information (Uddin, 2020), we considered them here as "noise" because even the functionally relevant components of intra-individual variation are confounders for our hypothesis. If Chinese subjects show increased inter-subject similarity merely because they show greater intra-subject stability, this complicates our interpretation of inter-subject similarity as being reflective of Eastern cultural norms about relationships between individuals. As such, we computed the power spectrum and each power spectral feature in 30-second sliding windows with no overlap. We then computed the signal-to-noise ratio as the intra-class correlation coefficient (ICC), treating each sliding-window estimate as a "rater" for each subject's EEG spectral feature (Bartko, 1966; Caceres et al., 2009; Fleiss & Shrout, 1978). We compared the ICCs between groups using a permutation test with 10,000 permutations.

The second method we used was to include various measures of artifact contamination as covariates in our group comparisons. We computed three metrics obtained from our preprocessing pipeline assessing artifact contamination: amount of data rejected by Artifact Subspace Reconstruction, percent variance retained after ICA component removal, and mean artifact probability of retained ICA components. The latter two are used in the HAPPE pipeline as metrics of preprocessing quality (Gabard-Durnam et al., 2018). These metrics were then used as covariates in our analyses as described

above. As an estimate of noise, we also entered intra-subject variability into the model, computed as the coefficient of variation of each parameter across sliding window estimates.

Finally, we attempted to control for amplifier differences by cross-comparing the EEG datasets: comparing CA1 with CN2, and CA2 with CN1. In each case, we preprocessed the data again in order to make the number of electrodes equivalent between the datasets. Then, we followed the same methods described above in order to compare the inter-subject variability in EEG power spectral features.

## **Results**

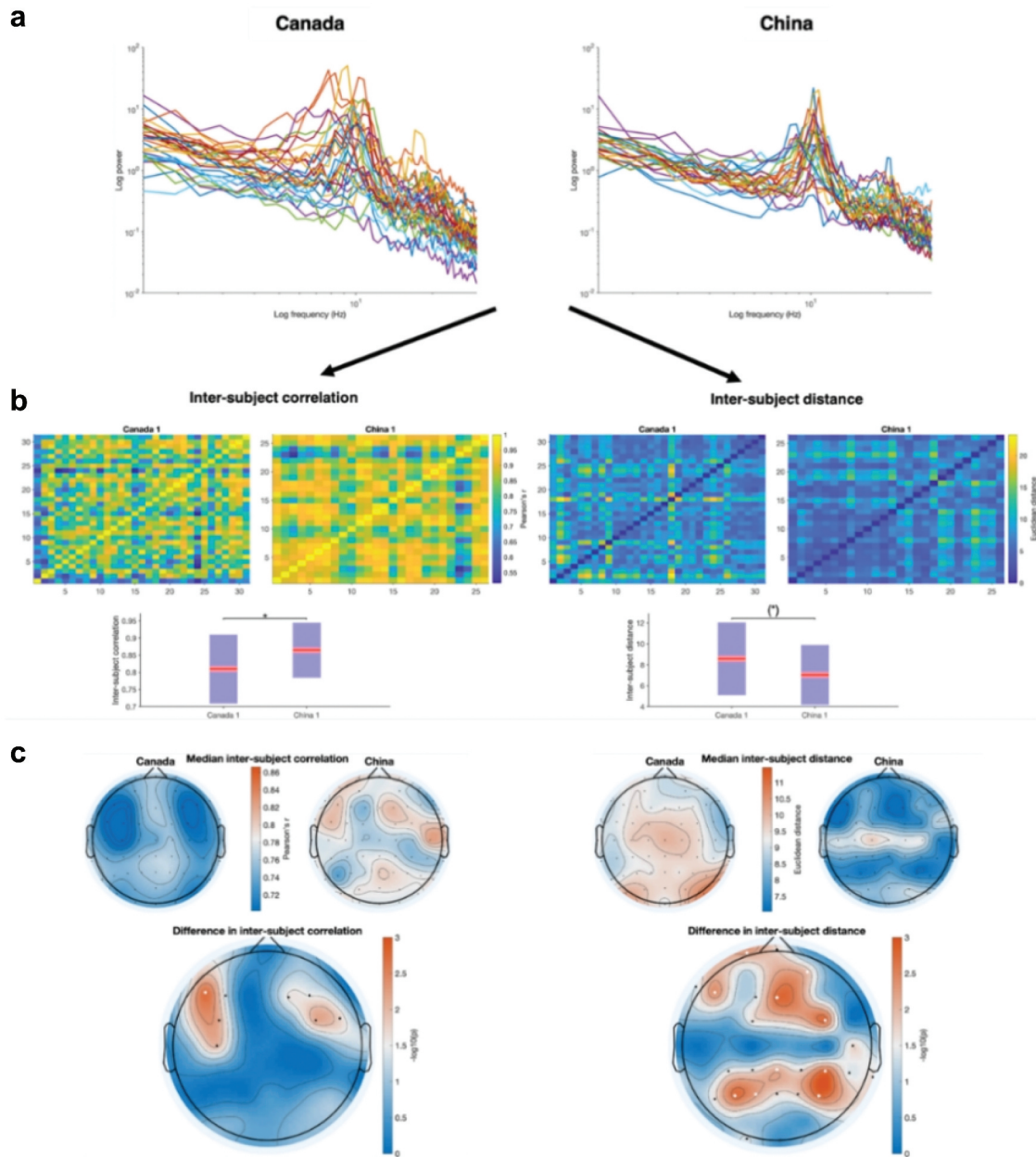
### **Chinese participants show less heterogeneity in resting state EEG spectral dynamics**

In the introduction, we predicted greater neural commonality between subjects would be observed in the Eastern rather than Western samples, according to their different cultural orientations. We tested to see whether this pattern of sharing versus idiosyncrasy could be observed in eyes-closed resting state EEG recordings.

First, we computed resting state EEG power spectra for each subject in the main Canadian and Chinese datasets (CA1 and CN1). We next compared the inter-subject variability of these power spectra using inter-subject correlation (ISC) and inter-subject distance (ISD) (Figure 2). A permutation test with 10,000 permutations showed a significant difference in ISC ( $z = -2.28$ ,  $p = 0.0202$ ) between the Canadian and Chinese datasets, with higher correlation between the Chinese subjects' power spectra than the Canadians. A permutation test also revealed a marginally significant difference in ISD ( $z = 1.81$ ,  $p = 0.0666$ ), with distances between subjects being larger in the Canadian sample than in the Chinese sample. We observed that these variability differences were mainly present in bilateral frontal regions for the ISC, and frontal and bilateral temporo-occipital regions for the ISD (Figure 2c). Together, these findings demonstrate that the spectral dynamics of resting state EEG are more consistent among Chinese participants than among Canadian subjects, where they are more heterogeneous.

Next, we computed features of the EEG spectral dynamics including alpha peak frequency and power in different frequency bands, and compared the relative variabilities of these features between the main Chinese and Canadian datasets. First, we compared the power in different frequency bands in terms of the means and variabilities of these power values between the two datasets (Figure 3a and b). While there were no

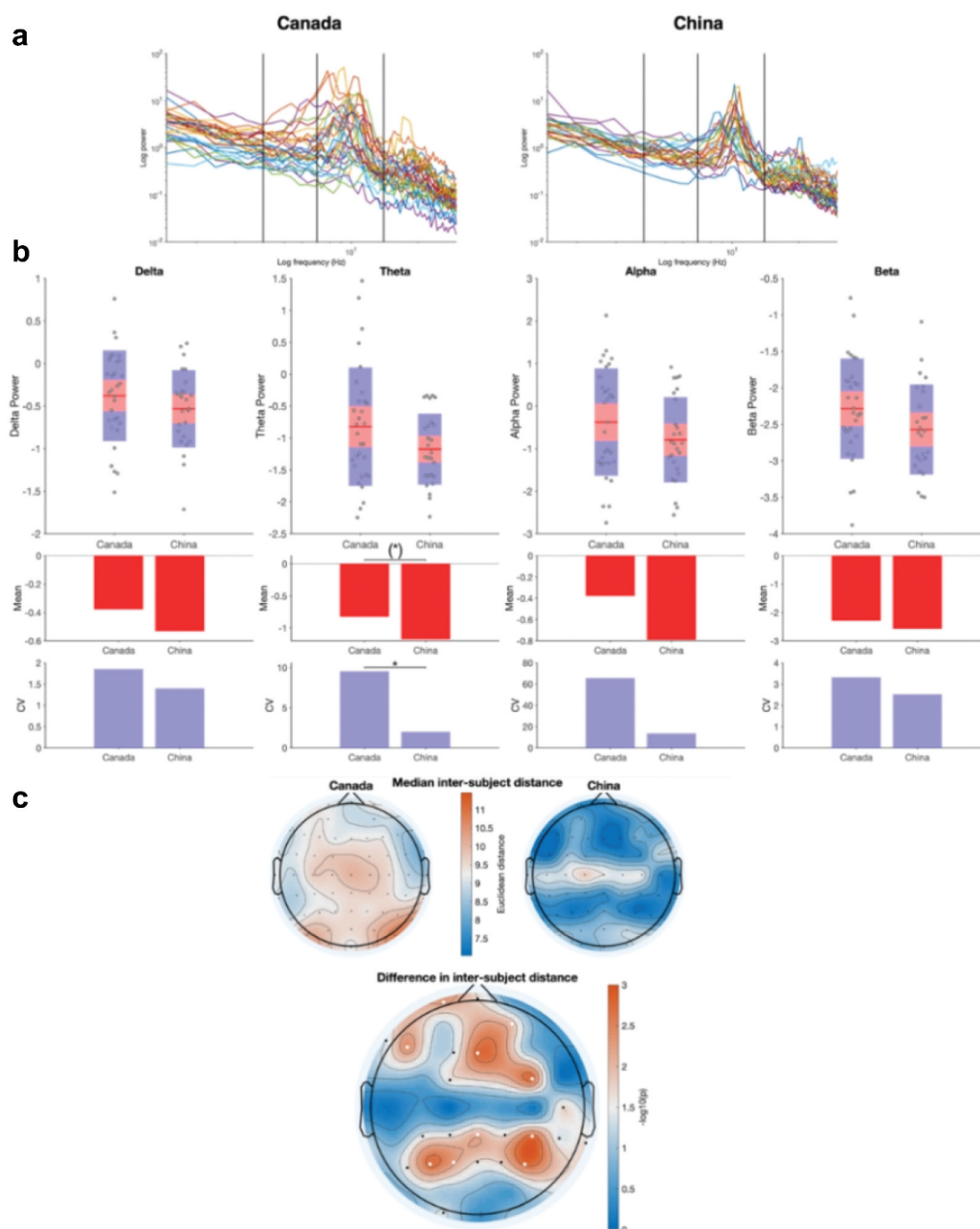




**Figure 2.** Comparison of inter-subject variability in EEG power spectra between the main Canadian and Chinese datasets (CA1 and CN1). A) log power spectra for each group, estimated with Welch's method; each line is one subject. B) Top: Inter-subject correlation (left) and Euclidean distance (right) matrices for each dataset. Bottom: Distribution of inter-subject correlation coefficients and Euclidean distances. Red line indicates mean, salmon-colored box indicates SEM, and purple box indicates SD. Asterisks indicate  $p$  values: (\*) =  $p < 0.1$ , \* =  $p < 0.05$ . C) topographical distribution of variability and group differences in variability of the power spectra, using inter-subject correlation (left) and inter-subject distance (right). Top: topographical distributions of the median inter-subject correlation (left) and Euclidean distances (right). Bottom: topographical distribution of  $p$ -values from a permutation test comparing the median inter-subject correlation (left) and Euclidean distance (right) between the Canadian and Chinese datasets.  $-\log_{10}$  of the  $p$ -value is plotted; all  $p$ -values are FDR corrected. White dots indicate significant electrodes at  $p < 0.05$  following FDR correction.

significant differences between the main datasets in mean power, we observed lower coefficient of variation (CV) in each frequency band in the Chinese dataset. This was significant in the theta band ( $z = -1.87$ ,  $p = 0.0462$ ), but not in any other band (delta:  $z = -0.819$ ,  $p = 0.439$ ; alpha:  $z = -1.48$ ,  $p = 0.141$ ; beta:  $z = 0.586$ ,  $p = 0.577$ ),

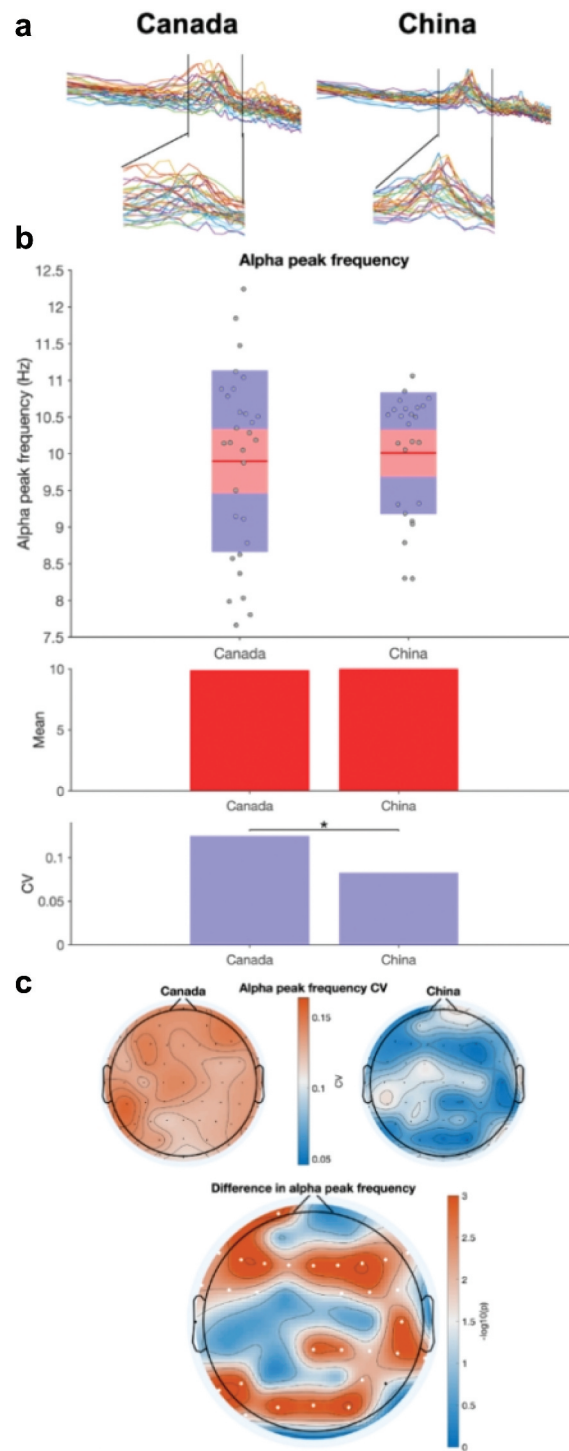
using the permutation procedure described in the methods for log-normal data. Considering the topography of the theta power results, a similar spatial pattern to the ISC/ISD results was observed, with variability differences being most pronounced in temporo-occipital regions (Figure 3c).



**Figure 3.** Inter-subject variability of power in different frequency bands. A) power spectral density (PSD) for the main Canadian and Chinese datasets, with schematic black bars to indicate the bounds of the frequency bands. B) Top: Box plots of the distributions of log-transformed delta, theta, alpha, and beta power. Red lines indicate mean, salmon box indicates SEM, and purple box indicates SD. Bottom: Bar plots of the means, and coefficients of variation of the data (CV calculated on the exponentiated data, as described in the methods). Asterisks indicate significant differences between groups: (\*) =  $p < 0.1$ , \* =  $p < 0.05$ , \*\* =  $p < 0.01$ . C) topographical distribution of variability and group differences in variability of theta power. Top: topographical distributions of the CV of theta power. Bottom: topographical distribution of  $p$ -values from the test comparing the CVs between the Canadian and Chinese datasets.  $-\log_{10}$  of the  $p$ -value is plotted; all  $p$ -values are FDR corrected. White dots indicate significant electrodes at  $p < 0.05$  following FDR correction.

Following observations of the power spectra, we then compared the samples based on variability of the alpha peak frequency (Figure 4a and b). It was found that the Chinese dataset displayed significantly lower CV in alpha peak frequency ( $\chi^2(1) = 4.06$ ,  $p = 0.0438$ ). No difference in the mean alpha peak frequency was found between samples ( $t(53) = -0.380$ ,  $p$

$= 0.705$ ). The differences in alpha peak frequency variability followed a similar pattern to the original power spectrum results, with differences being most pronounced in temporo-occipital and frontal regions, and with a tendency toward right-hemisphere lateralization (Figure 4c). The above findings suggest that theta power and alpha peak frequency are more



**Figure 4.** Comparison of variability in alpha peak frequency. A) power spectra, as in Figures 2 and 3, with alpha band highlighted. B) Top: Box plots of alpha peak frequency values for each dataset. Red line indicates mean, salmon-colored box indicates SEM, and purple box indicates SD; individual data points are also plotted in grey. Bottom: Bar plots of means and coefficients of variation of each dataset. Asterisks indicate significant differences between groups: (\*) =  $p < 0.1$ , \* =  $p < 0.05$ , \*\* =  $p < 0.01$ , \*\*\* =  $p < 0.001$ . C) topographical distribution of variability and group differences in variability of alpha peak frequency. Top: topographical distributions of the CV of alpha peak frequency. Bottom: topographical distribution of  $p$ -values from the test comparing the CVs between the Canadian and Chinese datasets.  $-\log_{10}$  of the  $p$ -value is plotted; all  $p$ -values are FDR corrected. White dots indicate significant electrodes at  $p < 0.05$  following FDR correction.

similar among subjects in the Chinese sample than in the Canadian sample.

We finally assessed whether the differences in variability observed in our EEG data were localized to particular regions, for example default-mode network (DMN) regions known to be involved in self-related processing (Murray et al., 2015; Northoff, 2016; Qin et al., 2020). To this end, we conducted the same analyses on several regions of interest, whose activity was calculated using exact Low-Resolution Electromagnetic Tomography (eLORETA; Pascual-Marqui et al., 2011). These results are described in the Supplementary Materials (Supplementary Fig. S4). In brief, no particular region or set of regions appears to be consistently modulated by culture; group differences in variability found using different measures appear to be prominent in multiple regions. However, group differences in both power spectrum inter-subject distance and alpha peak frequency variability showed a slight tendency toward right hemisphere lateralization. Overall, these findings suggests that the increased inter-subject consistency we observed in the Chinese subjects is not localized to specific regions. This, however, is a tentative inference given the low spatial resolution of source-localized EEG.

Taken together, the results show that Chinese participants have significantly more similar resting-state EEG spectral dynamics. This was manifest in the overall power spectrum, as well as in specific features such as alpha peak frequency and theta band power. These differences in homogeneity were spatially distributed, and occurred without comparable differences in mean power or peak frequency, suggesting an overall more shared neural features in Chinese participants.

### **Replication of results in independent datasets**

To increase the confidence in our results, we attempted to replicate our findings in two independent EEG datasets (see Methods and Supplementary Materials for more details). Preprocessing and analysis followed the same procedures as described above.

In general, the findings presented above were replicated in the additional datasets: the Chinese replication dataset displayed lower ISDs in their power spectra, as well as lower variability in theta power and alpha peak frequency, than the Canadian replication dataset (see Supplementary Fig. S1-3). Similar results were also observed in cross-comparisons, i.e., when comparing the main Canadian and replication Chinese datasets and vice versa (see Supplementary Fig. S6–10).

Additionally, except for the marginally significant difference in ISC of the power spectra between the two Chinese datasets ( $z = 1.79$ ,  $p = 0.0724$ ), no other significant differences were found in within-culture comparisons (see Supplementary Table S15). These results suggest that cultural shaping of variability in spontaneous neural activity is a robust phenomenon, not limited to our main samples.

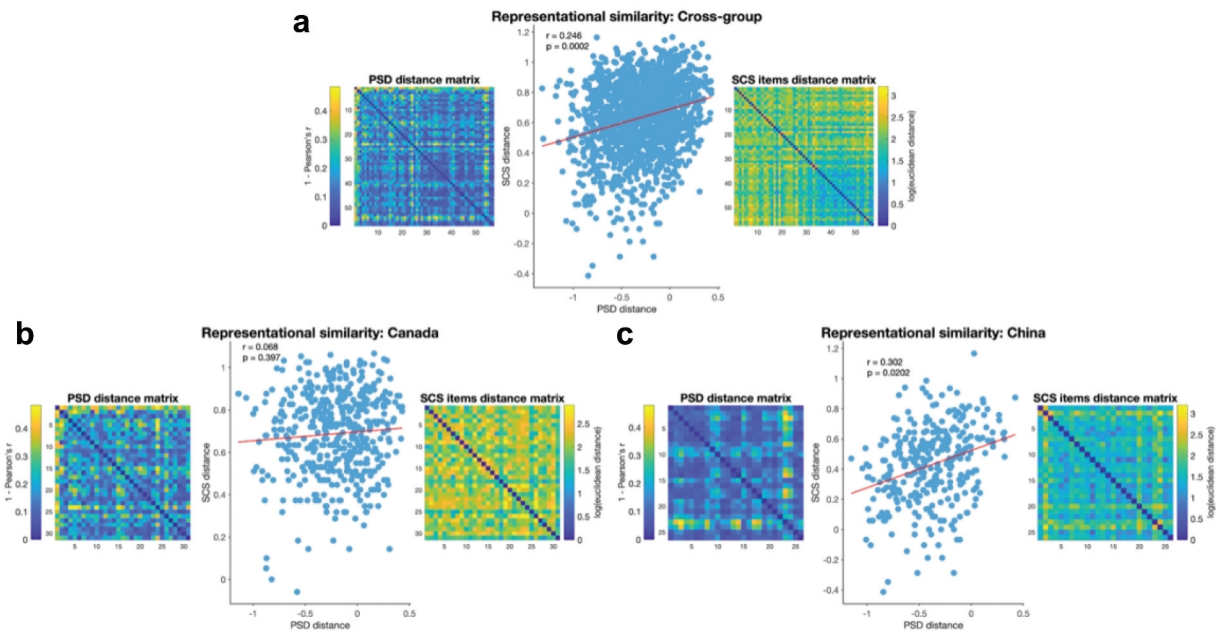
### **Representational similarity between EEG power spectra and SCS item response profiles**

Previous studies have found that neural similarity between individuals correlates with their personality similarity, as mentioned in the introduction. As our main datasets also had data from the Self-Consciousness Scale (SCS), we investigated the relationship between inter-subject variability of resting-state EEG dynamics and inter-subject variability of responses to the SCS items, using the inter-subject representational similarity analysis (Nguyen et al., 2019). The similarity of responses to the SCS items is used here as an example of personality similarity.

In brief, this procedure involves creating inter-subject similarity matrices for both the EEG power spectra and the SCS item response profiles and correlating the below-diagonal elements of these matrices: a significant correlation indicates that subjects which are similar in their EEG power spectra are also similar in their SCS responses, suggesting a link between the EEG metrics and personality. Significance of the representational similarity is assessed with a permutation test.

We observed significant representational similarity between the EEG power spectra and the SCS responses across both datasets (Figure 5a:  $r = -0.246$ ,  $p = 0.0002$ ): note that the sign of the correlation is negative because the Pearson correlation measures similarity while the Euclidean distance measures dissimilarity. However, the result may partially be influenced by the group differences: as such, we carried out the same representational similarity analyses within each of the cultural groups. Within the Canadian dataset alone, we did not observe significant representational similarity (Figure 5b:  $r = -0.0683$ ,  $p = 0.397$ ); however, we did observe significant representational similarity within the Chinese dataset alone (Figure 5c:  $r = -0.302$ ,  $p = 0.0202$ ). When combining the  $p$ -values from the independent tests using Fisher's method (Fisher, 1992), the overall effect was significant across both groups ( $p = 0.0468$ ). These results indicate that the closer the resting state EEG power spectra between individuals, the closer their responses to the Self-Consciousness Scale items, especially in the Chinese sample.





**Figure 5.** Inter-subject representational similarity analysis of EEG power spectra and self-Consciousness Scale item responses. A) shows the overall representational similarity across both groups; B) and C) show representational similarity within the main Canadian and Chinese datasets, respectively. Within each panel, the distance matrix (calculated as  $1 - \text{Pearson's } r$ ) of the EEG power spectrum is shown left, and the distance matrix for the SCS items (calculated as Euclidean distance) is shown right. A scatter plot of the representational similarity correlation is shown centrally: each dot is a pair of subjects. All  $p$  values shown are derived from a permutation test with 10,000 permutations.

In addition, a permutation ANOVA with 10,000 permutations on the distances between pairs of subjects' normalized 22-item responses showed a significant between-group difference ( $z = 2.97$ ,  $p < 0.001$ , Bonferroni-Holm corrected), with the inter-subject distances being larger in the Canadian dataset than the Chinese dataset, which was consistent with the pattern of EEG results (see supplementary Fig. S11A; see Supplementary Materials for details on the methods). Considering the results of the representational similarity analysis, group differences in inter-subject variability of responses to the Self-Consciousness Scale items might be related to group differences in inter-subject variability of resting state EEG dynamics.

### Control analyses: Demographics, and noise

**Demographics:** We controlled for the influences of demographic variables such as age and sex. General linear models were created including age, sex, and the sample-wise homogeneity of these variables as covariates (see Methods for detailed procedures). These results are reported in the supplementary materials (Supplementary Tables S1–7). In brief, while demographic factors had numerical effects on some of the results (such as the alpha peak frequency findings), no demographic factor emerged as a consistent

confounder, and findings generally remained significant in at least one of the main and replication datasets.

**Signal-to-noise ratio:** Differences in inter-subject variability in EEG could be due to differing signal-to-noise ratios in the EEG datasets. With this in mind, we performed three procedures to determine if signal-to-noise ratio influenced our results; results of these are reported in the supplementary materials. In the first procedure, we targeted intra-individual variability by computing each measure in 30-second sliding windows, and subsequently computed the intra-class correlation coefficient as a measure of intra-individual reliability (Bartko, 1966; Caceres et al., 2009; Fleiss & Shrout, 1978) of the data (with each 30-second window estimate serving as a “rater”). Reliability was generally higher in the Canadian datasets, indicating higher signal-to-noise ratio in these datasets: this is the opposite of what would be expected if technical artifacts in the Canadian datasets were driving the finding of increased inter-subject variability (Supplementary Fig. S5). In the second procedure, we included intra-subject variability (the operational definition of “noise” in the first procedure) and three metrics related to artifact contamination as covariates in our EEG analyses: our results were generally robust to the inclusion of these covariates (Supplementary Tables S8–14).



## Discussion

### *Cultural differences in population-level variability of brain dynamics*

While culture is known to shape individual variation in spontaneous brain activity (Knyazev et al., 2012, 2018; Kraus et al., 2021; Luo et al., 2020), it was not known prior to our study whether culture also shape population-level variability of spontaneous neural dynamics. We hypothesized that greater population-level commonality of brain's resting state dynamics would be observed in Eastern (Chinese) participants rather than Western (Canadian) participants. The reason is that the cultural orientations shown in East Asian societies (e.g., China), such as collectivism which emphasizes social connectedness, interpersonal harmony and collective goals (Hofstede, 1984; Hook et al., 2009; Triandis, 1988), interdependent self-construal and its preference for self-other harmony and conformity over deviance and uniqueness (Heine, 2001; Ishii et al., 2014; Kim & Markus, 1999; Kitayama et al., 2009, 2020; Markus & Kitayama, 1991; Torelli, 2006), preference for social learning over personal learning (Mesoudi et al., 2015), and tight society with strong norms and low tolerance for deviant behavior (Gelfand et al., 2011), may together encourage greater neural consistency among cultural members.

To test our hypothesis, a variety of datasets and novel methodological tools were employed. We observed that Chinese participants showed significantly higher inter-subject correlation and lower inter-subject distance in their EEG power spectra than Canadian participants, as well as lower variability in theta power and alpha peak frequency. Together, we demonstrate, for the first time, different relationships among subjects' resting state brain dynamics in Chinese and Canadian samples. These results point to more idiosyncratic neural dynamics in Canadian participants, compared with more shared neural features in Chinese participants.

Furthermore, the results may shed light on the interaction between brain and culture, namely, the "enculturation" of brain (Northoff, 2021). The results indicate that the influence of sociocultural environment goes beyond the individual attitudes, cognitions and neural traits, and is manifest in the group-level neural makeup of cultures.

### *Sociocultural context encoded in the spontaneous brain activity*

Notably, we saw higher neural commonality between subjects in the Chinese samples with respect to their resting state activity, without any cognitive task

demands. This suggests that the information of socio-cultural context (or inter-subjectivity) is already encoded in our brain's spontaneous activity independent of any specific, conscious cognitive tasks.

Recent studies have linked resting state brain dynamics to social cognition; the default mode network, a network active during resting state conditions and implicated in self-related processing (Huang et al., 2016; Northoff et al., 2006), has been of particular interest (Mars et al., 2012; Spreng & Andrews-Hanna, 2015; Spreng et al., 2020). Similarly, a recent study revealed that brain's spontaneous activity predicts animate (relative to inanimate) stimulus-induced activity (Scalabrini et al., 2019). These results suggest that the inter-subjectivity of our brain's spontaneous activity might reflect in part the inter-subjectivity constructed by social cognition within specific cultural contexts. However, it is also possible that lower neural variability simply reflects the neural correlate of lower psychological variability during the EEG recording, a plausible hypothesis given our findings regarding inter-subject representational similarity between the EEG power spectra and the Self-Consciousness Scale responses, and significantly lower inter-subject variability in self-report of self-consciousness in the Chinese dataset relative to the Canadian dataset (see Supplementary Materials for details). While our data are unable to contradict this possibility, we note that either interpretation cements our main conclusion, namely that population-level inter-subject variability varies considerably between Eastern and Western cultures.

In addition, many recent studies have showed correlations between neural similarity to stimuli or tasks and shared understanding of personality and the world, social coordination and intimate social relationship (De Bruin et al., 2023; Hou et al., 2020; Li et al., 2022; Liu et al., 2019; Matz et al., 2022; Nguyen et al., 2019; Parkinson et al., 2018; Reiner et al., 2021). For example, inter-subject similarity in personality predicts inter-subject synchronization of neural responses (Matz et al., 2022); similarity in the interpretation of narratives correlates with similarity in neural responses (Nguyen et al., 2019); and similarity in neural responses predicts friendship (Parkinson et al., 2018). We also observed a correlation between the inter-subject similarity of resting state EEG power spectra and the inter-subject similarity of the Self-Consciousness Scale responses, especially within the Chinese dataset. This supports Yeshurun et al.'s (2021) idea that our brains actively shape each other in social interactions to achieve neural alignment for mutual understanding and coordination.

The greater neural commonality shown in Chinese subjects may imply their more homogeneous understanding of personality and the world, which contributes

to their social harmony and social coordination. This is what Eastern cultures like Chinese culture value.

### **Methodological issues – Confounding factors and limitations**

We conducted various control analyses to rule out the potential impact of demographic factors, different EEG amplifiers, and noise in the EEG data. There are nevertheless some limitations remaining.

While we replicated our findings in an additional Chinese dataset and an additional Canadian dataset, we did not have data to extend our findings to other Eastern and Western cultures. Further work should attempt to replicate these findings in other cultures, like Japan and the UK. In addition, future work should better explore the relationship between neural similarity and cultural orientations, by using scales, such as the Self-Construal Scale (Singelis, 1994), the Individualism-Collectivism Scale (Singelis et al., 1995).

Our results preliminary show that inter-individual similarity in resting state dynamics correlates with inter-individual similarity in responses to the Self-Consciousness Scale items. This neural similarity may also correlate with similarity in other psychological scales. The relationship of resting-state neural similarity to a shared understanding of personality and the world and to social harmony and coordination remains to be further explored and confirmed.

Besides, the population of immigrants and the degree of cultural diversity may also contribute to the inter-individual variability, especially in Canada. Excluding the Asian subjects from the Canadian samples at least partially controlled this issue.

Finally, we did not consider differences in genetic homogeneity; if for instance Chinese participants are genetically more homogenous, it may explain their higher degree of homogeneity in resting state EEG dynamics.

### **Conclusion**

Eastern and Western cultures exhibit a variety of differences, for instance, collectivism vs. individualism, interdependence vs. independence, high frequency of social learning vs. personal learning, tightness vs. looseness, etc. These differences all center around the idea of collective vs. individual orientations, and all may constrain or promote variability among group members. Employing novel methods to test for cultural differences in population-level variability of neural phenotypes, we demonstrate that participants in Eastern cultures like China show greater neural commonality with each

other than Western participants from Canada, with respect to their resting state EEG dynamics. The results reveal that the sociocultural environment may shape not only the individual-level features of resting state brain dynamics, but also second-order statistics such as the population-level variability of such features. The results improve our understanding of cultural variation in brain dynamics by showing a complex relationship between individual-level psychological and cognitive features and the group-level sociocultural environment.

### **Disclosure statement**

No potential conflict of interest was reported by the author(s).

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### **Author contributions**

JX and GN conceived the idea. JX, SWT and GN wrote the manuscript together. A. Wolff, PQ, YZ, XS, JC, VK, A. Wolman, DS, JI, YW, and AS provided the main and replication EEG and Self-Consciousness Scale datasets (except China 2), and reviewed and edited the original draft. SWT provided advice on data analysis methods. SWT and JX analyzed the data and visualized the results with supervising and structuring by GN.

### **Data and code availability statements**

The datasets and codes used in this study are available from the corresponding authors via e-mail on request.

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