

Inter-brain Synchronization in the Alpha Band during Minimal Tactile Interaction

Chen Lam Loh^{1*}, Leonardo Zapata-Fonseca¹, Mark M. James¹, Guillaume Dumas^{2,3}, Tom Froese¹

1 Embodied Cognitive Science Unit, , Okinawa Institute of Science and Technology Graduate University, Onna-son, Okinawa, 904-0495, Japan

2 Department of Psychiatry and Addictology, University of Montréal, Montréal, Québec, Canada

3 Mila – Quebec AI Institute, University of Montréal, Montréal, Québec, Canada

* chen.loh@oist.jp

Abstract

Recently the minimal requirements for inter-brain coupling have attracted attention. Moreover, researchers have found that brains can couple not only when individuals are in the same space, but also during technologically mediated interactions. Here we investigate whether inter-brain synchronization occurs when both conditions of spatial isolation and minimal interaction are satisfied. In particular, we use a real-time interaction paradigm, the Perceptual Crossing Experiment where individuals must locate their partners in a minimal virtual space using tactile stimuli alone. We report novel findings that contribute to our understanding of inter-brain synchronization and the minimal conditions of social interaction in virtual spaces : 1)inter-brain synchronization is present in the Alpha band during online minimal interaction, 2)five behavioral patterns and three inter-brain patterns can be found in the PCE and 3)different behavioral patterns in the interaction environment recruited different inter-brain networks such that frontal-fronto-central synchrony occurs when people are further apart in space, interacting with a multitude of objects. These findings have important implications for the understanding of social interaction processes, such that inter-brain coupling can occur even without extensive communication channels.

Keywords :inter-brain synchrony, hyperscanning, perceptual crossing, haptic interaction, tactile modality

Word count :7101

Introduction

Hyperscanning, the simultaneous neuroimaging of more than one individual, has become a standard method to study intra- and inter-brain neurodynamics during real-time social interaction [19]. Although the term has been coined loosely, in this paper, we refer to inter-brain synchronization(IBS) as the phase synchronization of neural signals between individuals [26,60], and inter-brain coupling (IBC) as a general term for the association of neural signals between individuals, and also includes measures of amplitude correlation [76]. The coupling between brains has been thought to be

important for facilitating the transmission of information between brains, thus improving prediction of the other's action and leading to more complex joint behaviors [36]. Using electroencephalography (EEG) hyperscanning, IBS is found to occur in different frequency bands and brain regions, most commonly in the alpha and beta frequency bands [12, 26, 32, 45, 55, 77, 80, 86, 89, 90] and involve the prefrontal cortex (PFC) and right temporoparietal junction (rTPJ) [19, 28, 47, 85].

Tasks in hyperscanning experiments usually rely on visual or auditory stimuli, such as speech and communication tasks [44, 45, 77], musical performance tasks [70, 79], and cooperative joint action tasks [5, 86, 89]. In contrast, the tactile stimuli is more fundamental for establishing the presence of others [67] and humans are equipped with a high level of sensorimotor control in the hands that allows us to explore, manipulate and socially bond with touch [69]. Moreover, social touch alone is suggested to be associated with alpha band IBC in the somatosensory (frontal and central) regions and is important for the communication of empathy and social understanding [32]. However, touch-based interaction experiments in the hyperscanning literature typically involve face-to-face situations with the participants sharing similar environmental stimuli in the physical presence of each other [32, 72]. Therefore, in this paper, we explore IBC in a touch-based interaction experiment, the Perceptual Crossing Experiment (PCE) [7, 8, 23, 30, 38, 51, 91, 92].

In the current iteration of the PCE, participants interact with eyes closed in a shared one-dimensional (1D) virtual space through a minimalist haptic interface. The goal of the PCE is to cooperatively locate the other individual in the virtual space. Since the participants are not informed of the details of PCE before the experiment, in order to exchange information, they need to interact to create novel communication strategies which directly feed into the interaction. The idea that communication emerges through interaction is also mentioned by Hasson and colleagues [36]. However, the relationship between the minimality of the interaction and IBS is not yet clear. Recent findings of IBC between individuals near each other [54, 66] suggest that sharing the same environment could be one of the minimum requirements for IBC. Another study found that interaction in a virtual (but not physically isolated) environment can lead to similar IBC patterns compared to physical interaction [34], while IBC has been found to occur between interacting physically-separated individuals [89] but online video interactions lead to lower IBC [80]. Thus, PCE allows us to investigate whether interaction in a minimally shared environment can also lead to IBC. If IBC can occur in the PCE, this demonstrates that IBC can be established through minimal tactile interaction even if when interactants are physically isolated.

Using a public dataset that our group recently released [57], our aims are to investigate whether IBC in any frequency band can be observed during a minimal touch-based interaction using the PCE, and to investigate whether the behavioral variables also measured can be related to the IBC in an exploratory approach. We report robust IBC which occurs during the PCE and associations between the IBC and behavioral patterns in the alpha bands.

Materials and methods

Sample Description

Sixty-four participants (thirty-two dyads) took part in the ECSU-PCE study [57]. The sample included individuals from 24 nationalities who can understand and communicate in English. Participants' ages ranged from 18 to 68 years old (mean: 28.6 ± 8.9). Of the 64 participants, 39 identified as female. Most participants were blinded before the beginning of the experiment, so that they did not know with whom they would be

interacting. However, in three dyads, this was not possible: dyad number 32 included two classmates, and dyads number 15 and 25 were a couple. Out of the 32 dyads, dyad 31 had to be disregarded from the analysis due to technical difficulties during the EEG recordings. The experiment was approved by the OIST Human Subject Research Review Committee (HSR-2023-013). All participants gave their informed consent to participate in the study.

Task Procedure and Data Acquisition

The task was based on the PCE, a simple two-person interaction model that has been used in embodied cognitive science research to look into different aspects of social cognition, such as shared attention, mutual recognition, and the detection of social situations [7, 8, 23, 30, 38, 51, 91, 92]. In the PCE, dyads of participants were seated in 2 different rooms but with similar physical environments (Fig 1). Each player interacted through a haptic human-computer interface consisting of two hand-held components: one allowing a rotational movement and the other with a built-in button. Both components also had an integrated vibration motor that activated under certain conditions. With this interface, each player controlled the movements of an avatar along the perimeter of a circle, which served as a shared virtual space. In this space, each player could encounter three different objects (the avatar of the other player, a static immobile object and the shadow of the other player's avatar, which mimicked the movements of the avatar but at an offset with a fixed distance). Whenever a player overlapped with an object in the shared virtual environment, the vibration motor activated for that player in an all-or-nothing manner.

The objective of the task was to interact within the circular space and identify each other through the vibration patterns. Players were instructed to press a button whenever they felt that the crossed object was the avatar of the other player. Each player was only allowed to press once per trial, and during the instructions, they were encouraged to continue the interaction even after they pressed. The experiment consisted of 4 eye-closed resting sessions (REST) and 18 eye-closed task trials (TRIAL). The duration of each REST was 180 seconds, while each TRIAL was 60 seconds.

Dual-EEG data was simultaneously and continuously recorded throughout each experiment using 64-channel BrainAmp amplifiers (Brain Products(Germany)). Participants were fitted with a standard 64-channel Brain Product actiCAP snap set with sensors arranged in the international 10-20 system. The low- and high-cutoff frequencies were 0.016 Hz and 1000 Hz, respectively. The ground electrode was Fpz, and the common reference was FCz. The impedance was maintained below 25 k Ω . The sampling frequency was 1000 Hz, and an online Notch filter was applied at 60 Hz. The EEG data was recorded using the BrainVision Recorder (Version 1.20.0502) software provided by Brain Products.

Behavioral Data Analysis

Using the behavioral dataset, we derived a total of 9 behavioral variables. The first 5 variables were absolute differences between participants' avatar positions(P1avatar-P2avatar), between participants' own avatar and others' shadow positions (P1avatar-P2shadow and P2avatar-P1shadow), differences between participants' own avatar and own static positions of objects(P1avatar-P1static and P2avatar-P2static). The next 2 variables were the absolute differences between participants' avatar velocity and acceleration(P1vel-P2vel and P1acc-P2acc). These differences were computed and averaged for each 3s epochs during the task. The last 2 variables were the proportion of duration of mutual vibration, p_mutual_contact and dynamic time warping(DTW) [78] distance between participants' avatar velocities. For p_mutual_contact, the proportion of

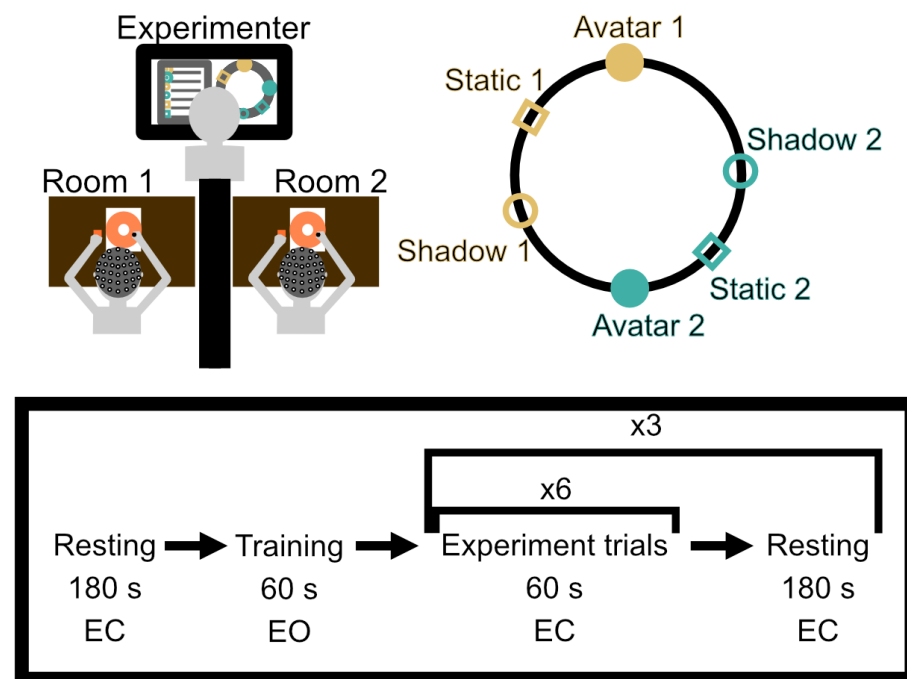


Fig 1. The Perceptual Crossing Experiment (PCE). The top of the figure shows two participants interacting in two different rooms in the minimally-shared space using the haptic human-computer interface. The bottom of the figure shows the experimental timeline; EC-eyes closed; EO-eyes open.

time when both participants' vibration motor simultaneously activated were computed for each 3s epoch. For the DTW, participants' avatar velocities were first calculated for each 3s epoch. Then, the velocities were normalised to values within the range [0,1] and smoothened with 20-point moving average. This procedure ensured that the DTW captured the distance between the moving patterns of both participants regardless of the magnitude. Finally, DTW was computed using the 'dtw' function in MATLAB. The DTW algorithm temporally matched the two signals and computed the sum of Euclidean distances between the two signals. All of the behavioral variables was normalized to values within the range [0,1]. An example of the behavioral variables could was plotted in S2 Fig.

Since the behavioral variables were computed for each 3s epoch of each dyad and trial, this resulted in a (DYADxTRIALxEPOCHxN) matrix, where N was the number of variables. We fed these data into a k-means algorithm [61] to analyse the behavioral patterns that could be observed during PCE. We used the 'kmeans' function in MATLAB for this purpose with the number of replicates set to 20. We first identified the optimal number of clusters using the elbow method and plotting the elbow plot of clustering cost against the number of clusters (S3 Fig). Subsequently, the optimal number of clusters was determined automatically by locating the elbow of the plot. The elbow was defined as the point having the maximum perpendicular distance from the straight line between the first and the last point of the elbow plot. The perpendicular distance for each point

was computed as follows:

$$\text{Distance} = \frac{|(y_2 - y_1)x - (x_2 - x_1)y + x_2y_1 - y_2x_1|}{\sqrt{(y_2 - y_1)^2 + (x_2 - x_1)^2}} \quad (1)$$

where (x_1, y_1) and (x_2, y_2) were the first and last points on the straight line respectively, x was the max-normalised number of clusters (horizontal axis), and y was the max-normalised cost (vertical axis).

The proportions of occurrence were calculated by summing the occurrences of each identified cluster over epochs, trials, or dyads.

The joint success(JS) rate was defined as the total number of joint recognitions of each other's avatar across all trials of each dyad, and normalized by the total number of trials per dyad. Therefore, it is a measure of the level of joint performance of each dyad.

EEG Data Analysis

Pre-processing of EEG data

We pre-processed the EEG data using the Hyperscanning Python Pipeline(HyPyP) [9] toolbox in combination with MNE-Python [33]. HyPyP was an open-source toolbox that was developed with the goal of standardising inter-brain connectivity analyses in the hyperscanning field. We kept the data at the original sampling rate of 1000 Hz. Using HyPyP, we first labelled the EEG data and split the EEG data into two subjects. We then applied a zero-phase finite impulse response(FIR)-filter of the range 1-100 Hz. The transition bandwidth for the high cut-off frequency was 5 Hz, while the low cut-off frequency was set to 'auto'. After average referencing of the data, we segmented the data into 3 s epochs for each trial, yielding 20 epochs per trial. The choice of 3 s epochs was based on a recent finding that shorter epochs could lead to spurious, inflated, and unreliable estimates of inter-brain coupling [94]. Then, we applied Infomax independent component analysis(ICA) with the number of included principal components set to 15. Artefactual ICA components were automatically detected and removed using a method based on ICLabel [58] and the function 'mne_iclabel.label_components'. We cleaned the resulting EEG epochs using the 'prep.AR_local' function. Details of the pre-processing procedure could be reviewed in the 'hypyp_preprocess.py' script or summarized in S1 Fig.

Measure of Inter-brain Synchronization

We quantified IBS as the phase synchronization between the neural signals of two EEG sensors. Precisely, IBS was calculated as the adjusted circular correlation coefficient (CCorr) between two neural signals [94]. The original CCorr measured the covariance between two phase signals and was previously shown to be a robust measure against spurious synchrony [17]. Because EEG signals do not usually have a well-defined mean phase between epochs, the adjusted CCorr accounts for the arbitrary mean by treating the signals as having a uniform distribution of phases. It has been shown that this stabilised the circular correlation coefficient estimates [94]. Following the code provided by Zimmermann and colleagues [94], the adjusted CCorr is defined as:

$$\text{Adjusted CCorr}(\phi, \psi) = \frac{|R^-| - |R^+|}{2\sqrt{\sum_{t=1}^T \sin^2\left(\phi(t) - \frac{\angle R^+ + \angle R^-}{2}\right) \sin^2\left(\psi(t) - \frac{\angle R^+ - \angle R^-}{2}\right)}} \quad (2)$$

where R is the circular mean of phase signals:

$$R^\pm = \sum_{t=1}^T e^{i(\phi(t) \pm \psi(t))} \quad (3)$$

and ϕ and ψ are the phase signals of the neural signals x and y respectively. For example, ϕ is estimated with:

$$\phi(t) = \angle \hat{x}(t) = \tan^{-1} \left(\frac{\Im\{\hat{x}(t)\}}{\Re\{\hat{x}(t)\}} \right) \quad (4)$$

$$\hat{x}(t) = x(t) + iH\{x(t)\} \quad (5)$$

where $H\{x(t)\}$ is the Hilbert transform of $x(t)$, $\hat{x}(t)$ is the analytic signal of $x(t)$, $\Im\{\hat{x}(t)\}$ is the imaginary component, and $\Re\{\hat{x}(t)\}$ is the real component of $\hat{x}(t)$. While the computed CCorr is bounded between $[-1, 1]$, we used the absolute value of CCorr, which bounds the coefficient between $[0, 1]$, as we were more interested in the magnitude of the synchronization rather than the direction of synchronization (whether in-phase or anti-phase). For the remainder of the article, CCorr is treated as the adjusted CCorr.

CCorr was implemented in the HyPyP toolbox and computed for all sensor pairs in all frequency bands of interest. To obtain the analytic signal, the default options of the 'hypyp.analyses.compute_freq_bands' which were zero-phase finite-impulse response(FIR) filters with Hamming windows, automatic filter order and automatic transition bandwidth, were applied as band-pass filters to the pre-processed signals prior to Hilbert transform. The frequency bands were Theta(4-7.5 Hz), Alpha-Low(7.5-10 Hz), Alpha-High(10-12.5 Hz), Beta-Low(12.5-20 Hz), Beta-High(20-30 Hz), Gamma-Low(30-58 Hz), and Gamma-High(62-100 Hz). We chose these frequency bands because of the previous findings of IBS and their relevance to social interaction [14, 26, 45, 89, 90]. Moreover, we further divided the Alpha, Beta, and Gamma bands into Low and High because the diversity of our study demographics (24 nationalities) also meant that there would be a large diversity in the band power distributions for the different dyads [2, 40].

Inter-brain Functional Connectivity

Since participants were exposed to a similar external environment and shared similar stimuli in the PCE task space, we needed to discriminate between spurious connections due to task similarity and genuine connections resulting from the interaction process. Therefore, we created a null distribution for CCorr by shuffling the dyad numbers, such that $31 \times 30 = 930$ surrogate dyads were created. The trial numbers, epoch numbers, frequency bands and sensor numbers were not shuffled. This resulted in dyad-shuffled CCorr which constituted the null distribution, where each of the observed CCorr was tested against this null distribution. For example, for each dyad, trial, epoch, band, and sensor-sensor connection, the observed CCorr was ranked in the null distribution and thresholded at the 97.5th percentile rank in the null distribution.

The dyad-shuffled surrogate method resulted in $31 \times 18 \times 20 \times 7$ matrices of binary functional connectivity(FC) which was more likely to be due to the genuine interaction process rather than similar task stimuli. To be more conservative, we further filtered out the weakest connections, retaining only the top 0.5% or top 0.1% of connections. This was done by first summing up all the FC matrices and thresholding at the 99.5th or top 99.9th percentile. This step resulted in one FC matrix for each frequency band, representing the significant inter-brain connections during the PCE task.

In the same way as the behavioral variables, the un-thresholded FC matrices for the Alpha-Low and Alpha-High band was first flattened into vectors resulting in $31 \times 18 \times 20 \times 4096$ (DYADxTRIALxEPOCHxN) matrices. Similarly, the optimal number of clusters was determined by using the elbow method and the inter-brain FC matrices in the Alpha-Low and Alpha-High band was clustered using this optimal number of clusters with the number of replicates set to 20. After labelling each epoch with a cluster number, we then pooled and summed the FC matrices for each cluster number. Finally, these clusters were thresholded separately at the 99.5th percentile, retaining only the top 5% of the strongest connections.

Regions of Interests

For the averaging of sensor-sensor FCs into ROI-ROI FCs, we grouped 40 sensors into 8 pre-defined ROIs, with each ROI containing 5 sensors. The ROIs were defined as right frontal (RF), left frontal (LF), right central (RC), LC (left central), right temporal (RT), left temporal (LT), right parietal (RP), and left parietal (LP). The clustering of EEG sensors into predefined regions of interest(ROI) provided a better SNR and easier interpretability while lowering the number of comparisons. Following previous research [55,80], we separated the ROIs into left and right ROIs to investigate whether there was a lateralization in inter-brain FC [25,80]. The sensors included in each ROI are showed in S4 Fig.

Statistical Methods

The Spearman correlation coefficient between the behavioral variables and the Alpha-Low and Alpha-High ROI-ROI was calculated using the 'corr' function in MATLAB. The function provided a p value based on testing against a null hypothesis of no correlation between the variables. For large samples, this is done by the approximating the ranked-sum statistic as a t-statistic distribution.

The contingency table was constructed by labelling all epochs with a behavioral or inter-brain cluster number and counting the number of occurrences for each cluster number. To test for association between the two sets of clusters, we applied chi-square test of independence on the contingency table for the inter-brain clusters and behavioral clusters. This was done with the 'chisq.test' function in R. For the post-hoc analyses of each cell, we used adjusted Pearson residuals [35] to account for the unbalanced counts among the rows and columns in the contingency table for inter-brain clusters and behavioral clusters. Adjusted Pearson residuals can be computed by:

$$\tilde{r}_{ij} = \frac{O_{ij} - E_{ij}}{\sqrt{E_{ij} \left(1 - \frac{m_i}{N}\right) \left(1 - \frac{n_j}{N}\right)}} \quad (6)$$

where O_{ij} represents the observed count in cell (i, j) , E_{ij} was the expected count under the null hypothesis of independence, m_i and n_j are the marginal sums for row i and column j , respectively, and N is the grand total count of all observed frequencies. Adjusted Pearson residual takes into consideration the row and column totals, thus providing a more precise measure of deviations from the expected counts. Furthermore, the asymptotic normality for Pearson residuals is not always observed in real data and using Pearson residuals alone can underestimate sample variability [15]. In contrast, adjusted Pearson residuals are asymptotically normal-distributed, providing more accurate statistical inferences than using Pearson residuals. These residuals can be interpreted as effect sizes. Larger values can be interpreted as stronger effects, positive values represent a positive association, and negative values represent a negative association between a category in the rows and a category in the columns. In particular, an association means that there is a relationship between the two categories, for example inter-brain cluster 1 and behavioural cluster 3, such that one category is more(positive) or less(negative) likely to occur with the other.

All p values were corrected for multiple comparisons with the Benjamini-Hochberg procedure, implemented via the 'fdr_bh' function in MATLAB. This controlled the false discovery rate at 0.05.

Software and Hardware

The EEG pre-processing and IBS computation were run in Python 3.11. The chi-square test was run in R Studio 3.6.3. The rest of the analyses were run in MATLAB 2022b

(Mathworks Inc, Natick, MA, USA). The EEG pre-processing, IBS computation and dyad-shuffled surrogate method were run on the computing clusters at OIST.

Results

Analysis of Behavioral Patterns

We applied a k-means clustering algorithm to the 9 behavioral variables(S2 Fig) to investigate the behavioral dynamics during PCE. Fig 2 shows the characteristics of the 5 identified behavioral clusters and their dynamics. From Fig 2A, it could be seen that clusters 1 and 4 were the clusters with the closest distances between the avatar positions and thus had larger $p_{\text{mutual-contact}}$ than the other clusters. In addition, clusters 1 and 4 were characterized by having one of the participants closer to his static object than the other participant and with both players having equal distances to the shadow objects of the other. Furthermore, the velocity differences between the participants avatar were similar compared to the other clusters. This suggested that cluster 1 and cluster 4 could represent the behavioral patterns during a successful interaction between participants in PCE. This was accentuated by the fact that the occurrences of cluster 1 and cluster 4 increased during each trial and plateauing around epoch 7 (18-21 s) after the start of each trial (Fig 2B), which showed that the participants were approaching each other during each trial.

In contrast, clusters 2, 3 and 5 were characterized by larger distances between the participant avatar positions and shorter periods of shared vibration between the interacting participants. These clusters had one participant closer to the shadow object than the other participant, suggesting that these clusters may represent the interaction patterns of one player chasing the shadow of the other. Additionally, cluster 5 could represent periods where both of the participants were interacting with their static objects. This could be shown with a longer duration of mutual vibration along low distance to static objects for both participants. The velocity differences for these 3 clusters were also slightly higher than those of cluster 1 and cluster 4, although there was no noticeable differences between the DTW distances and acceleration differences. The dynamics of these clusters during each trial Fig 2B shows that cluster 5 converged with a slower dynamics than clusters 2 and 3. Cluster 5 also converged to the lowest proportion compared to the other clusters, suggesting that participants first tend to identify their static objects before moving on to search for their partner in the space furthest from their static objects.

Fig 2C shows that the proportion for each cluster was largely independent of trial number. However, the interaction patterns largely differed between different dyads (Fig 2D). In particular, cluster 3 (0.2599 ± 0.0906) had the highest proportion across all dyads, followed by clusters 1 (0.1923 ± 0.0644) and 2 (0.1959 ± 0.0930), cluster 4 (0.1832 ± 0.0951), and lastly cluster 5 (0.1686 ± 0.0867). As cluster 3 had the characteristics of balanced distances to all of the objects including the avatar of the other participant, it could be drawn from this behavioral analysis alone that a popular strategy was to equally scan the whole space for different objects before converging to locate the other participant. Another simple explanation for cluster 3 was that this was this represented the starting configurations for each trial, but this does not explain why cluster 3 had the largest proportion even until epoch 10 (Fig 2B).

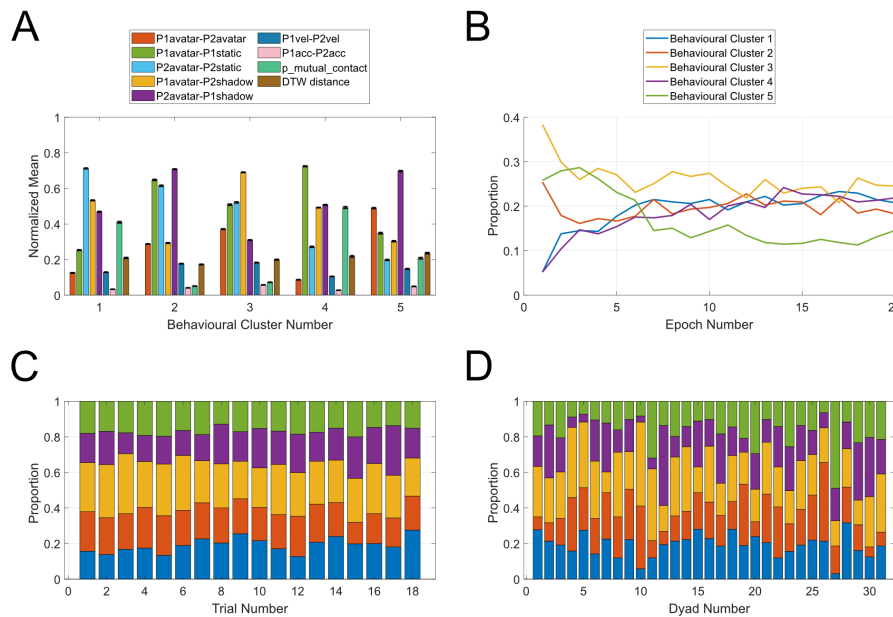


Fig 2. Behavioral pattern clusters identified using k-means and their dynamics. (A) Characteristics of each identified cluster. Each of the variables were averaged across all 3 s-epochs and normalized to the range [0,1]. avatar, participant avatar position; static, participant static object position; shadow, participant shadow object position; vel, velocity; acc, acceleration; DTW, dynamic time warping. Differences were computed as absolute differences. (B) Proportion for each cluster within a trial. Each epoch was 3 s. Clusters were color-coded for B, C and D. (C) Proportion for each trial across all dyads and epochs. (D) Proportion for each dyad across all trials and epochs.

Significant Inter-brain Synchronization in the Alpha-Low and Alpha-High band

We computed CCorr for each 3 s epoch between the EEG sensor signals of the 31 dyads. To identify genuine inter-brain connections that capture the nature of the interaction instead of the task itself, the dyad number was permuted via the dyad-shuffled surrogate method. The significant connections in the resulting binary FC matrices were then summed into density maps and the weak connections were filtered out based on the percentile. Fig 3 shows the top inter-brain connections after filtering. For the top 0.5% of the significant connections, we observed inter-brain connections between the participants in the Alpha-Low and Alpha-High bands. Notably, the connections involved the frontal, central, temporal and parietal regions. Filtering at 0.1% gave a clearer picture of the connections. There was more temporal connections in the Alpha-High band than the Alpha-Low band. Since we assumed that both individuals in a dyad were the same (there was no directionality in the design of the PCE, where none was instructed to lead), we averaged symmetrical connections between the top and lower triangle of the matrices. To ease interpretation, we averaged the sensor connections into ROIs. We observed that the connections were between LC-RC(0.02) for Alpha-Low, and RT-RP(0.02), RT-LF(0.04) for Alpha-High.

Interested in whether these 3 inter-brain ROI connections were related to the be-

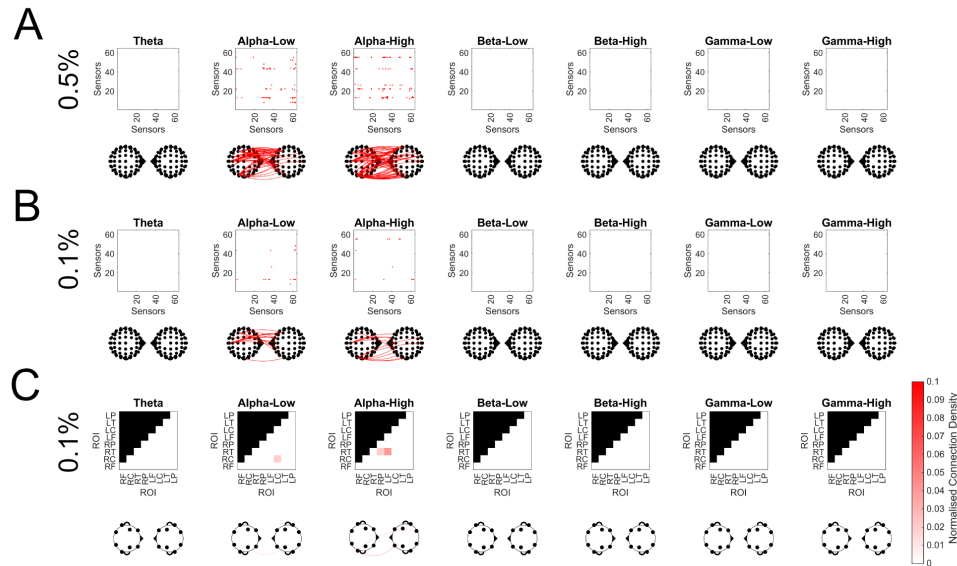


Fig 3. Significant inter-brain connections after dyad-shuffled surrogate method. (A) After filtering out sensor-sensor connections weaker than the top 0.5% threshold for all the frequency bands of interest, each red dot on the FC matrices represented the existence of an inter-brain connection, and each red curve on the head plots marked the connection between two heads that were facing each other. The frequency bands of interest were Theta(4-7.5 Hz), Alpha-Low(7.5-10 Hz), Alpha-High (10-12.5 Hz), Beta-Low (13-20 Hz), Beta-High(20-30 Hz), Gamma-Low(30-58 Hz), and Gamma-High(62-100 Hz). (B) Inter-brain connections filtered with 0.1 % threshold. (C) Inter-brain connections filtered with 0.1 % threshold and inter-brain sensor-sensor connections were averaged into regions of interest(ROI)-ROI connections. Symmetrical connections were averaged. The color scale shows the number of connections normalized by the total number of connections within each ROI-ROI.

havioral variables, we calculated the Spearman correlation between each of these 3 connections and the 9 behavioral variables (Table 1). After correcting for FDR, there were significant correlations between P1avatar-P2avatar and CCorr at LC-RC for Alpha-Low and RT-RP for Alpha-High ($p < 0.05$). Significant correlations were also observed between the avatar-shadow variables for all ROI-ROI ($p < 0.005$). Lastly, we also observed a significant negative correlation between P2avatar-P2static and CCorr(LC-RC) ($p < 0.005$). The correlation coefficients, though significant, showed very small values around 0.03. For the positive coefficients, the mean was 0.0357 ± 0.0107 . For the negative coefficients, the mean was 0.0383 ± 0.0097 .

Inter-brain Connectivity Patterns

Similarly to the behavioral analysis, for the Alpha-Low and Alpha-High frequency bands, we applied k-means clustering to the full inter-brain FC thresholded using the surrogate method. The optimal number of clusters was found to be 3. After labelling each epoch with a inter-brain cluster number and summing up the connectivities for each cluster, we further filtered out connections weaker than the top 0.5% of all connections for each cluster. Fig 4 and Fig 5 shows the resulting connectivity patterns for each inter-brain cluster and their dynamics. The 3 inter-brain clusters had distinct patterns

Table 1. Spearman correlation coefficients (ρ), 95% confidence intervals, and adjusted P-values between behavioral variables and inter-brain connections.

Behavioral Variable	Alpha-Low			Alpha-High					
	CCorr(LC-RC)			CCorr(RT-RP)			CCorr(RT-LF)		
	ρ	CI	P-value*	ρ	CI	P-value*	ρ	CI	P-value*
P1avatar-P2avatar	0.0345	[0.015, 0.053]	**0.0016	0.0238	[0.005, 0.042]	**0.0429	0.0161	[-0.002, 0.034]	0.1459
P1avatar-P1static	0.0138	[-0.004, 0.032]	0.2625	-0.0036	[-0.022, 0.014]	0.7946	-0.0020	[-0.020, 0.016]	0.8717
P2avatar-P2static	-0.0337	[-0.053, -0.014]	**0.0016	-0.0039	[-0.022, 0.014]	0.7946	0.0015	[-0.017, 0.019]	0.8717
P1avatar-P2shadow	-0.0301	[-0.049, -0.011]	**0.0034	-0.0522	[-0.071, -0.033]	**0.0000	-0.0374	[-0.056, -0.018]	**0.0003
P2avatar-P1shadow	0.0301	[0.011, 0.049]	**0.0034	0.0525	[0.033, 0.071]	**0.0000	0.0376	[0.018, 0.056]	**0.0003
P1vel-P2vel	-0.0077	[-0.026, 0.011]	0.4685	-0.0177	[-0.036, 0.001]	0.1375	-0.0190	[-0.037, -0.001]	0.1356
P1acc-P2acc	-0.0039	[-0.022, 0.014]	0.6819	-0.0103	[-0.029, 0.008]	0.3853	-0.0083	[-0.027, 0.010]	0.4858
p_mutual_contact	-0.0103	[-0.029, 0.008]	0.3536	-0.0183	[-0.037, 0.000]	0.1365	-0.0128	[-0.031, 0.005]	0.2620
DTW distance	-0.0107	[-0.029, 0.007]	0.3536	-0.0164	[-0.034, 0.002]	0.1459	-0.0167	[-0.035, 0.001]	0.1459

CI, 95% confidence intervals; CCorr, circular correlation coefficient; DTW, dynamic time warping; LF, left frontal; RC, right central; RP, right parietal; RT, right temporal.

* p values shown were corrected by the Benjamini-Hochberg method.

**Significance, $p < 0.05$

(Fig 4A). Cluster 3 had inter-brain connections concentrated mainly between the bilateral temporal regions, and was the most dominant cluster (Fig 4B, C, and D). For cluster 1, the connections were concentrated between the frontal regions and was the rarest cluster. Cluster 2 had a mixture of asymmetrical connections between the frontal-right temporal regions and frontal-left centroparietal regions.

As could be seen in Fig 4B and C, the proportions of these 3 clusters did not vary much within each trial and across trials. However, similar to the behavioral clusters in Fig 4D, the proportions of the inter-brain clusters, especially clusters 2 and 3 varied between the dyads. An exploratory analysis on the correlation between the JS rate and the dyadic proportion for each cluster revealed non-significant correlation (Cluster 1, $\rho = -0.2180$, $p = 0.4901$; Cluster 2, $\rho = -0.1287$, $p = 0.4901$; Cluster 3, $\rho = 0.1404$, $p = 0.4901$).

For the Alpha-High band, the resulting patterns and dynamics were similar to those of the Alpha-Low band (Fig 5). The only notable difference was in Cluster 2, where Alpha-Low showed more frontal-central connections but Alpha-High showed more frontal-temporal connections.

Exploration of the Association Between Behavioral and Inter-Brain Clusters

The frequency of occurrence for each inter-brain and behavioral cluster was shown in (Table 2). Interested in whether some of the inter-brain clusters occurred more frequently for some behavioral clusters and vice versa, we computed the conditional probabilities of each set of clusters. This was done by calculating the probability for each behavioral cluster conditioned on each inter-brain cluster, and vice versa. By visual inspection alone, inter-brain clusters seemed to have a similar distribution throughout the 5 behavioral clusters (Fig 6A). We could also see that different inter-brain clusters had a different preference of behavioral clusters (Fig 6B). For example, behavioral cluster 3 had a higher relative occurrence in inter-brain clusters 1 and 3 than inter-brain cluster 2. The Alpha-Low and Alpha-High bands showed similar patterns.

To objectively quantify the association between the behavioral and inter-brain clusters, we applied a chi-square test of independence on Table 2. We observed a significant association between the variables (Alpha-Low, $\chi^2(8) = 56.0977$, $n = 11160$, $p < 0.001$; Alpha-High, $\chi^2(8) = 56.6741$, $n = 11160$, $p < 0.001$). The effect size, calculated as

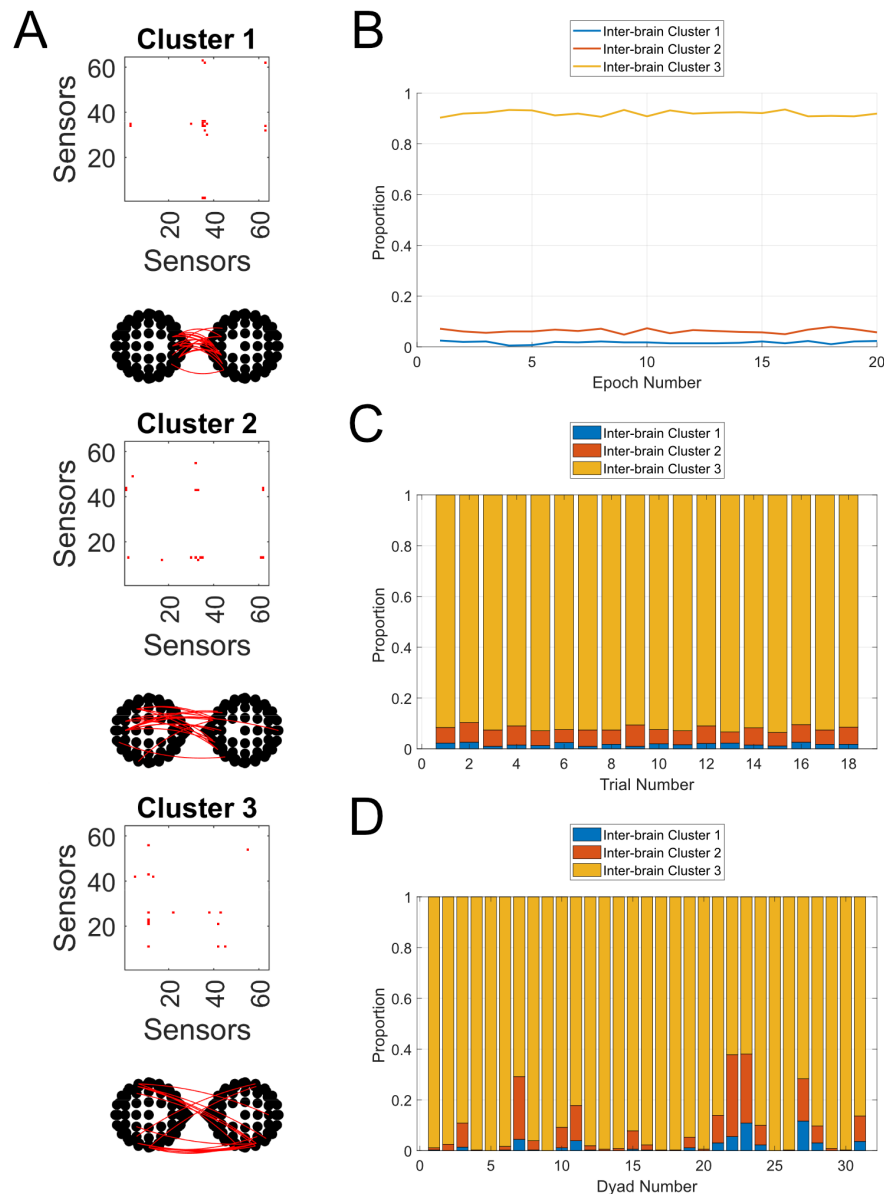


Fig 4. Inter-brain connectivity pattern clusters identified using k-means and their dynamics for the Alpha-Low band. (A) Inter-brain clusters for the Alpha-Low (7.5-10 Hz) frequency band. After summing up connectivity patterns across all epochs corresponding to each cluster, the sensor-sensor connectivity patterns were obtained by retaining the top 0.5% of connections within each cluster. (B) Proportion of each cluster over epochs within a trial. Each epoch was 3 s. Clusters were color-coded for B, C and D. (C) Proportion for each trial across all dyads and epochs. (D) Proportion for each dyad across all trials and epochs.

Cramer's V, was $w = 0.0251$ $w = 0.0252$ respectively, indicating very small effect sizes. Further post-hoc, local analyses (Table 3) on the adjusted Pearson residuals revealed a significant positive associations between inter-brain cluster 1 and behavioral clusters

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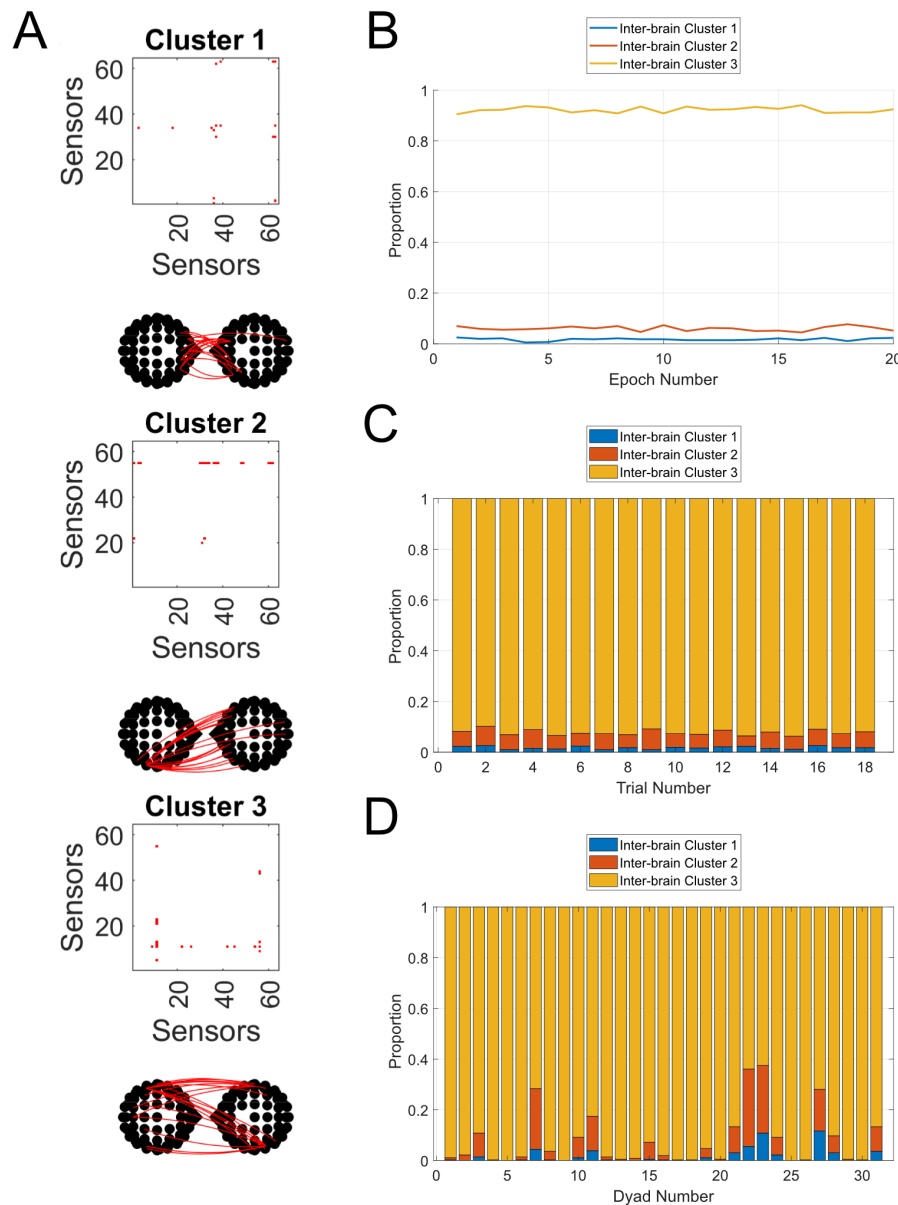


Fig 5. Inter-brain connectivity pattern clusters identified using k-means and their dynamics for the Alpha-High band. (A) Inter-brain clusters for the Alpha-Low (7.5-10 Hz) frequency band. After summing up connectivity patterns across all epochs corresponding to each cluster, the sensor-sensor connectivity patterns were obtained by retaining the top 0.5% of connections within each cluster. (B) Proportion of each cluster over epochs within a trial. Each epoch was 3 s. Clusters were color-coded for B, C and D. (C) Proportion for each trial across all dyads and epochs. (D) Proportion for each dyad across all trials and epochs.

2(Residual = 4.11, ($p < 0.001$)) and 5(Residual = 3.23, ($p < 0.01$)), but negative associations between inter-brain cluster 1 and behavioral clusters 1(Residual = -2.26, ($p < 0.05$)) and 3(Residual = -10.65, ($p < 0.0001$)). The residuals can be interpreted as

Table 2. Frequency of occurrences for each inter-brain and behavioral cluster under Alpha-Low and Alpha-High conditions.

Behavioral Cluster Number	Inter-Brain Cluster Number					
	Alpha-Low			Alpha-High		
	1	2	3	1	2	3
1	25	98	2023	25	92	2029
2	60	154	1972	60	149	1977
3	32	174	2695	32	168	2701
4	28	129	1888	28	122	1895
5	49	147	1686	49	141	1692

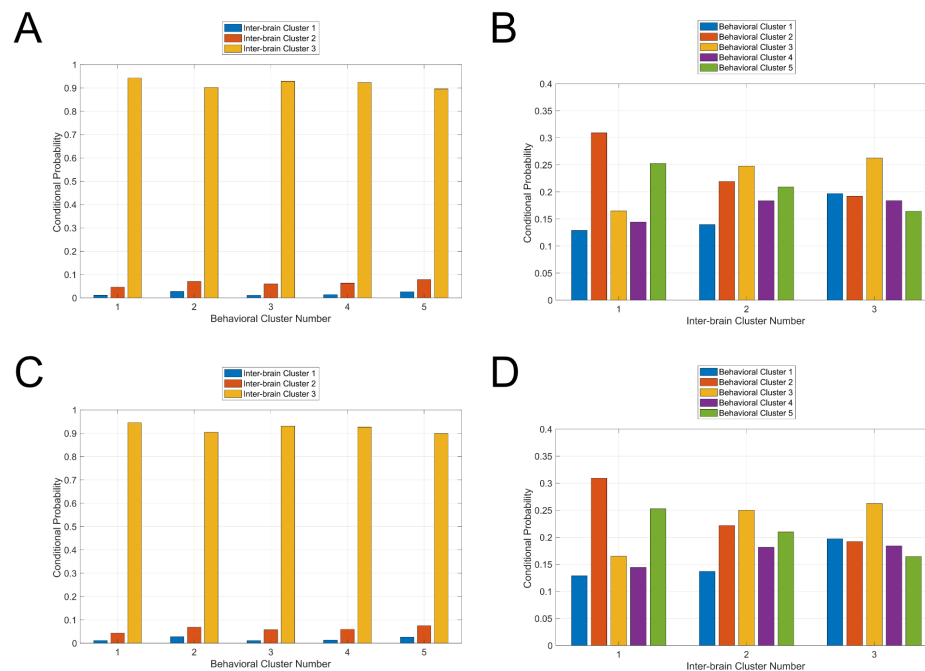


Fig 6. Conditional Probabilities of Behavioral and Inter-brain Clusters (A) Proportion of inter-brain clusters conditioned on the behavioral clusters. (B) Proportion of behavioral clusters conditioned on the inter-brain clusters. Probabilities shown were across all epochs for all trials and dyads.

effect sizes and follow a standard normal distribution(See Methods). Next, inter-brain cluster 2 showed strong significant negative association with behavioral cluster 1(Residual = -12.50, $p < 0.0001$) and positive association with behavioral cluster 5(Residual = 2.91, $p < 0.01$). Finally, inter-brain cluster 3 exhibited significant negative associations with behavioral cluster 2(Residual = -3.38, $p < 0.01$) and 5(Residual = -4.18, $p < 0.001$). We did not see any association between any of the inter-brain clusters and behavioral cluster 4. Post-hoc analyses for Alpha-High followed the same patterns(Table 4).

Table 3. Standardized residuals and P-values from the chi-square test between behavioral clusters and inter-brain clusters for the Alpha-Low band.

Behavioral Cluster Number	Inter-Brain Cluster Number					
	1		2		3	
	Res.	P-value*	Res.	P-value*	Res.	P-value*
1	-2.26	**0.0445	-12.50	**0.0000	1.28	0.2757
2	4.11	**0.0001	1.58	0.1893	-3.38	**0.0022
3	-10.65	**0.0000	-0.75	0.5636	0.61	0.6245
4	-1.41	0.2363	0.12	0.9006	0.19	0.9006
5	3.23	**0.0031	2.91	**0.0077	-4.18	**0.0001

Res., Adjusted Pearson residuals

**p* values shown were corrected by the Benjamini-Hochberg method.

**Significance, *p* < 0.05

Table 4. Standardized residuals and P-values from the chi-square test between behavioral clusters and inter-brain clusters for the Alpha-High band.

Behavioral Cluster Number	Inter-Brain Cluster Number					
	1		2		3	
	Res.	P-value*	Res.	P-value*	Res.	P-value*
1	-2.26	**0.0445	-13.08	**0.0000	1.28	0.2746
2	4.11	**0.0002	1.70	0.1475	-3.51	**0.0013
3	-10.83	**0.0000	-0.61	0.6567	0.57	0.6567
4	-1.41	0.2363	-0.41	0.7321	0.23	0.8194
5	3.22	**0.0032	2.88	**0.0086	-4.15	**0.0002

Res., Adjusted Pearson residuals

**p* values shown were corrected by the Benjamini-Hochberg method.

**Significance, *p* < 0.05

Discussion

To investigate whether neural signals between brains of physically isolated individuals could synchronize during minimal tactile interaction, we applied inter-brain analysis on a publicly available PCE dataset. Here we focus on explaining the novel findings and their significances. First, we discovered significant IBS during the PCE in the alpha bands. Second, we report behavioral and inter-brain patterns that can be found in the PCE. Third, we found associations between the significant inter-brain connection patterns and the behavioral patterns.

The discovery of significant IBS during PCE suggests that phase synchronization could occur between brains of interacting individuals even though they were physically isolated and the only means of communication was through the tactile stimuli representing this interaction dynamics in a virtual environment. IBS is observed in only the alpha band after retaining only the top 0.5% of connections(Fig 3A). This finding supports existing findings in the hyperscanning literature. In the experiments with physically isolated individuals engaged in an imitation task, Dumas and colleagues reported IBS in alpha-mu(8-12 Hz) between the right centro-parietal regions, beta(13-30 Hz) between the central and parieto-occipital regions, and gamma(30-48 Hz) between the centro-parietal and parieto-occipital regions [26]. Another study which involved physically isolated

participants engaged in a video game found IBS in the alpha(8-12 Hz), beta(13-30 Hz) and gamma(31-45 Hz) bands between the frontal, central, parietal and occipital regions [89]. For beta(13.5-29.5 Hz), remote interactions showed IBS between the right frontal and left temporal regions [80]. Regardless of the task, the current hyperscanning literature commonly reports IBC in the theta, alpha and beta and gamma bands [5, 6, 45, 46, 55, 56, 70, 77, 86, 88, 90]. However, gamma IBC is thought to be prone to muscular artefacts and proving gamma IBC requires a careful examination of the signal artefacts [39].

Due to the low spatial resolution of EEG [19, 79], the observed IBS cannot be linked to the actual underlying brain regions. However, we can speculate the regions involved by searching for correspondences between our findings and existing findings. In the PCE, most of the IBS connections are between the temporo-parietal ROIs(Fig 3A). The top 5% of connections show that 34.29% involve the RT cluster, followed by LT with 20.00%, LP with 17.14%, RC and RP both with 8.57%, RF and LC both with 5.71%, and LF with 0%, of 35 symmetrical ROI-ROI connections. This is consistent with temporal or parietal IBC in previous findings [20, 26, 60, 80, 85], with a focus on the rTPJ. The rTPJ is associated with social cognition [1, 4], along with other regions in the visual cortices, the parietal lobe, and the frontal motor areas for simultaneous action and perception [25]. Based on a recently published work on the probability of the underlying brain region for each EEG sensor of 20 participants [81], the sensors in the RT in the current article correspond to the inferior temporal gyrus(ITG), middle temporal gyrus(MTG), posterior superior temporal gyrus(STG), and angular gyrus(ANG). ITG, MTG and STG are regions within the temporal lobe, and the temporal lobe is involved in semantic and episode memory formation [52]. ITG is involved in general recognition, while MTG is involved in the visual perception of moving objects [16]. STG is involved in facial recognition and auditory perception [16, 37]. Located between the STG and MTG, the superior temporal sulcus(STS) is generally associated with aspects of social cognition such as multisensory integration and theory of mind [69], although it can be functionally divided further into sub-regions for the processing of different social stimuli [22]. Finally, right ANG is involved in attention to salient and task-relevant environmental stimuli, spatial cognition, theory of mind and conflict resolution [82]. The right posterior MTG and right ANG have been suggested to be part of the human mirror neuron system(MNS) involved in the observation and action execution in speech [18] and the social MNS pathway involves a more anterior and lateral activation than the non-social MNS pathway [93]. Furthermore, Naeem and colleagues have also suggested that simple social interactions likely involved MNS in the right hemisphere [71]. Therefore, we suggest that the IBC between RT-RT in our results involves the MNS pathway. The fact that these regions are synchronized between two brains implies that during the PCE, there is a synchronization of processes related to attention, perception, recognition, sensory integration and mentalizing to successfully locate the other participant. Additionally, this also suggested that there is a social component to the interaction, such that there is a coordination between the social regions of the brains across two individuals.

In the PCE, we observed similar patterns between Alpha-Low and Alpha-High. It was previously suggested that the low-alpha and high-alpha bands have functional differentiation and two orthogonal components(intersecting at 7-11 Hz and 10-13 Hz respectively) are believed to exist within the broad alpha range [49]. Functionally, low-alpha is related to task difficulty and attention processes and high-alpha is related to semantic processing [49, 50]. In an intra-brain study of mu suppression, both low-alpha(8-10 Hz) and high-alpha(10-12 Hz) are found to be associated with MNS, and high-alpha over the sensorimotor and frontal regions has been associated with top-down inhibitory processes [27]. The high-alpha-mu band(10-12 Hz), but not the low-alpha-mu band(8-10 Hz) was previously found to show higher intra-brain power suppression in

the right centro-parietal regions associated with activation of processes related to social interaction [71]. Another study pointed out that low-alpha(8-10 Hz) is more likely to be associated with MNS during action observation [29]. With regards to inter-brain findings, Moreau and colleagues recently reported differences in low-alpha(8-10 Hz) and high-alpha(11-13 Hz) IBS, with low-alpha associated with a more demanding social task and the high-alpha with the simultaneous, passive viewing of videos [68]. Here, the inter-brain connections in low-alpha are mostly located in the central ROIs while the connections for high-alpha are mostly between the frontal-temporal and right parietal-temporal ROIs, highlighting the role of the high-alpha band in social processing and low-alpha in sensorimotor processing.

Real-time coordination should be studied in an active(continuous and dynamic perception and action) [71] and naturalistic [48] interaction paradigm, but the complexity of a naturalistic interaction process means that it is difficult to fully describe the dynamics in one variable. Therefore, we computed several measures to represent the behavioral interaction processes. We then applied an unsupervised learning algorithm, k-means clustering to investigate the interaction patterns. K-means clustering is commonly used to classify brain states in the FC literature [3, 43, 64, 83, 95] and more recently in hyperscanning [13, 59], owing to its simplicity. The analysis of pattern clusters in the behavioral variables and inter-brain FCs provides a general picture of the types of inter-personal coordination and inter-brain connection patterns present during PCE, including how they vary over time. We identified five types of behavioral patterns(Fig 2A) and three types of inter-brain patterns(Fig 4A) in the alpha frequencies, with very low variation between replications. We did not observe large variations across trials(Fig 2C & Fig 4C) but noticed dyad-to-dyad variation in patterns(Fig 2D & Fig 4D). Upon closer examination of the dynamics(Fig 2B), the behavioral pattern clusters followed a pattern which covered around 18-21 s, and as such, could be combined into two groups - when participants were close together(Cluster 1 and 4) versus when they were far apart(Cluster 2, 3 and 5). Cluster 3 can be also interpreted as the cluster with similar distance to all the other objects. However, we could not discern any changes in the inter-brain patterns over time(Fig 4B). One reason could be that the time-scale of the dynamics was too fast to be captured by the 3-s windows. Future studies could employ a more fine-grained temporal analysis [13].

The significant associations between the inter-brain patterns and the behavioral patterns(Table 3 and Table 4) suggests that different inter-brain networks were activated depending on the behavioral dynamics of the players during every 3 s. When participants are close together, they are less likely to show alpha IBS between the frontal-frontal and frontal-centro-temporal regions(Inter-brain clusters 1 and 2). When participants are far apart, they are more likely to show alpha IBS between the frontal-frontal regions and frontal-centro-temporal regions(Inter-brain clusters 1 and 2). However, since frontal-frontal(inter-brain cluster 1) is less likely during behavioral cluster 3, this suggests that frontal-frontal inter-brain network is not recruited when there are multiple interactable objects within the vicinity. Lastly, IBS between bilateral temporal regions(Inter-brain cluster 3) are less likely when the participants are far apart. These associations suggest that frontal-associated but not bilateral temporal alpha networks are recruited when participants are far apart and still searching for each other in the space, and these networks are recruited less once they come into the vicinity of each other. IBC in the medial prefrontal cortex(PFC) is suggested to be associated with dyadic emotional co-regulation in parent-child relationships [10, 11] as well as similarity in executive functioning and social cognitive processes [65]. Moreover, in a meta-analysis, the PFC was suggested to be involved in cooperative behavior and attentional switching [20]. The frontal region is related to attentional focus, planning and cognitive regulation during motor sequence imagination [24], and leaders show frontal alpha suppression [53]. During

far-apart windows, we can assume that the participants feel similar uncertainty in the actual objects they are interacting with and thus, need to invest more effort to dissociate between the objects. However, when they come close to several objects, they become more certain that one of the objects is the avatar of the other. Future analyses should try to differentiate between the IBS patterns when interacting with a shadow versus a participant avatar.

Although the correlation between inter-brain ROI-ROI had a weak effect size (Table 1), the fact that the results of correlation and the correspondence analysis between the pattern clusters coincided suggests that the results are not spurious. For example, the LC-RC and RT-RP both showed a positive correlation with avatar distances, and we noticed that that close-together patterns are less likely to involve these ROI-ROIs but far-apart patterns are more likely to involve these ROIs-ROIs. However, we could not provide a sufficient explanation for the asymmetric correlations in the results for the avatar and shadow distances.

This work has several implications for ongoing discussions on the dynamics of social interaction in both physical and virtual environments. First, the capacity of even minimal and unfamiliar virtual environments to foster rich interpersonal neurodynamics speaks to the general sensitivity of our minds to social contexts and how others shape our potential actions [21], even in relatively limited social conditions. This finding challenges some early work in embodied cognitive science, which tended to be dismissive or critical of virtual spaces as settings for authentic social interaction [31, 62], aligning instead with recent philosophical work that, though not uncritical, has recognized the constructive potential of virtual spaces [41, 42, 73–75, 87]. Although we did not include it herein, we have gathered subjective reports from our participants in the PCE study and, as researchers, we are frequently struck by how richly social these minimal interactions are experienced. Future work will involve correlating these self-reports with our EEG and behavioral findings.

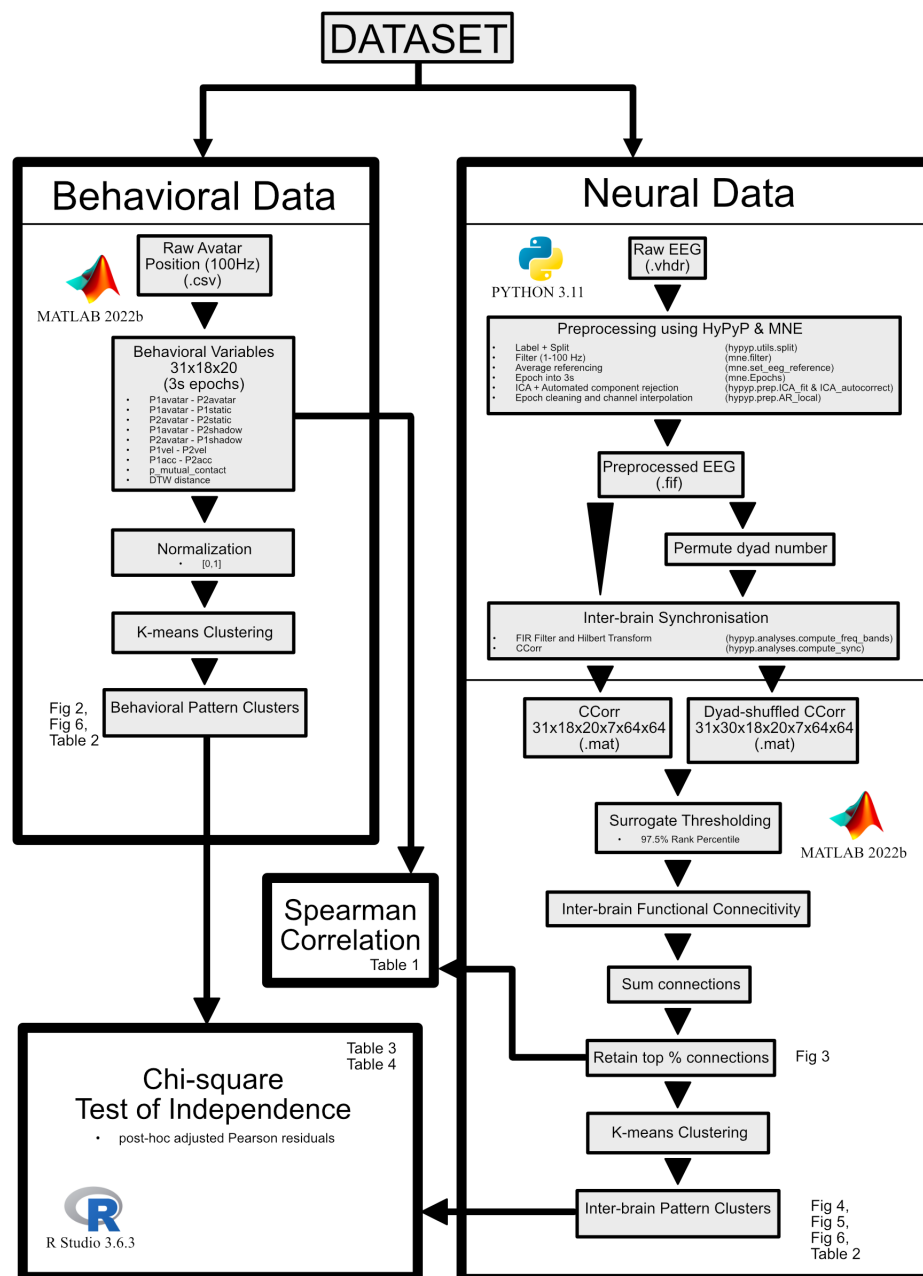
Another implication, given the richness observed in both subjective and objective data, is the potential value of integrating haptics into mediated virtual interactions. All else being equal, the more immersive an online environment is—the more sensory channels it engages—the greater the sense of co-presence, of genuinely being with another in that environment [84]. Here, we demonstrate how even basic haptics correlate with neurophysiological indicators of social connection, suggesting relatively accessible means of enhancing the sense of co-presence in online interactions. Finally, the shifting synchronous dynamics we observe in correlation with behavioral dynamics suggest a certain robustness and adaptability, possibly indicating the value of these nested dynamics in coordinating across changing spatiotemporal conditions. This aligns well with recent research emphasizing the adaptive value not only of synchrony but of our capacity to move in and out of synchrony across behavioral and physiological dynamics, thereby maintaining robustness in interaction even when coordination breaks down in specific dynamics [63]. Again, this points to the value of more immersive virtual environments, where the interpersonal dynamics that underpin social connection might benefit from a diverse range of means to realize coordination.

1 Data availability

All scripts including scripts for generating the tables and figures, as well as links to the complete (raw, pre-processed and analyzed) dataset could be accessed freely at <https://gitlab.com/oist-ecsu/ibspce2024>.

Supporting information

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S1 Fig.

Overview of the analysis plan Behavioral and inter-brain data were first analysed separately. Spearman correlation was computed between region of interests in the Alpha-Low(7.5-10 Hz) band and the behavioral variables. A contingency table of the behavioral and inter-brain clusters was created to investigate the association between behavioral and inter-brain clusters using chi-square test. The figure also pointed to where the figures and tables were created from. CCorr, circular correlation; DTW, dynamic time warping; EEG, electroencephalography.

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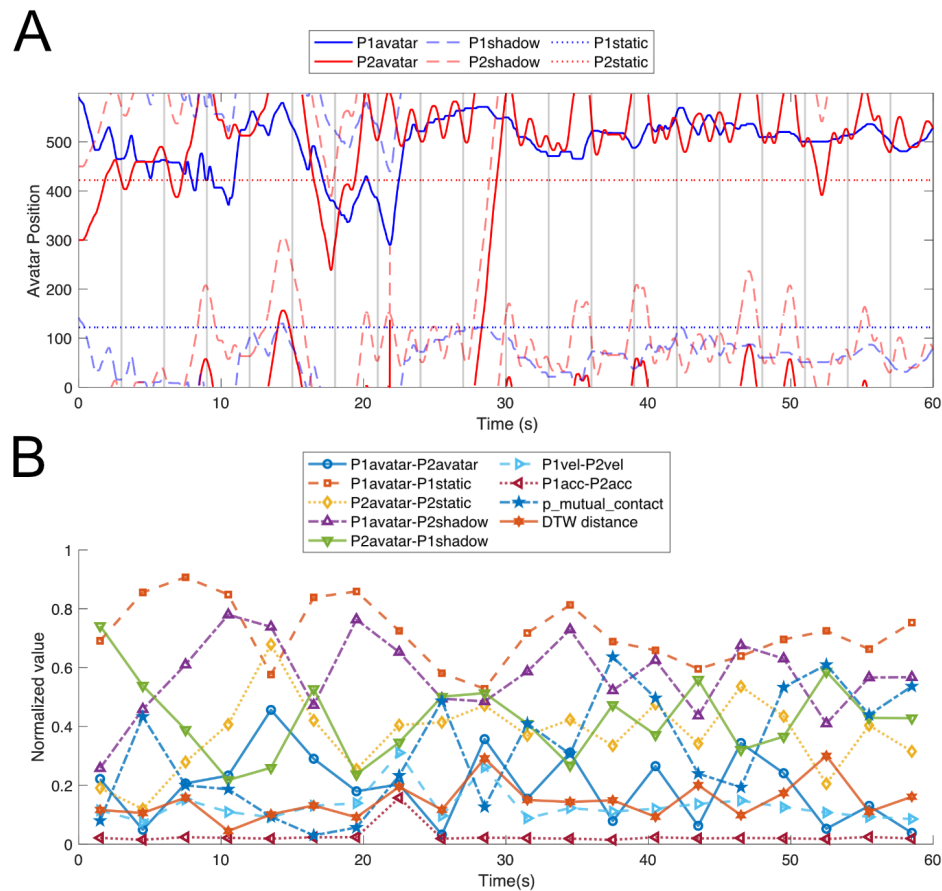
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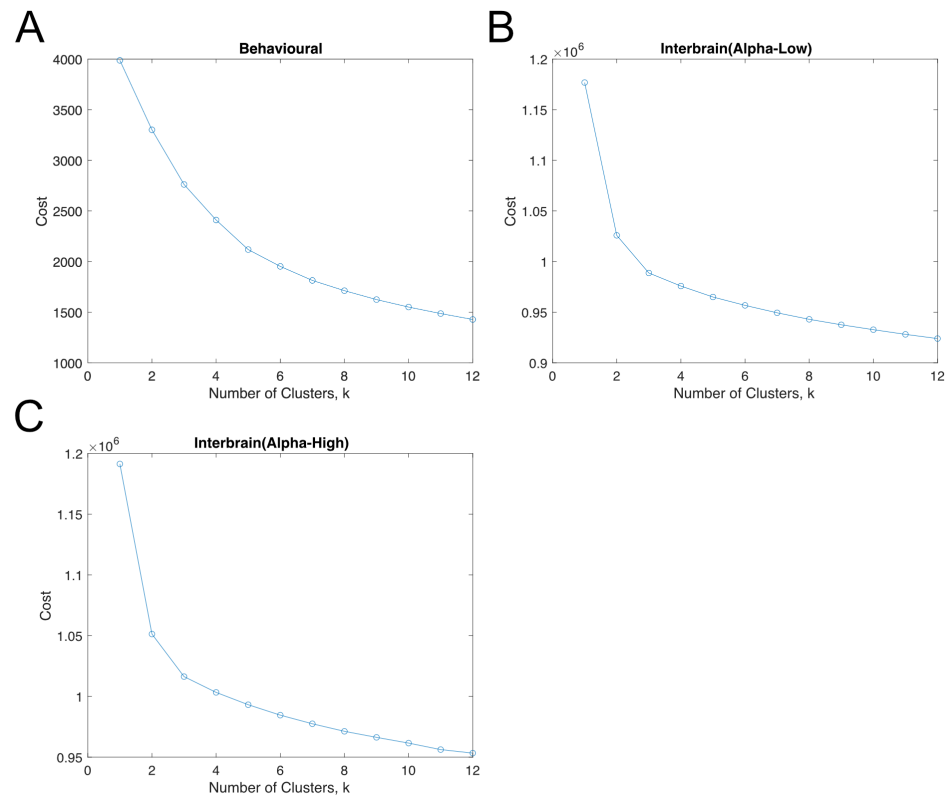
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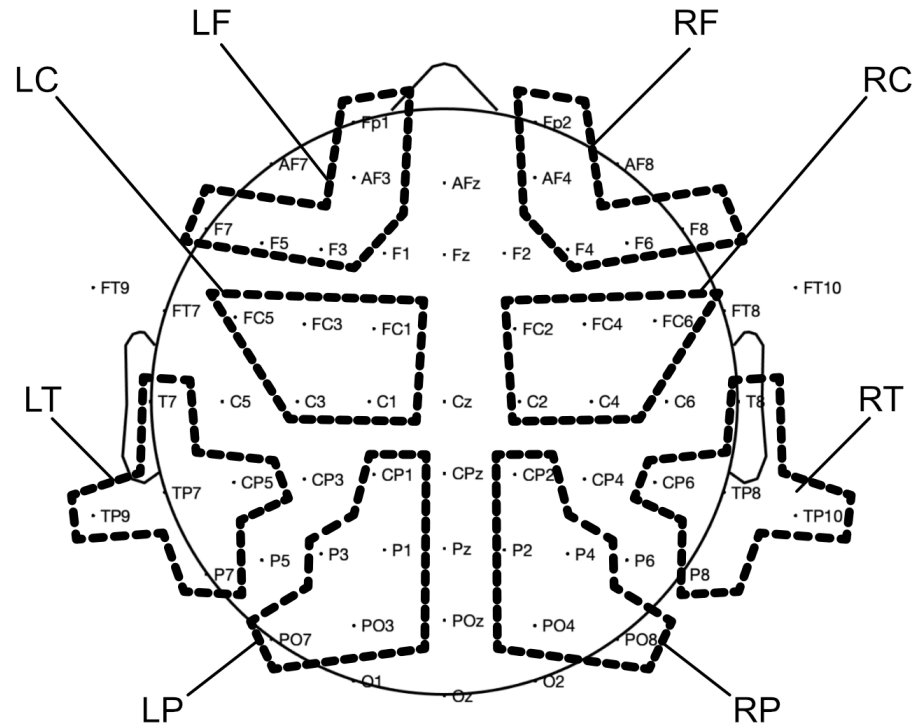
S2 Fig.

Example plot of behavioral data. (A) Avatar, shadow and static object positions of participant 1 and participant 2. Grey vertical lines mark 3-second windows; P1, participant 1; P2, participant 2; avatar, avatar position; shadow, shadow position; static, static object position. (B) Derived behavioral variables; DTW, dynamic time warping.



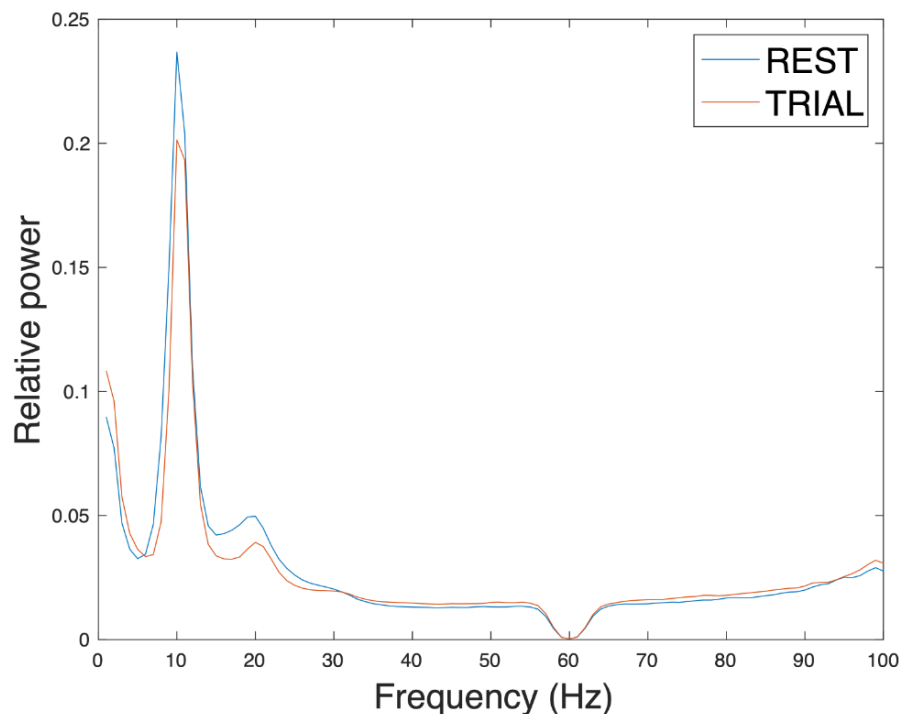
S3 Fig.

Elbow plots for the detection of the optimal number of clusters, k (A) Cost and k for the clustering of behavioral variables. The calculation of the optimal k could be understood as drawing a straight line from the first to the last point of the curve. The perpendicular distance from this line to the elbow curve was then calculated for each k. The optimal k was the k at which the perpendicular distance was maximum. Cost and k for the clustering of inter-brain patterns in the (B) Alpha-Low and (C) Alpha-High bands.

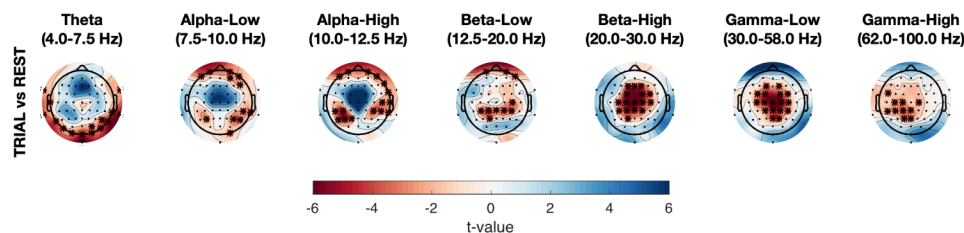


S4 Fig.

Regions of interest Head plot showing the grouping of 40 sensors into 8 regions of interests (ROIs); RF: Right Frontal; LF: Left Frontal; RC: Right Central; LC: Left Central; RT: Right Temporal; LT: Left Temporal; RP: Right Parietal; LP: Left Parietal.



S5 Fig. Relative Welch power spectral density for the 62 participants in the Perceptual Crossing Experiment, averaged over all epoch for resting phase and experimental trials. REST, resting phase; TRIAL, experimental trials.



S6 Fig. T-statistics of the differences in relative Welch power spectral density between resting phase and experimental trials. Asterisks(*) marked significant differences at a sensor and frequency band, tested using the MNE permutation cluster test. Dark red, TRIAL<REST; Dark blue, TRIAL>REST; REST, resting phase; TRIAL, experimental trials.

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