



Enhanced neural synchrony associated with long-term ballroom dance training

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ARTICLE INFO

Keywords:

Dance training

Neural similarity

Functional magnetic resonance imaging (fMRI)

Intersubject correlation (ISC)

Intersubject representational similarity analysis (ISRSA)

Frontal cortical-basal ganglia-thalamic circuits

ABSTRACT

Long-term dance training offers numerous benefits, including improvements in physical health, posture, body coordination, and mental health and well-being. Since dance is an art form of body-to-body communication, professional dancers may share feelings and thoughts on dance with their partners, owing to their shared training experiences. Considering this perspective, one may expect that professional dancers would demonstrate pronounced neural similarities when viewing dancing videos, which could be associated with their training duration. To test these hypotheses, we collected functional magnetic resonance imaging (fMRI) data while presenting ballroom dancing and neutral video clips with long durations (~100 s each) to 41 professional ballroom dancers (19 pairs of dance partners) and 39 age- and sex-matched nondancers. Our findings revealed that dancers exhibited broader and stronger neural similarities across the whole brain when watching dancing video clips, as compared to the control group. These increased neural similarities could be interpreted in at least two distinct ways. First, neural similarities in certain brain regions within the motor control circuit (i.e., frontal cortical-basal ganglia-thalamic circuit) were significantly correlated with dance-related information (e.g., dance partners' cooperation duration), which reinforced the impact of long-term dance training on neural synchronization. Second, neural similarities in other brain regions (e.g., memory-related brain regions) were significantly correlated with subjects' impression of the viewed videos (i.e., whether they have watched before, familiarity, and liking), which may not necessarily be directly linked to long-term dance training. Altogether, our study provided solid evidence for synchronized neural mechanisms in professional dancers due to long-term dance training.

1. Introduction

Dance is an expressive art form that involves real-time synchronization of coordinated body movements in response to perceived auditory patterns. It is a captivating and pleasurable activity that encompasses various aspects of human engagement, including motor skills, cognitive processing, visuospatial awareness, social interaction, and emotional expression (Burzynska et al., 2017; Hanggi et al., 2010). Although everyone may dance, professional dancers are well-trained in a particular form of dance and good at expressing emotional intentions using dance movements (Christensen et al., 2023). Long-term rigorous dance training would promote their coordination skills (Thullier and Moufti, 2004), esthetic awareness (Kirsch and Cross, 2018; Kirsch et al.,

2015), and abilities for the control of rhythmic movements (Miura et al., 2013). In line with these behavioral enhancements, recent neuroimaging studies have demonstrated that long-term dance training could lead to noticeable brain anatomical and functional alterations (Hanggi et al., 2010; Karpatei et al., 2017). For instance, dancers have exhibited increased brain volumes in the cingulate cortex, insula, and sensorimotor cortex (Rehfeld et al., 2018), as well as increased amplitudes of low-frequency resting-state functional magnetic resonance imaging (fMRI) fluctuations in the sensorimotor cortex (Lu et al., 2018), and enhanced resting-state functional connectivity in the cortico-basal ganglia loops (Li et al., 2015). Furthermore, professional dancers have shown greater activations in various brain areas, such as the premotor cortex, temporal cortex, and parahippocampal gyrus, when viewing

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<https://doi.org/10.1016/j.neuroimage.2023.120301>

Received 6 March 2023; Received in revised form 25 July 2023; Accepted 28 July 2023

Available online 29 July 2023

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dancing video clips of the dance form they have been trained in (Burzynska et al., 2017; Calvo-Merino et al., 2005).

Studies involving dancers often utilize video clips with a short duration (time length: 3–20 s) as stimuli. This choice is driven by the requirement of the traditional general linear model (GLM) analysis, which is the standard method to process fMRI data to isolate stimulus-induced signals from background noises and demands rapid alternations of stimulus on/off states (Lindquist and Wager, 2015). However, the use of short video clips has two important limitations. First, short video clips would inevitably activate brain responses that reflect transient changes of the stimuli but not associate with the video scene *per se*, e.g., the activation in the salience network (Seeley, 2019). Second, the short duration of the video clips would hamper the generation of a solid immersive experience, which is crucial to evoke strong and stable brain activations associated with the video scene. To address above issues, video clips with relatively longer durations (e.g., in a time scale of minutes) are required. Although the traditional GLM analysis could not be adopted, the analysis of fMRI data with long video clips could rely on a distinct statistical approach named intersubject correlation (ISC; Hasson et al., 2004; Kauppi et al., 2010; Nastase et al., 2019). ISC analysis is a model-free approach that can locate brain activations by assessing the similarities in hemodynamic responses across subjects (Hasson et al., 2004; Nastase et al., 2019). Since ISC analysis does not rely on *a priori* knowledge of the temporal composition of processes contributing to the measured signals, it has gained popularity in processing fMRI data collected in naturalistic environments, e.g., long video clips, yielding a series of novel findings (Bacha-Trams et al., 2018; Gruskin et al., 2020). For instance, ISC between two individuals during free viewing of naturalistic movies was found to be inversely related to their distance in real-world social networks (Parkinson et al., 2018). ISC between married couples while watching marital life-related movies predicted their marital satisfaction (Li et al., 2022). Additionally, highly central individuals exhibited higher neural similarities with others than less central individuals (Baek et al., 2022).

The ISC analysis strategy is also well suited for processing fMRI data when professional dancers view long dancing video clips to reveal neural mechanisms associated with the effect of long-term dance training. The application of ISC in the relevant field is well-established in literature. For example, Jola et al. (2013) investigated neural synchrony in both uni- and multi-sensory brain areas during watching unedited dance recordings. Similarly, Pollick et al. (2018) utilized ISC maps to define sensory and motor processing networks while participants viewed edited dance duets accompanied by a soundtrack. Additionally, Herbec et al. (2015) reported greater ISC for edited dance videos compared to unedited ones. Generally speaking, individuals who share similar feelings and interpretations of a viewed video would tend to exhibit synchronized neural responses, resulting in high neural similarities (Nguyen et al., 2019). Therefore, we proposed that compared to controls, professional dancers with similar dance training experiences would exhibit broader and/or higher neural similarities (i.e., more brain regions showing significant ISC and/or brain regions with higher ISC values) when viewing dancing video clips. Furthermore, the degree of neural similarity may increase with the amount of dancing practice. Specifically, professional duo dancers, such as ballroom dancers, who require coordination and emotional sharing during performances, are expected to demonstrate enhanced neural similarities as their paired training duration increases (i.e., positive correlations between ISC values and training durations) compared to random dancer pairs. Based on previous ISC studies on dance observation (Herbec et al., 2015; Jola et al., 2013; Pollick et al., 2018), we hypothesize that dancers would demonstrate superior neural synchrony in brain regions associated with motor and sensory processing, such as the precentral gyrus, postcentral gyrus, and temporal gyrus. Furthermore, given their familiarity with the movements in dancing videos and potentially prior exposure to these videos, as well as their heightened preference for dance content compared to control groups, we expect to observe significant neural

synchrony in memory-related and emotion-related brain regions for dancers, such as the hippocampal gyrus and prefrontal cortex (Sabatelli et al., 2011; Voss et al., 2019).

To examine these hypotheses, we conducted an fMRI experiment in which we presented four ballroom dancing video clips and four neutral video clips with relatively long durations (time length for each video clip: ~100 s) to 41 professional ballroom dancers (19 pairs of dance partners) and 39 age- and sex-matched nondancers. We applied the ISC analysis to investigate the impact of long-term dance training on neural synchrony, i.e., neural similarity, for ballroom dancers. Neural similarity, typically measured by calculating the correlation coefficients between pairs of participants, refers to the degree of correspondence or concordance in neural responses between different participants (Hasson et al., 2004). The relationships between ISC values and dance information (i.e., years of dance, years with dance partners, the number of dance partners, and the age started dancing) were examined to verify the impact of long-term dance training. In addition, intersubject representational similarity analysis (ISRSA; Chen et al., 2020; Nguyen et al., 2019), which is an extension of ISC, was employed to determine brain regions where the neural similarity reflected subjects' impression (e.g., degree of familiarity or preference) of the presented videos. Unlike ISC, which focuses on the correlation between pairs of participants, ISRSA relates ISC to individual traits and behaviors, operating at the level of single subjects. This is achieved by computing separate subject-by-subject distance matrices for brain data (e.g., ISC) and behavioral data, and then estimating the geometric relationships of these matrices using second-order isomorphism (Finn et al., 2020). The underlying principle is that individuals who exhibit greater behavioral similarity should also demonstrate greater similarity in their neural responses. The use of ISRSA analysis would be helpful in ruling out the possibility that the observed results associated with the long-term dance training were solely driven by the impression of the videos.

2. Methods

2.1. Participants

After excluding one male participant in the control group as his head motion exceeded 3 mm, a total of 80 healthy right-handed participants (41 professional ballroom dancers and 39 nondancers) were recruited from Beijing Sport University. All dancers have to meet the following criteria: (1) being listed as ballroom dancers by the Chinese Dance Sport Federation; (2) majoring in ballroom dancing in college; (3) having ballroom dancing experience for at least five years; (4) having participated in professional national dance sport competition at least once; and (5) practicing more than 10 h a week in the past three years. In contrast, the control group consisted of individuals who had no dancing experience or any other long-term professional kinematic training. All recruited participants had no history of neurological disorders, had normal or corrected-to-normal vision, had not consumed alcohol or coffee within 24 h before MRI scanning, and met all safety requirements for MRI. They have been provided informed consent prior to experiment and received monetary compensation for their participation. This study was approved by the Ethics Committee of the Institute of Psychology, Chinese Academy of Sciences.

2.2. Video clips

Four ballroom dancing video clips (time length for each video clip: 98–108 s) and four neutral video clips (time length for each video clip: 105–118 s) were meticulously selected and provided by the second author (Xiao Wang, a member of the China National DanceSport Professional team and an expert ballroom dancer who won many important accolades, such as the World Championship-quarterfinals, the Asian Single Dance Championship-2nd place, and the Chinese DanceSport Championship-2nd place). The dancing video clips present full

performances, from entrance to exit, featuring internationally renowned ballroom dancers Dmitry Zharkov and Olga Kulikova, in four styles (i.e., Quickstep, Waltz, Viennese Waltz, and Tango) in a world competition (WDSF GrandSlam Standard Finish Open 2018 Helsinki DanceSport Championships). Well-recognized prestigious dancers were selected to avoid judgment on the performance and reduce preference in dancing styles. Neutral video clips display natural scenes from four places (i.e., three in China: Beijing, Shenzhen, and Xinjiang; one in Germany) and predominantly show city buildings, forests, lakes, and hills etc. All video clips have high resolution and an inherent soundtrack to provide immersive enjoyment. Crucially, we did not perform any additional editing or cutting on the video clips to deliver a complete and immersive experience to the participants.

2.3. Experimental design

The whole experiment was composed of two separate runs (i.e., run 1 and run 2; Fig. 1A). Each run started with a 12 s rest, followed by four video clip blocks. During each video clip block, there was a 4 s prompt signaling the start of the video, three Likert scale rating tasks after playing the video (see below for details of the rating tasks), and a 20 s rest at the end of the block. The rest between successive blocks would help participants refocus their attention and maintain their concentration throughout the entire viewing session. The video clips were presented with the same order: Quickstep → Beijing → Waltz → Germany for run 1, and Viennese Waltz → Shenzhen → Tango → Xinjiang for run 2. Please note that we presented video clips in the same order for all participants to ensure consistency and eliminate potential confounds arising from variances in stimulus presentation (Baek et al., 2022;

Parkinson et al., 2018). This practice aligns with recommendations by Baek et al. (2022) and Parkinson et al. (2018), presenting video clips in the same sequential order during scanning would minimize the variability in neural responses that may result from differences in the presentation of stimuli rather than from inherent individual-level differences, specifically for the purpose of conducting ISC analysis (Chen et al., 2020). The three Likert scale ratings were as follows: (1) Have you watched this video clip before (0 = Have not watched it before; 1 = Not sure; 2 = Have watched it before)? (2) Are you familiar with the content in this video clip (0 = Very unfamiliar; 1 = Unfamiliar; 2 = Neutral; 3 = Familiar; 4 = Very familiar)? (3) Do you like this video clip (0 = Very dislike; 1 = Dislike; 2 = Neutral; 3 = Like; 4 = Very like)?

During the experiment, participants were instructed to passively watch video clips but attentively in a relaxing state. The stimuli were presented using a projector and a back-projection mirror mounted in the scanner suite. Participants shifted ratings using two buttons in their left hand and selected a rating using one button in their right hand. E-prime 2.0 (Psychology Software Tools Inc., USA) was used to control the presentation of video clips and record information of behavioral reactions.

For each rating task, a two-way mixed-design analysis of variance (ANOVA) with a within-subject factor (video type: dancing or neutral video clips) and a between-subject factor (participant type: dancer group or control group) was performed on normalized ratings (i.e., the mean ratings for each video type was normalized to the range from 0 to 1, by subtracting each participant's answer from the minimal score obtained and subsequently dividing it by the maximal score recorded across all participants on the same scale). If the data were normally distributed, parametric ANOVA analysis was conducted using the *pingouin* package (Vallat, 2018); if not, non-parametric ANOVA analysis was conducted

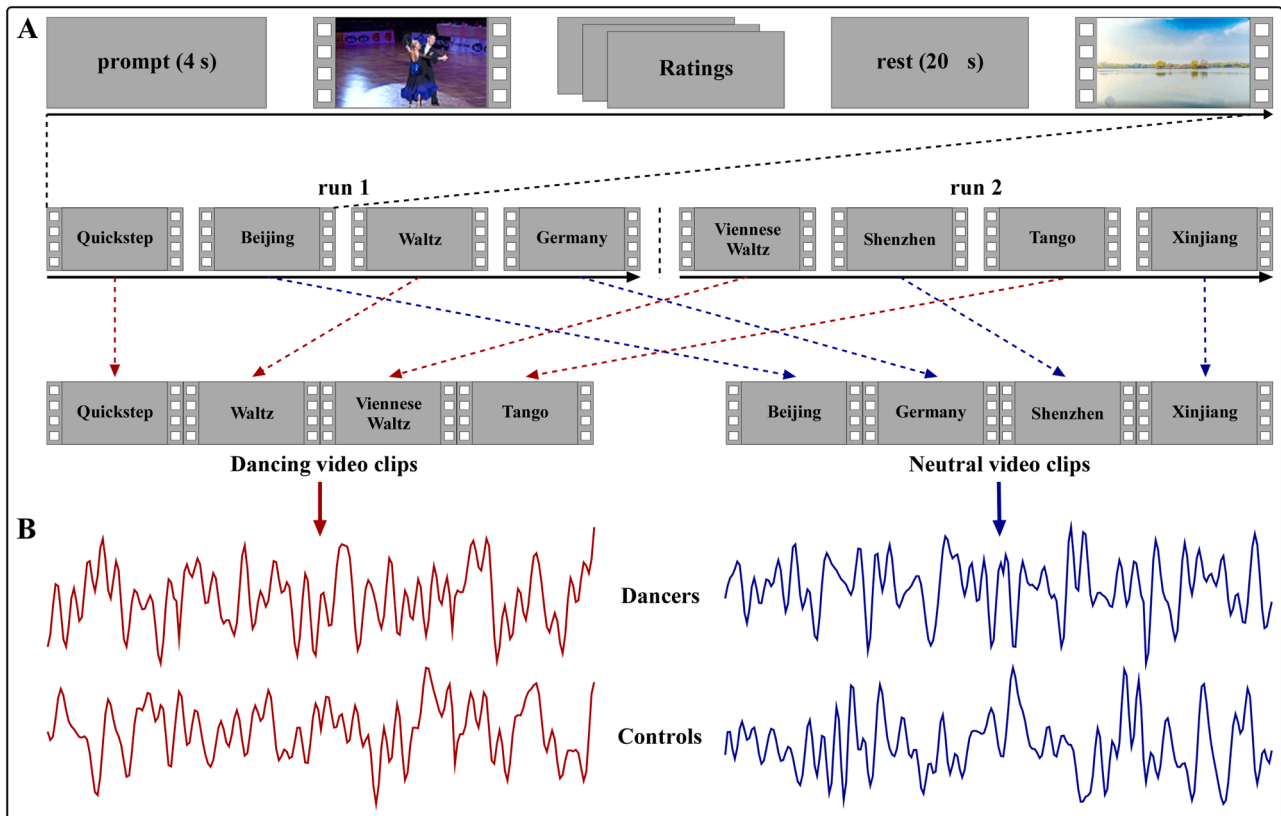


Fig. 1. The experimental flowchart and representative fMRI BOLD timeseries. (A) All participants viewed the same set of video clips in the same order, with two video types presented alternatively. Dancing video clips include four different dance styles (i.e., Quickstep, Waltz, Viennese Waltz, and Tango), and neutral video clips showcase natural scenes from four different places (i.e., Beijing, Germany, Shenzhen, and Xinjiang). (B) fMRI images collected when subjects viewed video clips were extracted and concatenated according to the video type. Mean BOLD timeseries for every subregion in Brainnetome Atlas were extracted for further data analyses.

using the *ARTool* package (Wobbrock et al., 2011). Additionally, rating differences for each video clip were assessed individually using statistical tests, either independent-sample t-tests or Mann-Whitney U tests, depending on the nature of the data and the assumptions of the tests.

2.4. MRI data acquisition

MRI data were collected using a 3T GE Discovery MR 750 scanner with an 8-channel head coil at the Magnetic Resonance Imaging Research Center, Institute of Psychology, Chinese Academy of Sciences, China. High-resolution T1-weighted structural images were obtained using a 3D SPGR sequence (192 sagittal slices, repetition time [TR] = 6.7 ms, echo time [TE] = 2.9 ms, flip angle [FA] = 12°, field of view [FOV] = 256 × 256 mm², voxel size = 1 × 1 × 1 mm³). Task fMRI images (run 1 and run 2) were obtained using an echo-planar imaging sequence (TR = 2000 ms, TE = 30 ms, FA = 90°, FOV = 224 × 224 mm², voxel size = 3.5 × 3.5 × 3.5 mm³, slices = 37, no slice spacing, interleaved slice ordering). The OptoActive™ active noise canceling headphones (Optoacoustics Ltd., Israel), which could actively reduce noise generated by the MRI scanner, were used to provide high-quality audio sounds.

2.5. MRI data preprocessing

Task fMRI images were preprocessed using Data Processing Assistant for Resting-State functional MRI toolbox (Yan and Zang, 2010) as follows: removed the first five volumes; slice timing; motion correction; regressed out nuisance regressors including Friston's 24 head motion parameters, white matter and CSF signals; regressed out an overall

linear trend; scaled all timeseries to mean; filtered with a bandpass of 0.01–0.1 Hz (Kauppi et al., 2010); adjusted T1 images to be parallel to anterior commissure – posterior commissure line; co-registered T1 images to functional images; segmented T1 images via the Diffeomorphic Anatomical Registration using Exponentiated Lie algebra (DARTEL; Ashburner, 2007) method with the East Asian template for affine regularization to obtain the nonlinear deformation field between native and Montreal Neurological Institute (MNI) space; normalized functional images to the standard MNI space with the deformation field; resampled voxel size into 3 × 3 × 3 mm³; and smoothed with a 6-mm full width half maximum (FWHM) Gaussian kernel. The maximal head motions were required to be within 3 mm translation and 3° rotation in any direction throughout the scanning for all participants, and outliers were subsequently excluded from further analyses.

The fMRI images while watching each video clip were extracted and then concatenated according to the video type (Fig. 1A), yielding in total 209 and 227 images for dancing video and neutral video, respectively. In this case, fMRI images collected during motor responses were not included in our data analysis, i.e., time intervals with motor-related activations were discarded. The mean timeseries from every subregion in the Brainnetome Atlas (Fan et al., 2016), which parcellates the brain into a total of 210 cortical areas and 36 subcortical regions based on their anatomical and functional connectivity patterns, were then extracted for further analysis (Fig. 1B).

2.6. Intersubject correlation analysis (ISC)

ISC analysis (Chen et al., 2020; Nastase et al., 2019; Nummenmaa et al., 2018) was performed using the python package *nltools* 0.4.7 from

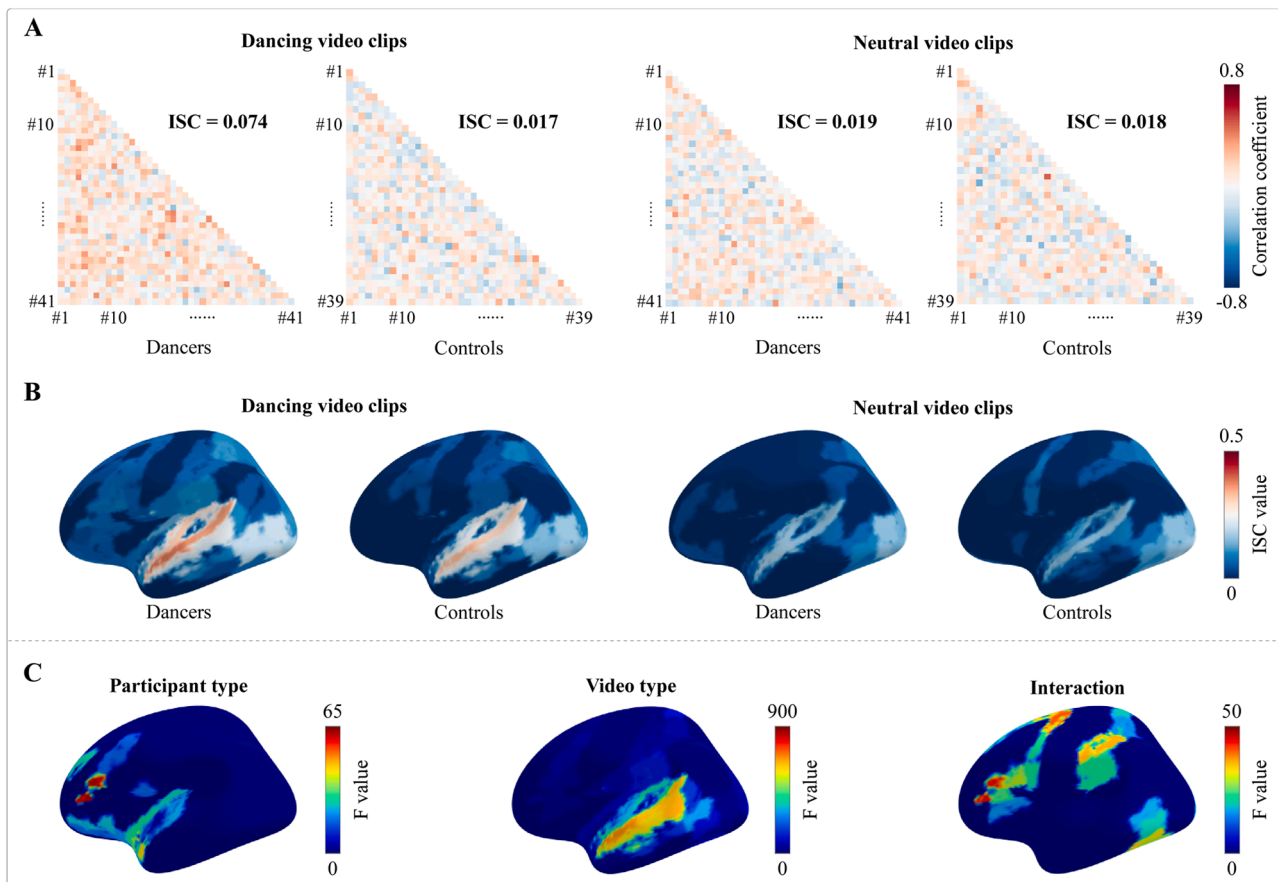


Fig. 2. Whole brain ISC results. (A) ISC similarity matrices (the lower triangle part) of a representative subregion (i.e., the left inferior frontal sulcus) at four different experimental conditions. (B) Whole brain ISC distributions in different experimental conditions. (C) Whole brain statistical results: *left*, the main effect of participant type; *middle*, the main effect of video type; and *right*, the interaction effect. Significance was declared if $p_{\text{bonf}} < 0.05$. ISC: intersubject correlation.

Cosan Lab (<https://cosanlab.github.io/nltools>). First, pairwise Pearson correlations between the timeseries of one participant and other participants were calculated to generate intersubject correlation matrices for each brain subregion (Fig. 2A) and each experimental condition, yielding 2 (dancer group and control group) $\times$ 2 (dancing and neutral video clips) $\times$ 246 (246 subregions) ISC matrices. The overall ISC value for each experimental condition was obtained by calculating the median of the lower triangle in each ISC matrix. The p -values were obtained by comparing the ISC value and the null distribution that was generated by subject-wise bootstrapping of the pairwise similarity matrix 10,000 times, and calculating the percentage of samples from the distribution that was less than the observed ISC value. It should be noted that the *nltools* toolbox converts the perfect correlations in bootstrapped pairwise similarity, caused by repeat resample, to NaNs to minimize these outliers on the summary statistic. Bonferroni correction was applied wherever multiple comparisons occurred, therefore significance was declared in the ISC analysis if $p < 0.0002$ ($0.05/246 \approx 0.0002$).

Two-way mixed-design ANOVA with a within-subject factor (video type: dancing and neutral video clips) and a between-subject factor (participant type: dancer group and control group) was performed on ISC values from all 246 subregions to evaluate the condition difference of the neural synchronization at the whole-brain level. Furthermore, the same two-way mixed-design ANOVA was performed on individual ISC values (i.e., the mean pairwise Pearson correlation coefficients between one participant and other participants) for each subregion. Post-hoc pairwise comparisons were performed to isolate subregions, in which (1) significantly higher neural similarities were observed for dancers than controls while watching dancing video clips, (2) no significant group difference was observed while watching neutral video clips, (3) significantly higher neural similarities for dancers was observed while watching dancing video clips than neutral video clips, and (4) no significant difference for controls was observed while watching the two types of video clips (Fig. 3A). Significance was declared in post-hoc analyses if $p < 0.05/\text{number of subregions showed significant interaction effects}$ (i.e., Bonferroni correction).

Moreover, a series of statistical analyses were performed on data collected from dancers while watching dancing video clips to further

assess the impact of long-term ballroom dance training. First, potential outliers were excluded using a criterion of three standard deviations from the mean. Bayesian correlation analyses were then performed to examine the relationship between individual ISC values and dance information (i.e., years of dance, years with dance partners, the number of dance partners, and the age started dancing). The Bayes factor (BF) explicitly provides evidence for or against the null hypothesis of no correlation. The interpretation of BF values was as follows: (1) 1–3.2: barely worth mentioning evidence for the alternative hypothesis; (2) 3.2–10: substantial evidence; (3) 10–100: strong evidence; (4) >100: decisive evidence; and (5) <1: substantial evidence for the null hypothesis (SamPenDu, 2015). Second, an independent-sample t -test was performed to compare ISC values of dance partners (i.e., the correlation coefficient between one male dancer and his dance partner) and the mean ISC values between one male dancer and all other female dancers to assess whether the neural similarity between dance partners would be superior to other random pairs. Third, Bayesian correlation analysis was conducted to assess the possible correlation between ISC values of dance partners and their cooperation duration (in years).

Furthermore, we conducted ISC analysis on an individual basis for each video clip. This involved estimating the ISC values for each video clip and participant, and then calculating the mean ISC values for each type of video clip (i.e., ballroom dancing video and neutral video). This procedure generated an ISC matrix for each experimental condition, consisting of 2 (dancer group and control group) $\times$ 2 (dancing and neutral video clips) conditions. These ISC matrices were subjected to the same statistical analyses as described previously.

2.7. Intersubject representational similarity analysis (ISRSA)

To assess whether the neural similarity could be affected by subjects' impression of the presented video clips, ISRSA (Chen et al., 2020; Gruskin et al., 2020; van Baar et al., 2019) was performed to compare the ISC matrices with rating similarity matrices using second-order statistics akin to representational similarity analysis (Finn et al., 2020; Kriegeskorte and Kievit, 2013; Kriegeskorte et al., 2008). The *nltools* was also used for performing ISRSA analysis. The rating similarity matrices

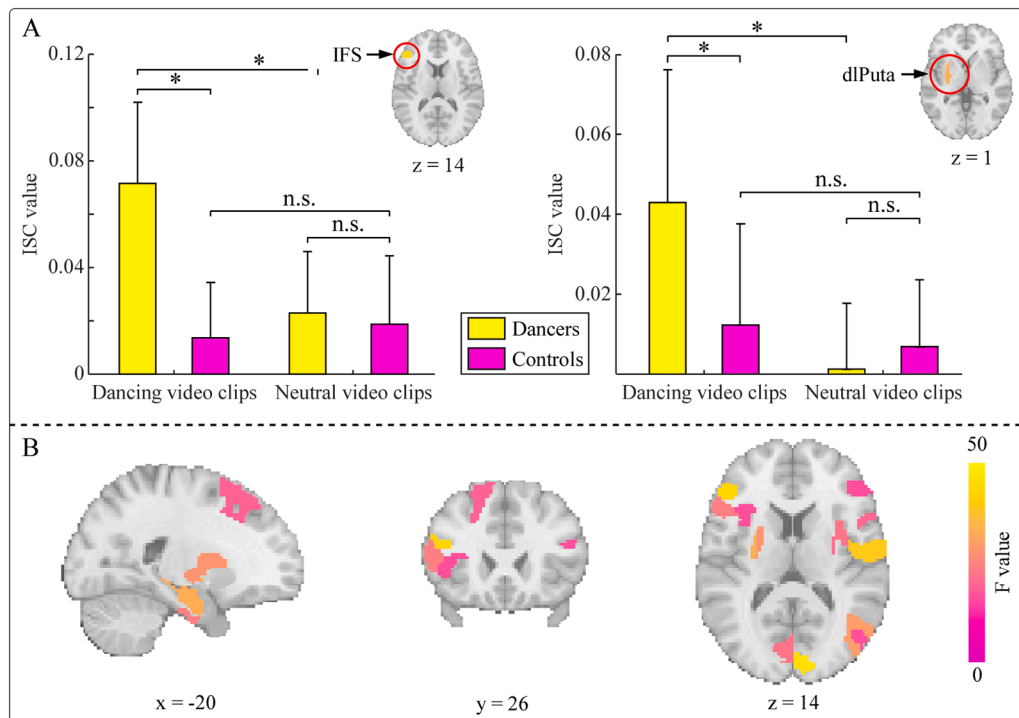


Fig. 3. Brain regions with ISC values showing significant interactions. (A) The comparisons of ISC values among experimental conditions in the left IFS (left) and left dorsolateral putamen (right). (B) Brain subregions with (1) significantly higher neural similarities for dancers than controls while watching dancing video clips, (2) no significant group difference while watching neutral video clips, (3) significantly higher neural similarities for dancers while watching dancing video clips than neutral video clips, and (4) no significant difference for controls while watching the two types of video clips. ISC: intersubject correlation; IFS: inferior frontal sulcus; dlPut: dorsolateral putamen; n.s.: not significant; *: $p_{\text{bonf}} < 0.05$.

were generated using the Anna Karenina (AnnaK) model (Finn et al., 2020) to test the prediction that people who score high on a given rating scale share similar patterns of brain activity, while those who score lower demonstrate greater variability. The AnnaK model, derived from the famous opening line of Leo Tolstoy's novel, characterizes similarity by employing a metric that reflects the absolute position on the scale. In our study, we adopted a ranking approach to assess scores and measure similarity between two subjects by calculating the normalized mean value of their respective ranks. Consequently, a higher AnnaK score indicates that both subjects occupy higher positions in the ranking.

Specifically, 246 ISC matrices were obtained from all participants, and three pairwise rating similarity matrices (i.e., whether they have watched before, familiarity, liking) were constructed. Only the video type in which ratings showed significant group differences was considered in ISRSA. Spearman correlation analysis between each of the ISC matrices and each of the rating similarity matrices was performed, for a total of 246×3 times. Subject labels were randomly permuted for one of the two similarity matrices 10,000 times, and the correlation coefficients between the two matrices were recalculated to generate a null distribution. The p -values were obtained by comparing the real correlation coefficients and the null distribution. Significance was declared in ISRSA analyses if $p < 0.0002$ ($0.05/246 \approx 0.0002$).

3. Results

3.1. Demographic information and behavioral results

In total, 41 dancers (21 males, age: 21.78 ± 2.36 , 19 pairs of dance partners plus two single males and one single female) and 39 controls (19 males, age: 21.00 ± 2.14) were included in the final analyses (Table 1). There were no significant differences in age ($t[78] = 1.55$, $p = 0.126$) or years of education ($t[78] = 1.16$, $p = 0.249$) between dancers and controls.

Normalized ratings about the impression of the video clips were summarized in Table 2. Overall, 7 dancers and 27 controls reported that they had not viewed any of the four dancing video clips; 37 dancers and 37 controls reported that they had not watched any of the four neutral video clips. Q-Q plot showed that the ratings of 'whether have watched before' were not normally distributed. Two-way mixed-design ANOVA showed a significant interaction between the two factors (i.e., video type and participant type) (Table S1; $F[1,78] = 93.67$, $\eta^2_p = 0.55$, $p < 0.001$). Non-parametric Mann-Whitney U tests showed significant differences between dancers and controls when watching dancing video clips ($z = 6.13$, $p < 0.001$) but not neutral video clips ($z = 0.20$, $p = 0.842$). Moreover, non-parametric Mann-Whitney U tests revealed that there were significant differences between dancers and controls for different dancing video clips (Table S2). However, no significant differences were observed between dancers and controls for each neutral video clip

Table 1
Demographic data and dance information (mean $\pm$ standard deviation).

	Dancers ($n = 41$)	Controls ($n = 39$)	t	p value
Sex (male/female)	21/20	19/20		
Age (year)	21.78 ± 2.36	21.00 ± 2.14	1.55	0.126
Education (year)	15.15 ± 2.03	14.67 ± 1.63	1.16	0.249
Years of dance	8.93 ± 2.21			
Years with dance partners	8.33 ± 1.84			
The number of dance partners	3.17 ± 1.48			
The age started dancing	10.61 ± 2.82			

Years of dance refer to the duration of dance training for dancers, including basic training without a fixed dance partner and official training with a fixed dance partner; years with dance partners refer to the number of years that the dancer has officially danced with a fixed partner; the number of dance partners refers to the number of fixed partners with which the dancer has danced.

Table 2

Ratings on the video clips and the whole brain ISC values (mean $\pm$ standard deviation) in different experimental conditions.

	Dancers ($n = 41$)		Controls ($n = 39$)	
	dancing clips	neutral clips	dancing clips	neutral clips
Ratings on the video clips				
Whether have watched before	0.62 ± 0.35	0.04 ± 0.10	0.10 ± 0.14	0.03 ± 0.07
Familiarity	0.70 ± 0.17	0.28 ± 0.16	0.34 ± 0.20	0.34 ± 0.21
Liking	0.81 ± 0.15	0.57 ± 0.17	0.60 ± 0.16	0.67 ± 0.15
Mean whole-brain ISC value	0.08 ± 0.07	0.04 ± 0.05	0.06 ± 0.07	0.04 ± 0.05

(Table S2).

Q-Q plot illustrated that the ratings of familiarity and liking were nearly normally distributed. Two-way mixed-design ANOVA also showed significant interactions between the two factors (Table S1; familiarity: $F[1,78] = 83.30$, $\eta^2_p = 0.52$, $p < 0.001$; liking: $F[1,78] = 39.65$, $\eta^2_p = 0.34$, $p < 0.001$). Post-hoc pairwise t-tests showed significant differences between dancers and controls when watching dancing video clips (familiarity: $t[74.50] = 8.45$, $p < 0.001$; liking: $t[76.63] = 6.11$, $p < 0.001$). Significant differences were also observed for dancers when they were watching dancing video clips and neutral video clips (familiarity: $t[40] = 13.09$, $p < 0.001$; liking: $t[40] = 6.59$, $p < 0.001$). In addition, neutral video clips were more liked in the control group than in the dancer group ($t[77.65] = -2.64$, $p = 0.010$) and were more liked than dancing video clips for controls ($t[38] = -2.04$, $p = 0.048$), likely attributable to the beautiful natural scenes depicted in the neutral video clips. Independent-sample t-tests revealed significant differences between dancers and controls for each dancing video clip (Table S2). Additionally, significant differences were observed between dancers and controls for familiarity and liking ratings of certain neutral video clips. Specifically, the neutral video clips exhibiting Beijing showed significant group differences in familiarity ($t[78] = -2.54$, $p = 0.013$) and liking ($t[40] = -2.76$, $p = 0.007$). Similarly, the neutral video clips exhibiting Xinjiang demonstrated a significant difference in liking between the two groups ($t[78] = -2.18$, $p = 0.033$) (Table S2). No other significant differences were observed (all $p > 0.05$).

3.2. Intersubject correlation results

Whole-brain ISC values showed a significant main effect for video type ($F(1, 490) = 202.60$, $\eta^2_p = 0.29$, $p < 0.001$) and a significant interaction effect ($F(1, 490) = 49.16$, $\eta^2_p = 0.09$, $p < 0.001$). The main effect for participant type was marginally significant ($F(1490) = 3.88$, $\eta^2_p = 0.01$, $p = 0.050$). Post-hoc pairwise comparisons showed that both dancers ($t(245) = 14.28$, $p < 0.001$) and controls ($t(245) = 5.40$, $p < 0.001$) had higher neural similarity when they were viewing dancing video clips than neutral video clips. Moreover, dancers showed higher neural similarity than controls when they were watching dancing video clips ($t(490) = 3.62$, $p < 0.001$), but not for neutral video clips ($t(490) = -0.54$, $p = 0.593$), which resulted in the marginal significance for the main effect of participant type.

The bootstrapping test revealed that in total 175 (Fig. 2B, the first plot), 100 (Fig. 2B, the second plot), 80 (Fig. 2B, the third plot), 84 (Fig. 2B, the fourth plot) out of 246 subregions showed significant neural synchronization (i.e., ISC values) for dancers and controls when viewing dancing and neutral video clips, respectively. High ISC values were predominantly observed in the primary visual cortex and temporal cortex across all four conditions, while dancers viewing dancing video clips showed wider neural synchrony in more subregions, such as the frontal gyrus, precentral gyrus, postcentral gyrus, insular gyrus,

amygdala, and basal ganglia. Among all the observed ISC values, the highest ISC value of 0.45 was found in the right rostral superior temporal gyrus when dancers viewed dancing video clips. Two-way mixed-design ANOVA performed for each subregion showed that 32, 137, and 61 subregions had significant main effects for participant type and video type, and significant interaction, respectively (Fig. 2C). A significant main effect for participant type was mainly observed in the frontal gyrus (i.e., the right medial superior frontal gyrus area 10, bilateral dorsal middle frontal gyrus, left inferior frontal junction, middle frontal gyrus area 46, and left inferior frontal sulcus), superior temporal gyrus, amygdala, hippocampus, and parahippocampal gyrus; a significant main effect for video type was mainly observed in the temporal and parietal gyrus; and a significant interaction was mainly observed in the inferior frontal gyrus (IFG), precentral and postcentral gyrus, and inferior parietal lobule. Post-hoc pairwise comparisons revealed that 28 subregions, with (1) significantly higher neural similarities for dancers than controls while watching dancing video clips, (2) no significant

group difference while watching neutral video clips, (3) significantly higher neural similarities for dancers while watching dancing video clips than neutral video clips, and (4) no significant difference for controls while watching the two types of video clips (Fig. 3B& Tables 3 & S3). Those subregions were mainly situated in bilateral IFG, parahippocampal gyrus, and basal ganglia.

In the additional ISC analysis conducted on each individual video clip, we observed some ISC differences among different videos (Fig. S1). However, when examining the results using mean ISC values for each condition, we observed consistent ISC outcomes and statistical results between the previous concatenated analysis approach and the current itemized analysis approach (Fig. S2).

For dancers, Bayesian correlation analyses revealed positive correlations of individual ISC values with the number of partners in the right rostradorsal inferior parietal lobule ($r = 0.42$, $BF = 5.05$) and with the age started dancing in the right lateral amygdala ($r = 0.42$, $BF = 4.89$). Moreover, negative correlations of individual ISC values were observed

Table 3

Brain regions with ISC values showing significant interactions between the factors ‘participant type’ and ‘video type’.

Brain subregions	Hemi	MNI			Participant type × video type			Dancing clips		Dancer group	
		x	y	z	F	p_{bonf}	η_p^2	t	p_{bonf}	t	p_{bonf}
Superior Frontal Gyrus (dorsolateral area 8)	L	−18	24	53	19.11	< 0.05	0.20	3.84	< 0.05	4.32	< 0.05
Inferior Frontal Gyrus (dorsal area 44)	L	−46	13	24	29.07	< 0.05	0.27	4.18	< 0.05	7.23	< 0.05
Inferior Frontal Gyrus (inferior frontal sulcus)	L	−47	32	14	43.62	< 0.05	0.36	9.94	< 0.05	8.16	< 0.05
Inferior Frontal Gyrus (inferior frontal sulcus)	R	48	35	13	15.97	< 0.05	0.17	4.19	< 0.05	9.06	< 0.05
Inferior Frontal Gyrus (caudal area 45)	L	−53	23	11	24.08	< 0.05	0.24	4.75	< 0.05	6.42	< 0.05
Inferior Frontal Gyrus (opercular area 44)	L	−39	23	4	16.09	< 0.05	0.17	4.26	< 0.05	7.51	< 0.05
Inferior Frontal Gyrus (ventral area 44)	R	54	14	11	19.86	< 0.05	0.20	4.36	< 0.05	5.14	< 0.05
Orbital Gyrus (medial area 14)	L	−7	54	−7	21.77	< 0.05	0.22	5.25	< 0.05	5.84	< 0.05
Orbital Gyrus (medial area 11)	L	−6	52	−19	20.69	< 0.05	0.21	4.57	< 0.05	6.29	< 0.05
Parahippocampal Gyrus (rostral area 35/36)	R	28	−8	−33	20.82	< 0.05	0.21	4.31	< 0.05	6.03	< 0.05
Parahippocampal Gyrus (entorhinal cortex)	L	−19	−12	−30	23.93	< 0.05	0.23	6.59	< 0.05	6.30	< 0.05
Parahippocampal Gyrus (entorhinal cortex)	R	19	−10	−30	31.57	< 0.05	0.29	7.09	< 0.05	6.16	< 0.05
Parahippocampal Gyrus (temporal agranular insular cortex)	R	22	1	−36	28.93	< 0.05	0.27	5.03	< 0.05	5.10	< 0.05
Parahippocampal Gyrus (medial area)	R	19	−36	−11	32.26	< 0.05	0.29	4.30	< 0.05	7.28	< 0.05

Brain regions	Hemi	MNI			Participant type × video type			Dancing clips		Dancer group	
		x	y	z	F	p_{bonf}	η_p^2	t	p_{bonf}	t	p_{bonf}
Inferior Parietal Lobule (caudal area 39)	R	45	−71	20	29.34	< 0.05	0.27	5.36	< 0.05	11.86	< 0.05
Precuneus (medial area 7)	L	−5	−63	51	32.18	< 0.05	0.29	6.27	< 0.05	5.56	< 0.05
Precuneus (medial area 7)	R	6	−65	51	43.93	< 0.05	0.36	5.49	< 0.05	10.77	< 0.05
Postcentral Gyrus (area 1/2/3)	R	56	−10	15	39.26	< 0.05	0.33	4.49	< 0.05	8.10	< 0.05
Postcentral Gyrus (area 2)	R	48	−24	48	45.60	< 0.05	0.37	6.48	< 0.05	9.02	< 0.05
Insular Gyrus (dorsal dysgranular insula)	R	38	5	5	21.95	< 0.05	0.22	3.67	< 0.05	5.07	< 0.05
Cuneus (rostral cuneus gyrus)	L	−5	−81	10	22.20	< 0.05	0.22	5.05	< 0.05	10.38	< 0.05
Cuneus (caudal cuneus gyrus)	R	8	−90	12	45.97	< 0.05	0.37	6.07	< 0.05	6.17	< 0.05
Occipital Cortex (area V5/MT+)	R	48	−70	−1	16.01	< 0.05	0.17	4.71	< 0.05	6.14	< 0.05
Hippocampus (rostral area)	L	−22	−14	−19	32.65	< 0.05	0.30	7.40	< 0.05	6.85	< 0.05
Basal Ganglia (globus pallidus)	L	−22	−2	4	27.96	< 0.05	0.26	4.85	< 0.05	7.74	< 0.05
Basal Ganglia (ventromedial putamen)	R	22	8	−1	28.96	< 0.05	0.27	5.36	< 0.05	10.06	< 0.05
Basal Ganglia (dorsal putamen)	L	−28	−5	2	33.38	< 0.05	0.30	4.64	< 0.05	8.76	< 0.05
Basal Ganglia (dorsal putamen)	R	29	−3	1	20.01	< 0.05	0.20	4.62	< 0.05	6.20	< 0.05

The columns under the “Dancing clips” and “Dancer group” summarized the post-hoc results comparing dancers vs. controls while viewing dancing video clips and comparing dancing vs. neutral video clips for dancers, respectively. Specifically, these brain subregions showed significantly higher neural similarities (1) for dancers than controls while watching dancing video clips and (2) for dancers while watching dancing video clips than neutral video clips. Brain subregions were named after Brainnetome Atlas. Hemi: hemisphere.

with years of dance in the left occipital thalamus ($r = -0.40$, $BF = 3.53$) and with the age started dancing in the right caudal cuneus gyrus ($r = -0.40$, $BF = 3.64$; Fig. 4A). Please refer to Chen et al. (2021) for details regarding the subregions of the thalamus. Independent-sample t -test showed that neural similarity between the 19 pairs of dance partners was not superior to other random pairs in any subregion (all $p > 0.05$). However, Bayesian correlation analysis revealed that ISC values between pairs of dance partners and their cooperation duration (in years) were positively correlated in the left globus pallidus ($r = 0.56$, $BF = 3.76$; Fig. 4B).

3.3. Intersubject similarity representational results

Since significant group differences were mainly observed in ratings when viewing dancing video clips, data for this video type were used in the ISRSA analysis (Fig. 5). Variations in ‘whether have watched before’ ratings were reflected in the left inferior frontal sulcus ($r = 0.13$, $p < 0.05$). Variations in ‘familiarity’ ratings were reflected in the left rostral hippocampus ($r = 0.14$, $p < 0.05$), right parahippocampal gyrus (entorhinal cortex; $r = 0.13$, $p < 0.05$), and left intermediate ventral inferior temporal gyrus (ITG; $r = 0.09$, $p < 0.05$). Variations in ‘liking’ ratings were reflected in the right medial superior frontal gyrus ($r = 0.16$, $p < 0.05$), left ventral IFG ($r = 0.11$, $p < 0.05$), and left precentral gyrus (tongue and larynx region; $r = 0.11$, $p < 0.05$). In all these subregions analyzed, significantly higher neural similarity was consistently observed in dancers than in controls when viewing dancing video clips.

4. Discussion

In this study, we investigated the impact of long-term ballroom dancing on neural synchrony among dancers, and we obtained three main findings. First, dancers showed wider and stronger neural similarities across the whole brain, especially in bilateral IFG, parahippocampal gyrus, and basal ganglia, when watching dancing video clips than controls did. Second, neural similarities were significantly correlated with dance information in regions within the frontal cortical-basal ganglia-thalamic circuits (Alexander, 1994; Lehericy et al., 2006), e.g., correlations between ISC values between pairs of dance partners and their cooperation duration in the left globus pallidus. Third, neural similarities in certain brain regions were associated with subjects’ impression (i.e., whether they have watched before, familiarity, liking)

of the viewed videos, e.g., variations in ‘familiarity’ ratings were reflected in the left rostral hippocampus, right parahippocampal gyrus, and left ITG. Correlations with these two sets of behavioral data suggested that the effect of long-term dance training could be mainly reflected by neural synchrony in the frontal cortical-basal ganglia-thalamic circuits, as the influence of the video impression on neural synchrony, although including part of the frontal region, was mainly observed in other (e.g., memory related) brain regions. Altogether, our study provided novel and solid evidence for synchronized neural mechanisms in professional dancers due to long-term dance training.

4.1. Difference in neural similarities between dancers and controls

Long-term dance training can enhance the perception and prediction of the skilled actions (Abernethy and Zawi, 2007; Calvo-Merino et al., 2005; Cheung and Bar, 2012), as well as improve esthetic perception (Kirsch and Cross, 2018; Kirsch et al., 2015) and the control of rhythmic movements (Miura et al., 2013). In other words, professional dancers are able to detect some micro-movements, anticipate future movement, experience a deeper level of appreciation, and even “dance” with the dancer in their own brains. Therefore, it is reasonable to expect that dancers would exhibit higher levels of neural synchrony in comparison to controls when they are processing dancing-related information. As expected, we showed that the neural activities of dancers were more synchronized than controls when watching dancing video clips, but not when viewing neutral video clips. In particular, the enhanced neural synchrony was mainly observed in the bilateral IFG, parahippocampal gyrus, and basal ganglia (Table 3). Interestingly, our observation was strikingly similar with the findings reported in a previous study (Cross et al., 2006), which recorded weekly neural changes in dancers as they learned and rehearsed novel and complex dance sequences over the course of 5 weeks. It was found that activities in the left inferior parietal lobule, IFG and parahippocampal gyrus was modulated as a function of dancers’ ratings of their own ability to perform the observed movements and their motor experience.

The IFG, a key component of the human mirror-neuron system (Rizzolatti and Craighero, 2004), was often found to be significantly activated during sensory observation (Engel et al., 2008; Zhou et al., 2022). It has been found to decode intentions from subtle kinematic features (Koul et al., 2018) and integrate contextual information into

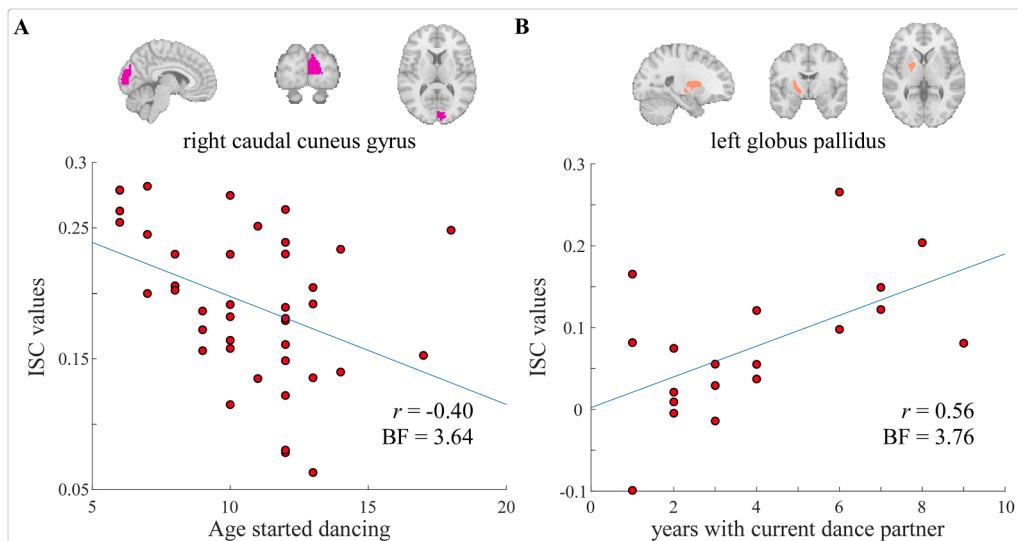


Fig. 4. Correlations between ISC values and dance information for dancers. (A) Individual ISC values were negatively correlated with the age started dancing in the right caudal cuneus. (B) Paired ISC values between dance partners were positively correlated with the duration of their cooperation (in years) in the left globus pallidus. ISC: intersubject correlation; BF: Bayes factor.

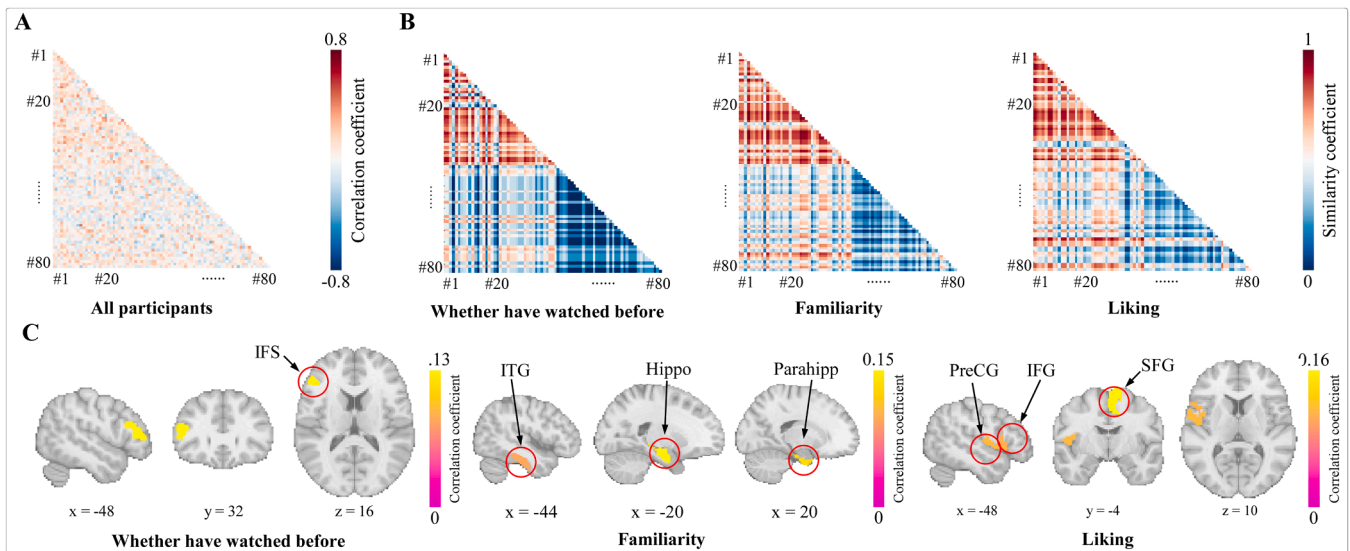


Fig. 5. Whole brain ISRSA results. (A) ISC matrix of all participants in the left inferior frontal sulcus while viewing dancing videos. (B) Rating similarity matrices obtained using the AnnaK model. (C) Brain subregions with rating similarity reflecting neural similarity. Specifically, rating similarity on ‘whether have watched before’ was reflected in the left IFS (left); ‘familiarity’ rating similarity was reflected in the left rostral hippocampus, right parahippocampal gyrus (entorhinal cortex), and left intermediate ventral ITG (middle); ‘liking’ rating similarity was reflected in the right medial SFG, left ventral IFG, and left precentral gyrus (tongue and larynx region) (right). Significance was declared if $p_{\text{bonf}} < 0.05$. ISC: intersubject correlation; ISRSA: intersubject representational similarity analysis; IFS: inferior frontal sulcus; ITG: inferior temporal gyrus; Hippo: hippocampus; Parahippo: parahippocampal gyrus; PreCG: precentral gyrus; IFG: inferior frontal gyrus; SFG: superior frontal gyrus.

motion prediction (El-Sourani et al., 2020). Apart from its role in motor processing, the IFG is involved in various other functions. A meta-analysis investigating the spatio-functional diversity of the IFG identified four distinct clusters (Liakakis et al., 2011). In the left hemisphere, these clusters are associated with empathy processing, semantic and phonological processing, and working memory, respectively, while the cluster in the right hemisphere is related to movement control. Our results align closely with the clusters associated with semantic and phonological processing, working memory, and movement control. The high neural similarities observed in the IFG of ballroom dancers may stem from their extensive training in performing basic body movements and synchronizing with movements/soundtracks from the early stages of their training. As a result, it is not surprising that professional dancers are able to mirror dance movements in their brains in a more similar way, as their neural networks have been shaped by their dance training.

The parahippocampal gyrus, located inferior to the hippocampus, is associated with episodic memory related to associative memory, source memory, and processing of emotional stimuli (Aminoff et al., 2013). Previous studies showed that exercise, such as dancing, has significant effects on the parahippocampal gyrus, represented as increased neural excitability and increased volume of gray/white matter (see Loprinzi 2019 for a review). It is possible that the dancing video clips actively activated the dancers’ past dancing experiences, which were encoded in the parahippocampal gyrus, along with the emotions embedded in the dance. Therefore, the increased neural similarity observed in the parahippocampal gyrus while viewing dancing video clips could be attributed to the dancers’ retrieval of their past experiences and emotions related to the dance.

The basal ganglia, especially putamen (i.e., bilateral dorsal putamen and right ventromedial putamen), also showed strong neural synchrony while watching dancing video clips. This could be attributed to the rhythm of dance, as previous studies have shown that bilateral putamen was significantly activated when listening to beat rhythmic stimuli (Grahn and Brett, 2007, 2009). Further research by Grahn and Rowe (2013) confirmed that putamen was responsible for predicting the internal generation of the beat, rather than simply detecting the beat. In the present study, it is likely that the professional dancers were much

more familiar with the rhythm of the dance and were better able to predict the beat in a similar manner. As a result, the putamen would have been activated similarly for dancers due to their ability to anticipate and generate the rhythmic patterns of the dance in a similar way. Alternatively, the activation observed in the basal ganglia can be attributed to the fact that, for dancers, dance movements become well-established motor routines. This implies that during the observation of dance performances, a form of simulation of the performance takes place, which is typically implemented through the basal ganglia-thalamo-cortical loops (Alexander et al., 1986; Calvo-Merino et al., 2005).

4.2. The effect of long-term dance training on neural similarities

While we observed enhanced neural synchrony in several brain regions when dancers viewed dancing video clips, it is possible that these findings are not solely related to the effect of long-term dance training. To investigate the specific neural effects of dance training, we performed correlation analyses between individual ISC values and dance-related information. We observed a positive correlation between the age at which individuals began dancing and neural similarity in the right caudal cuneus gyrus of the visual network. This finding may suggest that dancers who started dancing at a younger age exhibited more similar patterns of primary visual processing when observing dance video. However, it is important to note that the correlations with dance practice in our study were not particularly robust. As a result, these findings may require additional evidence to firmly support the drawn conclusions.

The left globus pallidus, another subregion in the basal ganglia, showed high neural similarity among all dancers, with increased similarity between dance partners as their cooperation prolonged. Previous studies have demonstrated that the globus pallidus plays a crucial role in controlling conscious and proprioceptive movements (Javed and Cascella, 2022) and in supporting the sensorimotor process involved in kinematic adaption (Seidler et al., 2006). Our result further suggests that the left globus pallidus may also contribute to the control of the movement, e.g., when to turn or wiggle, rather than the movement *per se*. This

is supported by the fact that male and female dancers would perform different body movements, although their movements become increasingly coordinated with prolonged cooperation.

Notably, we did not observe a significant difference in neural similarities between pairs of dance partners and random pairs. This finding could be attributed to the fact that all participants in our study were professional ballroom dancers with long-term training (mean training duration: 8.93 ± 2.21 years). It is possible that these dancers had already reached a high level of expertise, resulting in a ceiling effect where their neural responses to dancing videos were highly synchronized, regardless of whether the neural similarities were assessed between paired partners or random pairs. To further investigate the relationship between neural synchrony and paired training, it may be advantageous to consider using a different participant sample with variations in skills, such as comparing high-level ballroom dancers with low-level ballroom dancers. This approach may help provide more insights into the specific neural mechanisms underlying the coordination and synchronization observed between dance partners.

4.3. The influence of video impression on neural similarities

To isolate brain activities that may not be necessarily related to long-term dance training, we conducted ISRSA to explore the relationship between neural similarities and the subjects' impressions of the viewed videos. We observed that neural similarities in some other brain regions reflected participants' impressions of the videos (i.e., whether they have watched before, familiarity, liking). Variations in 'whether have watched before' were reflected in the left inferior frontal sulcus, where participants who were more likely to have seen the videos before displayed stronger neural synchrony. This brain region is implicated in various cognitive functions, including cognitive control, working memory, semantic processing, and etcetera (Guenther et al., 2015; Ruland et al., 2022). Participants who were more familiar with the dancing video clips showed higher neural similarity in the left rostral hippocampus, right parahippocampal gyrus, and left ITG. Since the hippocampus is a traditional brain region for memory retrieval (Voss et al., 2019) and the ITG is responsible for object representations (Ranganath, 2006), our findings suggest that people who were more familiar with the video content could interpret it and retrieve relevant memories in a similar way. Moreover, variations in 'liking' ratings were reflected in the right medial superior frontal gyrus, left precentral gyrus and adjacent ventral IFG. These brain regions were identified to be related with 'motor function' according to the Neurosynth, a meta-analytic platform that employs a large-scale, automated synthesis of fMRI data to decipher the associations between coordinates of interest and related terms, ranked by their probability of association (Yarkoni et al., 2011). This indicates that participants who like the dancing videos more were more likely to show similar neural responses in these motor-related areas. In other words, they were more likely to imitate dancing in the brain along with dance video clips.

It should be noted that significant group differences of neural similarities between dancers and controls were observed in all brain regions identified by ISRSA when they were viewing dancing video clips. In the meantime, dancers scored higher on all impression ratings than controls. This means that group differences in neural similarities may not be associated with the long-term dance training, and similar results may be obtained if participants with no dance training were highly familiar with the video content.

4.4. Limitations and future directions

Our study has several limitations that could be addressed in the future. First, the possible variance within dancers was not fully considered, particularly given that professional dancers were presented with videos of well-recognized prestigious dancers. While this design may have reduced dancers' judgments of the performance, it could also

have resulted in a homogeneity of performance across all dancers. Notably, to address potential biases introduced by judgmental viewing, it is recommended that future studies consider implementing post-questionnaires after participants have viewed all video clips. This design would provide a more optimal approach compared to asking participants to rate likeability immediately after viewing each video clip, which could be considered as a prime for judgmental viewing. Second, the relationship between dance partners' concordance and their neural similarity was not fully tested. Although we checked the correlation between dance partners' cooperation duration and their neural similarity, the concordance between partners is difficult to evaluate and may not be fully determined by their cooperation duration alone. Future studies could recruit dancers with varying levels of expertise, not only professional dancers, to solve this issue. Third, the same set of video clips was presented in the same order to all participants (normally required for the ISC analysis), which could confound the order effect and video type effect. Fortunately, the interaction effect, which is the focus of our study, could not be influenced by this fix-order experimental design. Randomizing the presentations of stimuli, which could offer certain advantages, could be considered in future studies. Furthermore, it is worth noting that contrasting a ballroom dance performance with a scene video may not be the optimal choice and could be improved in future studies, since the scenes may not serve as a strong contrast to elicit significant ISC in neural responses (Wang et al., 2010). Additionally, although videos of different lengths were used in our study to enhance the immersive experience, using videos of equal length would be more appropriate to eliminate the potential impact of video duration on the neural similarity results. Fourth, it would have been beneficial to incorporate a distinct set of controls, such as dancers who possess similar experience levels but engage in different forms of physical activity or dance, to optimize our study design. This design would have provided a more targeted exploration of the neural mechanisms specifically associated with ballroom dance. However, we were unable to pursue this design due to the considerable challenges encountered in recruiting an adequate number of eligible participants, e.g., pairs of classical ballet dancers, within our circumstances. Fifth, our findings were obtained based on correlational analyses, and longitudinal studies are needed to establish a causal link between dance training and neural synchrony. Sixth, while we employed ISRSA to identify brain regions exhibiting significant neural synchrony associated with participants' familiarity, liking, or whether they had seen the stimuli before, this approach may not completely eliminate their potential influences of these factors. The dilemma we faced was presenting stimuli (i.e., dance video clips) that were likely to be familiar to the dancers but not necessarily to the controls. This dilemma could potentially be addressed by recruiting a sample consisting of high-level dancers and low-level dancers, which may help minimize these individual differences (e.g., familiarity).

5. Conclusions

In conclusion, our study explored the impact of long-term ballroom dance training on neural synchrony among dancers. We found that dancers exhibited stronger and broader neural similarities in the brain when viewing dancing video clips than controls. Correlations with two sets of behavioral data suggested that the effect of long-term dance training could be predominantly reflected in neural synchrony within the frontal cortical-basal ganglia-thalamic circuits, while the influence of subjects' impression of viewed videos on neural synchrony was mainly observed in other, e.g., memory-related, brain regions. Overall, our study provides robust and innovative evidence for synchronized neural mechanisms in professional dancers due to long-term dance training.

Data and code availability statement

The data and code that support the findings of this study are

available from the corresponding author upon reasonable request. A demonstration of the dancing video clip used in our study titled "Waltz" is available at the following website: <https://www.youtube.com/watch?v=2nr8UcHi2xE>.

CRedit authorship contribution statement

Xiao Wu: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization. **Xiao Wang:** Conceptualization, Investigation, Resources. **Xue-Jing Lu:** Conceptualization, Writing – review & editing, Funding acquisition. **Ya-Zhuo Kong:** Conceptualization, Methodology, Writing – review & editing, Project administration, Funding acquisition. **Li Hu:** Conceptualization, Methodology, Writing – original draft, Writing – review & editing, Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare no commercial or financial conflict of interest.

Data availability

Data will be made available on request.

Acknowledgments

L.H. is supported by Beijing Natural Science Foundation (JQ22018) and the National Natural Science Foundation of China (32071061). X.L. is supported by the National Natural Science Foundation of China (32171077) and a grant from the Youth Innovation Promotion Association, CAS. All authors are supported by the Scientific Foundation of the Institute of Psychology, Chinese Academy of Sciences (E2CX4015).

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.neuroimage.2023.120301](https://doi.org/10.1016/j.neuroimage.2023.120301).

References

- Abernethy, B., Zawi, K., 2007. Pickup of essential kinematics underpins expert perception of movement patterns. *J. Mot. Behav.* 39, 353–367.
- Alexander, G.E., 1994. Basal ganglia-thalamocortical circuits: their role in control of movements. *J. Clin. Neurophysiol.* 11, 420–431.
- Alexander, G.E., DeLong, M.R., Strick, P.L., 1986. Parallel organization of functionally segregated circuits linking basal ganglia and cortex. *Annu. Rev. Neurosci.* 9, 357–381.
- Aminoff, E.M., Kveraga, K., Bar, M., 2013. The role of the parahippocampal cortex in cognition. *Trends Cogn. Sci.* 17, 379–390.
- Ashburner, J., 2007. A fast diffeomorphic image registration algorithm. *Neuroimage* 38, 95–113.
- Bacha-Trams, M., Alexandrov, Y.I., Broman, E., Gleason, E., Kaupila, M., Kautonen, J., Ryyppo, E., Sams, M., Jaaskelainen, I.P., 2018. A drama movie activates brains of holistic and analytical thinkers differentially. *Soc. Cogn. Affect. Neurosci.* 13, 1293–1304.
- Baek, E.C., Hyon, R., Lopez, K., Finn, E.S., Porter, M.A., Parkinson, C., 2022. In-degree centrality in a social network is linked to coordinated neural activity. *Nat. Commun.* 13, 1118.
- Burzynska, A.Z., Finc, K., Taylor, B.K., Knecht, A.M., Kramer, A.F., 2017. The dancing brain: structural and functional signatures of expert dance training. *Front. Hum. Neurosci.* 11, 566.
- Calvo-Merino, B., Glaser, D.E., Grezes, J., Passingham, R.E., Haggard, P., 2005. Action observation and acquired motor skills: an fMRI study with expert dancers. *Cereb. Cortex* 15, 1243–1249.
- Chen, F., Lv, X., Fang, J., Li, T., Xu, J., Wang, X., Hong, Y., Hong, L., Wang, J., Wang, W., Wang, C., 2021. Body-mind relaxation meditation modulates the thalamocortical functional connectivity in major depressive disorder: a preliminary resting-state fMRI study. *Transl. Psychiatry* 11, 546.
- Chen, P.A., Jolly, E., Cheong, J.H., Chang, L.J., 2020. Intersubject representational similarity analysis reveals individual variations in affective experience when watching erotic movies. *Neuroimage* 216, 116851.
- Cheung, O.S., Bar, M., 2012. Visual prediction and perceptual expertise. *Int. J. Psychophysiol.* 83, 156–163.
- Christensen, J.F., Bruhn, L., Schmidt, E.M., Bahmanian, N., Yazdi, S.H.N., Farahi, F., Sancho-Escanero, L., Menninghaus, W., 2023. A 5-emotions stimuli set for emotion perception research with full-body dance movements. *Sci. Rep.* 13, 8757.
- Cross, E.S., Hamilton, A.F., Grafton, S.T., 2006. Building a motor simulation de novo: observation of dance by dancers. *Neuroimage* 31, 1257–1267.
- El-Sourani, N., Trempler, I., Wurm, M.F., Fink, G.R., Schubotz, R.I., 2020. Predictive impact of contextual objects during action observation: evidence from functional magnetic resonance imaging. *J. Cogn. Neurosci.* 32, 326–337.
- Engel, A., Burke, M., Fiehler, K., Bien, S., Rosler, F., 2008. How moving objects become animated: the human mirror neuron system assimilates non-biological movement patterns. *Soc. Neurosci.* 3, 368–387.
- Fan, L., Li, H., Zhuo, J., Zhang, Y., Wang, J., Chen, L., Yang, Z., Chu, C., Xie, S., Laird, A.R., Fox, P.T., Eickhoff, S.B., Yu, C., Jiang, T., 2016. The human brainnetome atlas: a new brain atlas based on connective architecture. *Cereb. Cortex* 26, 3508–3526.
- Finn, E.S., Gleason, E., Khojandi, A.Y., Nielson, D., Molfese, P.J., Handwerker, D.A., Bandettini, P.A., 2020. Idiosyncrasy: from shared responses to individual differences during naturalistic neuroimaging. *Neuroimage* 215, 116828.
- Grahn, J.A., Brett, M., 2007. Rhythm and beat perception in motor areas of the brain. *J. Cogn. Neurosci.* 19, 893–906.
- Grahn, J.A., Brett, M., 2009. Impairment of beat-based rhythm discrimination in Parkinson's disease. *Cortex* 45, 54–61.
- Grahn, J.A., Rowe, J.B., 2013. Finding and feeling the musical beat: striatal dissociations between detection and prediction of regularity. *Cereb. Cortex* 23, 913–921.
- Gruskin, D.C., Rosenberg, M.D., Holmes, A.J., 2020. Relationships between depressive symptoms and brain responses during emotional movie viewing emerge in adolescence. *Neuroimage* 216, 116217.
- Guenther, F.H., Tourville, J.A., Bohland, J.W., 2015. Speech production. *Toga, A.W. (Ed.). Brain Mapping. Academic Press, Waltham*, pp. 435–444.
- Hanggi, J., Koeneke, S., Bezzola, L., Jancke, L., 2010. Structural neuroplasticity in the sensorimotor network of professional female ballet dancers. *Hum. Brain Mapp.* 31, 1196–1206.
- Hasson, U., Nir, Y., Levy, I., Fuhrmann, G., Malach, R., 2004. Intersubject synchronization of cortical activity during natural vision. *Science* 303, 1634–1640.
- Herbec, A., Kauppi, J.P., Jola, C., Tohka, J., Pollick, F.E., 2015. Differences in fMRI intersubject correlation while viewing unedited and edited videos of dance performance. *Cortex* 71, 341–348.
- Javed, N., Cascella, M., 2022. Neuroanatomy, globus pallidus. *StatPearls. StatPearls, Treasure IslandFL [Internet]*.
- Jola, C., McAleer, P., Grosbras, M.H., Love, S.A., Morison, G., Pollick, F.E., 2013. Uni- and multisensory brain areas are synchronised across spectators when watching unedited dance recordings. *J. Perception* 4, 265–284.
- Karpati, F.J., Giacosa, C., Foster, N.E.V., Penhune, V.B., Hyde, K.L., 2017. Dance and music share gray matter structural correlates. *Brain Res.* 1657, 62–73.
- Kauppi, J.P., Jaaskelainen, I.P., Sams, M., Tohka, J., 2010. Inter-subject correlation of brain hemodynamic responses during watching a movie: localization in space and frequency. *Front. Neuroinform.* 4, 5.
- Kirsch, L.P., Cross, E.S., 2018. The influence of sensorimotor experience on the aesthetic evaluation of dance across the life span. *Prog. Brain Res.* 237, 291–316.
- Kirsch, L.P., Dawson, K., Cross, E.S., 2015. Dance experience sculpted aesthetic perception and related brain circuits. *Ann. N. Y. Acad. Sci.* 1337, 130–139.
- Koul, A., Cavallo, A., Cauda, F., Costa, T., Diano, M., Pontil, M., Becchio, C., 2018. Action observation areas represent intentions from subtle kinematic features. *Cereb. Cortex* 28, 2647–2654.
- Kriegeskorte, N., Kievit, R.A., 2013. Representational geometry: integrating cognition, computation, and the brain. *Trends Cogn. Sci.* 17, 401–412.
- Kriegeskorte, N., Mur, M., Bandettini, P., 2008. Representational similarity analysis - connecting the branches of systems neuroscience. *Front. Syst. Neurosci.* 2, 4.
- Lehericy, S., Bardinet, E., Tremblay, L., Van de Moortele, P.F., Pochon, J.B., Dormont, D., Kim, D.S., Yelnik, J., Ugurbil, K., 2006. Motor control in basal ganglia circuits using fMRI and brain atlas approaches. *Cereb. Cortex* 16, 149–161.
- Li, G., He, H., Huang, M., Zhang, X., Lu, J., Lai, Y., Luo, C., Yao, D., 2015. Identifying enhanced cortico-basal ganglia loops associated with prolonged dance training. *Sci. Rep.* 5, 10271.
- Li, L., Huang, X., Xiao, J., Zheng, Q., Shan, X., He, C., Liao, W., Chen, H., Menon, V., Duan, X., 2022. Neural synchronization predicts marital satisfaction. *Proc. Natl. Acad. Sci. U. S. A.* 119, e2202515119.
- Liakakis, G., Nickel, J., Seitz, R.J., 2011. Diversity of the inferior frontal gyrus—a meta-analysis of neuroimaging studies. *Behav. Brain Res.* 225, 341–347.
- Lindquist, M.A., Wager, T.D., 2015. Principles of fMRI. *LeanPub*.
- Loprinzi, P.D., 2019. The effects of physical exercise on parahippocampal function. *Physiol. Int.* 106, 114–127.
- Lu, Y., Zhao, Q., Wang, Y., Zhou, C., 2018. Ballroom Dancing promotes neural activity in the sensorimotor system: a resting-state fMRI study. *Neural Plast.* 2018, 2024835.
- Miura, A., Kudo, K., Nakazawa, K., 2013. Action-perception coordination dynamics of whole-body rhythmic movement in stance: a comparison study of street dancers and non-dancers. *Neurosci. Lett.* 544, 157–162.
- Nastase, S.A., Gazzola, V., Hasson, U., Keysers, C., 2019. Measuring shared responses across subjects using intersubject correlation. *Soc. Cogn. Affect. Neurosci.* 14, 667–685.
- Nguyen, M., Vanderwal, T., Hasson, U., 2019. Shared understanding of narratives is correlated with shared neural responses. *Neuroimage* 184, 161–170.
- Nummenmaa, L., Lahnakoski, J.M., Gleason, E., 2018. Sharing the social world via intersubject neural synchronisation. *Curr. Opin. Psychol.* 24, 7–14.

- Parkinson, C., Kleinbaum, A.M., Wheatley, T., 2018. Similar neural responses predict friendship. *Nat. Commun.* 9, 332.
- Pollick, F.E., Vicary, S., Noble, K., Kim, N., Jang, S., Stevens, C.J., 2018. Exploring collective experience in watching dance through intersubject correlation and functional connectivity of fMRI brain activity. *Prog. Brain Res.* 237, 373–397.
- Ranganath, C., 2006. Working memory for visual objects: complementary roles of inferior temporal, medial temporal, and prefrontal cortex. *Neuroscience* 139, 277–289.
- Rehfeld, K., Luders, A., Hokenmann, A., Lessmann, V., Kaufmann, J., Brigadski, T., Muller, P., Muller, N.G., 2018. Dance training is superior to repetitive physical exercise in inducing brain plasticity in the elderly. *PLoS ONE* 13, e0196636.
- Rizzolatti, G., Craighero, L., 2004. The mirror-neuron system. *Annu Rev Neurosci* 27, 169–192.
- Ruland, S.H., Palomero-Gallagher, N., Hoffstaedter, F., Eickhoff, S.B., Mohlberg, H., Amunts, K., 2022. The inferior frontal sulcus: cortical segregation, molecular architecture and function. *Cortex* 153, 235–256.
- Sabatinelli, D., Fortune, E.E., Li, Q., Siddiqui, A., Krafft, C., Oliver, W.T., Beck, S., Jeffries, J., 2011. Emotional perception: meta-analyses of face and natural scene processing. *Neuroimage* 54, 2524–2533.
- SamPenDu**, 2015. **Bayes factors MATLAB functions**. [figshare](https://figshare.com/projects/SamPenDu/120301).
- Seeley, W.W., 2019. The salience network: a neural system for perceiving and responding to homeostatic demands. *J. Neurosci.* 39, 9878–9882.
- Seidler, R.D., Noll, D.C., Chintalapati, P., 2006. Bilateral basal ganglia activation associated with sensorimotor adaptation. *Exp. Brain Res.* 175, 544–555.
- Thullier, F., Moufti, H., 2004. Multi-joint coordination in ballet dancers. *Neurosci. Lett.* 369, 80–84.
- Vallat, R., 2018. Pingouin: statistics in Python. *J. Open Source Softw.* 3, 1026.
- van Baar, J.M., Chang, L.J., Sanfey, A.G., 2019. The computational and neural substrates of moral strategies in social decision-making. *Nat. Commun.* 10, 1483.
- Voss, M.W., Soto, C., Yoo, S., Sodoma, M., Vivar, C., van Praag, H., 2019. Exercise and hippocampal memory systems. *Trends Cogn. Sci. (Regul. Ed.)* 23, 318–333.
- Wang, H., Freeman, J., Merriam, E.P., Hasson, U., Heeger, D.J., 2010. Temporal scramble disrupts eye movements to naturalistic videos. *J. Vis.* 10, 528–528.
- Wobbrock, J.O., Findlater, L., Gergle, D., Higgins, J.J., 2011. The aligned rank transform for nonparametric factorial analyses using only ANOVA procedures. In: *Proceedings of the ACM Conference on Human Factors in Computing Systems*. Association for Computing Machinery, Vancouver, British Columbia, Canada, pp. 143–146.
- Yan, C.G., Zang, Y.F., 2010. DPARSF: a MATLAB toolbox for "Pipeline" data analysis of resting-state fMRI. *Front. Syst. Neurosci.* 4, 13.
- Yarkoni, T., Poldrack, R.A., Nichols, T.E., Van Essen, D.C., Wager, T.D., 2011. Large-scale automated synthesis of human functional neuroimaging data. *Nat. Methods* 8, 665–670.
- Zhou, Z., Chen, S., Li, Y., Zhao, J., Li, G., Chen, L., Wu, Y., Zhang, S., Shi, X., Chen, X., Xu, S., Ren, M., Chang, S., Shan, C., 2022. Comparison of sensory observation and somatosensory stimulation in mirror neurons and the sensorimotor network: a task-based fMRI study. *Front. Neurol.* 13, 916990.