

# Synergy of the mirror neuron system and the mentalizing system in a single brain and between brains during joint actions

Angela Ciaramidaro<sup>a,b,1,\*</sup>, Jlenia Toppi<sup>c,d,1</sup>, Pascal Vogel<sup>b,e</sup>, Christine M. Freitag<sup>b</sup>, Michael Siniatchkin<sup>b,f</sup>, Laura Astolfi<sup>c,d</sup>

<sup>a</sup> Department of Biomedical, Metabolic and Neural Sciences, University of Modena and Reggio Emilia, Viale Allegri 9, 42121 Reggio Emilia, Italy

<sup>b</sup> Department of Child and Adolescent Psychiatry, Psychosomatics, and Psychotherapy, University Hospital, Goethe-University, Deutschordenstraße 50, 60528 Frankfurt/Main, Germany

<sup>c</sup> Department of Computer, Control, and Management Engineering, Univ. of Rome "Sapienza", Via Ariosto 25, 00185 Rome, Italy

<sup>d</sup> Neuroelectrical Imaging and Brain Computer Interface Laboratory, Fondazione Santa Lucia IRCCS, Via Ardeatina 306/354, 00179 Rome, Italy

<sup>e</sup> Institute of Neurophysiology, Neuroscience Center, Goethe University, Heinrich-Hoffmann-Str. 7, 60528 Frankfurt/M, Germany

<sup>f</sup> Clinic of Child and Adolescent Psychiatry, Psychosomatics and Psychotherapy, University Hospital Aachen, RWTH Aachen University, Pauwelsstraße 30, 52074 Aachen, Germany

## ARTICLE INFO

### Keywords:

EEG-Hyperscanning  
Theory of mind  
Mirror neurons system  
Joint actions  
Source analysis

## ABSTRACT

Cooperative action involves the simulation of actions and their co-representation by two or more people. This requires the involvement of two complex brain systems: the mirror neuron system (MNS) and the mentalizing system (MENT), both of critical importance for successful social interaction. However, their internal organization and the potential synergy of both systems during joint actions (JA) are yet to be determined. The aim of this study was to examine the role and interaction of these two fundamental systems—MENT and MNS—during continuous interaction. To this hand, we conducted a multiple-brain connectivity analysis in the source domain during a motor cooperation task using high-density EEG dual-recordings providing relevant insights into the roles of MNS and MENT at the intra- and interbrain levels.

In particular, the intra-brain analysis demonstrated the essential function of both systems during JA, as well as the crucial role played by single brain regions of both neural mechanisms during cooperative activities. Specifically, our intra-brain analysis revealed that both neural mechanisms are essential during Joint Action (JA), showing a solid connection between MNS and MENT and a central role of the single brain regions of both mechanisms during cooperative actions. Additionally, our inter-brain study revealed increased inter-subject connections involving the motor system, MENT and MNS. Thus, our findings show a mutual influence between two interacting agents, based on synchronization of MNS and MENT systems. Our results actually encourage more research into the still-largely unknown realm of inter-brain dynamics and contribute to expand the body of knowledge in social neuroscience.

## 1. Introduction

Human life is characterized by people (inter-)acting with other people. Individuals constantly interact with other individuals and coordinate their mental and physical resources to achieve a common goal. Social interactions in which individuals jointly pursue a shared goal are called Joint Actions (JA) (Sebanz et al., 2006), a complex social phenomenon that requires at least two individuals to follow a sequence of

actions in a coordinated manner. During JA people mutually predict the consequences of their co-actor's behavior through internal action simulation and representation of the co-actor's task (called co-representation) to allow mutual action prediction and motor adaptation (Miss et al., 2022, Ruissen and de Bruijn, 2016, Knoblich et al., 2011, Vesper et al., 2010, Sebanz et al., 2003, Sebanz et al., 2005).

JA are studied through paradigms such as grasping or pulling (Era et al., 2018, Meyer et al., 2016, Kourtis et al., 2013, Newman-Norlund

\* Corresponding author at: Department of Biomedical, Metabolic and Neural Sciences, University of Modena and Reggio Emilia, Viale Allegri 9, 42121 Reggio Emilia, Italy.

E-mail address: [angela.ciaramidaro@unimore.it](mailto:angela.ciaramidaro@unimore.it) (A. Ciaramidaro).

<sup>1</sup> These authors contributed equally.

<https://doi.org/10.1016/j.neuroimage.2024.120783>

Received 17 July 2024; Received in revised form 4 August 2024; Accepted 12 August 2024

Available online 24 August 2024

1053-8119/© 2024 The Authors. Published by Elsevier Inc. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

et al., 2008), joint interference tasks (Sebanz et al., 2005, Iani et al., 2014), social play (Gräfenhain et al., 2009, Babiloni et al., 2007), and joint musical performance (Vanzella et al., 2019, Novembre et al., 2016). Neuroimaging studies have described the involvement of two distinct large-scale neural systems in JA (Newman-Norlund et al., 2008, Abe et al., 2019, Chaminade et al., 2012): the human "mirror neuron system" (MNS) which underpins action simulation and consists of the premotor cortex (PMC), the anterior intraparietal sulcus (aIPS), and the superior temporal sulcus (STS); and the "mentalizing system" (MENT), which supports co-representation and is characterized by activations in the precuneus (Prec), the temporoparietal junction (TPJ), and the medial prefrontal cortex (mPFC) (for a review, see Van Overwalle and Baetens, 2009). While MNS is primarily involved in understanding and simulating actions, MENT is crucial for understanding others' intentions and mental states. However, the interaction and potential overlap between these systems during JA are not fully understood, and it remains unclear whether MNS or MENT predominates during JA. Studies have described their roles as complementary, independent, or even opposed (Isoda, 2016, Caramidaro et al., 2014, Sperduti et al., 2014, Alcalá-López et al., 2019). However, the following two key aspects of the interaction between MNS and MENT during JA remain unclear: i) the specific internal network organization of each system and ii) whether and how the two systems are connected.

The majority of studies on JA are based on fMRI measures (Newman-Norlund et al., 2008, Abe et al., 2019, Chaminade et al., 2012, Becchio et al., 2012), which have poor temporal resolution, that makes it difficult to explore the mutual influence and causal influence between specific brain regions and between the two systems. Causality in the statistical sense requires capturing the precise temporal dynamics and directionality of interactions, which is not guaranteed by fMRI due to its slow temporal resolution. Additionally, the dynamics of the BOLD response are not uniform across different brain regions, complicating the analysis of causality and increasing the risk of obtaining spurious connections. EEG, on the other hand, provides superior temporal resolution, allowing the capture of rapid neural dynamics and causal relationships associated with JA. Previous EEG studies mainly focused on event-related potentials (ERPs) to investigate motor-related brain activity (Kourtis et al., 2014, Kourtis et al., 2013, Kourtis et al., 2010) and response inhibition (Tsai et al., 2006) or used spectral approach to assess the modulation of EEG rhythms (Kourtis et al., 2013, Kourtis et al., 2010, Fitzpatrick et al., 2019, Oberman et al., 2007) during JA. However, these studies often do not leverage the full potential of EEG's temporal resolution for analyzing the complex dynamics of JA, particularly in the spectral domain.

In the last two decades, a significant paradigm shift has been proposed to move from the one-brain paradigm to the multi-brain paradigm in order to capture the "togetherness" of sharing mental and motor resources that typically underlie social interactions. Accordingly, a two-person setting (known as hyperscanning) was implemented in association with a multivariate and multi-subject analysis to characterize the intricate and unpredictable temporal evolution of the interaction within a dyad during JA (Hari et al., 2015, Hari et al., 2016, Babiloni and Astolfi, 2014). The spectral analysis of EEG data is particularly valuable in hyperscanning studies as it allows the examination of frequency-specific neural synchronization between interacting individuals.

Regarding JA, hyperscanning studies based on fNIRS have uncovered patterns of interbrain synchronization through cognitively demanding tasks on interpersonal coordination (Novembre et al., 2016, Cheng et al., 2022, Chen et al., 2020, Kruppa et al., 2021, Zhang et al., 2017, Pan et al., 2017, Hu et al., 2017, Cui et al., 2012). They reported differences in inter-brain synchronization between fNIRS channels or cortical regions of interest (ROIs) due to social factors or to the degree of shared intentionality. Furthermore, EEG hyperscanning studies assessed synchronization, coherence, or alignment between subjects at the scalp level, ranging from coordination tasks (Shiraishi and Shimada, 2021,

Dodel et al., 2020, Konvalinka et al., 2014, Dumas et al., 2020, Mu et al., 2016), imitation (Dumas et al., 2010), cooperation during social game (Zhang et al., 2019, Liu et al., 2021) to complex musical performance (Novembre et al., 2016, Gugnowska et al., 2022, Zamm et al., 2021, Müller et al., 2018, Sängler et al., 2012). To our knowledge, only two studies addressed the hyperscanning analysis of JA in the source domain. A dual MEG study (Zhou et al., 2016) on repetitive simple hand actions reported a phase–amplitude coupling between leader and follower in bilateral sensorimotor and occipital cortices. An EEG-hyperscanning study reported local neural synchronization in different frontal regions (the inferior frontal gyrus and the ventromedial prefrontal cortex) during unconscious finger movements by two subjects (Yun et al., 2012). None of these studies studied the relationship between MENT and MNS systems during cooperative actions.

A previous work by the authors of the present work (Astolfi et al., 2020) demonstrated that indices extracted from multi-subject scalp EEG brain networks are modulated by the degree and type of interaction, allowing a better discrimination between social (joint action) and non-social conditions than indices derived from single-subject analyses. However, the multi-subject circuitry at the level of the brain sources involved in JA were not assessed, limiting our understanding of the underlying neural mechanisms.

Therefore, the purpose of the current study was to examine the role and relationship of these two fundamental systems—MENT and MNS—during continuous interaction. To this end, we performed a high-density EEG hyperscanning study and exploited a multi-brain connectivity analysis in the source domain providing insights at intra- and inter-brain levels. In particular, we aim to investigate:

- i. The neuronal activations and functional organization of the MNS and MENT systems in the single brain (intra-brain analysis, within and between different systems);
- ii. Whether there is a mutual influence between the activation of homologous neural systems between the two agents (inter-brain between the corresponding neural systems);
- iii. Whether there is an influence between MNS activation in one agent and MENT activation in the other, and vice-versa (inter-brain analysis across both neural systems).

## 2. Material and methods

### 2.1. Participants

Thirty-two male subjects (mean age 25.28; SD= 4.39) arranged in 16 dyads participated in the study. They were all right-handed, had normal or corrected-to-normal vision and were free of chronic somatic and neurological diseases and any mental disorder, i.e. values below the borderline cut-off in all scales of the Young Adult Self-Report (YASR) (Achenbach, 1997). The study was approved by the Ethics Committee of the Medical Faculty, Goethe Universität Frankfurt/Main (Germany). All participants gave written informed consent according to the Convention of Helsinki and received a lump sum payment of 45 euros for taking part in the experiment.

### 2.2. Experimental design

Each dyad performed a computer game representing a Joint Action, which consisted of lifting a virtual ball placed on a moving bar from the bottom of the screen up to a target area located at the top of the screen (goal), by controlling both sides (left and right) of such a bar. The ball was free to roll down the bar if the correct balance was not maintained. In order to increase complexity, we introduced an obstacle in the center of the screen.

We used a modified version of the JA paradigm introduced in (Newman-Norlund et al., 2008, Bosga and Meulenbroek, 2007), in which we added to the human joint condition an analogous non-human

(PC) joint condition, and a solo condition. The joint condition provided both agents the same goal, which was to reach the target area avoiding an obstacle in the middle of the screen. In order to execute the task in concert with the other player without rolling the ball down, each player used his right index finger to adjust one side of a single virtual bar. The Joint condition was successful only if both agents worked together. In the other two conditions the two participants played simultaneously but separately two independent games. In the PC condition each participant controlled one side of the virtual bar using the right index finger while the other side was controlled by the computer. In the Solo condition both subjects were asked to solve the task individually. Instead of playing as a team, they played alone by controlling both sides of the virtual bar by their right index and middle fingers.

In all conditions, the two subjects played and were recorded simultaneously and weren't allowed to verbally communicate. In addition, we included a baseline condition in which the subjects were sitting in front of the screen, watched the same bar used during the experiments moving through the screen, and had to press buttons with the same fingers and timing as during the experiment, but with no relation to what was happening on the screen.

The conditions were presented block-wise, in random order. Each block consisted of 60 trials of approximately 8 s with an inter-trial interval of 2 s. In the Solo and PC conditions, when a subject finished a trial before the other did, the former's game was paused in order to ensure that all trials started simultaneously.

Stimuli were presented by using MATLAB Psychtoolbox (The MathWorks, Version R2009) and were displayed on two 19" LCD monitors (Fujitsu Siemens Scenic view L9ZA, resolution 1280 × 1024) at a refresh rate of 150 Hz.

### 2.3. EEG hyperscanning recordings

The neuroelectrical hyperscanning recordings were performed with two synchronized 64-channel EEG acquisition systems (Brain Product GmbH, Germany - for each subject: 61 EEG + 3EOG channels, reference on linked mastoids, ground at Fpz). Data were collected with a sampling frequency of 250 Hz. In order to delete the sources of variance between the two systems, we used a calibration signal to equalize the different gains.

### 2.4. Behavioral data

Behavioral data were collected during the paradigm administration. In particular, for each trial, task condition we collected the following behavioral parameters: i) number of successful trials (number of trials in which the ball reached the goal zone); ii) trial duration (trial length in seconds for successful trials only); iii) ball height (height reached by the ball at the end of the trial, normalized according to the maximum). As for Joint condition behavioral data referred to the dyad while in PC and Solo conditions they were extracted separately for each dyad member.

## 2.5. EEG analysis

### 2.5.1. Pre-processing of EEG signals

The pre-processing procedure was performed by means of Brain Vision Analyzer 1.0 (Brain Products GmbH). EEG signals were band-pass filtered in the range 1-45 Hz and ocular artifacts were removed by means of Independent Component Analysis. For most of the subjects we removed one component, the one mostly related to blink artifacts, in a few cases two components. In order to keep the simultaneity of the data recorded from the two subjects also in their offline processing, in the Joint condition we took the entire duration of each trial as a window of interest, since the two subjects played simultaneously the game; in the PC and Solo conditions we considered the time interval between the simultaneous beginning of the trial for the subjects and the trial conclusion for the faster player, since they played different games. Each

window was then further segmented in epochs of 1s and a semi-automatic procedure based on a threshold criterion ( $\pm 80\mu\text{V}$  in absolute value) was then applied to highlight the presence of artifacts. Once the trial was marked as "bad" for one subject, it was removed from the data of both participants, to maintain the alignment between the two subjects' data. On average, we removed less than 10 % of the trials collected per condition and per subject. No statistical differences were found among the number of epochs preserved in the three experimental conditions.

### 2.5.2. EEG source localization

Sources of EEG activity were localized by means of the standardized Low-Resolution Tomography (sLORETA) technique (Pascual-Marqui, 2002) implemented in Loreta software (Pascual-Marqui et al., 1999, Pascual-Marqui et al., 1994). EEG data were re-referenced to the Common Average Reference before entering the reconstruction procedure. The regularized linear inverse approach was applied to the EEG data in order to project the scalp activities in the whole gray matter of the brain. As a solution of the forward model reproducing the electromagnetic propagation from the active sources to the EEG sensors, we used a lead field matrix obtained from the application of the Boundary Element Method (Fuchs et al., 2002) to the MNI152 realistic head model (Mazziotta et al., 2001). In particular, we used a 3D lead field matrix modeling the propagation of 6239 active sources (distributed in the whole gray matter at 5mm spatial resolution towards the EEG sensors). The regularization parameter  $\lambda$  used for sLORETA solution was computed by means of a cross-validation approach (Tikhonov and Arsenin, 1977). The solution of the source localization problem for each subject and each experimental condition consisted of a waveform for each of the 6239 dipoles used to model the gray matter. These data were used for the spectral analysis reported in this work. To perform the connectivity analysis, we considered the waveforms related to specific regions of interest (ROIs), obtained by selecting the dipole closest to the spatial centroid of each of them. In particular, we selected 12 ROIs that specifically compose the MNS, MENT and the motor circuit involved in JA task (Van Overwalle and Baetens, 2009, Mayka et al., 2006). In particular, we considered for MNS: posterior superior temporal sulcus right (pSTS\_R; 50, -55, 10) and left (pSTS\_L; -50, -55, 10), anterior intraparietal sulcus right (aIPS\_R; 40, -40, 45) and left (aIPS\_L; -40, -40, 45), premotor cortex right (PMC\_R; 40, 5, 40) and left (PMC\_L; -40, 5, 40); for MENT: medial prefrontal cortex (mPFC; 0, 50, 20), precuneus (Prec; 0, -60, 40), temporoparietal junction right (TPJ\_R; 50, -55, 25) and left (TPJ\_L; -50, -55, 25) and for Motor Circuit (MC): left primary motor cortex (M1\_L; -37, -21, 58) and supplementary motor area proper (SMAp; -2, -7, 55). Coordinates in brackets refer to the MNI system. A figure containing ROIs localization can be found in the Supplementary Materials (see tab. S1).

### 2.5.3. Whole-brain spectral analysis

Power spectral density (PSD) was computed for each source in the gray matter by means of the Welch periodogram on non-overlapping data segments of 1s each tapered with the Hann window. PSD was then averaged in four frequency bands: theta (4-8Hz), alpha (8.5-12 Hz), beta (12.5-30 Hz) and gamma (31-40 Hz). The spectral analysis was performed for each subject and each experimental condition.

### 2.5.4. Single-brain connectivity

Single-brain connectivity networks were estimated by means of the Partial Directed Coherence (PDC) (Baccalá and Sameshima, 2001) computed on the waveforms reconstructed for the 12 ROIs selected in the study. PDC is a multivariate spectral index providing an estimation of the frequency-resolved influence directed from each ROI in our dataset toward each of the others using a single model for the entire network. PDC values were averaged in the same frequency bands used in spectral analysis. The analysis was performed for each participant ( $N = 32$ ) and each experimental condition (Joint, PC, Solo and baseline).

### 2.5.5. Graph theory at single-brain level

We investigated the properties of the brain networks obtained by PDC by using indices derived from graph theory (Rubinov and Sporns, 2010). To quantify the level of engagement of each brain area in the network we extracted the degree index, a local measure derived from graph theory quantifying the number of connections involving each node. We computed the degree index for each node (12 ROIs), each band (theta, alpha, beta), each subject ( $N = 32$ ) and each experimental condition (Joint, PC, Solo).

To investigate and quantify the communication within and between MNS and MENT, we extracted their related circuits from the general network and defined indices measuring the intra-circuit ( $D_{intra}$ ) and inter-circuit ( $D_{inter}$ ) connection densities as follows:

$$D_{intra} = \frac{N_C}{N_{TOT}^{intra}} \quad (1)$$

$$D_{inter} = \frac{N_{C1 \rightarrow C2}}{N_{TOT}^{inter}} \quad (2)$$

where C generically refers to a single brain circuit,  $N_C$  is the number of connections within the generic circuit C (intra-circuit connections), i.e. going from a node in C to another node in C,  $N_{TOT}^{intra}$  is the maximum number of connections possibly linking nodes within C, C1 and C2 generically refer to two specific different brain circuits,  $N_{C1 \rightarrow C2}$  is the number of connections going from a node in C1 to a node in C2,  $N_{TOT}^{inter}$  is the maximum number of connections possibly going from C1 to C2.  $D_{intra}$  was computed for MNS and MENT, while  $D_{inter}$  was calculated separately for the two directions (from MNS to MENT and viceversa). All the indices were obtained for each frequency band, experimental condition and subject.

The single-brain connectivity estimation and the graph theory computations were performed in the Matlab environment (MATLAB, R2020a).

### 2.5.6. Multiple-brain connectivity

After the single-subject connectivity analysis, we built a multiple-brain connectivity model for each dyad involved in the study. To this purpose, we fed the multivariate autoregressive model at the basis of PDC computation with the same data used for the single subject analysis, simultaneously acquired for the two subjects and considered as a unique dataset. In order to avoid spurious links in the multiple-brain connectivity (Burgess, 2013) due to amplitude differences in the signals recorded from different individuals, we normalized the data coming from each subject in the couple by a z-score before their inclusion in the estimate. We employed an extension of PDC to the multi-subject case, optimized for hyperscanning purposes (Babiloni and Astolfi, 2014), whose accuracy was demonstrated in previous hyperscanning studies (Astolfi et al., 2020, Toppi et al., 2022, Ciaramidaro et al., 2018, Toppi et al., 2016, Astolfi et al., 2011, Astolfi et al., 2010, Fallani et al., 2010). The resulting model provides magnitude, direction and spectral content of the functional connections exchanged between different brain areas for each subject (intra-connections) and between the two subjects (inter-connections). PDC values were averaged in the same frequency bands previously used for the single-subject connectivity. The analysis was performed for each dyad and for each experimental condition (Joint, PC, Solo and baseline).

### 2.5.7. Graph theory at multiple-brain level

To investigate the properties of the multiple-brain networks obtained for our dyads, we used a set of indices partly derived from the graph theory for neuroscience (Rubinov and Sporns, 2010) and partly defined ad hoc for multiple-subject connectivity (Astolfi et al., 2020, Ciaramidaro et al., 2018, Toppi et al., 2016).

To quantify the involvement of the different ROIs in the multiple-brain network communication, like in the single-brain analysis, we

computed the degree index for each ROI of each subject in the dyad and then we averaged it for the two subjects, to obtain an average degree for each brain region considered in the study. We performed the analysis for each band, experimental condition and dyad.

To investigate the inter-subject communication between the two brain circuits relevant for the task (MNS and MENT), we introduced here an index, the inter-circuits density (ICD) defined as follows:

$$ICD_{C1 \rightarrow C2} = \frac{N_{C1 \rightarrow C2} + N_{C2 \rightarrow C1}}{N_{TOT}} \quad (3)$$

where C1 and C2 represent two generic brain circuits;  $N_{C1 \rightarrow C2}$  is the number of connections going from a node in C1 of subject 1 to a node in C2 of subject 2,  $N_{C2 \rightarrow C1}$  the number of connections going from a node in C1 of subject 2 to a node in C2 of subject 2 and  $N_{TOT}$  is the total number of connections possibly linking nodes of C1 with those in C2 for both subjects. In this study the circuits under investigation are four: mirror neuron system in subject 1 (MNS1), mentalizing circuit in subject 1 (MENT1), mirror neuron system in subject 2 (MNS2) and mentalizing circuit in subject 2 (MENT2). Thus, we obtained four indices for each frequency band, experimental condition and dyad:  $D_{MNS \rightarrow MNS}$  (MNS1  $\rightarrow$  MNS2 & MNS2  $\rightarrow$  MNS1),  $D_{MENT \rightarrow MENT}$  (MENT1  $\rightarrow$  MENT2 & MENT2  $\rightarrow$  MENT1),  $D_{MNS \rightarrow MENT}$  (MNS1  $\rightarrow$  MENT2 & MNS2  $\rightarrow$  MENT1),  $D_{MENT \rightarrow MNS}$  (MENT1  $\rightarrow$  MNS2 & MENT2  $\rightarrow$  MNS1).

The multiple-brain connectivity estimation and the graph theory computations were performed in the Matlab environment (MATLAB, R2020a).

### 2.5.8. Statistical analysis

ANOVA on behavioral data. Data were analyzed by repeated measures one-way ANOVAs, with as within factor the TASK type (Joint, PC and Solo) and as dependent variables the three parameters (trial duration, ball height and number of successful trials) considered separately. Means were subsequently compared using the Newmann-Keuls post hoc test.

Grand Average Spectral Maps. PSD values obtained for each dipole were statistically compared across participants ( $N = 32$ ) between the different experimental conditions by means of a non-parametric statistical approach to obtain spectral activation maps. A permutation test ( $N = 10000$  permutations) was applied to the three statistical contrasts - Joint vs PC, Joint vs Solo, PC vs Solo - using the paired t-value as a measure of distance between the two distributions. A non-parametric approach is preferred for this class of data since it corrects for multiple testing and does not rely on Gaussianity assumption (Nichols and Holmes, 2002).

Grand Average Single-brain and Multiple-brain Connectivity Networks. We statistically compared single-brain and multiple brain connectivity networks among the experimental conditions, across participants ( $N = 32$ ) and dyads ( $N = 16$ ), respectively, by means of a right-tail dependent sample t-test applied to the statistical contrast between Joint condition and each of the two high baseline condition PC and Solo. The statistical test was performed for each connection, each direction and each frequency band.

Single-brain and Multiple-brain adjacency matrices extraction. To convert single-brain and multiple-brain networks into binary adjacency matrices for the graph indices computation, the PDC matrices obtained for each dyad, frequency band and condition were contrasted with the corresponding ones estimated for the baseline. We considered the 95th percentile of the PDC values distribution constructed during the baseline as a statistical threshold for each participant or dyad. We assigned 1 to the entries corresponding to connections with a weight statistically higher than the threshold and 0 to the entries corresponding to connections for which the PDC value was below the threshold. A total of 12 (3 experimental conditions X 4 frequency bands) binary and directed (non-symmetrical) adjacency matrices were obtained for each dyad and used to compute the graph theory indices.



**ANOVA on single-brain and multiple-brain graph theory indices.** For each of the indices used to characterize both single and multiple-brain networks, we performed a one-way repeated measures ANOVAs using the index as dependent variable and the experimental condition (3 levels: Joint, PC, Solo) as within factor. The test was applied to the ROIs' degree for single-brain and multiple analysis and to connection densities defined for measuring the interaction between MNS and MENT at single and multiple brain levels. The analysis was performed for each of the frequency bands, separately. The ANOVAs were computed by using STATISTICA (StatSoft Inc., Version 8.0). Newmann-Keuls post hoc test was used to assess differences between means.

**Correlation between multiple-brain graph theory indices and behavioral data.** Pearson correlation was computed between connection densities defined for measuring the interaction between MNS and MENT at multiple brain levels and the behavioral data (ball height, trial length and number of successful trials).

For all the statistical tests carried out in this work, we set a significance level ( $\alpha$ ) equal to 0.05 adjusted by means of False Discovery Rate (FDR) to mitigate type I errors coming from multiple comparisons.

### 3. Results

#### 3.1. Behavioral data

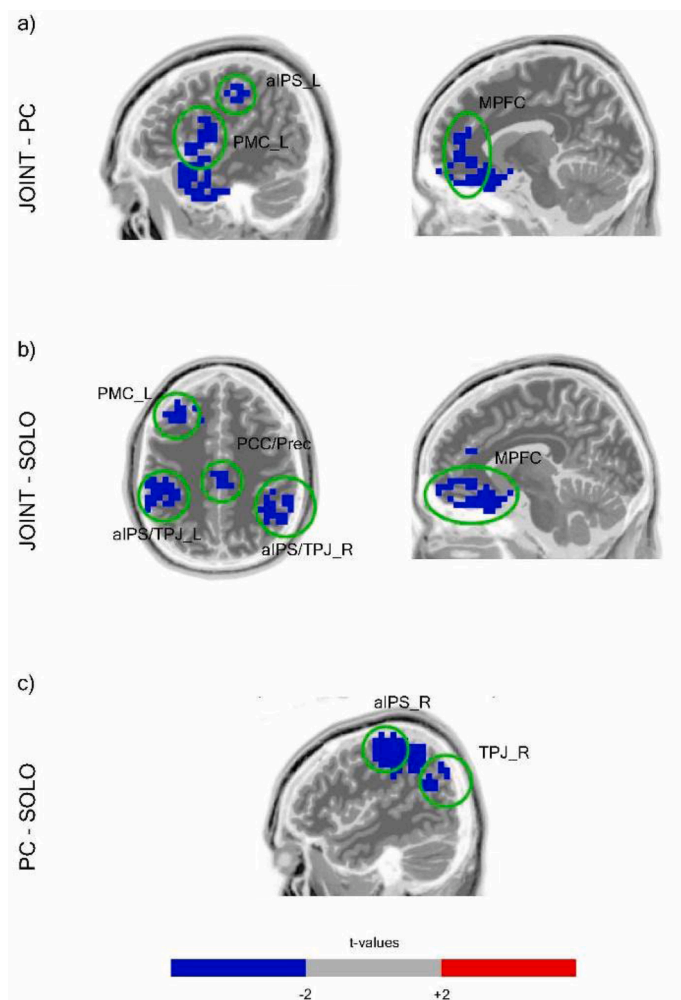
As for ANOVAs applied to behavioral data, we did not find any significant effect induced by the TASK for trial duration [ $F(2,30) = 1.915$ ;  $p = 0.164$ ] and ball height [ $F(2,30) = 2.585$ ;  $p = 0.093$ ]. The only significant effect was found for the number of successful trials [ $F(2,30) = 79.703$ ;  $p = 0.00001$ ] which resulted significantly higher in Joint condition, followed by Solo and then PC condition. In particular, participants made more errors in the PC condition (36.77 % successful rate) in contrast to the Joint (66.35 % successful rate) and Solo condition (61.15 % successful rate). Post hoc comparisons revealed significant differences for the Joint condition compared with the PC and the Solo condition. Differences were also found for the Solo condition compared with the PC condition.

#### 3.2. EEG data

The results section is composed of two parts. The single-brain analysis describes the whole-brain spectral activation maps and the intra-brain connectivity networks obtained for the group of subjects ( $N = 32$ ), by contrasting the joint condition with Solo and PC, and quantifies the role of specific ROIs and the connection density within and between MNS and MENT circuits. The multiple-brain analysis returns the multiple-subject connectivity networks obtained for the group of dyads ( $N = 16$ ) and quantifies the involvement of specific brain areas and the communication between MNS and MENT of the two subjects under the different experimental conditions.

##### 3.2.1. Single-brain analysis

**3.2.1.1. Whole-brain spectral analysis.** The spectral activation maps obtained for the pairwise contrast (FDR-corrected) between the three experimental conditions in the source domain are shown in Fig. 1 (theta band) and S1 (all bands). Table 1 summarizes the areas activated in the four frequency bands for the three pairwise comparisons and revealed that the contrast JA compared to the Solo or PC condition evidenced specific activations in (key) regions of the MNS and MENT circuits, whereas the comparison conditions PC and Solo showed activations in the posterior part of brain areas involved in the MNS and MENT circuits and motor activation. Fig. 1-a illustrates a significant theta-band desynchronization in the Joint condition with respect to the PC exclusively in the mPFC, PMC\_R and aIPS\_R. A similar desynchronization in the mPFC was found for the contrast JA compared to the Solo condition



**Fig. 1.** Group statistical spectral maps obtained by comparing the PSD of the three experimental conditions (Joint vs PC, Joint vs Solo and PC vs Solo) in the source domain in theta band. We used non-parametric statistics, with a significance level of 0.05, FDR-corrected. Blue voxels report significant desynchronizations. No significant synchronizations (red voxels) were found in this frequency band. Green circles highlight spectral activations in areas related to MNS or MENT. The spectral activations, reconstructed using the three-dimensional MNI152 model, were visualized on a more realistic model, the Colin27 - T1 weighted, with both models co-registered in MNI space. Images were generated using the Loreta Viewer utility, available at (<http://www.uzh.ch/kevinst/loretaOldy.htm>).

accompanied by a pronounced desynchronization also in the posterior cingulate cortex (PCC), Precuneus (Prec), PMC\_L, bilateral aIPS and bilateral TPJ (Fig. 1b). In the comparison PC vs Solo, the most prominent findings were detected in the posterior area, in particular a desynchronization current density in TPJ\_R and aIPS\_R. Also, the other frequency bands (alpha, beta and gamma) showed exclusively brain activations belonging to the MNS and MENT circuits (with the exception of a motor activation in the Alpha band for the comparison PC and Solo) (see table 1 and supplemental materials).

##### 3.1.2. Single-brain connectivity analysis

The connectivity networks obtained from the single-brain analysis performed on each of the 32 subjects for Joint conditions were statistically compared against PC and Solo conditions to obtain grand-average connectivity patterns like those reported in Fig. 2 for all the frequency bands. The resulting network includes regions from all the three systems (MNS, MENT and MC; Fig. 2-a and 2-b). In theta and alpha bands, the results show a significantly increased connectivity between the regions

**Table 1**

List of brain areas significantly involved in the four frequency bands (theta, alpha, beta, gamma) for the three statistical comparisons (Joint vs PC, Joint vs Solo, PC vs Solo). List of abbreviations: aIPS (anterior intraparietal sulcus), dmPFC - dorsal medial prefrontal cortex, L - left, M1 - primary motor cortex, mPFC - medial prefrontal cortex, PCC - posterior cingulate cortex, PMC - premotor cortex, Prec - precuneo, R -right, SMA - supplementary motor area, TPJ - temporo-parietal junction.

	Joint vs PC	Joint vs Solo	PC vs Solo
<b>Theta</b>	MPFC	MPFC	aIPS_R
	PMC	PCC/Prec	TPJ_R
	aIPS_L	PMC_L	
<b>Alpha</b>		aIPS/TPJ_bil	
	MPFC	MPFC	SMA_L
		PCC/Prec	M1_R
		M1_R	
<b>Beta</b>	dmPFC	TPJ_R	PMC_R
	TPJ_R	Prec	
<b>Gamma</b>	PCC/Prec	PCC/Prec	Prec
	aIPS/TPJ_bil	aIPS/TPJ_bil	

in the left hemisphere and the medial regions (mPFC and Prec) in the Joint condition when compared to the other two conditions. The theta band showed in addition a significant role of the PMC\_R in the Joint condition vs Solo. The beta band revealed similar but less dense connectivity patterns for the contrast Joint vs Solo and a significant role of the PMC\_R and Prec in the Joint condition vs PC. Sporadic connections resulted from the pairwise comparisons between connectivity patterns obtained in the gamma band.

The ANOVAs performed to evaluate the role of single ROIs (degree index) in the three conditions highlighted higher involvement in Joint condition with respect to PC and Solo for the PMC (left and right), the mPFC, the Prec and the SMAp in the theta band. Alpha showed significant result in aIPS\_L, in bilateral PMC, in Prec and M1, whereas beta bands evidenced an effect of task condition on the degree values in aIPS\_L, right PMC, rTPJ and M1\_L (see Fig. 3 and Tables S2 and S3 in supplemental materials). No significant differences were found for any of the other ROIs. No significant results were found for the gamma band.

As for the communication within and between MNS and MENT systems, the results of the ANOVA computed on intra-circuit (Intra MNS and Intra MENT) and inter-circuit connection (MNS-MENT and MENT-MNS) densities in the three conditions are shown in Fig. 4 and reported in supplemental materials (Tables S4 and S5). Only the density of the connections within MNS in alpha band and of those going from MNS to MENT in theta and alpha bands are significantly modulated by the experimental conditions. In particular, the communication within MNS and from MNS to MENT are significantly higher in Joint condition with respect to PC and Solo (Fig. 4 for alpha band and Fig. S2 for the other bands), as revealed by Newmann-Keuls' post-hoc test.

### 3.1.2. Multiple-brain connectivity analysis

The connectivity networks obtained from the multiple-brain analysis performed on each of the 16 dyads were statistically compared between conditions to obtain grand-average connectivity patterns like those reported in Fig. 5 for the beta band and Fig. S3 for all the bands. These results show a significantly increased inter-subject connectivity involving almost all the areas in the three considered systems, for the Joint condition when compared to the other two conditions. Similar results were obtained for the other frequency bands, with a lesser interaction between the two brains in the gamma band (Fig. S3).

The ANOVAs performed to evaluate the role of single ROIs (degree index) in the three conditions returned significant results in the same ROIs and same bands as obtained for the single-subject connectivity analysis, i.e. for the left aIPS, the PMC (left and right), the Prec, the left TPJ, and the SMAp in the theta, and similar also for alpha. Beta showed significant results in bilateral PMC, mPFC and left M1 (see also Tables S6 and S7 in suppl. material). A graphical representation of such results is

reported in Fig. 6, that shows the condition for which the degree of each ROI was significantly stronger than in the other two conditions (Newmann-Keuls' post-hoc test).

Results of the ANOVAs performed to evaluate how the inter-circuit density (MNS $\leftrightarrow$ MNS, MENT $\leftrightarrow$ MENT, MNS $\rightarrow$ MENT, MENT $\rightarrow$ MNS) in the multiple-subjects networks is modulated by the type of interaction were shown in Fig. 7 for theta band (other bands are reported in Figure S4 and Tables S8 and S9 of supplemental materials). Newmann-Keuls' post-hoc test showed a significantly higher MNS $\leftrightarrow$ MNS inter-circuits density for the joint condition with respect to the other two conditions in theta (Fig. 7), alpha and beta bands (Fig. S4). Similar behavior was found for MNS $\rightarrow$ MENT inter-circuits density in theta band (Fig. 7) and for MENT $\rightarrow$ MNS inter-circuits density in theta (Fig. 7) and alpha bands (Fig. S4).

**Table 2**

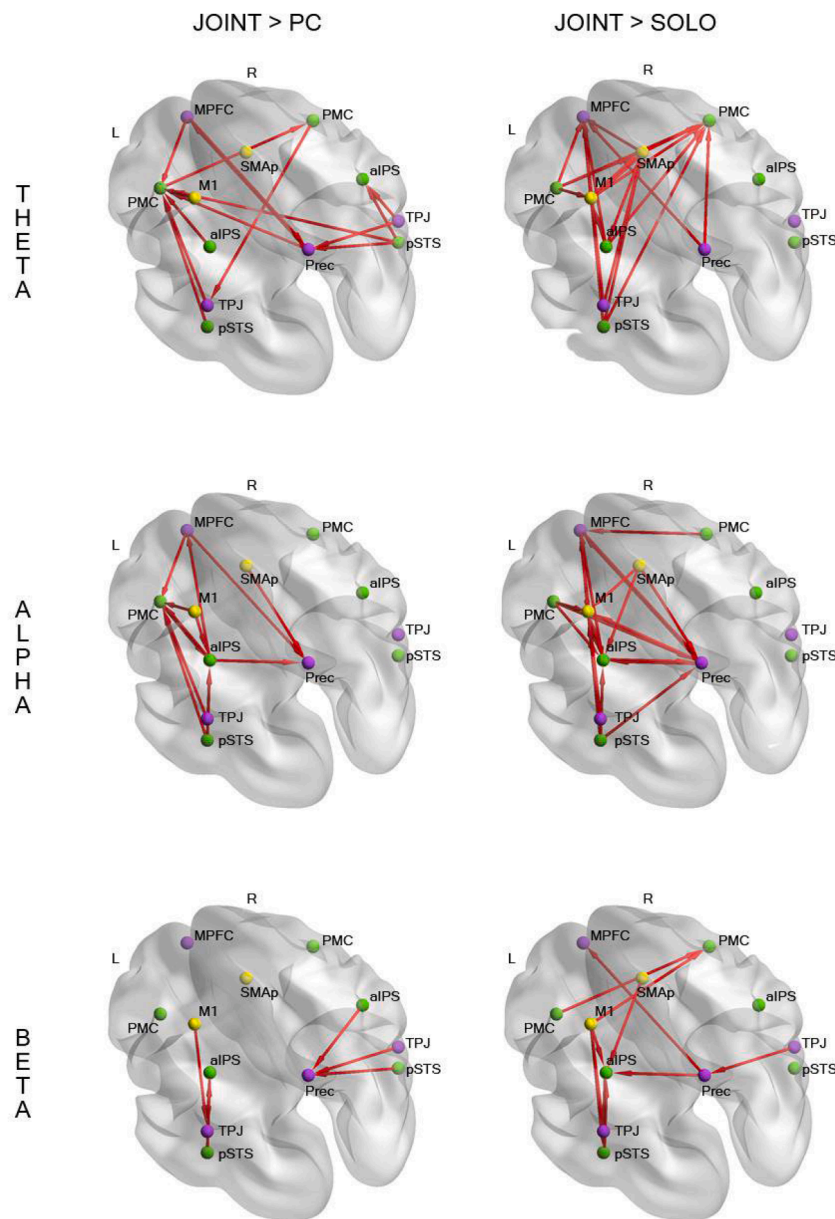
## 4. Discussion

Successful JA is based on action simulation and co-representation, which involves complex brain networks. The primary goal of the current study was to characterize the neural correlates of JA during ongoing social interaction in the context of a multi-brain connectivity analysis in the source domain, providing relevant information about the role in social function of two essential systems, the human MNS and MENT, and describing their influence at both intra-brain and inter-brain levels.

### 4.1. Joint action in a single brain

In our first investigation, we focused on identifying the brain regions involved during joint and individual actions by using a virtual bar-balancing task in which participants were required to cooperate with a human agent or to act alone or with a PC. In the joint condition, the dyad's shared goal was to reach the target area avoiding the obstacle in the middle of the screen. In order to successfully complete this task cooperatively with another person, both agents have to collaborate together to reach the goal without rolling the ball down, actually controlling one side of a single virtual bar with their right index finger. Behaviorally, we found that successful interaction with a human agent resulted in higher trials, while the PC condition had the lowest number of successful trials. This may be due to the human agent's different attitude towards cooperation and responsiveness compared to a human and requires high levels of interpersonal motor coordination and co-representation. Consequently, we hypothesized that the human "mirror neuron system" (MNS) and the mentalizing system (MENT) would be more active in the joint condition than in the other conditions (Solo and PC).

We found activation of several brain regions of the MNS and MENT during the JA condition, showing stronger activations in mPFC, TPJ and Precuneus (three brain regions of the MENT) complemented by enhanced activation in bilateral aIPS and left PMC (brain regions of the MNS). These findings support previous fMRI data showing the critical role of both systems (Newman-Norlund et al., 2008, Alcalá-López et al., 2019, Becchio et al., 2012, Chauvigné et al., 2018): during JA individuals are required to continuously consider their partner's actions by i) adjusting their behavior through the integration of the partner's actions within their own actions, which is supported by the MNS, and ii) understanding the intentions of others and disentangling mental states using an inference-based mechanism (MENT). In particular, it has been proposed that MNS might play an important role during JA by eliciting the neural representation of an observed action in one's own motor systems, thus providing a plausible neural mechanism for integrating one's own and observed actions into a common representation (Bonini et al., 2022, Rizzolatti et al., 2001). The MENT appears to be involved in the integration of the flow of social salient signals produced by both partners during joint actions, providing relevant information to infer the partners' intentions (Abe et al., 2019, Carter and Huettel, 2013, Geng



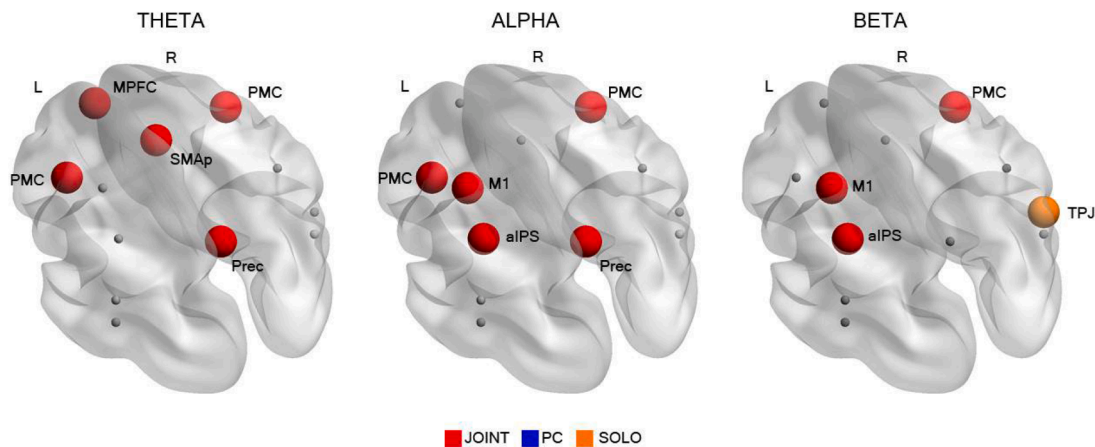
**Fig. 2.** Grand Average ( $N = 32$ ) INTRA-BRAIN Connectivity patterns. The networks were obtained by statistically comparing the single-brain patterns obtained for the Joint condition with those achieved for PC and Solo conditions (paired t-test,  $p < 0.05$  FDR corrected, one-side test, right tail). Each ROI is represented by a sphere whose color codes for the brain circuit: green for MNS, purple for MENT, yellow for MC. Statistically significant connections (Joint > Solo or Joint > PC) between ROIs are represented by means of red directed arrows.

and Vossel, 2013). Our results based on EEG data confirm that both neural systems are involved in JA and sustain cognitive processes that are associated with social interaction (Vogeley, 2017). Moreover, our results revealed a solid connection between MNS and MENT (Fig. 2). These results confirm that single brain regions of these mechanisms are central “nodes” during JA enabling two agents to be engaged in cooperative actions.

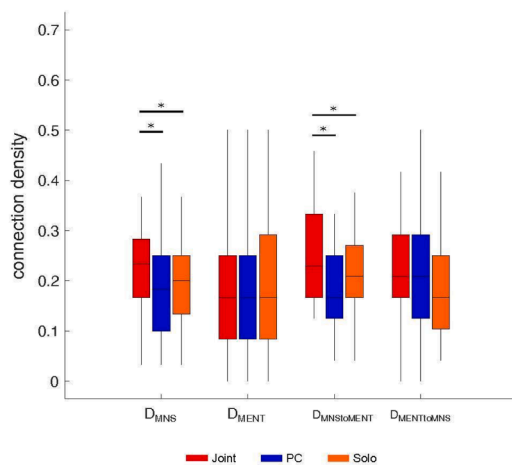
Furthermore, we were interested in distinguishing functional roles of both systems, by quantifying the connections involving each brain region. We demonstrated that in different bands during JA, the number of connections involving PMC (bilateral), mPFC, Prec, left aIPS and right TPJ was higher than in the other two conditions (PC and Solo). As known, the PMC is associated with motor resonance generating temporal predictions and is involved in determining the timing of turn-taking during joint actions (Bolt and Loehr, 2021, Hadley et al., 2015). In our JA condition both agents controlled one side of the same

virtual bar by alternately pressing a button with the right index finger: the correct timing alternation between the agents was fundamental to reach the goal and to prevent the ball free to roll down. It follows that the involvement of the PMC in the JA condition was essential in this task. Furthermore, the aIPS subserves the execution of hand goal-oriented movements (Van Overwalle and Baetens, 2009, Tunik et al., 2007) and the comprehension of actions with immediate goals (de C. Hamilton and Grafton, 2008). As already introduced, also part of the MENT contributes to JA, which is confirmed by our results, showing a prominent involvement of the mPFC. The mPFC, a key component of the mentalizing system (Ciaramidaro et al., 2014, Vogeley, 2017, Walter et al., 2004) and is assumed to be involved in coding one’s own and the other person’s action over time allowing a joint representation of the goal’s action (Dolk et al., 2012, Humphreys and Bedford, 2011, Frith and Frith, 2007). TPJ and Prec are also two neural areas belonging to the mentalizing system (Walter et al., 2004, Ciaramidaro et al., 2007,





**Fig. 3.** Graphical representation of the results of repeated measures ANOVA conducted on ROI degree index computed at intra-brain level in three frequency bands. For each ROI we use a sphere whose color and dimension are representative of the results of the statistical analysis. In particular we used: red when the degree of the ROI is significantly higher in Joint condition with respect to the others; blue when the degree of the ROI is significantly higher in PC condition with respect to the others; orange when the degree of the ROI is significantly higher in Solo condition with respect to the others; grey when no significant differences resulted from the ANOVA. The significance was evaluated by means of Newmann-Keuls' post-hoc test.



**Fig. 4.** Bar diagram reporting the results of the repeated measures ANOVA conducted on the intra-circuit and inter-circuit connection densities computed at intra-brain level for alpha band. The symbol \* highlights a significant difference between two levels of the within factor (Joint, PC, Solo) as revealed by Newmann-Keuls' post-hoc test. The results obtained for the other frequency bands are reported in Fig. S2.

Gallagher et al., 2002, Vogeley et al., 2001, Goel et al., 1995) and are involved in self-other distinction (Newman-Norlund et al., 2008, Abe et al., 2019). Specifically, it has been proposed that the TPJ appears to be implicated in two sets of functions relevant to JA: reorientation of attention and social cognitive functions ranging from the processing of socially relevant movements and cues, to inferring social intentions (Abe et al., 2019). The degree of cooperation between partners during joint action is thus reflected in the activation in TPJ, which is important for deducing the partner's intent. To do this, it manages and extracts the flow of data relevant to a goal-oriented joint action, enabling the execution of joint movements only when self- and other-movement planning overlaps (Dumas et al., 2020, Era et al., 2020). Similarly, it has been proposed that Prec is part of the network used to determine a sense of agency and self-other distinction (Abe et al., 2019, Vogeley et al., 2001, Vogeley and Fink, 2003). In the current experiment, it is plausible that during JA the participants are more focused on monitoring their own behaviors in order to better disambiguate their own actions from those generated by the co-agent.

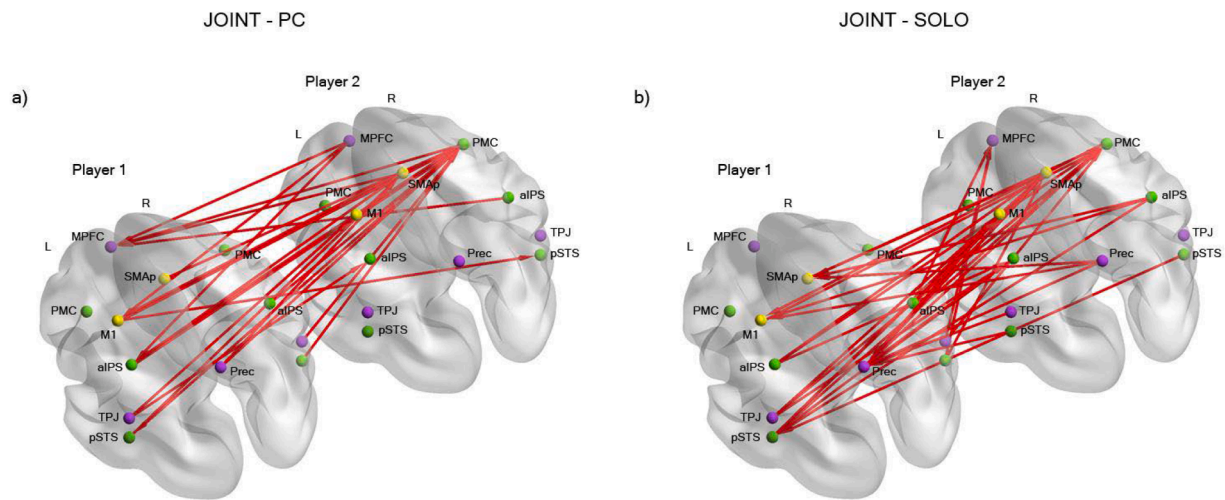
Although it is claimed that each single brain area of both systems is essential and serves its specific function during successful interaction, it is still unclear how these areas are functionally connected within and between the two systems. In line with this, we also aimed to investigate the reciprocal influence of each brain area within his circuits and between circuits. By comparing the JA conditions with respect to PC and Solo we found a significantly stronger density of connections within the MNS in alpha band, and a significantly stronger density of connections directed from MNS to MENT (theta and alpha bands).

The increased communication flow from MNS to MENT corroborates the hypothesis that MNS is involved in the early stages of social cognition, underlying an initial, fast and automatic processing of socially salient stimuli in JA, whereas MENT is assumed to be involved in the 'late' stages of controlled processes of evaluation of socially relevant information (Vogeley, 2017, Spunt and Lieberman, 2013, Keysers and Gazzola, 2007). Our results confirmed that, at the intra-brain level, MNS and MENT are two complementary mechanisms that support two different functional roles during interaction with others: Automatic behavior identification is supported by the MNS and inferring the actor's mental state is supported by the mentalizing system (Van Overwalle and Baetens, 2009, Kilner, 2011, Apperly, 2008, de Lange et al., 2008). The claim is that, while MNS is related to the early, automatic processing of spatial or body-related information, and it sends this information to MENT. In turn, MENT, pertaining to a late, controlled processing of information connected to the inner experience of people - including oneself - is influenced by the information received from MNS.

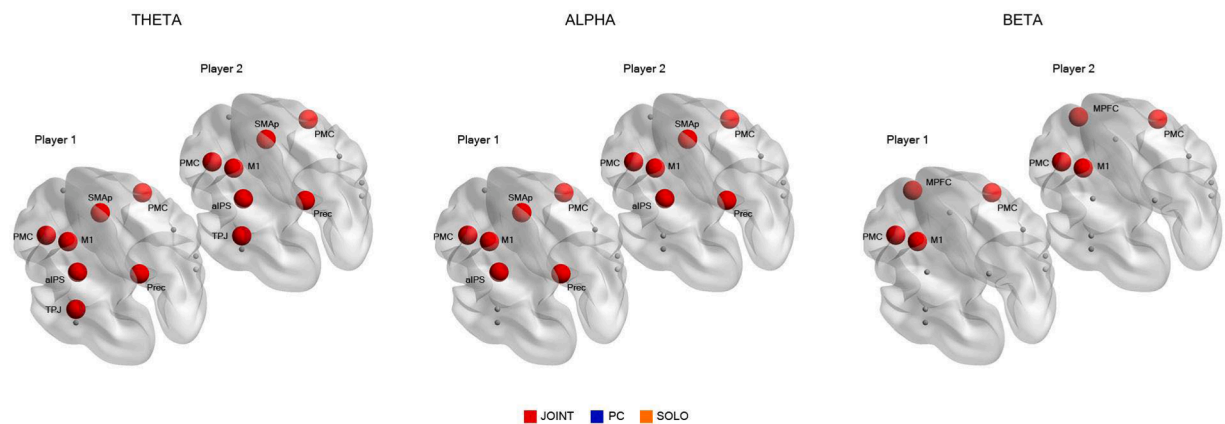
#### 4.2. Joint actions between brains

When two people interact, perceived information is conveyed between their brains, enabling people to anticipate and instantly adjust to the behavior of others and to represent shared action goals. In terms of neural activation, it follows that the neural mechanisms involved in the agents should be reciprocally influenced. Consequently, an important contribution of the present study was to explore the complex and unpredictable interaction between a specific dyad in terms of neural mechanisms in relation to the specific inter-brain contributions of MNS and MENT by implementing a multi-brain connectivity analysis in the source domain, a methodology that allowed us to capture the interaction as an autonomous property of the "dual system" and to explain how the brains of a dyad work (Hari, 2017). In line with previous hyperscanning studies (Dumas et al., 2020) our analyses initially included all EEG frequency bands relevant to physiological waking states. Through





**Fig. 5.** Grand Average ( $N = 16$  dyads) INTER-BRAIN Connectivity patterns in beta band. The networks were obtained by statistically comparing the multiple brain networks obtained in the Joint condition with those related to PC and Solo conditions (paired t-test,  $p < 0.05$  FDR corrected, one-side test, right tail). Each ROI is represented by a sphere whose color codes for the brain circuit: green for MNS, purple for MENT, yellow for MC. Statistically significant connections (Joint > Solo or Joint > PC) between ROIs are represented by means of red directed arrows.



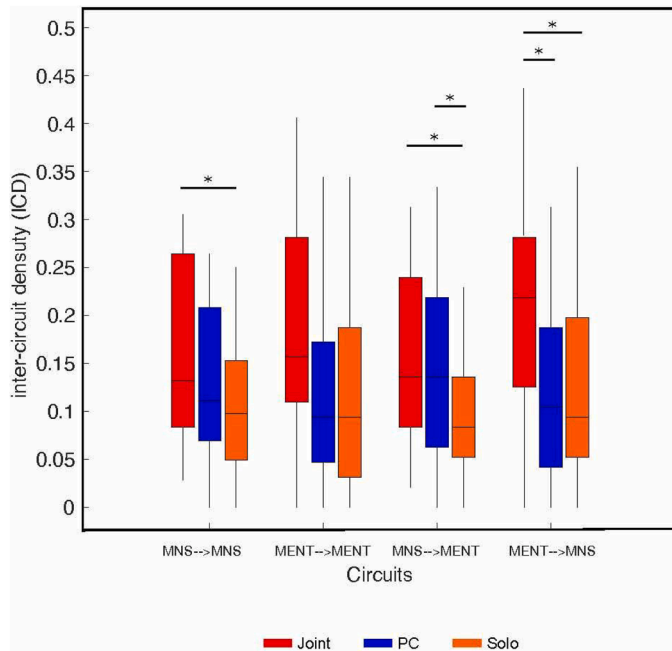
**Fig. 6.** Graphical representation of the results of the repeated measures ANOVA conducted on inter-circuit density in the multiple brain network for theta, alpha and beta bands. The centroid of each ROI for each subject is indicated by a sphere. The color of each sphere indicates which condition shows the (significantly) stronger degree for that ROI: red when it is significantly higher in the Joint condition with respect to the others; blue when it is significantly higher in PC condition (not occurring); orange when it is significantly higher in Solo condition (not occurring); gray when no significant differences resulted from the ANOVA (Newmann-Keuls' post-hoc test).

subsequent statistical tests and power analysis, we excluded the Gamma band, focusing instead on the Theta, Alpha, and Beta bands.

Our results delineated a significantly increased inter-subject connectivity involving MNS, MENT and MC in all the analyzed frequency bands during JA compared to Solo and PC conditions. Such finding confirmed the band-unspecific behavior of multiple-brain networks highlighted in previous studies on social cognitive process. In particular, fronto-central and occipital-temporal regions resulted as mainly involved in theta band (Dumas et al., 2012, Moreau et al., 2020), while alpha and beta bands were mostly associated to sensorimotor and cognitive coordination processes and motor related activities, respectively (Konvalinka et al., 2014, Tognoli et al., 2007, Novembre et al., 2014, Ménoret et al., 2014).

An increased inter-brain connectivity between two brains during interaction versus non-interaction conditions has already been reported in previous studies (Astolfi et al., 2020, Astolfi et al., 2010, Dumas et al., 2012, Lindenberger et al., 2009). However, to our knowledge, here we described for the first time, an increased specific connectivity in MENT and MNS systems. In particular, at inter-brain level we found similar results as for the single-subject connectivity, i.e. the left aIPS, mPFC,

bilateral PMC, the Prec, the left M1, and the SMAp in all the bands although to different degree. Nevertheless, the multi-brain connectivity study here proposed enables us to build on the findings at the individual level and to make a distinctive contribution to the description of how the brains of a dyad works in terms of neural modulation of MNS and MENT. In fact, the inter-brain level data demonstrated functional connectivity between the MNS systems of both agents during JA and reciprocal effect between the MNS and MENT systems of the two subjects showing a reciprocal influence of these mechanisms guiding social interaction. In addition, the correlation analysis revealed that the more our participants play and interact together, the more integrated the circuits are. We claim that, during JA interbrain synchronies may steer social interaction. This process seems to begin with neural activity in the MNS and MENT of one individual (Subject 1), which evokes cooperative behavior. This behavior, in turn, triggers the MNS and MENT in the second individual (Subject 2), resulting in an adaptive cooperative behavioral response. This is corroborated by the finding of hyperscanning studies stating that participation in social interaction directly affects motor interbrain synchronization among people's reciprocal encoding and interpretation of intention (for review see 73, 105). A new theoretical and experimental



**Fig. 7.** Bar diagram reporting the results of the repeated measures ANOVA reported in Tab.5 (theta band). The symbol \* highlights a significant difference between two levels of the within factor experimental condition (Joint, PC, Solo) as revealed by Tukey’s post-hoc test. The results obtained for the other frequency bands are reported in Fig. S4.

perspective suggests that inter-individual synchronization acts as a ‘forward or prediction’ model and implies that higher-level activations of the brain anticipate or predict lower-level events (Miyata et al., 2021, Friston, 2008, Friston and Frith, 2015). This feedback loop reduces discrepancies between predicted and actual outcomes, improving the accuracy of the brain’s interpretations (Friston and Frith, 2015). Thus, accordingly we suggest that the synchronization in the mentalizing network may represent the upper-level forward model of co-representation (monitoring and predicting the goal-directed behavior of self and others), which sends top-down prediction signals to the MNS. The MNS represents the action simulation, by predicting the consequences of the co-actor’s behavior, and sending feedback to the upper-level prediction represented by the mentalizing network, refining such predictions and forming hierarchical representation. fMRI-hyperscanning studies have shown that the parietal part of the motor neuron (MNS) is crucial for pair-specific forward internal modeling of action representation. This process, known as “resonance,” allows observers to internalize another person’s behaviors, offering a first-person viewpoint (Miyata et al., 2021, Yoshioka et al., 2021, Koike et al., 2019). Synchronization was also found in the motor prefrontal cortex (mPFC) and rTPJ, which are essential for uniquely human social cognition (Bilek et al., 2015, Bilek et al., 2022, Saxe, 2006). mPFC is involved in processing triadic interactions between minds and objects, while rTPJ function is proposed as the basis of unique neural synchrony (Abe et al., 2019, Bilek et al., 2015, Saxe, 2006).

To summarize, the results of our inter-brain analysis suggest the complementarity of both systems but also their synergy across subjects. We demonstrated that the use of a hyperscanning setting together with multiple-brain modeling enables us to address whether there is an influence i) between the activation of the homologous neural systems in the two agents (MNS-MNS and MENT-MENT), and ii) between the MNS activation in one agent and the MENT activation in the other, and vice-versa. The synergy between MNS and MENT during a dual exchange seems to be strong and bidirectional, including the effect of the MNS of each subject toward the MENT of the other and reversed.

**Table 2** Results of the statistical correlation (Pearson correlation) between connection densities defined for measuring the interaction between MNS and MENT at multiple brain levels and the behavioral data (ball height, trial length and number of successful trials). We highlighted in bold significant results. (p-values below the significance level of 0.05 corrected by means of False Discovery Rate).

	THETA			ALPHA			BETA			GAMMA		
	MNS→MNS	MENT→MENT	MNS→MENT	MNS→MNS	MENT→MENT	MNS→MENT	MNS→MNS	MENT→MENT	MNS→MENT	MNS→MNS	MENT→MENT	MNS→MENT
<b>Ball Height</b>	0.37	-0.04	0.26	0.21	0.48	0.32	0.20	0.42	-0.13	0.24	0.20	0.14
<b>Trial Length</b>	0.63	0.39	0.56	0.49	0.68	0.63	0.65	0.71	0.59	0.72	0.70	0.67
<b>Suc Trials</b>	0.29	-0.07	0.17	0.15	0.38	0.26	0.16	0.35	-0.11	0.19	0.20	0.15

Significant positive correlations were found between trial length and ICD within MNS in all the four bands, ICD within MENT in alpha and beta bands, ICD from MNS to MENT and from MENT to MNS in alpha, beta and gamma bands (see Table 2). we set a significance level ( $\alpha$ ) equal to 0.05 adjusted by means of False Discovery Rate (FDR) to mitigate type I errors coming from multiple comparisons.

### 4.3. Limitations of the study

Our sample only included male subjects, and thus, the results are not representative of both sexes. But evidence suggests that it is possible to expect changes on joint actions effects related to the perceived similarity between both agents (Wang et al., 2018, Miyata et al., 2021) and the gender composition of pairs should affect the joint action, given that gender is one of the most salient types of social categorization (Friston, 2008). Consequently, it seems necessary to investigate Joint actions with greater statistical power that include male and female participants or consider gender-related variables measuring same-gender pairs and mixed-gender pair.

In this work we decided to use the sLORETA approach for localizing EEG sources since for the level of noise we estimated in our data and the depths of the sources we included in the study, it gives the best solution in terms of both localization error and ghost sources (Grech et al., 2008). Moreover, being a non-parametric approach, dipole sources are distributed in the whole brain volume covering the entire gray matter, thus ensuring a good spatial sampling of the regions of interest. However, the selection of a specific source localization approach would have affected the results obtained. Future studies should confirm the results obtained by applying other localization approaches thus generalizing the findings and making them untied with respect to the method applied.

Furthermore, the innovative methodological approach employed in this work allowed to describe the interaction between MNS and MENT systems at intra- and inter-subject levels considering the interaction established during the entire experimental session as a static phenomenon overlooking all the aspects related to the transient, namely the establishment of the relationship and its temporal evolution along the game. In fact, the high complexity of the model used to characterize such interaction requires a substantial amount of data which is satisfied only using the entire dyadic dataset as input of the algorithms employed. Future studies should address this issue by proposing new approaches able to keep in the computation the temporal aspects of the interaction and thus providing an estimate of the multiple-brain model at single trial level. This would ensure the possibility to track the establishment of the interaction and follow its evolution along time.

### 5. Conclusion

Neuroscience is still in its early stages, but a two-person approach can clarify open questions and formulate new hypotheses about human social interaction. The study explored the MNS and MENT systems during JA, revealing a bidirectional synergy between them. This highlights the collaborative nature of human cognition and the importance of studying social interaction from a multi-subject perspective. The findings suggest a need for a multiple-brain approach to understand human social behavior in real-world settings.

### Data sharing

Fully anonymized data can be made available to researchers upon request regarding scientific aspects (such as data analysis).

### CRediT authorship contribution statement

**Angela Ciaramidaro:** Writing – original draft, Supervision, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Jlenia Toppi:** Writing – original draft, Supervision, Methodology, Funding acquisition, Data curation, Conceptualization. **Pascal Vogel:** Writing – review & editing, Methodology. **Christine M. Freitag:** Writing – review & editing, Conceptualization. **Michael Siniatchkin:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Laura Astolfi:** Writing – original draft, Supervision, Resources, Methodology, Investigation, Conceptualization.

### Declaration of competing interest

The authors of this article have no conflicts of interest, financial or otherwise, to disclose.

### Data availability

Data will be made available on request.

### Acknowledgment

The study was supported by the Italian Ministry of University and Research—PRIN (20207S3NB8), Sapienza University of Rome—Progetto di Ateneo 2022 (RM1221816C8C757C) and SEED-PNR 2021, by Bit-Brain award 2020 (2962-B2B), by “FAR: PROGETTO DI RICERCA INTERDISCIPLINARE MISSION ORIENTED” Inter-brain synchronization during face-to-face interaction: EEG-hyperscanning during empathic and cooperative interaction in Autism (Funding: University of Modena and Reggio) and by Italian Ministry of Health (GR2019-12369207).

### Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.neuroimage.2024.120783](https://doi.org/10.1016/j.neuroimage.2024.120783).

### References

- Abe, M.O., et al., 2019. Neural correlates of online cooperation during joint force production. *Neuroimage* 191, 150–161.
- T. Achenbach, *Manual for the Young Adult Self-Report and Young Adult Behavior Checklist* (1997).
- Alcalá-López, D., Vogeley, K., Binkofski, F., Bzdok, D., 2019. Building blocks of social cognition: mirror, mentalize, share? *Cortex* 118, 4–18.
- Apperly, I.A., 2008. Beyond simulation-theory and theory-theory: Why social cognitive neuroscience should use its own concepts to study “theory of mind. *Cognition* 107, 266–283.
- Astolfi, L., et al., 2010. Neuroelectrical hyperscanning measures simultaneous brain activity in humans. *Brain Topogr.* 23, 243–256.
- Astolfi, L., et al., 2011. Imaging the social brain by simultaneous hyperscanning during subject interaction. *IEEE Intell. Syst.* 26, 38–45.
- Astolfi, L., et al., 2020. Raising the bar: Can dual scanning improve our understanding of joint action? *Neuroimage* 216, 116813.
- Babiloni, F., Astolfi, L., 2014. Social neuroscience and hyperscanning techniques: past, present and future. *Neurosci. Biobehav. Rev.* 44, 76–93.
- Babiloni, F., et al., 2007. High resolution EEG hyperscanning during a card game. *Annu. Int. Conf. IEEE Eng. Med. Biol. Soc.* 4957–4960, 2007.
- Bacalá, L.A., Sameshima, K., 2001. Partial directed coherence: a new concept in neural structure determination. *Biol. Cybern.* 84, 463–474.
- Becchio, C., Manera, V., Sartori, L., Cavallo, A., Castiello, U., 2012. Grasping intentions: from thought experiments to empirical evidence. *Front. Human Neurosci.* 6.
- Bilek, E., et al., 2015. Information flow between interacting human brains: Identification, validation, and relationship to social expertise. *Proc. Natl. Acad. Sci.* 112, 5207–5212.
- Bilek, E., et al., 2022. Directed coupling in multi-brain networks underlies generalized synchrony during social exchange. *Neuroimage* 252, 119038.
- Bolt, N.K., Loehr, J.D., 2021. The motor-related brain activity that supports joint action: a review. *Acta Psychol. (Amst)* 212.
- Bonini, L., Rotunno, C., Arcuri, E., Gallese, V., 2022. Mirror neurons 30 years later: implications and applications. *Trends Cogn. Sci.* 26, 767–781.
- Bosga, J., Meulenbroek, R.G.J., 2007. Joint-action coordination of redundant force contributions in a virtual lifting task. *Motor Control* 11, 235–258.
- Burgess, A.P., 2013. On the interpretation of synchronization in EEG hyperscanning studies: a cautionary note. *Front. Hum. Neurosci.* 7, 881.
- Carter, R.M., Huettel, S.A., 2013. A nexus model of the temporal-parietal junction. *Trends Cogn. Sci.* 17, 328–336.
- Chaminade, T., Marchant, J., Kilner, J., Frith, C., 2012. An fMRI study of joint action—varying levels of cooperation correlates with activity in control networks. *Front. Human Neurosci.* 6.
- Chauvigné, L.A.S., Belyk, M., Brown, S., 2018. Taking two to tango: fMRI analysis of improvised joint action with physical contact. *PLoS One* 13, e0191098.
- Chen, Y., et al., 2020. The influence of prior intention on joint action: an fNIRS-based hyperscanning study. *Soc. Cognit. Affect. Neurosci.* 15, 1340–1349.
- Cheng, X., Guo, B., Hu, Y., 2022. Distinct neural couplings to shared goal and action coordination in joint action: evidence based on fNIRS hyperscanning. *Soc. Cognit. Affect. Neurosci.* 17, 956–964.



- Ciaramidaro, A., et al., 2007. The intentional network: how the brain reads varieties of intentions. *Neuropsychologia* 45, 3105–3113.
- Ciaramidaro, A., Becchio, C., Colle, L., Bara, B.G., Walter, H., 2014. Do you mean me? Communicative intentions recruit the mirror and the mentalizing system. *Soc. Cognit. Affect. Neurosci.* 9, 909–916.
- Ciaramidaro, A., et al., 2018. Multiple-brain connectivity during third party punishment: an EEG hyperscanning study. *Sci. Rep.* 8, 6822.
- Cui, X., Bryant, D.M., Reiss, A.L., 2012. NIRS-based hyperscanning reveals increased interpersonal coherence in superior frontal cortex during cooperation. *Neuroimage* 59, 2430–2437.
- de C. Hamilton, A.F., Grafton, S.T., 2008. Action outcomes are represented in human inferior frontoparietal cortex. *Cereb. Cortex* 18, 1160–1168.
- de Lange, F.P., Spronk, M., Willems, R.M., Toni, I., Bekkering, H., 2008. Complementary systems for understanding action intentions. *Curr. Biol.* 18, 454–457.
- Dodel, S., Tognoli, E., Kelso, J.A.S., 2020. Degeneracy and complexity in neuro-behavioral correlates of team coordination. *Front. Hum. Neurosci.* 14, 328.
- Dolk, T., Liepelt, R., Villringer, A., Prinz, W., Ragert, P., 2012. Morphometric gray matter differences of the medial frontal cortex influence the social Simon effect. *Neuroimage* 61, 1249–1254.
- Dumas, G., Nadel, J., Soussignan, R., Martinerie, J., Garnero, L., 2010. Inter-brain synchronization during social interaction. *PLoS One* 5, e12166.
- Dumas, G., Martinerie, J., Soussignan, R., Nadel, J., 2012. Does the brain know who is at the origin of what in an imitative interaction? *Front. Hum. Neurosci.* 6.
- Dumas, G., Moreau, Q., Tognoli, E., Kelso, J.A.S., 2020. The human dynamic clamp reveals the fronto-parietal network linking real-time social coordination and cognition. *Cereb. Cortex* 30, 3271–3285.
- Era, V., Candidi, M., Gandolfo, M., Sachelì, L.M., Aglioti, S.M., 2018. Inhibition of left anterior intraparietal sulcus shows that mutual adjustment marks dyadic joint-actions in humans. *Soc. Cognit. Affect. Neurosci.* 13, 492–500.
- Era, V., Aglioti, S.M., Candidi, M., 2020. Inhibitory theta burst stimulation highlights the role of left aIPS and right TPJ during complementary and imitative human-avatar interactions in cooperative and competitive scenarios. *Cereb. Cortex* 30, 1677–1687.
- Fallani, F.D.V., et al., 2010. A graph-theoretical approach in brain functional networks. Possible implications in EEG studies. *Nonlinear Biomed Phys* 4 (Suppl 1), S8.
- Fitzpatrick, P., Mitchell, T., Schmidt, R.C., Kennedy, D., Frazier, J.A., 2019. Alpha band signatures of social synchrony. *Neurosci. Lett.* 699, 24–30.
- Friston, K., Frith, C., 2015. A Duet for one. *Conscious. Cogn.* 36, 390–405.
- Friston, K., 2008. Hierarchical Models in the Brain. *PLoS Comput. Biol.* 4, e1000211.
- Frith, C.D., Frith, U., 2007. Social cognition in humans. *Curr. Biol.* 17, R724–R732.
- Fuchs, M., Kastner, J., Wagner, M., Hawes, S., Ebersole, J.S., 2002. A standardized boundary element method volume conductor model. *Clin. Neurophysiol.* 113, 702–712.
- Gallagher, H.L., Jack, A.I., Roepstorff, A., Frith, C.D., 2002. Imaging the intentional stance in a competitive game. *Neuroimage* 16, 814–821.
- Geng, J.J., Vossel, S., 2013. Re-evaluating the role of TPJ in attentional control: contextual updating? *Neurosci. Biobehav. Rev.* 37, 2608–2620.
- Goel, V., Grafman, J., Sadato, N., Hallett, M., 1995. Modeling other minds. *Neuroreport* 6, 1741–1746.
- Gräfenhain, M., Behne, T., Carpenter, M., Tomasello, M., 2009. Young children's understanding of joint commitments. *Dev. Psychol.* 45, 1430–1443.
- Grech, R., et al., 2008. Review on solving the inverse problem in EEG source analysis. *J. Neuroeng. Rehabil.* 5, 25.
- Gugnowska, K., et al., 2022. Endogenous sources of interbrain synchrony in duetting pianists. *Cereb. Cortex* 32, 4110–4127.
- Hadley, L.V., Novembre, G., Keller, P.E., Pickering, M.J., 2015. Causal role of motor simulation in turn-taking behavior. *J. Neurosci.* 35, 16516–16520.
- Hari, R., Henriksson, L., Malinen, S., Parkkonen, L., 2015. Centrality of social interaction in human brain function. *Neuron* 88, 181–193.
- Hari, R., Sams, M., Nummenmaa, L., 2016. Attending to and neglecting people: bridging neuroscience, psychology and sociology. *Philosophical. Transact. Royal Society B: Biol. Sci.* 371, 20150365.
- Hari, R., 2017. From brain–environment connections to temporal dynamics and social interaction: principles of human brain function. *Neuron* 94, 1033–1039.
- Hu, Y., Hu, Y., Li, X., Pan, Y., Cheng, X., 2017. Brain-to-brain synchronization across two persons predicts mutual prosociality. *Soc. Cognit. Affect. Neurosci.* 12, 1835–1844.
- Humphreys, G.W., Bedford, J., 2011. The relations between joint action and theory of mind: a neuropsychological analysis. *Exp. Brain Res.* 211, 357–369.
- Iani, C., Anelli, F., Nicoletti, R., Rubichi, S., 2014. The carry-over effect of competition in task-sharing: evidence from the joint Simon task. *PLoS One* 9, e97991.
- Isoda, M., 2016. Understanding intentional actions from observers' viewpoints: A social neuroscience perspective. *Neurosci. Res.* 112, 1–9.
- Keyers, C., Gazzola, V., 2007. Integrating simulation and theory of mind: from self to social cognition. *Trends Cogn. Sci.* 11, 194–196.
- Kilner, J.M., 2011. More than one pathway to action understanding. *Trends Cogn. Sci.* 15, 352–357.
- Knoblich, G., Butterfill, S., Sebanz, N., 2011. Chapter three - psychological research on joint action: theory and data. In: Ross, B.H. (Ed.), *Psychology of Learning and Motivation, Advances in Research and Theory*. Academic Press, pp. 59–101.
- Koike, T., et al., 2019. Role of the right anterior insular cortex in joint attention-related identification with a partner. *Soc. Cognit. Affect. Neurosci.* 14, 1131–1145.
- Konvalinka, I., et al., 2014. Frontal alpha oscillations distinguish leaders from followers: multivariate decoding of mutually interacting brains. *Neuroimage* 94, 79–88.
- Kourtis, D., Sebanz, N., Knoblich, G., 2010. Favouritism in the motor system: social interaction modulates action simulation. *Biol. Lett.* 6, 758–761.
- Kourtis, D., Sebanz, N., Knoblich, G., 2013. Predictive representation of other people's actions in joint action planning: an EEG study. *Soc. Neurosci.* 8, 31–42.
- Kourtis, D., Knoblich, G., Sebanz, N., 2013. History of interaction and task distribution modulate action simulation. *Neuropsychologia* 51, 1240–1247.
- Kourtis, D., Knoblich, G., Woźniak, M., Sebanz, N., 2014. Attention allocation and task representation during joint action planning. *J. Cogn. Neurosci.* 26, 2275–2286.
- Kruppa, J.A., et al., 2021. Brain and motor synchrony in children and adolescents with ASD—a fNIRS hyperscanning study. *Soc. Cognit. Affect. Neurosci.* 16, 103–116.
- Lindenberger, U., Li, S.-C., Gruber, W., Müller, V., 2009. Brains swinging in concert: cortical phase synchronization while playing guitar. *BMC Neurosci.* 10, 22.
- Liu, H., Zhao, C., Wang, F., Zhang, D., 2021. Inter-brain amplitude correlation differentiates cooperation from competition in a motion-sensing sports game. *Soc. Cogn. Affect. Neurosci.* 16, 552–564.
- Ménoiret, M., et al., 2014. Neural correlates of non-verbal social interactions: a dual-EEG study. *Neuropsychologia* 55, 85–97.
- Müller, V., Sänger, J., Lindenberger, U., 2018. Hyperbrain network properties of guitarists playing in quartet. *Ann. N.Y. Acad. Sci.* 1423, 198–210.
- Mayka, M.A., Corcos, D.M., Leurgans, S.E., Vaillancourt, D.E., 2006. Three-dimensional locations and boundaries of motor and premotor cortices as defined by functional brain imaging: a meta-analysis. *Neuroimage* 31, 1453–1474.
- Mazziotta, J., et al., 2001. A probabilistic atlas and reference system for the human brain: international consortium for brain mapping (ICBM). *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 356, 1293–1322.
- Meyer, M., van der Wel, R.P.R.D., Hunnius, S., 2016. Planning my actions to accommodate yours: joint action development during early childhood. *Philosoph. Transact. Royal Society B: Biol. Sci.* 371, 20150371.
- Miss, F.M., Adriaense, J.E.C., Burkart, J.M., 2022. Towards integrating joint action research: Developmental and evolutionary perspectives on co-representation. *Neurosci. Biobehav. Rev.* 143, 104924.
- Miyata, K., et al., 2021. Neural substrates for sharing intention in action during face-to-face imitation. *Neuroimage* 233, 117916.
- Moreau, Q., Candidi, M., Era, V., Tieri, G., Aglioti, S.M., 2020. Midline frontal and occipito-temporal activity during error monitoring in dyadic motor interactions. *Cortex* 127, 131–149.
- Mu, Y., Guo, C., Han, S., 2016. Oxytocin enhances inter-brain synchrony during social coordination in male adults. *Soc. Cogn. Affect. Neurosci.* 11, 1882–1893.
- Newman-Norlund, R.D., Bosga, J., Meulenbroek, R.G.J., Bekkering, H., 2008. Anatomical substrates of cooperative joint-action in a continuous motor task: virtual lifting and balancing. *Neuroimage* 41, 169–177.
- Nichols, T.E., Holmes, A.P., 2002. Nonparametric permutation tests for functional neuroimaging: a primer with examples. *Hum. Brain Mapp.* 15, 1–25.
- Novembre, G., Ticini, L.F., Schütz-Bosbach, S., Keller, P.E., 2014. Motor simulation and the coordination of self and other in real-time joint action. *Soc. Cogn. Affect. Neurosci.* 9, 1062–1068.
- Novembre, G., Sammler, D., Keller, P.E., 2016. Neural alpha oscillations index the balance between self-other integration and segregation in real-time joint action. *Neuropsychologia* 89, 414–425.
- Oberman, L.M., Pineda, J.A., Ramachandran, V.S., 2007. The human mirror neuron system: a link between action observation and social skills. *Soc. Cognit. Affect. Neurosci.* 2, 62–66.
- Pan, Y., Cheng, X., Zhang, Z., Li, X., Hu, Y., 2017. Cooperation in lovers: An fNIRS-based hyperscanning study. *Hum. Brain Mapp.* 38, 831–841.
- Pascual-Marqui, R.D., Michel, C.M., Lehmann, D., 1994. Low resolution electromagnetic tomography: a new method for localizing electrical activity in the brain. *Int. J. Psychophysiol.* 18, 49–65.
- Pascual-Marqui, R.D., et al., 1999. Low resolution brain electromagnetic tomography (LORETA) functional imaging in acute, neuroleptic-naive, first-episode, productive schizophrenia. *Psychiatry Res.* 90, 169–179.
- Pascual-Marqui, R.D., 2002. Standardized low-resolution brain electromagnetic tomography (sLORETA): technical details. *Methods Find Exp. Clin. Pharmacol.* 24 (Suppl D), 5–12.
- Rizzolatti, G., Fogassi, L., Gallese, V., 2001. Neurophysiological mechanisms underlying the understanding and imitation of action. *Nat. Rev. Neurosci.* 2, 661–670.
- Rubinov, M., Sporns, O., 2010. Complex network measures of brain connectivity: uses and interpretations. *Neuroimage* 52, 1059–1069.
- Ruisen, M.I., de Bruijn, E.R.A., 2016. Competitive game play attenuates self-other integration during joint task performance. *Front. Psychol.* 7.
- Sänger, J., Müller, V., Lindenberger, U., 2012. Intra- and interbrain synchronization and network properties when playing guitar in duets. *Front. Human Neurosci.* 6.
- Saxe, R., 2006. Uniquely human social cognition. *Curr. Opin. Neurobiol.* 16.
- Sebanz, N., Knoblich, G., Prinz, W., 2003. Representing others' actions: just like one's own? *Cognition* 88, B11–B21.
- Sebanz, N., Knoblich, G., Prinz, W., 2005. How two share a task: corepresenting stimulus-response mappings. *J. Exp. Psychol. Hum. Percept. Perform.* 31, 1234–1246.
- Sebanz, N., Bekkering, H., Knoblich, G., 2006. Joint action: bodies and minds moving together. *Trends Cogn. Sci.* 10, 70–76.
- Shiraishi, M., Shimada, S., 2021. Inter-brain synchronization during a cooperative task reflects the sense of joint agency. *Neuropsychologia* 154, 107770.
- Sperduti, M., Guionnet, S., Fossati, P., Nadel, J., 2014. Mirror Neuron System and Mentalizing System connect during online social interaction. *Cogn. Process* 15, 307–316.
- Spunt, R.P., Lieberman, M.D., 2013. The busy social brain: evidence for automaticity and control in the neural systems supporting social cognition and action understanding. *Psychol. Sci.* 24, 80–86.
- Tikhonov, A.N., Arsenin, V.I., 1977. Solutions of ill-posed problems.
- Tognoli, E., Lagarde, J., DeGuzman, G.C., Kelso, J.A.S., 2007. The phi complex as a neuromarker of human social coordination. *Proc. Natl. Acad. Sci. USA* 104, 8190–8195.

- Toppi, J., et al., 2016. Investigating cooperative behavior in ecological settings: an EEG hyperscanning study. *PLoS One* 11, e0154236.
- Toppi, J., et al., 2022. A novel approach to measure brain-to-brain spatial and temporal alignment during positive empathy. *Sci. Rep.* 12, 17282.
- Tsai, C.-C., Kuo, W.-J., Jing, J.-T., Hung, D.L., Tzeng, O.J.-L., 2006. A common coding framework in self–other interaction: evidence from joint action task. *Exp. Brain Res.* 175, 353–362.
- Tunik, E., Rice, N.J., Hamilton, A., Grafton, S.T., 2007. Beyond grasping: representation of action in human anterior intraparietal sulcus. *Neuroimage* 36 (Suppl 2), T77–T86.
- Van Overwalle, F., Baetens, K., 2009. Understanding others' actions and goals by mirror and mentalizing systems: a meta-analysis. *Neuroimage* 48, 564–584.
- Vanzella, P., et al., 2019. fNIRS responses in professional violinists while playing duets: evidence for distinct leader and follower roles at the brain level. *Front. Psychol.* 10.
- Vesper, C., Butterfill, S., Knoblich, G., Sebanz, N., 2010. A minimal architecture for joint action. *Neural. Netw.* 23, 998–1003.
- Vogeley, K., Fink, G.R., 2003. Neural correlates of the first-person-perspective. *Trends Cogn. Sci.* 7, 38–42.
- Vogeley, K., et al., 2001. Mind reading: neural mechanisms of theory of mind and self-perspective. *Neuroimage* 14, 170–181.
- Vogeley, K., 2017. Two social brains: neural mechanisms of intersubjectivity. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 372, 20160245.
- Walter, H., et al., 2004. Understanding intentions in social interaction: the role of the anterior paracingulate cortex. *J. Cogn. Neurosci.* 16, 1854–1863.
- Wang, M.-Y., et al., 2018. Concurrent mapping of brain activation from multiple subjects during social interaction by hyperscanning: a mini-review. *Quantit. Imag. Med. Surg.* 8, 81937.
- Yoshioka, A., et al., 2021. Neural substrates of shared visual experiences: a hyperscanning fMRI study. *Soc. Cognit. Affect. Neurosci.* 16, 1264–1275.
- Yun, K., Watanabe, K., Shimojo, S., 2012. Interpersonal body and neural synchronization as a marker of implicit social interaction. *Sci. Rep.* 2, 959.
- Zamm, A., et al., 2021. Behavioral and neural dynamics of interpersonal synchrony between performing musicians: a wireless EEG hyperscanning study. *Front. Human Neurosci.* 15.
- Zhang, M., Liu, T., Pelowski, M., Jia, H., Yu, D., 2017. Social risky decision-making reveals gender differences in the TPJ: a hyperscanning study using functional near-infrared spectroscopy. *Brain Cogn.* 119, 54–63.
- Zhang, D., Lin, Y., Jing, Y., Feng, C., Gu, R., 2019. The dynamics of belief updating in human cooperation: findings from inter-brain ERP hyperscanning. *Neuroimage* 198, 1–12.
- Zhou, G., Bourguignon, M., Parkkonen, L., Hari, R., 2016. Neural signatures of hand kinematics in leaders vs. followers: a dual-MEG study. *Neuroimage* 125, 731–738.