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Raising the bar: Can dual scanning improve our understanding of joint action?

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ABSTRACT

Two-person neuroscience (2 PN) is a recently introduced conceptual and methodological framework used to investigate the neural basis of human social interaction from simultaneous neuroimaging of two or more subjects (hyperscanning). In this study, we adopted a 2 PN approach and a multiple-brain connectivity model to investigate the neural basis of a form of cooperation called joint action. We hypothesized different intra-brain and inter-brain connectivity patterns when comparing the interpersonal properties of joint action with non-interpersonal conditions, with a focus on co-representation, a core ability at the basis of cooperation. 32 subjects were enrolled in dual-EEG recordings during a computerized joint action task including three conditions: one in which the dyad jointly acted to pursue a common goal (joint), one in which each subject interacted with the PC (PC), and one in which each subject performed the task individually (Solo).

A combination of multiple-brain connectivity estimation and specific indices derived from graph theory allowed to compare interpersonal with non-interpersonal conditions in four different frequency bands. Our results indicate that all the indices were modulated by the interaction, and returned a significantly stronger integration of multiple-subject networks in the joint vs. PC and Solo conditions. A subsequent classification analysis showed that features based on multiple-brain indices led to a better discrimination between social and non-social conditions with respect to single-subject indices. Taken together, our results suggest that multiple-brain connectivity can provide a deeper insight into the understanding of the neural basis of cooperation in humans.

1. Introduction

Successful interactions depend upon our capacity to cooperate with others, and are based on the human ability to give sense to another person's behavior, to adjust and to synchronize one's actions with those of others: cooperation involves mutual and reciprocal interaction between two minds. A particular form of cooperation, whereby at least two agents coordinate their motor actions pursuing a common goal, is joint action (Bratman, 1992; Clark, 1996; Engemann et al., 2012; Sebanz et al., 2006). According to Bratman (1992), a shared cooperative activity (i.e. joint action) includes three features: (i) mutual responsiveness, i.e. each participating agent attempts to be responsive to the intentions and actions of the other; (ii) appropriate commitment to the joint activity (an intention in favor to the joint activity, even if with different motivations); (iii) commitment to mutual support, i.e. each agent is committed to supporting the efforts of the other to play his/her role in the joint activity. Successful joint actions depend on the ability to dynamically adjust the individual action planning by simultaneously taking into account the actions performed by one's co-actor (Becchio et al., 2008; Vesper et al., 2009). This ability, called co-representation or shared representation, is based on the representation of the other's relevant actions by simulating and integrating own and other's action in real time (Bekkering et al., 2009; Sebanz et al., 2006).

From a neurophysiological perspective, joint actions have been

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related to two cognitive brain mechanisms: the mirror neuron system (MNS), responsible for action simulation (Newman-Norlund et al., 2008; Rizzolatti and Craighero, 2004), and the mentalizing system, supporting the representation of other minds (Apperly and Butterfill, 2009; Frith, 2012; Gallagher and Frith, 2003). Enhanced activations of both systems have been reported in studies in which individuals were engaged in online interactions, including motor coordination (Chaminade et al., 2012), joint attention (Schilbach et al., 2010), and the observation of a joint action (Eskenazi et al., 2015). Literature also reports studies investigating joint action by means of different motor and interpersonal coordination paradigms (Bosga and Meulenbroek, 2007; Knoblich and Jordan, 2003; Konvalinka et al., 2010; Miles et al., 2009; Ondobaka et al., 2012; Richardson et al., 2007; Sacheli et al., 2018; Schmitz et al., 2017; Sebanz et al., 2005), by the mirror game paradigm (Hart et al., 2014), and by communicative interaction via ambiguous stimuli (Manera et al., 2011). However, these studies used the traditional single-person approach investigating an "isolated mind" and did not exploit the simultaneous measurement of both agents typically involved in joint actions. Thus, the link between brain modulations in interacting agents is still not explored.

It was demonstrated that if two agents behave cooperatively and in a synchronized way in order to achieve a common goal, their brain activities synchronize too (Hasson et al., 2012). Recently, a new conceptual and methodological framework was proposed to investigate the neural basis of human social interaction: the two-person neuroscience (2 PN). 2 PN focuses on studying the dual exchange rather than the individual behavior alone, by using simultaneous neurophysiological recordings from two or more subjects, commonly referred to as hyperscanning or dual scanning (Montague et al., 2002; Babiloni and Astolfi, 2014; Hari et al., 2015). Despite this being a very promising framework, hyperscanning studies show typical technical and practical limitations, ranging from an artificial setting to imprecise spatial or temporal resolution. Disentangling different factors producing a modulation of brain activity is currently a challenge for both data analysis and experimental design (Burgess, 2013; Hari et al., 2015). A viable way to untangle the social interaction from two-persons data is the estimation of multiple-brain connectivity (also referred to, in some studies, as hyperconnectivity). Thereby, temporal correlations (or causality in the statistical sense (Wiener, 1956)) between brain signals of different subjects during their interaction are studied to understand how each subject's brain activity is correlated with the other subject's one. Inter-subject connectivity was described by fMRI (Bilek et al., 2015; King-Casas et al., 2005), MEG (Campi et al., 2013) and EEG studies, which allow for a more ecological setting (Toppi et al., 2016a; Müller et al., 2013; Dumas et al., 2012b; Sänger et al., 2012; Astolfi et al., 2011, 2010; De Vico Fallani et al., 2010; Lindenberger et al., 2009; Babiloni et al., 2006). The use of indices derived from graph theory has allowed characterizing the multiple brain system by means of its properties (Ciaramidaro et al., 2018; De Vico Fallani et al., 2010). Despite the advancements in the field, the added value and potentiality of analyzing social and non-social conditions provided by multiple-brain analysis with respect to the single-brain analysis has not been yet clearly quantified. In fact, although recent literature reports an increase in works about inter-subject connectivity, no study, to our knowledge, focused on demonstrating the advantages of analyzing the subjects' data as a unique system with respect to analyze them separately.

Just a few hyperscanning studies using EEG and fNIRS have tested cooperative joint action. In particular, they focused on motor planning tasks (Konvalinka et al., 2014; Kourtis et al., 2013; Dumas et al., 2010, 2012a, 2012b), guitarists playing (Vanzella et al., 2019; Müller et al., 2018, 2013; Sänger et al., 2012), joint attention (Szymanski et al., 2017), conversation (Pérez et al., 2017; Kawasaki et al., 2013) and cognitive joint performance (Balconi et al., 2018a, 2018b; Cui et al., 2012). However, none of these studies focused on the co-representation, an ability that is at the basis of joint action. Here we aim to disentangle the ability to share representations during real-time interpersonal coordination: by using EEG-hyperscanning within a 2 PN framework, we intend to test if the study of inter-brain connectivity in a multiple-subject approach can provide an effective tool for discriminating the interpersonal properties of joint action tasks with respect to non-interpersonal conditions.

In this study, in contrast to previous works, we focused on the co-representation, and in particular on how the awareness of interacting or not with a human agent will affect the motor synchronization task. For this reason, we modified a motor interpersonal coordination task proposed in previous studies (Newman-Norlund et al., 2008; Bosga and Meulenbroek, 2007) by adding to the human joint condition an analogous non-human condition, representing the joint coordination with a computer, and a solo condition, in which each subject was asked to perform the task individually (Fig. 1). In all conditions, neural activity from both subjects was recorded simultaneously by means of 64-channel EEG. In a preliminary study (Astolfi et al., 2014) we reported a first analysis of the inter-subject connectivity in a dyad, exploring two graph indices that varied in the interactive condition.

In summary, we based this study on the hypothesis that multiple-brain analysis during a real-time joint action task will be able to elicit EEG signatures of shared representation in both interacting agents. In particular, we expected: i) different inter-brain connectivity patterns in the human joint task with respect to the PC condition; ii) different connectivity patterns in the joint task with respect to the Solo condition; iii) that the indices derived from the multiple-brain networks can quantify such differences, accurately discriminate the joint action from the other two conditions and correlate with performances in the joint condition, as a possible way to explain a successful cooperation; iv) that multiple-brain analysis can return a deeper characterization of the role of agency and co-representation in social tasks with respect to a classical single subject analysis, and thus that indices derived from the multiple-brain networks can prove an effective tool to increase our ability to understand the neural basis of social tasks.

2. Methods

2.1. Participants

Thirty-two male subjects aged between 18 and 30 (mean age 25.28; SD = 4.39) were enrolled in the study. Participants were recruited by advertisements in local schools and at university. All participants were right-handed with normal or corrected-to-normal vision. Psychiatric disorders were excluded by the Young Adult Self-Report (YASR) (Achenbach, 1997). All participants scored below the borderline range of any first-order scale. In addition, a semi-structured medical interview was done to exclude chronic somatic and neurological conditions. Participants were arranged in 16 dyads, each composed of two male strangers with an acceptable age gap.

All participants provided written informed consent according to the convention of Helsinki. The study was approved by the ethical committee of the Medical Faculty of the Goethe Universität Frankfurt/Main (Germany). The subjects received a lump sum payment of 45 euros for taking part in the experiment.

2.2. Experimental design

Each pair of subjects performed the Joint Action task, implemented through a computer game. The task consisted of lifting a virtual ball from the bottom of the screen up to a target region located at the top of the screen (goal), by controlling both sides (left and right) of a moving bar on which the ball was placed. The ball was free to roll down the bar, if the correct balance was not kept (see Fig. 1). In order to increase complexity, we introduced an obstacle in the middle of the screen. We used a modified version of the paradigm (Bosga and

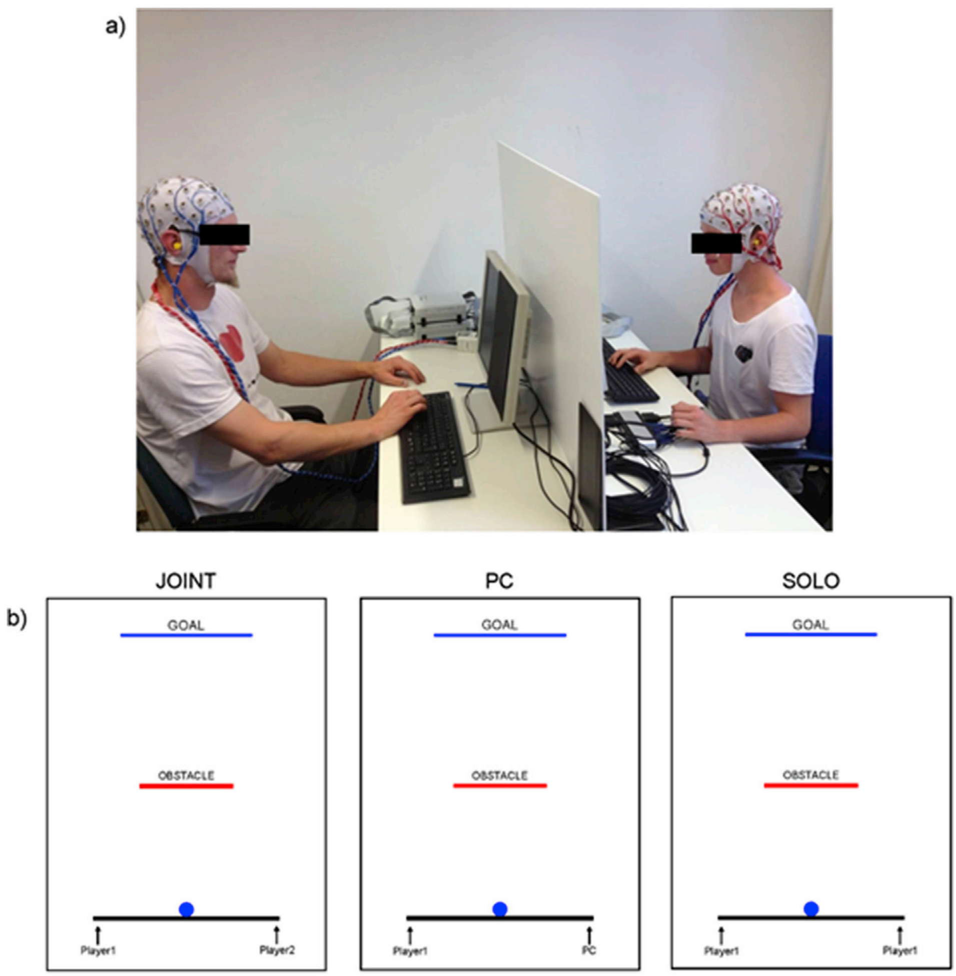

Fig. 1. a) Hyperscanning Experimental Setup. Subjects were seated face to face, separated by a barrier which did not allow them to look at each other, and wore earplugs to avoid that the noise of pressing buttons would facilitate their motor synchrony. b) Graphical representation of the three conditions included in the paradigm. The goal of the game was to lift the virtual bar by keeping it balanced, so to make the virtual ball on its top reach the target area (in blue in the upper part of the screen) without rolling away from the bar or hitting the obstacle (the red line). In the Joint Condition, the subjects jointly controlled the bar, one side (and one response button) each. In the PC Condition, each subject did the same task but with the PC, controlling one side of the bar and one response button. In the Solo Condition, the subjects were asked to solve the task individually (though simultaneously), and each of them controlled both sides of their bar and both response buttons.

Meulenbroek, 2007; Newman-Norlund et al., 2008) by adding to the human joint condition an analogous non-human (PC) joint condition, and by considering a solo condition. Consequently, our task included three main conditions: Joint condition, Solo condition, and PC condition. In the Joint condition, the dyad jointly worked at the same task. Each subject controlled one side of the virtual bar by pressing a button with his right index finger. The PC condition represents the joint coordination with a non-human agent and like in the Joint condition, each subject controlled a side of the virtual bar using the right index finger while the other side was controlled by the PC. In the Solo condition each subject was asked to perform the task individually, by controlling both sides of the virtual bar by using the right index and middle fingers. In all the conditions, both subjects played and were recorded simultaneously and weren't allowed to 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 than during the experiment, but with no relation to what was happening on the screen (low baseline).

Each of the three experimental conditions consisted of 60 trials of approximately 8 s (inter-trial interval = 2 s). The conditions were presented block-wise, in random order. In the Solo and PC conditions, in case one person finished a trial before the other did, the game of the former would pause in order to assure that all trials started simultaneously.

Stimuli presentation was realized by using MATLAB (The MathWorks, Version R2009b). Stimuli were displayed on two 19″ LCD monitors (Fujitsu Siemens Scenicview L9ZA, resolution 1280 × 1024) at a refresh rate of 150 Hz.

2.3. Analysis of behavioral data

For each trial of the task we saved the following parameters: i) trial duration (trial length in seconds); ii) height reached by the ball at the end of the trial, normalized according to the maximum (ball height); iii) the score of correct trials (i.e. those in which the ball reached the goal zone).

Data were analyzed (using STATISTICA 12) by a repeated measures one-way ANOVA considering as dependent variables the three parameters (trial length, ball height and correct trials) and as within factor the TASK type (Joint, PC and Solo). Means were subsequently compared using Newmann-Keuls post hoc test.

We did not find any significant effect induced by the TASK for trial length [$F(2,30) = 1.915$; $P = 0.164$] and ball height [$F(2,30) = 2.585$; $P = 0.093$]. The only significant effect was found for the number of goals [$F(2,30) = 79.703$; $P = 0.00001$]. Post hoc comparisons revealed

Table 1
Average performances in the three experimental conditions (Joint, PC, Solo) captured by the behavioral variables i) trial length (trial duration in seconds), ii) ball height (% of trial completion), and iii) goals (% of correct trials). Values are represented as mean (±SD).

	Trial Length (in sec)	Ball Height (%)	Goal (%)
Joint	7.32 (1.04)	87.31 (3.00)	66.35 (12.79)
PC	7.02 (0.76)	83.43 (4.60)	36.77 (15.12)
Solo	6.48 (0.67)	87.31 (3.45)	61.15 (17.75)

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 (see Table 1).

2.4. Simultaneous multi-subject EEG recordings

The neuroelectrical hyperscanning recordings were performed with a 128-channel EEG acquisition system (Brain Product GmbH, Germany - for each subject: 61 EEG + 3EOG channels, reference on linked mastoids, ground at Fpz). The EEG/EOG signals were collected with a sampling frequency of 250 Hz. In order to delete the sources of variance between the four amplifiers due to the electrical noise and the impedance of the electrodes, the same calibration signal was delivered to all the devices to adjust their sensitivities and to equalize their different gains.

2.5. Pre-processing of EEG signals

EEG signals were band-pass filtered in the range 1–45 Hz. Independent Component Analysis (ICA) was used to remove ocular artifacts. We discarded only one ICA component from the estimated set, the one in which the blink artifact was identified. EEG traces were segmented in relation to the specific timing of the paradigm: in the Joint Condition we focused on the period in which the two subjects jointly controlled the bar; in PC and Solo we considered only the period between the simultaneous beginning of the trial for the subjects and the trial conclusion for the fastest of the two. These intervals were further segmented in epochs of 1s each. Then, a semi-automatic procedure, based on a threshold criterion (±80 μV), was applied to remove the residual artifacts. On average, we removed less than 10% of the total amount of trials collected per condition per subject. Only the artifacts-free epochs common to both subjects were considered in the further analyses. No statistical differences were found in the number of epochs preserved for the three different experimental conditions.

The pre-processing procedure was entirely performed by means of Brain Vision Analyzer 1.0 (Brain Products GmbH).

2.6. Multiple-brain connectivity estimation

A subset of 15 channels (Fp1, Fp2, F5, Fz, F6, T7, C3, Cz, C4, T8, P3, Pz, P4, O1 and O2) among the 61 recorded was selected for each subject, in order to increase the accuracy of the connectivity estimates. Data recorded simultaneously for both players was jointly subjected to connectivity estimation (multiple-brain connectivity). In particular, we used an extension of Partial Directed Coherence (PDC) to the multi-subject case, optimized for hyperscanning purposes (Babiloni and Astolfi, 2014), whose accuracy was demonstrated in previous hyperscanning studies (Ciaramidaro et al., 2018; Astolfi et al., 2011, 2010; De Vico Fallani et al., 2010). Such estimator 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) (see Fig. 2). For further information about PDC and its extension to multiple-subject case, see the Supplementary Data. The resulting PDC values were then averaged in four bands of interest: theta, on average 3–7 Hz, alpha, on average 8–12 Hz, beta, on average 13–29 Hz and gamma, on average 30–40 Hz.

In order to avoid the estimation of spurious links in the multiple-brain connectivity (Burgess, 2013) due to differences in the amplitude of the signals recorded from different individuals, we applied the following mitigation actions: i) data coming from each subject in the couple were normalized by means of a z-score before being included in the estimate, ii) the significance of estimated networks was then assessed through an asymptotic approach theorizing PDC null-case distribution (Toppi et al., 2016b). The asymptotic statistic approach allowed to obtain threshold values related to the null-case (significance level 0.05, corrected by means of False Discovery Rate - FDR) which were used for the construction of the connectivity matrices. Specific thresholds were computed for each (directed) connection in the network and each frequency band.

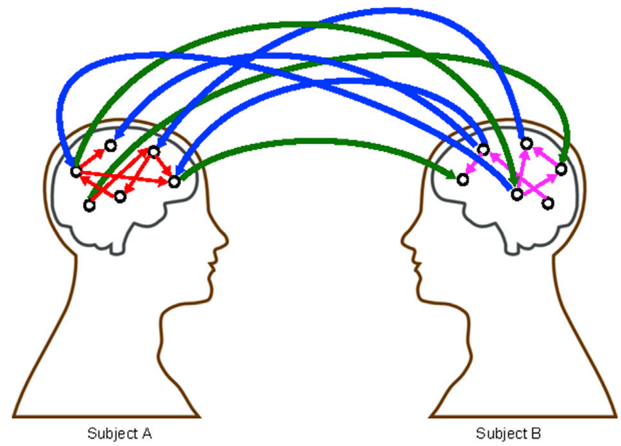

Fig. 2. Conceptual scheme of a multiple brain connectivity model. Red and purple arrows refer to the intra-subject connectivity for subject A and B, respectively. Green arrows refer to connectivity directed from subject A to subject B and blue arrows refer to the connectivity directed from subject B to subject A. The entire connectivity network is derived, in a fully multivariate way, on the basis of the whole dataset.

2.7. Graph theory in multiple-brain networks

To quantify the main properties of the multiple-brain networks (including intra- and inter-brain connectivity) at the level of the single dyad, we computed a set of indices, some derived from the classical graph theory (Rubinov and Sporns, 2010) and others defined ad hoc to capture relevant properties of multiple-subject connectivity (Ciaramidaro et al., 2018). In particular, we focused on specific indices measuring the integration of the two-subject network, some positively correlated (the higher the integration, the higher the index value): Global Efficiency, Local Efficiency, Clustering, Inter-Brain Density-IBD, Path Length and Degree, and some negatively correlated (the lower the integration, the higher the index value): Divisibility and Modularity. Further details about the indices are reported in Tab.S1.

To evaluate the added value of considering the two subjects as a unique system we extracted graph indices also from the single subject connectivity matrices. To this purpose, we used a subset of indices (Global Efficiency, Local Efficiency, Clustering, Path Length and Degree) since IBD and inter-brain Divisibility and Modularity cannot be computed for single-brain connectivity matrices.

For each dyad, experimental condition and frequency band we built a binary directed adjacency matrix G as a squared matrix of dimensions N X N (where N is the number of nodes of the graph). Each element G_{ij} represents the connection directed from node i to node j. G_{ij} is equal to 1 if the connection directed from i to j in the task is significantly different ($p < 0.05$) with respect to the baseline, and 0 if the statistical test does not return any significant difference for that connection and direction. Our adjacency matrices are non-symmetrical ($G_{ij} \neq G_{ji}$) and therefore keep the information about directionality, which we subsequently used to compute indices formulated for directed graphs.

The analysis pipeline, including multiple brain connectivity estimation and graph theory computation, was performed in Matlab environment (MATLAB, R2018a).

2.8. Statistical analysis

2.8.1. Connectivity patterns group analysis

We computed PDC between the two subjects' brain signals by means of the same (previously described) procedure for all conditions (Joint, PC and Solo). Successively, we statistically compared (dependent samples *t*-

test, $p < 0.05$) the resulting connections with their homologous connections across conditions (i.e. Joint vs Solo, Joint vs PC and PC vs Solo) to reliably isolate the brain-to-brain causality specifically active during the Joint condition, where the two subjects are interacting with each other, in contrast to those active when both subjects are simultaneously engaged in a joint coordination with a non-human agent (the PC), or in an individual coordination (Solo), in order to disentangle the co-representation ability. The statistical test was performed for each connectivity link, each direction and each frequency band and was corrected for multiple comparisons by means of False Discovery Rate (FDR) under dependence assumptions (Benjamini and Yekutieli, 2001).

2.8.2. Single dyad analysis

To quantify the main properties of the multiple-subjects brain networks (including intra- and inter-brain connectivity) at the single dyad level we performed a task-baseline comparison (independent samples *t*-test, $p < 0.05$) to characterize each condition for each dyad. While PC and Solo conditions were meant to disentangle co-representation, to characterize each condition we used a low baseline, reproducing the common aspects of the task (visual stimulation, motor planning and execution). During the baseline, the subjects sat in front of the screen, watched the same bar used during the experiment moving through the screen and the instruction was to randomly press the buttons with the same fingers, but with no relation to what was happening on the screen. By this procedure, spurious connectivity that could result as a consequence of the fact that the subjects are involved in a similar and temporally related task (they are exposed to the same stimuli and environment), can be removed, ensuring a correct estimation (Astolfi et al., 2011; Burgess, 2013).

2.8.3. Graph theory analysis of connectivity networks

To compute graph indices, the PDC matrices obtained for each dyad, frequency band and condition were contrasted with their homologous estimated during the low baseline, returning adjacency matrices. We assigned 1 to the entries corresponding to connections resulting statistically different from the low baseline and 0 to the entries for which the test did not return any difference. 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 extract the graph theory indices listed in Tab.S1. The entire procedure was performed for multiple- and single-subject networks.

2.8.4. ANOVA on graph indices

The indices computed for the multiple-subject networks as well as for the single subject networks were subjected to one-way repeated measures ANOVA considering as main within factor the experimental conditions (Joint, PC, Solo). Newman-Keuls' post hoc tests were then applied to further investigate the significant factors. ANOVA was computed separately for each frequency band and for indices extracted from single-brain and multiple-brain networks. Statistical analysis on graph indices was computed by means of STATISTICA (StatSoft Inc., Version 8.0).

2.9. Classifying social behavior through multiple-subject connectivity indices

To test if and how the information provided by multiple-subject connectivity is suitable to characterize the joint task, we performed a classification study, in which graph indices were used as features of a Support Vector Machine classifier with linear kernel to discriminate three different pairs of classes: Joint-Solo, Joint-PC, PC-Solo. We built a classifier for each classification and each frequency band and computed the related accuracy. To explore to which extent such analysis can be empowered by the multiple-subjects approach, we statistically compared the accuracy obtained with single-subject indices (intra-brain connectivity) with that obtained by multiple-brain indices (independent sample *t*-test, significance level = 0.05). The classification analysis was performed in Matlab environment (MATLAB, R2018a).

2.10. Correlation of inter-brain indices with behavioral data

Correlation between inter-brain indices (obtained for each dyad and each frequency band) and behavioral data (average values for each dyad) was performed to test the hypothesis that the indices can not only discriminate different tasks but also be modulated according to the degree of cooperation in the Joint condition. As measures of successful interaction we used the average time during which subjects were able to keep the ball on the bar (trial length), the number of correct trials (goals score) and the average maximum height achieved by the dyad (ball height). The correlation was performed for the Joint condition and repeated for the four frequency bands.

3. Results

3.1. Multiple-brain connectivity

The multi-subject statistical patterns obtained by the comparison of each connection with its homologous across conditions (i.e. Joint vs Solo, Joint vs PC and PC vs Solo) are reported in Fig. 3 for the alpha band. Results in the other frequency bands are reported in the Supplementary Data, Figs. S1–S3. For each comparison, the red connections represent the inter-subject links that are significantly strengthened in the first condition with respect to the second, while the blue ones report the result of the opposite comparison. Fig. 3 shows how the inter-brain links significantly strengthened in Joint vs. Solo and Joint vs. PC are denser than those obtained in all the other comparisons. A similar behavior can be described for the other frequency bands (see Figs. S1–S3).

3.2. Graph theory analysis of multiple-subject networks

The results of the ANOVAs performed for the multiple-brain indices are reported in Table 2 and illustrated in Fig. 4 for the alpha band (the complete results are reported in Fig. S4). The corresponding effect sizes can be found in Table S4 of the Supplementary Data.

ANOVA results showed that all the indices were significantly modulated by the type of interaction (Joint, PC and Solo) only for the multiple-subject approach. In particular, we found significant differences between the Joint condition and the two other conditions. In contrast, no significant differences were obtained between Solo and PC. Results of the ANOVAs related to the single subject indices are reported in the Supplementary Data (Tab.S2).

3.3. Classifying social behavior through multiple-subject connectivity indices

Table S3 and Table 3 report the results of the classification study in terms of accuracy achieved by the single subject and the dual subject approach, respectively (see also Fig. 5 and Fig.S5 for the scatter plots of global and local efficiencies). While the maximum classification accuracy achieved by the classical single subject approach was of 75% for a single index (Global Efficiency in the beta band, see Table S3), the results obtained with multiple brain indices indicate multiple classification accuracies higher than 75% for Joint-PC and Joint-Solo classification (Table 3; best results: 88% in theta and in alpha band). On the contrary, the PC-Solo classification never returned results significantly different from chance. Such results confirm that the differences found with the ANOVA performed on the group are robust also at the single dyad level and produce results that cannot be achieved by the single subject connectivity analysis. Moreover, the statistical comparison between classification accuracies obtained by a single and dual approach highlighted how the performances are significantly higher when the indices are extracted from multiple-brain networks than from the single-brain networks (theta: $p = 0{,}00057$; alpha: $p = 0{,}0001$; beta: $p = 0{,}036$; gamma: $p = 0{,}0024$).

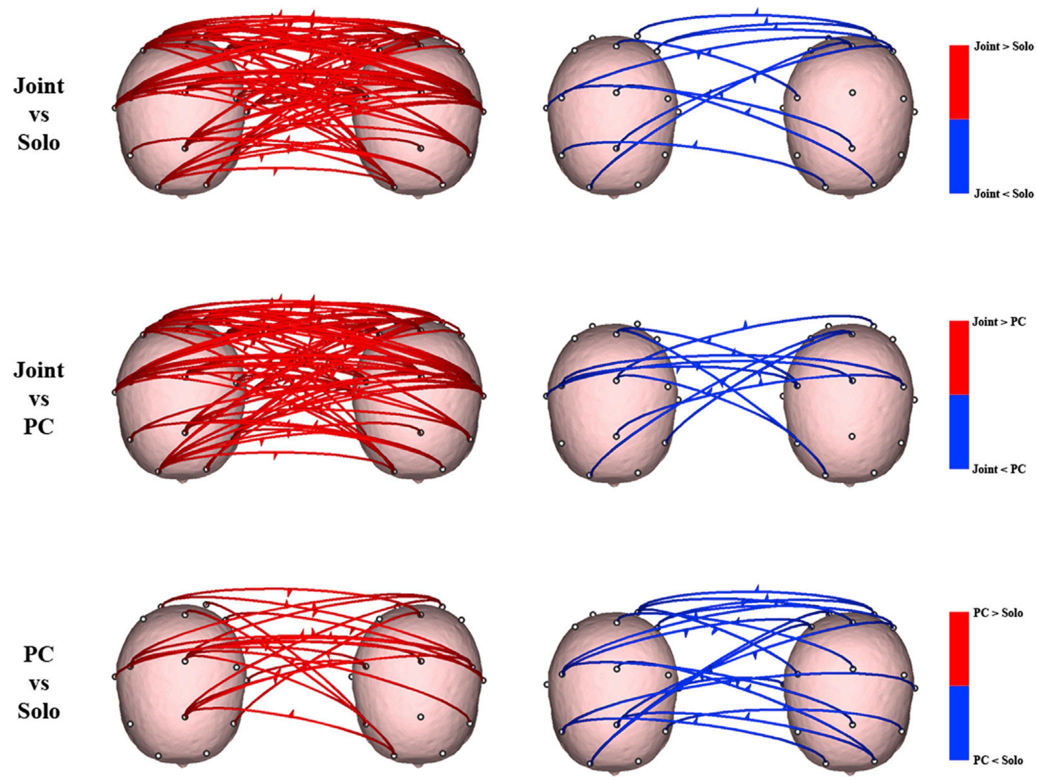

Fig. 3. Statistical inter-brain causality patterns in alpha band. The networks were obtained by statistically comparing the three different levels of interaction: Joint vs Solo, Joint vs PC and PC vs Solo (paired *t*-test, $p < 0.05$ FDR corrected). The heads are seen from above, the nose pointing to the bottom of the page. The arrows indicate the existence of a statistical causality between the activity recorded on the scalp of the two subjects (15 electrodes each).

3.4. *Correlation of inter-brain indices with behavioral data*

Results of the correlation study revealed a significant positive correlation between the trial length and IBD, Global Efficiency, Local Efficiency and Degree, while a negative correlation was found between the same behavioral index and Divisibility and Modularity (Table 4). No significant correlation was found for the other behavioral data.

4. Discussion

In this work we studied the contribution of a multiple-subject approach to the investigation of shared actions in a dyadic interaction. We pursued the main aim to prove if inter-brain connectivity can be a valid instrument to investigate the co-representation ability during synchronized interactive conditions with respect to non-interactive conditions.

4.1. *Interdependent synchronized interactions: shared representation during joint actions*

4.1.1. *Co-representation*

Our first aim was to describe EEG signatures of shared representation in interacting agents, by means of indices derived from the multiple-brain networks.

To this purpose, we used a modified version of a motor interpersonal coordination task including three different conditions: the *Joint action condition*, in which the dyad jointly performed the motor task, a non-human interactive situation that we called *PC condition* and the *Solo condition*, viz an individually performed motor action. The novelty of this study consists of including two different factors that should be controlled during a dual motor task: the number of (co)-represented agents (Solo vs Joint) and the sense of agency in terms of human and non-human (PC vs Joint). By using two different baseline conditions, we were able to show that multiple-brain analysis allows characterizing the difference in terms of shared representation in real-time interactive tasks. In fact, by means of Solo condition we disentangled the individual from the dual contribution, while by introducing the non-human agent we were able to demonstrate that the differences found were not only related to the number of agents involved, but also to the presence of two intentional minds. During the joint action condition, our subjects had to continuously and mutually adapt to each other, generating, on a moment-to moment basis, a coupled behavior guided by a common goal. To increase complexity and to assure co-representation we introduced an obstacle in the middle of the screen (Sebanz et al., 2006) so that, in order to be successful, our subjects needed to co-represent the relevant aspects of the partner's actions. In the PC condition, the subjects were continuously engaged to adapt their behavior in accordance to the feedback generated by the PC, but a co-representation was not possible, due to the non-human nature of the cooperating agent. Similarly, no form of shared representations was present during the Solo condition.

4.1.2. *Multi-subject patterns*

Results of our group analysis (Fig. 3 and Figs. S1–S3) showed that the inter-brain links were significantly stronger in the Joint vs. PC and Solo condition, indicating the existence of a statistical causality between the activity recorded on the scalp of the two subjects in that condition. No differences in terms of inter-brain links were observed between the PC and the Solo conditions. We interpreted these links as a sign of interdependent synchronization based on shared representations exclusively present in the joint action condition.

4.1.3. *Integration of multi-subject networks in the joint, PC and Solo conditions*

Such results were also confirmed by the values obtained for graph theory indices across the different experimental conditions. In particular, we selected the indices quantifying integration properties, since they

Table 2
Results of the ANOVA performed considering the graph theory indices obtained for the inter-subject networks as dependent variables and the type of interaction (Joint, PC, Solo) as within factor. The tests were computed separately for the four bands. For each ANOVA we reported the F-value, the corresponding significance level p and the results of Newman-Keuls post-hoc test (●Results of the ANOVA performed considering the graph theory indices obtained for the inter-subject networks as dependent variables and the type of $p < 0.05$). *Note: GlobEff = Global Efficiency;* LocEff = *Local Efficiency; Clust = Clustering; PL = Path Length; IBD = Inter-Brain Density; Div = Divisibility; Mod = Modularity; Deg = Degree.*

Graph Indices	Theta					Alpha					Beta					Gamma				
	F (2,30)	p	J vs S	J vs PC	PC vs S	F (2,30)	p	J vs S	J vs PC	PC vs S	F (2,30)	p	J vs S	J vs PC	PC vs S	F (2,30)	p	J vs S	J vs PC	PC vs S
GlobEff	25.98	<0.00001	●	●		30.91	<0.00001	●	●		14.07	0.00005	●	●		16.7	0.0001	●	●	
LocEff	12.53	0.00011	●	●		11.27	0.00022	●	●		8.26	0.0014	●	●		6.32	0.005	●	●	
Clust	8.07	0.0016	●	●		6.42	0.0048	●	●		10.18	0.0003	●	●		16.27	0.00002	●	●	
PL	1.42	0.257				0.31	0.733				0.6	0.56				6.98	0.0032	●	●	
IBD	18.74	<0.00001	●	●		24.19	<0.00001	●	●		21.36	<0.00001	●	●		23.34	<0.00001	●	●	
Div	3.50	0.043	●	●		4.03	0.028	●	●		7.91	0.0017	●	●		8.38	0.0013	●	●	
Mod	0.18	0.84				3.35	0.049	●	●		5.14	0.012	●	●		7.4	0.0025	●	●	
Deg	18.68	0.00001	●	●		22.36	<0.00001	●	●		21.43	<0.00001	●	●		25.533	<0.00001	●	●	

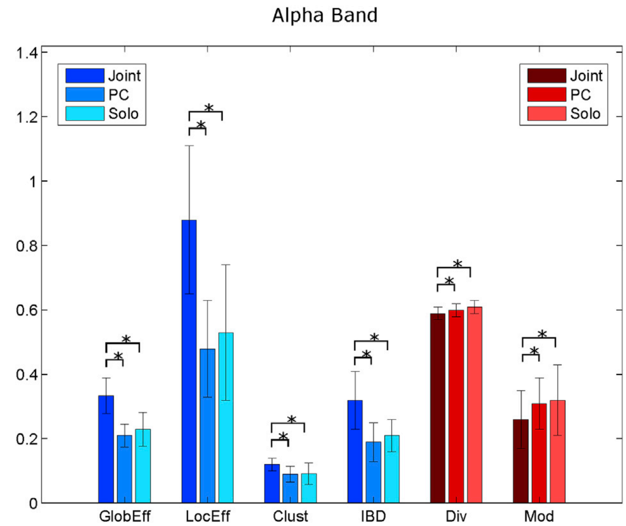

Fig. 4. Results of the ANOVA performed on indices computed on the multiple-brain networks, considering as within factor the type of interaction (Joint, PC, Solo). Indices directly proportional to the network integration are reported in blue, while those inversely proportional are depicted in red. Corresponding F and p values are reported in Table 1. Asterisks indicate statistically significant differences as returned by the Newman-Keuls post-hoc test. Note: GlobEff = Global Efficiency; LocEff = Local Efficiency; Clust = Clustering; IBD= Inter-Brain Density; Div = Divisibility; Mod = Modularity.

have been demonstrated to be the most sensitive to variations in the structure of multi-subject networks (Astolfi et al., 2011, 2010). In the case of networks comprising two interdependent synchronized persons, we expected a more efficient configuration, characterized e.g. by high values of IBD and global efficiency and by low values of modularity and divisibility (Ciaramidaro et al., 2018; De Vico Fallani et al., 2010). In literature, there's an agreement on the fact that the brain-to-brain networks become increasingly efficient and integrated as the level of interaction between subjects intensifies (Falk and Bassett, 2017; Toppi et al., 2015). In line with these expectations, we obtained significant differences - in the direction of a higher integration – specifically between the Joint condition and the two control conditions (see Table 2, Fig. 4 and Fig. S4).

During an individual action, the agent makes predictions about the action course, that he compares with the ongoing feedback. During a joint action the predictions concerns also the actions of the other agent (Pacherie, 2011), as we automatically represent the partner's action in our motor planning and we are able to anticipate the goal of the motor action of the partner, leading to successful interaction (Sahaï et al., 2017). Consequently, in contrast to an individual action, the agent needs additional planning to take into consideration the partner's specific goal. More importantly, these predictions are co-represented in both agents. We might speculate how the high integration between the two subjects (high IBD/global efficiency and low divisibility/modularity) could be a direct measure of such simultaneous and reciprocal co-representation during the joint action. Humans consider a joint action with a human partner different than with computer agents (Limerick et al., 2014) as the participants are aware that the PC is a non-intentional agent. A co-representation is not possible and the "PC mind" is perceived as opaque (Sahaï et al., 2017). This is in line with what we speculated, since when no co-representation is made by the subjects (as in PC or Solo conditions) the network efficiency drastically falls down. It was suggested that when the partner of a joint action is a human agent, a kind of "sense of agency" for the partner, called "we-agency" or "we-mode" (Limerick et al., 2014), takes place. By acting with a PC this particular sense of agency is inhibited.

We found no difference between PC and Solo conditions in multi-subject network indices. This might be due to the fact that we selected

Table 3
Classification accuracy achieved using graph indices derived from multiple-subject connectivity networks as features. A binary linear Fisher classifier was built for each pair of classes (Joint-PC, Joint-Solo, PC-Solo) and for each combination of graph indices (reported on x and y axis). The classification was repeated separately for the four frequency bands. Classification accuracies above 70% were highlighted in bold. Note: GlobEff = Global Efficiency; LocEff = Local Efficiency; Clust = Clustering; PL= Path Length; IBD= Inter-Brain Density; Div = Divisibility; Mod = Modularity.

		GlobEff			LocEff			Clust			PL			IBD			Div			Mod		
		J vs PC	J vs S	PC vs S	J vs PC	J vs S	PC vs S	J vs PC	J vs S	PC vs S	J vs PC	J vs S	PC vs S	J vs PC	J vs S	PC vs S	J vs PC	J vs S	PC vs S	J vs PC	J vs S	PC vs S
Theta	**GlobEff**				**78**	**81**	53	**81**	**72**	38	**81**	**75**	47	**81**	**75**	25	**75**	**75**	41	**75**	**78**	38
	LocEff							**72**	**75**	53	**75**	**78**	50	69	**84**	53	**72**	**88**	44	**75**	**88**	56
	Clust										69	**72**	25	**78**	**78**	25	63	**72**	16	66	**75**	31
	PL													**72**	**75**	28	69	66	31	66	69	34
	IBD																**78**	66	22	**81**	**78**	41
	Div																			50	44	44
	Mod																					
Alpha	**GlobEff**				**88**	**78**	47	**88**	**75**	47	**84**	**75**	56	**84**	**75**	50	**84**	**75**	53	**88**	**72**	47
	LocEff							**75**	**81**	34	**78**	**75**	56	**75**	**75**	50	**72**	**75**	44	69	69	47
	Clust										**78**	66	53	**75**	**75**	41	69	**75**	41	**72**	66	41
	PL													**78**	**75**	56	**75**	63	53	**78**	63	63
	IBD																**75**	**72**	44	**78**	**72**	28
	Div																			56	63	53
	Mod																					
Beta	**GlobEff**				**75**	59	47	**81**	59	66	**78**	69	59	**78**	59	59	**78**	63	47	**75**	66	44
	LocEff							**72**	63	66	**75**	59	28	66	63	50	**72**	63	28	**75**	69	34
	Clust										**75**	47	66	**78**	63	59	**81**	59	66	66	56	63
	PL													**75**	59	53	63	**72**	34	66	69	34
	IBD																66	59	50	**81**	63	56
	Div																			59	56	41
	Mod																					
Gamma	**GlobEff**				**72**	66	66	**78**	**72**	59	**78**	**72**	50	**78**	66	59	**81**	69	56	**75**	**72**	59
	LocEff							**75**	69	38	**81**	66	53	**72**	59	50	66	63	50	63	59	50
	Clust										**78**	**72**	56	**75**	**72**	59	**75**	**72**	53	**72**	69	56
	PL													**81**	**72**	56	**78**	69	66	**78**	69	69
	IBD																69	59	56	**78**	63	56
	Div																			59	50	53
	Mod																					

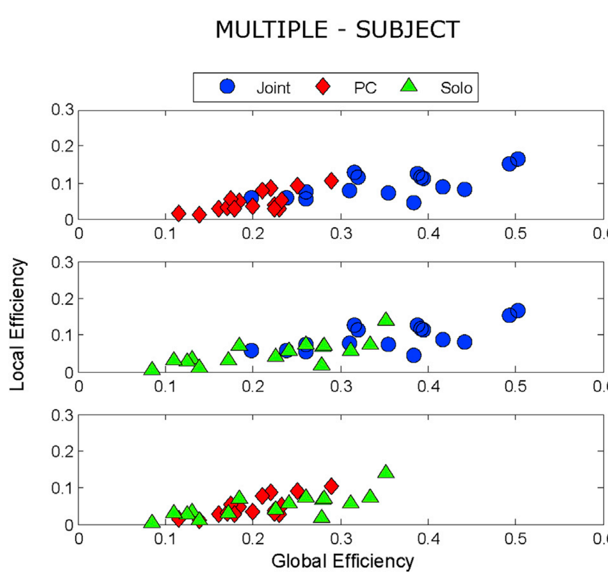

Fig. 5. Scatterplots reporting the values of Global Efficiency (on x-axis) and Local Efficiency (on y-axis) computed on multiple-subject networks in Alpha band. The scatterplots report the three different modalities of social interaction (Joint: blue circles, PC: red diamonds, Solo: green triangles).

indices characterizing the integration of the pair, while in both conditions the two subjects played simultaneously without any reciprocal influence. Moreover, the estimated connectivity patterns are statistically contrasted against a low-baseline condition, so that brain-to-brain connections due to the simultaneous execution of a motor task are subtracted to the networks, thus we do not expect further sources of integration of the multi-subject network.

4.1.4. Network properties at different frequency bands

The higher network integration during Joint condition with respect to the others was found in all the frequency bands (Fig. 3, Figs. S1–S3). However (Fig. S4), the low frequency bands (theta and alpha) show higher levels of integration between the two subjects (higher local efficiency, higher global efficiency and lower modularity) with respect to the high frequency bands (beta and gamma). This confirms what was already described in previous works on guitarists (Müller et al., 2018) where the multiple-brain networks show a more efficient organization (small-world topology) at lower frequencies when compared with higher frequencies.

4.1.5. Directionality of the networks

All the indices here reported were computed on directed adjacency matrices and take into account the direction of the interaction. However, we didn't report graph indices specifically measuring the symmetry in the information flow exchanged between the two subjects, as the joint action paradigm we used implies a symmetrical role of the participants and we did not expect a predominant direction. To check this hypothesis, we statistically compared the number of connections directed from Player 1 to Player 2 with those directed to the opposite direction (from Player 2 to Player 1). No statistical differences were found between the two directions in any experimental condition or frequency band.

4.2. Multiple-subject connectivity as an effective tool to investigate joint actions

With this study, we wanted to show that multiple-brain analysis can return a deeper characterization of shared representation in social tasks with respect to a classical single subject analysis. To this purpose, we used indices derived from the multiple-brain networks to discriminate

Table 4
Results of the statistical correlation between behavioral data (trial length, ball height at the end of trial and percentage of correct trials) and graph theory indices extracted from the inter-subjects network elicited during Joint condition. Significant correlations are highlighted in bold ($p < 0.05$, corrected by means of False Discovery Rate). Note: GlobEff = Global Efficiency; LocEff = Local Efficiency; Clust = Clustering; PL= Path Length; IBD= Inter-Brain Density; Div = Divisibility; Mod = Modularity; Deg = Degree.

		GlobEff	LocEff	Clust	PL	IBD	Div	Mod	Deg
Theta	**Trial Length**	**0,69**	**0,61**	**0,64**	−0,24	**0,86**	**−0,57**	**−0,62**	**0.85**
	Ball Height	0,25	−0,03	0,14	−0,21	0,18	0,20	0,13	0.15
	Goal	0,08	−0,18	0,05	−0,22	0,08	0,20	0,12	0.04
Alpha	**Trial Length**	**0,69**	**0,67**	**0,64**	0,11	**0,88**	−0,51	−0,55	**0.88**
	Ball Height	0,14	0,19	0,26	0,15	0,30	0,09	0,00	0.27
	Goal	0,05	0,17	0,28	0,13	0,22	0,11	0,04	0.19
Beta	**Trial Length**	**0,78**	**0,72**	**0,50**	0,24	**0,81**	−0,32	−0,27	**0.81**
	Ball Height	0,23	0,18	0,21	−0,15	0,25	0,02	0,04	0.25
	Goal	0,08	0,01	0,09	−0,29	0,14	0,06	0,09	0.13
Gamma	**Trial Length**	**0,80**	**0,83**	**0,58**	0,35	**0,73**	−0,32	−0,13	**0.75**
	Ball Height	0,21	0,25	0,16	0,11	0,14	0,05	0,17	0.15
	Goal	0,07	0,18	0,04	−0,05	0,04	0,09	0,24	0.05

social and non-social tasks and compared the results with those obtained with indices derived from single subject analysis.

The literature reports a few ecological studies using EEG-hyperscanning for the investigation of joint actions (Balconi et al., 2018a; Konvalinka et al., 2014; Müller et al., 2018, 2013; Pérez et al., 2017; Sänger et al., 2012), most of which focused on the synchronization ability or the interpersonal coordination during joint actions (for example, guitarists playing in ensemble or spontaneous imitation, Dumas et al., 2010, 2012a; 2012b). Such studies exploited dual scanning to provide insights in the comprehension of the mechanisms at the basis of joint action, but they did not focus on co-representation, or they did not consider baseline conditions able to disentangle such aspect (probably because of the task complexity). The introduction of appropriate (low and high) baselines is fundamental for disentangling the true social interaction between subjects (Hari et al., 2015). Accurate hyperscanning needs an appropriate selection of reference conditions, since similar - or even correlated - brain activities can result from the exposure of the subjects to common stimuli, from a simultaneous execution of the same task or from other confound elements (Babiloni and Astolfi, 2014).

In previous works (Toppi et al., 2016a; Astolfi et al., 2010) we showed the importance of the analysis of simultaneously collected data to capture the “here and now” of the interaction and the temporal relationship between the two brains by means of a comparison with “shuffled” dyads (pairing data from subjects recorded during different sessions or belonging to different teams). Here, we had a further purpose: to investigate the co-representation ability during synchronized interactive conditions, with a particular focus on the effects of agency. Thus, we included two control conditions (Solo and PC) in which the two subjects were still simultaneously recorded during a synchronization task, by removing the synchronization with a human agent (PC condition) and the synchronization with any external agent (Solo condition). A higher inter-subject connectivity during the Joint condition (with respect to Solo and PC) can thus be due only to the fact that both were performing a social task (which is what our hypothesis implied).

4.2.1. Methodological considerations

In this work, we used a multivariate spectral measure, the PDC, in combination with graph theory indices, in order to investigate the directed links between any given pairs of EEG signals in terms of intra- and inter-connections. PDC provides a spectral, multivariate and directed analysis, three features that fit the aims of this study. In fact, EEG signals have an oscillatory nature that makes it particularly important to use a spectral estimator; that is why we preferred a partial coherence-based measure over a correlation-based one. As for the directionality, as discussed in the previous paragraph we didn’t expect a prevalent direction in the functional links between the subjects, due to the symmetrical nature of the task. However, directionality still holds important information about the network organization: graph indices have a different formulation for directed graphs and are influenced by the direction of single connections. So, while we checked for (and correctly found) a balance in the interbrain connections, we still exploited the information hold by the directionality provided by PDC in the indices we used in this study.

PDC returned a model of the system formed by the two subjects during the three conditions (Joint, PC and Solo). Such model includes an intra-brain connectivity pattern (for each subject) as well as a pattern of inter-brain causal links, that together form a complex multi-subject network (Fig. 2). The use of a multivariate approach in such context gives the advantage to construct a network including all the possible information sources (i.e. the two subjects) instead of deriving it from the computation of similarity measures between couples of electrodes.

As for the ocular artifacts’ rejection, we decided to use ICA as it is currently the most conservative among correction approaches. In fact, since EEG and ocular activity are bidirectionally mixed (Oster and Stern, 1980), the regression of eye artifacts can lead to remove neural activity, especially from electrodes located over frontal and periocular sites (Astolfi et al., 2006; Jung et al., 2000). Among decomposition approaches, PCA could be used to the purpose, but it has shown limitations in the complete separation of eye artifacts from brain signals, especially when they have comparable amplitudes (Jung et al., 2000). Moreover, PCA aims at finding orthogonal directions of greatest variance in the data, while there is no reason for neurobiologically distinct artifact and EEG sources to be spatially orthogonal. ICA, on the contrary, can collect concurrent activity arising from spatially overlapping artifact and EEG source distributions (Jung et al., 2000). We also checked that ICA had clearly separated eye artifacts into a single component with physiologically plausible scalp map and we removed just that single component from the data (1 out of 61).

4.2.2. Multiple-vs single-subject analysis

In order to prove if multiple-brain connectivity can provide an advancement in understanding the brain basis of joint actions with respect to the traditional single subject analysis we compared the ability of graph indices extracted from single-subject (Table S2; Table S3; Fig. S5) or multiple-subject networks (Table 2, Table 3, Fig. 5) to discriminate the different experimental conditions by means of classification. ANOVA results indicate that both single-subject and multiple-subject indices discriminated the Joint condition from the other two, but the classification analysis showed that features based on multiple-brain indices led to higher classification accuracies. In line with our hypothesis, both analysis returned a discrimination between Joint-PC and Joint-Solo classes, but the single subject classification reached significantly weaker scores (the best score was 75% for a single index, Global Efficiency in beta band). In contrast, the accuracy achieved by multiple brain indices showed multiple scores over the 75%, with a maximum of 88%, thus confirming the strength of the dual approach. The best accuracy percentages were obtained at lower frequencies (theta, alpha) for indices derived from multiple-brain networks, and at higher frequencies (beta and gamma) for indices computed considering only intra-brain connections. This is in line with what has already been found in previous works on guitarists, which highlighted how intra-brain connections primarily involve higher frequencies (i.e., beta), whereas interbrain connections primarily operate at lower frequencies (i.e., delta and theta) (Müller et al., 2013).

4.2.3. Correlation with behavioral measures

Successful interaction was also analyzed in terms of behavioral measures. Although our participants spent equal time to reach the same ball height in all conditions, the number of successful trials (when the ball reached the goal zone) differed between conditions. The highest number of successful trials was achieved in the Joint condition, whereas the lowest one in the PC condition. This may reflect an advantage provided by the interaction with a human agent, that can simultaneously co-represent the ongoing action, and, in contrast, the difficulty to act with a non-human agent. The stance towards a PC is confirmed to be different with respect to a human agent, since the PC necessarily shows a different attitude toward cooperation and responsiveness with respect to a human being. So, it is not surprising that during this condition the participants encountered more difficulties to reach the goal zone.

In Joint condition, we found a significant positive correlation between the trial length and the indices of IBD, Global Efficiency, Local Efficiency, Degree, as well as a negative correlation with Divisibility and Modularity. This suggests that our multiple-brain data are also modulated in accordance with the degree of cooperation - or successful interaction - between subjects.

5. Limitations and future advancements

This work has some inherent limitations that may be addressed in future studies. First of all, the signals were acquired by scalp EEG. While this choice fits the hypothesis of this study - which was to exploit multiple-subject models to provide indices to quantify the cooperative behavior in a cooperative joint action and to be related to the behavioral and social content of the experiment - on the other hand the multiple-brain connectivity networks we provided do not include any information on the spatial localization of the brain sources that were involved in cooperative joint action. Future studies could combine advanced source localization methods and multiple-brain connectivity approaches to provide a 2 PN neurofunctional model of the brain circuits that constitute that basis of the joint action that is established between two subjects.

Secondly, the sample we analyzed is limited to 32 subjects. Notwithstanding the sample dimension, however, there are two main considerations that support our conclusions about the role of agentivity in joint actions: (i) they are mainly based on the significant results obtained by the ANOVA in terms of differences between Joint and PC/Solo conditions, which are significant even with a small sample size; on the other hand, the small group dimension could be responsible for the lack of differences between PC and Solo, which was not, however, used to draw any conclusion about our hypothesis; (ii) we performed the classification analysis with the purpose to infer if the conclusions obtained in the group via the ANOVA could be replicated at the single dyad analysis. The results of the classification confirmed our conclusion.

To our knowledge, this is the first study in which different motor coordination acts have been classified on the basis of co-representation by means of indices derived from multiple-subject EEG measures. We show that the discrimination achieved by a multiple-brain methodology can provide a qualitative and quantitative accuracy that was not achieved by a traditional single person approach. Future studies on a larger sample and including source localization will focus on the specific role of brain circuits in the shared representation as depicted by the dual scanning, by investigating the joint action data in the source domain. Nevertheless, our results show how even at the sensor-level a multiple-brain methodology can help to depict the complexity of the social phenomena intrinsic during a joint action - i.e. the social exchange between two minds - and can better characterize a dynamical mutual interacting system like the one established during a joint action.

Declaration of competing interestCOI

The authors declare no competing interests.

CRediT authorship contribution statement

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.neuroimage.2020.116813.

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