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Gesture in hyperscanning during observation. Inter-brain connectivity

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ABSTRACT

Non-verbal communication is a joint action defined by the use of different gestures' types. The present research aimed to investigate the electrophysiological (EEG) correlates during the observation of affective, social and informative gestures in non-verbal communication between encoder and decoder. Moreover, the hyperscanning paradigm allows investigating the individuals' inter-brain connectivity. Regarding gestures' type, the study's results showed a decrease of alpha (increased brain activity), and an increase of delta and theta brain responsiveness and inter-brain connectivity for affective and social gestures in frontal and posterior areas for informative ones. Concerning gestures' valence, an increase of left frontal theta activity and inter-brain connectivity was observed. Finally, about the inter-agents' role, the same brain responses and inter-brain connectivity patterns emerged both in encoder and decoder. This study allows discovering neural responses underlying gestures' type and valence during action observation, highlighting the validity of hyperscanning to investigate inter-brain connectivity mechanisms.

Keywords: gestures observation; hyperscanning; EEG; inter-brain connectivity

1. Introduction

Hyperscanning is configured as a recent research paradigm that allows the simultaneous recording of the neural activity of two or more individuals involved in social interaction or in a joint action (Balconi et al., 2017; Montague et al., 2002). This research paradigm broadens the horizons of neuroscience, allowing for the investigation of the activity of two or more interacting brains and the observation of individuals' brain functioning during social and emotional interactions, such as communicative exchanges, cooperation, and competition dynamics (Astolfi et al., 2011; Balconi et al., 2018; King-Casas et al., 2005; Liu et al., 2015). Although hyperscanning lends itself to the application of different devices, such as functional near-infrared spectroscopy (fNIRS) and functional magnetic resonance imaging (fMRI), which allow for the investigation of the cerebral regions most involved in some brain processes, the use of EEG in hyperscanning provides an excellent temporal resolution, allowing for the acquisition of more ecological and real-time events (Balconi & Molteni, 2015; Balconi & Vanutelli, 2017). The application of EEG in hyperscanning, indeed, records any inter-brain synchronization mechanisms that occur at different frequency band oscillations, including alpha (8–12 Hz), beta (14–20 Hz), delta (0.5–4 Hz) and theta (4–8 Hz) bands, which are implicated in different cognitive processes, such as attention, perception, and emotions (Balconi & Fronda, 2020; Balconi & Vanutelli, 2017; Balconi et al., 2015).

Specifically, the term brain synchronization refers to individuals' mechanisms of neural coupling that occur during the performance of joint activities or synchronized behaviors (Hasson et al., 2012; Pan et al., 2017), in which the co-regulation of actions and feelings is based on specific cortical synchronization in the inter-agents inducing a state of vicarious activation (Hasson et al., 2012; Keysers & Gazzola, 2009). These similar patterns of vicarious activation between individuals lead to a phenomenon defined as "brain-to-brain coupling".

In light of this evidence, in the present study, the brain responses of two interacting individuals (the encoder, who reproduces the gesture, and the decoder, who receives the gesture) were investigated during the observation of different types of gestures (affective, social, and informative) with positive or negative valence. The aim of the present study, therefore, was to observe the brain responses and the presence of possible neural coupling and synchronization mechanisms involved in the non-verbal communicative exchange, in which brain-to-brain coupling is paralleled by gestural synchronization between individuals. Indeed, it has been shown that communicative interaction creates a common environment in which individuals mutually adapt their actions, synchronizing their body and mind (Konvalinka et al., 2010).

Specifically, in order to investigate the possible inter-agents' neural coupling mechanisms involved in the observation of different gestures' types, functional neural connectivity, which is intended as the temporal correlation between spatially remote neurophysiological events (Balconi & Fronda, 2020), was considered. The measurement of neural connectivity provides information about the simultaneous coupling between two series of bio-signal data collected by different inter-agents allowing for the observation of inter-agents' brain synchronization mechanisms involved in the observation of particular types of gestures.

Moreover, some studies have demonstrated that gestures' observation was supported by the involvement of mirroring mechanisms that created a direct link between inter-agents (Holle et al., 2008; Huxham et al., 2009), allowing better planning and understanding of the motor intention and the meaning of actions observed (Balconi & Canavesio, 2013; Freedberg & Gallese, 2007; Gallese, 2006; Rizzolatti & Craighero, 2004; Rizzolatti et al., 2001) and leading to the development of implicit coupling mechanisms between individuals.

Specifically, gestures' observation seems to be an authentic ability in human beings (Decety et al., 1997), who are easily able to distinguish biological movement from non-biological ones. Moreover, gestures' observation allows the understanding, recognition, and imitation of actions, leading individuals' to the mental simulation of the observed action by activating specific brain areas involved in this process, such as the lower parietal lobule, the dorsal and primary premotor cortex, the ventral premotor cortex and the dorsolateral and prefrontal cortex (Costantini et al., 2005; Holle et al., 2008; Huxham et al., 2009).

In light of previous evidence, we expected to observe a different modulation of brain responsiveness and inter-brain connectivity of high and low frequency bands concerning the type and the valence of the observed gesture. In particular, we expected to reveal a greater frontal brain responsiveness and inter-brain connectivity of high-frequency bands, which are more involved in the attentional processes (Balconi & Fronda, 2020; Puzzo et al., 2011; Quandt et al., 2012), and of low-frequency bands, which are more involved in emotional processes (Balconi & Fronda, 2020; Balconi et al., 2015; Balconi & Pozzoli, 2005; Knyazev, 2007), during the observation of affective and social gestures. In particular, considering the meaning of social gestures, which have the purpose of starting, managing, or ending relationships (Balconi & Fronda, 2020; Balconi et al., 2020; Fronda & Balconi, 2020; Kendon, 2017), and of affective ones, aimed at influencing the emotional state of other individuals, the frontal region appears to be the most involved in order to comprehend others' mental states and intentions (Balconi & Bortolotti, 2013; Balconi & Fronda, 2020; Bressem & Müller, 2017; Crivelli & Balconi, 2017; Rameson & Lieberman, 2009; Rosso et al., 2004). On the contrary, we expected to observe an increase of high and low frequency bands activity in temporo-parietal area for the observation of informative gestures, which require more involvement of attentional processes and cognitive effort (Perry et al., 2011; Rushworth et al., 2001). Indeed, considering the meaning of informative gestures, aimed at directing the attention of the decoder towards a specific object in the surrounding environment (Enfield, 2001), we expected to observe a greater activation of the parietal region more involved in attentional processes related to body movements (Perry et al., 2011; Sato et al., 2009).

Instead, considering gestures' valence (positive or negative), we expected to observe a different frontal brain responsiveness and inter-brain connectivity of low-frequency bands, more involved in emotional processes (Balconi & Caldiroli, 2011; Calbris, 2011; Hanslmayr, et al., 2005; Knyazev et al., 2009; Kita, 2009), during the observation of positive gesture compare to negative ones. Indeed, according to the model of the neural signatures of affective experience (Balconi et al., 2015; Davidson, 1992), positive stimuli seems to activate more the left frontal cortex compared to the right one.

Finally, considering the inter-agents' role (encoders and decoders), we did not expect to observe differences in brain responsiveness and inter-brain connectivity of encoder and decoder, due to the presence for both of them of mirroring mechanisms involved in the gestures' observation and to implicit coupling mechanisms that occur during the communicative exchange.

2. Method

2.1 Subjects

The present research was conducted on a sample of seventeen dyads of participants (Mage= 24,09; SDage= 3,45).

Specifically, participants who were not previously familiar with each other were recruited and they were coupled in dyads composed by members of the same gender. One member of the couple was randomly assigned the role of encoder, while the other one was given the role of decoder. Participants recruitment occurred according to the following inclusion criteria: age over 18 and under 40, absence of cognitive and neurological deficits and normal or correct visual acuity.

Moreover, participants voluntarily took part in the research after signing informed consent. The conduct of this study was approved by the local ethics committee of the Department of Psychology of the Catholic University of the Sacred Heart of Milan and follows the principles and guidelines of the Helsinki Declaration.

2.2 Procedure and materials

In order to conduct the research, the participants were asked to observe 60 videos that reproduced a non-verbal communicative interaction between two actors characterized by the use of different types of gestures (affective, social and informative) with a positive and negative valence.

The presentation of the videos took place via a computer screen placed at a distance of 60 cm from the members of the couple, sitting facing each other, and the videos were administered through the use of the E-Prime 2.0 software. In addition, in order to prevent participants' fatigue, the 60 videos were administered in three blocks consisting of 20 randomly presented stimuli. Specifically, the videos reproduced 10 positive affective gestures, 10 negative affective gestures, 10 positive social gestures, 10 negative social gestures, 10 positive informative gestures, 10 negative informative gestures. The three types of gestures reproduced with positive and negative valence had different purposes: the affective ones were aimed at transmitting affective states of well-being or malaise to the interlocutor, the social ones had the aim of starting, maintaining or interrupting a relationship with the interlocutor; finally, the informative ones were aimed at direct the attention of the interlocutor towards a specific object in the environment (Balconi & Fronda, 2020; Balconi et al., 2020; Fronda & Balconi, 2020). For the latter type of gesture, the positive or negative connotation was attributed according to the content of the context phrase presented before the video starts. In particular, the execution of the experiment required both members of the dyads to observe the video reproduced, then the encoder was asked to reproduce the gesture observed to the decoder who have only to receive the reproduced gesture passively.

The structure of the task was the following: the presentation of a blank screen (2 sec); the presentation of a scene context (4 sec), to help individuals to understand the meaning of the gesture observed; the video reproducing the gesture to be observed (3 sec).; the presentation of a black screen (4 sec), the presentation of a slide with the "go" signal to indicate encoder to reproduce the gesture (4 sec) (Figure 1a).

The stimuli were previously validated by a sample of 14 judges (Mage = 28.34, SDage = 0.04) (Balconi & Fronda, 2020). In particular, some gestures characteristics, such as commonality, frequency of use, complexity, social meaning, familiarity, and emotional impact were evaluated using a Likert scale of 7 points (Balconi et al., 2020; Fronda & Balconi, 2020).

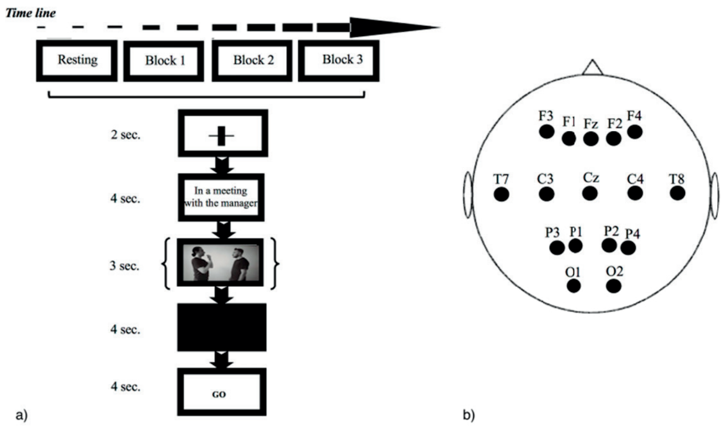

Figure 1. (a) The figure represents the experimental procedure. Brackets represents the experimental window used for EEG analysis. (b) Representation of EEG channels location (F3, F1, Fz, F2, F4, T7, C3, Cz, C4, T8, P3, P1, P2, P4, O1, O2)

2.3 EEG recording and analysis

EEG signal was recorded by two 16-channel EEG systems (V-AMP: Brain Products, München; LiveAmp: Brain Products, GmbH, Gliching, Germany). In particular, two ElectroCaps were used for the electrodes placement on the following cerebral positions: F3, F1, Fz, F2, F4, T7, T8, C3, Cz, C4, P3, P1, P2, P4, O1, and O2 positions (Figure.1b). An EOG electrode was placed on the external canthi. Data collection of each individual was monitored with electrode impedance of 5 kΩ. For data sampling 1000 Hz was used. Moreover, an input filter of 0.01–200 Hz and a 50 Hz notch filter were employed (Balconi & Fronda, 2020). To the filtering of data offline a 0.5–40 Hz bandpass filter was used, and a common offline average reference was calculated (Ludwig et al., 2009) to reduce signal-noise. Regarding signals evaluation, artifacts were excluded and ocular artifacts were corrected with an algorithm that uses a regression analysis in combination with the artifacts average. Subsequently, data were extracted into low and high-frequency bands, as delta (0.5–4 Hz), theta (4–8 Hz), alpha (8–12 Hz), and beta (14–20 Hz). The mean EEG power for each frequency band was calculated by averaging data related only to the gesture observation phase (3 sec.) and not the following execution phase (Balconi & Fronda, 2020).

3. Results

3.1 EEG: Theta band activity

For data analyses, regarding EEG dependent measures, three sets of analysis were conducted: (i) An ANOVA applied on single subject was performed to observe the effect of independent measures on each frequency band (alpha, beta, delta and theta), not considering the couple (single-brain analysis); (ii) A set of analyses was performed on the calculation of inter-brain connectivity for each frequency band (alpha, beta, delta and theta), within each dyad. The calculation of inter-brain connectivity for each couple of encoder/decoder, was aimed to calculate the synchronization values within each dyad for each measure.

The partial correlation coefficient Πij was computed to obtain inter-brain connectivity by normalizing the inverse of the covariance matrix $\Gamma = \Sigma^{-1}$ (Balconi & Fronda, 2020):

$$\Gamma = (\Gamma_{ij}) = \Sigma^{-1} \text{ inverse of the covariance matrix}$$
$$\Pi_{ij} = (-\Gamma_{ij})/\sqrt{\Gamma_{ii}\Gamma_{jj}} \text{ partial correlation matrix}$$

(iii) Subsequently, a second ANOVA was applied to these inter-brain measures, in order to observe variations of inter-brain connectivity as a function of the experimental conditions.

The degrees of freedom were corrected using Greenhouse-Geisser epsilon for all the ANOVA tests and post-hoc comparisons were applied to the data (contrast analyses). Moreover, for multiple comparisons Bonferroni test was applied. Finally, the normality of the data distribution was tested with kurtosis and asymmetry tests supporting the distribution normality assumption.

3.2 Single-brain analyses

The following independent measures were used for single-brain analyses: Role (encoder/decoder, 2), Valence (positive/negative, 2), Lateralization (left/right, 2), Gesture (social/ affective/informative, 3), and ROI (regions of interest, 4). Considering left and right same sides, four specific ROIs were calculated for frontal channels (F3,F1-F2,F4), central channels (C3,C4), temporo-parietal channels (T7,P1-T8,P2) and occipital channels (O1,O2).

3.2.1 Delta band

For delta band, ANOVA revealed a significant Gesture x ROI interaction effect ($F[6,148] = 9.76$; $p < 0.001$; $\eta^2 = 0.35$).

From post-hoc comparisons, an increase of activity of delta band was observed in the frontal cerebral region compared to central, temporo-parietal and occipital ones in relation to affective and social type of gestures respect to informative type of gestures (for all post-hoc comparisons $p \leq .001$) and an increase of delta activity emerged in temporo-parietal (posterior) region (for all post-hoc comparisons $p \leq .001$) for informative type of gestures compared to other ones (Figure 2a).

3.2.2 Theta band

Considering theta band, a significant interaction effect for Valence x Lateralization x Gesture x ROI ($F[6,148] = 9.07$; $p < 0.001$; $\eta^2 = 0.35$) emerged by ANOVA. Post-hoc comparisons reported an increase of activity of theta band in frontal cerebral region compared to central, temporo-parietal and occipital ones regarding affective and social type of gestures respect to informative type of gestures (for all post-hoc comparisons $p \leq .001$). Finally, an increase of left frontal theta activity, respect to the right frontal one, has emerged for positive type of gestures ($F[1,22] = 9.12$; $p < 0.001$; $\eta^2 = 0.36$) (Figure 2b).

3.2.3 Alpha band

For alpha band, ANOVA revealed a significant Gesture x ROI interaction effect ($F[6,148] = 7.63$; $p < 0.001$; $\eta^2 = 0.30$). In particular, a decrease of alpha power (increase of alpha brain activity) has emerged in frontal cerebral region compared to central, temporo-parietal and occipital ones (for all post-hoc comparisons $p \leq .001$) for affective and social type of gestures respect to informative type of gestures and in temporo-parietal (posterior) area (for all post-hoc comparisons p ≤ .001) for type of informative gestures respect to affective and social type of gestures (Figure 2c).

3.2.4 Beta band

Regarding beta band, a significant Gesture x ROI interaction effect ($F[6,148] = 8.88$; $p < 0.001$; $\eta^2 = 0.32$) has emerged.

Post-hoc comparisons revealed an increase of activity of beta band in temporo-parietal (posterior) area (for all post-hoc comparisons p ≤ .001) for informative type of gestures compared to affective and social type of gestures (Figure 2d).

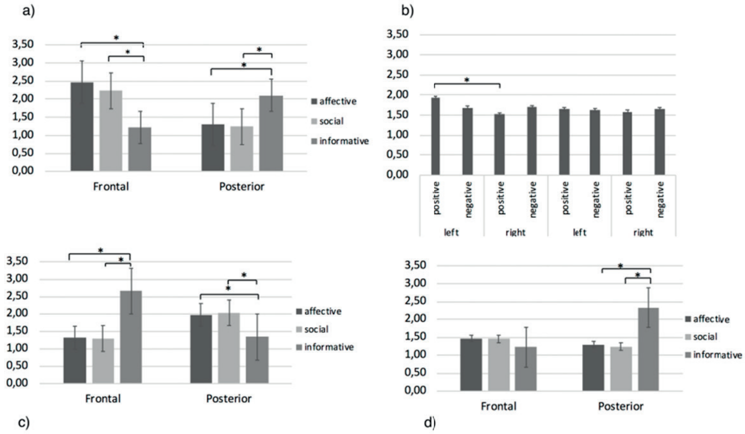

Figure 2. (a) Bar chart of frontal and posterior (temporo-parietal) delta brain responsiveness for affective, social, and informative gestures. The bar chart represents an increase of delta brain responsiveness in the frontal area for affective and social gestures and in posterior (temporo-parietal) area for informative ones. Bars depict ∓1SE. Stars point out statistically significant pairwise comparisons. (b) Bar chart of theta brain responsiveness for left and right side in frontal and posterior (temporo-parietal) cerebral regions. The bar chart shows an increase of theta activity in the left frontal side for positive gestures. Bars depict ∓1SE. Stars point out statistically significant pairwise comparisons. (c) Bar chart of alpha brain responsiveness (decrease of alpha power) related to affective, social and informative gestures in the frontal and

posterior (temporo-parietal) cerebral regions. The bar chart shows an increase of alpha brain responsiveness (decrease of alpha activity) in the frontal area for affective and social gestures and in the posterior area for informative gestures. Bars depict ∓1SE. Stars point out statistically significant pairwise comparisons. (d) Bar chart of beta brain responsiveness for affective, social, and informative gestures in the frontal and posterior (temporo-parietal) regions. The bar chart shows an increase of beta brain responsiveness in the posterior area for informative gestures. Bars depict ∓1SE. Stars point out statistically significant pairwise comparisons

3.3 Inter-brain analyses

From the raw database of each band, inter-subjects correlational indices were calculated to compute the synchronization for each dyad. Subsequently, these correlation coefficients were used as dependent variables into mixed-model ANOVA tests, with the following repeated factors: Role, Valence, Lateralization, Gesture and ROI.

3.3.1 Delta band

Concerning delta band, ANOVA shows a significant interaction effect for Gesture x ROI ($F[6,148] = 8.90$; $p < 0.001$; $\eta^2 = 0.34$).

Post-hoc comparisons proved an increase of delta inter-brain connectivity in frontal cerebral region compared to central, temporo-parietal and occipital ones for affective and social type of gestures and in temporo-parietal (posterior) cerebral region compared to others for informative type of gestures (for all post-hoc comparisons $p \leq .001$) (Figure 3ab).

3.3.2 Theta band

Considering theta band, a significant Valence x Lateralization x Gesture x ROI interaction effect emerged by ANOVA ($F[6,148] = 10.75$; $p < 0.001$; $\eta^2 = 0.38$). Post-hoc comparisons reported an increase of theta inter-brain connectivity in frontal area compared to central, temporo-parietal and occipital ones for affective and social type of gestures. Moreover, an increase of theta inter-brain connectivity was observed for positive gestures in the left cerebral side compare to the right one ($F[1,22] = 9.76$; $p < 0.001$; $\eta^2 = 0.37$) (Figure 3c-d).

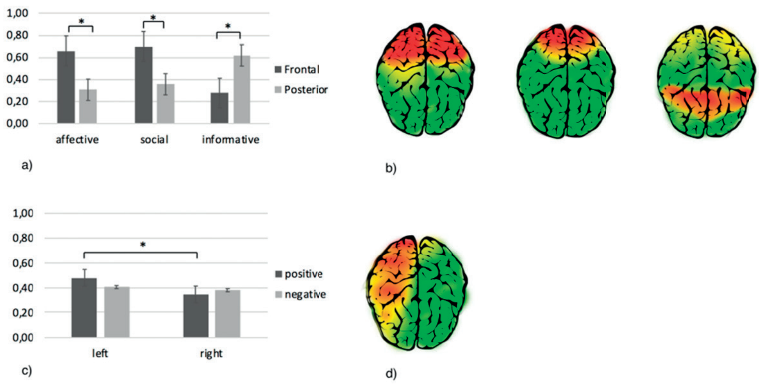

Figure 3. (a) Bar chart of frontal and posterior (temporo-parietal) delta inter-brain connectivity regarding affective, social, and informative gestures. The bar chart shows an increase of delta inter-brain connectivity in the frontal cerebral region according to affective and social gestures and in the temporo-parietal cerebral region according to informative ones. Bars depict ∓1SE. Stars point out statistically significant pairwise comparisons. (b) Delta inter-brain connectivity representation for affective, social, and informative types of gestures. Red color represents the increase of delta inter-brain connectivity. (c) Bar chart of theta inter-brain connectivity for left and right side. The bar chart shows an increase of theta inter-brain connectivity in the left side for positive gestures. Bars depict ∓1SE. Stars point out statistically significant pairwise comparisons. (d) Theta inter-brain connectivity representation for positive gestures in the left and right side. The red area represents the increase of theta inter-brain connectivity

3.3.3 Alpha band

Considering alpha band, ANOVA revealed a significant interaction effect for Gesture x ROI ($F[6,148] = 9.54$; $p < 0.001$; $\eta^2 = 0.37$).

From post-hoc comparisons, an increase of alpha inter-brain connectivity emerged in frontal cerebral area more than central, temporo-parietal and occipital ones for affective and social type of gestures and in temporo-parietal area (posterior) for informative type of gestures (for all post-hoc comparisons $p \leq .001$) (Figure 4a-b).

3.3.4 Beta band

Considering beta band, a Gesture x ROI interaction effect was found ($F[6,148] = 12.09$; $p < 0.001$; $\eta^2 = 0.40$). In particular, post-hoc comparisons revealed an increase of beta inter-brain connectivity in posterior area (temporo-parietal) than frontal, central and occipital one for informative type of gestures (for all post-hoc comparisons $p \leq .001$) (Figure 4c-d).

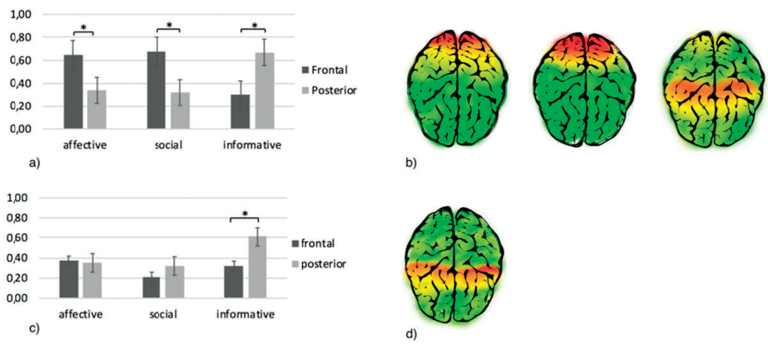

Figure 4. (a) Bar chart of frontal and posterior (temporo-parietal) alpha inter-brain connectivity for affective, social, and informative gestures. The bar chart shows an increase of frontal alpha inter-brain connectivity for affective and social gestures and of posterior alpha inter-brain connectivity for informative gestures. Bars depict ∓1SE. Stars point out statistically significant pairwise comparisons. (b) Alpha inter-brain connectivity representation for affective, social, and informative gestures. Red color represents the increase of alpha inter-brain connectivity. (c) Bar chart of beta inter-brain connectivity for affective, social, and informative gestures in the frontal and posterior (temporo-parietal) regions. The bar chart shows an increase of beta inter-brain connectivity in posterior (temporo-parietal) region for informative gestures. Bars depict ∓1SE. Stars point out statistically significant pairwise comparisons. (d) Beta inter-brain connectivity representation for informative gestures. Red color represents the increase of beta inter-brain connectivity

4. DISCUSSION

The present study aimed to observe the modulation of individuals' brain responsiveness and inter-brain connectivity during a non-verbal communicative interaction, characterized by the observation of social, affective and informative type of gestures with positive and negative valence. Regarding the main objectives, we expected to observe: (i) a different brain responsiveness and inter-brain connectivity related to the type (affective, social and informative) and the valence (positive and negative) of the gestures observed; (ii) a similar patterns of brain responsiveness and inter-brain connectivity both in the encoder and the decoder during the observation of affective, social and informative gestures with positive and negative valence.

First of all, it is interesting to note how the present research has allowed for the investigation of individuals' brain responsiveness and brain-to-brain coupling mechanisms implicated in a non-verbal communicative exchange, which requires tuning between inter-agents. Specifically, the possibility to observe individuals' brain activity during a real non-verbal interaction was provided by the hyperscanning paradigm, which has allowed for the investigation of the implicit coupling mechanisms that occur in individuals during the performance of joint actions (Balconi et al., 2017; Knoblich et al., 2011), introducing an innovative perspective for the analysis of the social brain functioning (Balconi et al., 2017; Holper et al., 2012).

Considering the results of the research, according to the first hypothesis, a different brain responsiveness of high and low frequency bands has emerged for affective, social, and informative gestures.

Specifically, regarding high-frequency bands activity, a decrease in alpha power was observed in the frontal area for affective and social gestures and in the temporal-parietal (posterior) area for informative ones. This different modulation of alpha activity in specific brain regions could be due to the functional meaning of the gestures observed. Indeed, the decrease of alpha activity in the frontal area for affective and social gestures, which are aimed at maintaining or interrupting social interactions and expressing affective states, may be due, firstly, to the involvement of sensorimotor processes involved in social and emotional dynamics, and, secondly, to attentional processes related to the gestures meaning understanding (Puzzo et al., 2011; Quandt et al., 2012). Instead, a decrease of alpha power in the temporal-parietal region for informative gestures, which are aimed at directing the decoder's attention towards a specific object within the environment, is suggested to be related to the implementation of more specifically visuospatial and attentional mechanisms (Posner et al., 1984; Rushworth et al., 2001). On the contrary, an increase of beta activity was observed in the posterior region during the observation of informative gestures. This result could be due because posterior beta activity appears to be involved in control and attentional processes related to visual stimuli (Hanslmayr et al., 2005; Kamiński et al., 2012).

In light of this evidence, considering the meaning of informative gestures, finalized to direct the decoder's attention towards a specific point in the surrounding environment (Balconi & Fronda, 2020; Balconi et al., 2020; Enfield, 2001; Fronda & Balconi, 2020; Kita, 2009), a functional beta response can be observed for the informative content of this type of gesture.

Considering low-frequency band activity, instead, an increase in delta activity was observed in the frontal area for affective and social gestures, probably due to an increase in individuals' emotional involvement (Balconi & Caldiroli, 2011; Balconi & Bortolotti, 2012, 2013; Balconi & Fronda, 2020; Rameson & Lieberman, 2009) and cognitive attentional and motivational investment for a type of gesture more linked to affective and social spheres (Balconi & Fronda, 2020; Balconi et al., 2020; Knyazev et al., 2009; Fronda & Balconi, 2020; Knyazev, 2007).

On the contrary, for informative gestures, an increase in delta activity in the temporal-parietal region was observed, attributable to the presence of more perceptual processes implicated in the observation and execution of action (Balconi & Fronda, 2020; Holle et al., 2008; Huxham et al., 2009). For the theta band, instead, only an increase in the frontal activity for affective and social gestures has emerged. This result could be due to the fact that theta band turns out to be directly involved in the emotional response processes linked to the perception of stimuli considered particularly salient for individuals (Balconi et al., 2015; Balconi & Fronda, 2020; Knyazev, 2007).

In light of this result, it is interesting to note that for the theta band, unlike other frequency bands, did not occur an increase of activity in the temporo-parietal region for informative gestures, underlining the specific role of this frequency band as a marker of emotional responses elicited by affective and social gestures.

Thus, concerning the different modulations of cortical activity based on the observed gestures, a clearer picture emerges from greater frontal area involvement during the observation of affective and social gestures, as well as that of the posterior areas during the observation of informative ones. Specifically, the frontal areas could be more involved in affective and social gestures due to their engagement in regulation of social processes, emotional sharing, and theory of mind related to the understanding of others' emotional and mental states (Balconi et al., 2017; Bressem & Müller, 2017; Calbris, 2011; Fragopanagos et al., 2005; Kalbe et al., 2010; Kendon, 2017; Liotti & Mayberg, 2001; Petrican & Schimmack, 2008). On the other hand, the posterior (temporal-parietal) area could be more involved in response to informative gestures due to the implication of this cerebral region in processes of sustained and directed attention (Centelles et al., 2011; Szymanski et al., 2017; Walker et al., 2009).

In addition, considering the results of gestures' valence on the neural activity, an increase in the left frontal activity compared to the right one was observed in the theta band according to positive gestures. This result could be interpreted according to the theory of neural signatures of affective experience (Balconi & Fronda, 2020; Balconi & Vanutelli, 2016; Balconi et al., 2015; Davidson, 1992), which postulates a greater activation of the left frontal region for positive stimuli, inducing an "approach behavior", and of the right frontal ones for negative stimuli, inducing an "avoidance behavior" (Balconi & Fronda, 2020; De Stefani et al., 2013).

It is interesting to underline how this result was observed only for theta band, highlighting the emotional-valence meaning of this low-frequency band.

In addition to single-brain modulation, also considering inter-brain connectivity results, according to our hypothesis, a different modulation of inter-brain activity in specific brain areas according to gesture type has emerged, confirming the same trend of single brain responsiveness. In particular, an increase of alpha, delta, and theta inter-brain connectivity was observed in frontal areas for affective and social gestures and of alpha, delta and beta activity in posterior areas (temporal-parietal) for informative ones.

Pointing out this evidence, it is interesting to note the presence of a similar trend for single and inter-brain analyses which, on the one hand, emphasizes the functional specialization of the frontal areas for affective and social gestures and of the posterior areas for informative ones; on the other hand, it also underlies a synchronous activation of these brain areas in the two members of the dyads (encoder and decoder), highlighting the presence of a maximum degree of tuning between individuals, since the inter-brain connectivity level reflects the co-activation of the individual members of the dyads (Centelles et al., 2011; Szymanski et al., 2017; Walker et al., 2009).

In addition, the increase in inter-cerebral connectivity in frontal and temporal-parietal areas could support the presence of mirroring processes that create a direct link between gestures' observation and execution (Balconi & Fronda, 2020; Rizzolatti & Sinigaglia, 2010), allowing a better understanding of the motor intentions underlying actions and a better comprehension of interlocutor's behavior (Buccino et al., 2004; Iacoboni et al., 2005; Rizzolatti & Craighero, 2004; Rizzolatti & Luppino, 2001), that lead inter-agents to internally simulate others' experience (the observed gesture), reaching a greater level of attunement with each other (Rizzolatti & Sinigaglia, 2010; Shepherd et al., 2009).

These results might explain also the role of the inter-agent individuals, according to the second hypothesis, that indicate the absence of differences between brain responsiveness in encoder and decoder during observation. This result could be due to the presence of mirror mechanisms during the gestural observation, that allows individuals to understand other mental states, perceiving themselves in joint actions and developing "resonance mechanisms" and consequent implicit brain-coupling processes (Balconi et al., 2018; Holle et al., 2008; Huxham et al., 2009; Lindenberger et al., 2009). Indeed, non-verbal communicative interaction, also in the case of a simple observation, as a shared action leads individuals to automatically align their behavior at different levels (Hari et al., 2015), leading to the implementation of interpersonal coupling models (Cui et al., 2012; Knoblich et al., 2011).

5. Conclusion

The results of this study allow us to provide an overview of the functioning of specific brain areas during the observation of different gestures' categories characterizing a communicative interaction between two individuals. In addition, the present results allow us to discover the brain tuning mechanisms during action observation, highlighting the validity of hyperscanning as a paradigm able to provide information about inter-brain response and implicit brain coupling, underlying social and interpersonal interactions. Despite the potential of this study, some limitations can be observed that could be expanded in future research. A first limitation is related to the sample size, which if increased in future studies would improve the strength of empirical observations. Secondly, we only collected electroencephalography activity. In this regard, in future studies the recording of hemodynamic or peripheral activity could be integrated with the use of neuroimaging tools (as fNIRS).

Finally, future studies could consider observing possible effects related to gender through the formation of dyads composed by individuals of different sex.

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