Mirroring and brain connectivity of gesture observation

Giulia Fronda [1, 2]

[1] *International Research Center for Cognitive Applied Neuroscience (IrcCAN), Università Cattolica del Sacro Cuore, Milan, Italy*

[2] *Research Unit in Affective and Social Neuroscience, Department of Psychology, Università Cattolica del Sacro Cuore, Milan, Italy*

giulia.fronda@unicatt.it

Abstract

Non-verbal communication involves different channels, as gestures, to communicate different information. The present study ai ms investigating the electrophysiological (EEG) correlates underlying the use of affective, social, and informative gestures during gesture observation by an encoder (who observed to reproduce the gestures successively) and decoder (who simply observed the gestures). Mirroring mechanisms were considered for a gesture observation task. Results showed an increase of frontal alpha, delta, and theta brain responsiveness and intra-brain connectivity for affective and social gestures; and of posterior (temporo-parietal) alpha activity and alpha and delta intra-brain connectivity for informative ones. Concerning inter-agents' role, similar responses were found for all gestures. Regarding gesture valence, an increase of delta and theta activity was observed for positive gestures on the left cerebral side. This study, therefore, revealed the function of gestures' type and valence in influencing individuals' brain activity, showing the presence of mirroring mechanisms underlying gesture observation.

Keywords: gestures; observation; EEG; mirroring

1. Introduction

Among the various bodily forms of expression, gestures are configured as a set of motor actions that characterize individuals' verbal and non-verbal communication (McNeill, 1992, 2013), allowing, emphasizing, and completing the transmission of different information (Cabrera et al., 2017). Given gestures' multifunctionality, several neuroscientific studies have focused on brain patterns and cognitive processes underlying gesture observation (Cabrera et al., 2017, 2020) demonstrating the presence of different cerebral areas involved in gesture perception (Caspers et al., 2010; Chong et al., 2008; Molenberghs et al., 2012).

As revealed by different studies (Cabrera et al., 2020; Schippers et al., 2010), gesture observation activates specific cerebral networks (Caspers et al., 2010), such as the mirror neural system, which appears to support actions predictive and understanding processes (Balconi & Fronda, 2020a,b, 2021a,b; Costantini et al., 2005; Kilner & Blakemore, 2007; Rizzolatti & Sinigaglia, 2010; Urgen et al., 2013). Specifically, certain brain areas, such as fronto-parietal regions, appear to be involved in mirroring mechanisms underlying actions understanding (Costantini et al., 2005), providing a direct link between gesture observation and execution (Balconi et al., 2020, 2021; Balconi & Fronda, 2020a,b, 2021a,b; Fronda & Balconi 2020; Holle et al., 2008).

In this perspective, the direct bond between gesture perception and production by mirroring function provides the involvement of sensorimotor processes related to previous experiences with the observed gesture (Hamilton et al., 2004; Hecht et al., 2001; Quandt et al., 2012, 2013; Schütz-Bosbach & Prinz, 2007). The involvement of sensorimotor processes during gesture observation was also demonstrated by different studies that have used electroencephalography (EEG) to investigate the brain correlates underlying gesture perception (Balconi & Fronda, 2020b; Muthukumaraswamy et al., 2004; Pineda, 2005; Quandt et al., 2012, 2013). Specifically, EEG, compared to neuroimaging techniques, has proved to be a good neuroscientific tool for the recording of individuals' neural activity (Balconi at al., 2018a; Balconi & Fronda, 2020a,b, 2021a,b; Balconi & Molteni, 2016; Koike et al., 2015) by obtaining a better temporal resolution and providing useful information on functional and local brain networks underlying gesture perception (Buzsáki & Draguhn, 2004; Muthukumaraswamy et al., 2004; Pineda, 2005; Quandt et al., 2012, 2013; Singer, 1999).

About gesture observation, as demonstrated by previous studies (Balconi & Fronda, 2020b; Muthukumaraswamy et al., 2004; Pineda, 2005; Quandt et al., 2012, 2013), it appears to be associated with changes in both high- and low-frequency bands oscillations.

Specifically, high-frequency bands, such as alpha (8–13 Hz) and beta (14–20 Hz), are particularly involved in sensorimotor mechanisms underlying gesture observation (Balconi & Fronda, 2020b; Mizelle et al., 2010; Puzzo et al., 2011; Quandt et al., 2012; Van Ede et al., 2011) and, in some specific characteristics, like familiarity or speed profile (Wriessnegger et al., 2013) of the observed gesture; while low-frequency bands, such as delta (0.5–4 Hz) and theta (4–8 Hz), are more implicated in emotional processes underlying gesture perception (Balconi & Fronda, 2020b; Holle et al. 2012; Knyazev 2007).

In the present study, the use of EEG in hyperscanning allowed us to investigate the brain responsiveness and intra-brain connectivity of two individuals involved in a non-verbal communicative exchange: the encoder, who observed the gesture to be subsequently reproduced, and the decoder, who observed the gesture to be subsequently received. In particular, the use of hyperscanning paradigm allows us to simultaneously record the neural activity of the two individuals involved in the exchange, providing the possibility to observe the potential presence of differences or similarities in neural responses (Liu et al., 2015; Ruby & Decety, 2004; Stone et al., 2019), during the observation of different types of gesture in term of their category and valence, such as affective, social, and informative gestures of positive and negative valence.

The use of hyperscanning allows investigating individuals' functional connectivity that reflects the correlation between two time series (Friston, 2011) providing information about the activation of inter-agents' individuals and events spatially remote (Balconi et al., 2017b; Balconi & Fronda 2020a,b, 2021a,b; Chaudhary et al., 2011; Zhao et al., 2014). In particular, functional connectivity allows exploring intra-brain links, showing the connectivity within brain regions in single subjects (encoder and decoder) during the non-verbal communication (Balconi & Fronda 2020a,b, 2021a; Falk & Bassett, 2017; Simony et al., 2016) characterized by the use of affective, social and informative gestures with positive or negative valence. Functional connectivity allows information to be obtained on the synchronic and diachronic aspects underlying gestural communication (Vanutelli et al., 2016) that produces a continuous better synchronization, increasing the intra-brain links between brain areas, creating implicit coupling mechanisms in response to mirroring for gesture observation (Balconi & Pagani, 2015; Liu et al., 2015).

In particular, affective gestures are aimed to transmit emotional content or to influence interlocutor emotional states (Balconi & Fronda 2020a,b, 2021a,b; Balconi et al., 2020, 2021; Fronda & Balconi 2020; Tomasello et al., 2005); social gestures are aimed at establishing a social relationship with the interlocutor (Balconi & Fronda, 2020a,b, 2021a,b; Balconi et al., 2020, 2021; Fronda & Balconi, 2020; Bressem & Müller, 2017; Kendon, 2017), and informative gestures are aimed at transmitting information relating to the description of a mental or physical state (Balconi & Fronda 2020a,b, 2021a,b; Balconi et al., 2020, 2021; Fronda & Balconi, 2020; Enfield et al., 2007; Kita, 2009). With respect of valence, positive gestures, instead, are aimed at initiating or establishing a relationship with the interlocutor or communicating positive states, while negative ones are aimed to interrupt a relationship or communicate negative states. Regarding gestures valence, different previous studies, according to the dual system model of neural signatures, have demonstrated a different frontal asymmetry in response to positive and negative gestures observation (Balconi et al., 2015; Balconi & Fronda 2020a,b, 2021a,b; Balconi et al., 2020,2021; Davidson 1992; Fronda & Balconi, 2020).

In light of this evidence, firstly, considering gestures category, we expected to observe an increase of frontal brain responsiveness and intra-brain connectivity of high-frequency bands, which are more involved in sensorimotor processes related to gesture observation (Balconi & Fronda, 2020b; Mizelle et al., 2010; Puzzo et al., 2011; Quandt et al., 2012; Schneider et al., 2008; Van Ede et al., 2011; Yuval-Greenberg & Deouell, 2007), and of low-frequency bands, which are more involved in emotional processes related to gesture perception (Balconi & Fronda 2020b; Knyazev, 2007), during the observation of social and affective gestures, compared to informative ones. Indeed, considering the nature of social and affective gestures, frontal areas are the most implicated in socio-emotional and relational processes (Balconi & Caldiroli, 2011; Balconi & Bortolotti, 2012, 2013; Balconi & Fronda, 2020a,b, 2021a,b; Balconi et al., 2011, 2012, 2020, 2021; Fronda & Balconi, 2020; Rameson & Lieberman, 2009; Rosso et al., 2004). Furthermore, we expected to observe a decrease of alpha power (increased brain activity), and an increase of delta and theta brain responsiveness and intra-brain connectivity in temporo-parietal area according to the observation of informative gestures, which require more involvement of attentional processes (Balconi & Fronda, 2020b; Perry et al., 2011; Rushworth et al., 2001).

Secondly, considering instead gesture valence, we expected to observe, for affective, social, and informative gestures, a different frontal asymmetry in relation to positive and negative gesture (Balconi & Fronda, 2020a,b, 2021a,b; Balconi et al., 2015, 2020, 2021; Davidson, 1992; Fronda & Balconi, 2020). In particular, we expected to observe an increase of delta and theta right frontal activity during the observation of negative gestures which, given their purpose, can induce individuals to an "avoidance" behaviour; while, an increase of delta and theta left frontal activity during the observation of positive gestures which induce individuals to an "approach" behavior (Balconi & Fronda, 2020b; De Stefani et al., 2013).

Finally, considering the inter-agents role (encoder or decoder), we expected to observe a similar brain responsiveness and intra-brain connectivity both in the encoder and in the decoder, due to the presence of mirror mechanisms during others' gesture observation, that allow individuals to understand other mental states, perceiving themselves in joint action and developing "resonance mechanisms" and implicit brain coupling processes (Balconi & Fronda, 2020b, 2021a; Balconi et al., 2018b; Holle et al., 2008; Lindenberger et al., 2009).

2. Methods

2.1 Participants

The present study was conducted on a sample of thirteen dyads of participants (M_{age} = 23.33; SD_{age} = 2.67) of the same sex. Specifically, dyads were composed by individuals not involved in a friendship or familiar relation. For each dyad, two different roles (encoder or decoder) were randomly assigned to participants. For the participants' recruitment, specific inclusion and exclusion criteria were selected. In particular, inclusion criteria requested the recruitment of individuals aged between 18 and 40 years, with normal or correct visual acuity and normal manual ability. Instead, the following exclusion criteria have been adopted: the presence of clinical or neurological disorders and the experience of stressful events in the last 6 months. The conduction of the research was approved by the local ethics committee of the Department of Psychology of the Catholic University of the Sacred Heart and followed the principles and guidelines of the Helsinki Declaration. In addition, participants took part in the experiment only after having signed the informed consent.

2.2 Procedure

The conduction of the research provided that participants were arranged sitting facing each other at a distance of 60 cm from a computer, used for the administration of 60 videos randomly shown in three blocks.

Firstly, participants were asked to observe the 60 videos, administered through the use of E-Prime 2.0 software (E-prime2 software, Tools Psychology Software Inc., Sharpsburg, Pennsylvania, USA). These videos reproduced 10 positive social gestures, which aimed to start or maintain a social relationship with the interlocutor; 10 negative social gestures, which aimed to interrupt the relationship with the interlocutor; 10 positive affective gestures, aimed at communicating an emotional positive state to the interlocutor; 10 negative affective gestures, aimed at transmitting a negative emotional state to the interlocutor; 10 positive informative gestures, and 10 negative informative gestures, used to describe a good or bad physical or psychological state to the interlocutor. For informative gestures, the positive or negative valence was determined by a context sentence (for example the informative gesture in which the encoder move the hand upwards with the palm up indicating to the encoder to stand up was preceded by this context: “On the train, someone occupies a reserved place”) shown before the video presentation to allow participants to understand the gesture meaning better (Balconi & Fronda, 2020a,b, 2021a,b; Balconi et al., 2020, 2021; Fronda & Balconi, 2020).

Specifically, videos reproduced a non-verbal communicative interaction between two actors, one of whom reproduced a gesture (encoder), which could be affective, social and informative of positive or negative valence, towards another individual who received the gesture (decoder).

Secondly, participants were asked to reproduce the gestures observed according to their roles. In particular, the encoder had to reproduce the gesture observed towards the decoder, which was only asked to receive the gesture. For the task administration, the following structure was used, consisting of: the presentation of an empty screen (2 sec.), the presentation of a slide containing a contextual sentence to allow individuals to better understand the meaning of the gesture observed (4 sec.), the video with the gesture to be observed (3 sec.), the presentation of an inter-stimulus (4 sec.), and the presentation of a slide containing a “go” signal to inform participants to reproduce the gesture (4 sec.) (Figure 1).

Videos reproducing gestures were previously validated by 14 judges (M_{age} = 28.34, SD_{age} = 0.04), using a seven-point Likert scale, for the assessment of the following gestures’ characteristics: commonality, frequency of use, complexity, social significance, familiarity, and emotional impact (Balconi et al., 2020, 2021; Balconi & Fronda, 2020a,b, 2021a,b; Fronda & Balconi, 2020). Statistical analyses were subsequently carried out on the following scores to define the categories of stimuli and verify the homogeneity of the previous characteristics. Similarly, experimental subjects were submitted to the same evaluation of gesture after viewing them (after gesture reproduction). Similar effects were found for the subjects, as observed for judges.

2.3 EEG recording and analysis

For the recording of the EEG signal, two 16-channel EEG systems were used (V-AMP: Brain Products, München; LiveAmp: Brain Products, GmbH, Gliching, Germany). Specifically, with the use of two ElectroCaps, electrodes were placed on individuals’ scalps on F3, F1, Fz, F2, F4, T7, T8, C3, Cz, C4, P3, P1, P2, P4, O1, and O2 positions (Figure 2). Furthermore, an EOG electrode was placed on the external canthi (Balconi & Fronda, 2020a,b, 2021a,b).

For each individual, 5 kΩ electrode impedance was monitored for data collection, and 1000 Hz was used for data sampling with a 0.01–200 Hz input filter and a 50 Hz notch filter. A 0.5–40 Hz bandpass filter was used to filter the acquired data offline. A common offline average reference was calculated (Ludwig et al., 2009) to reduce problems associated with signal-noise. For signals evaluation, portions of data containing artifacts were excluded, and an algorithm using regression analysis in combination with the artifacts average was utilized for ocular artifacts correction. Finally, 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) (Keil et al. 2003). The mean EEG power was calculated by averaging data related only to the gesture observation phase, using a 3-second segment.

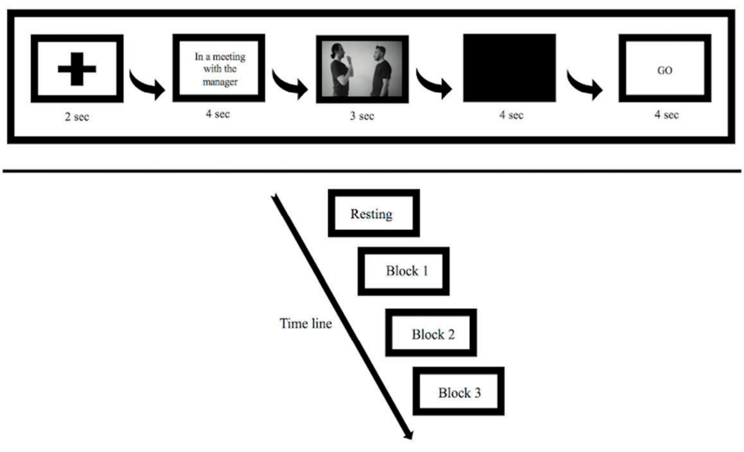

Figure 1. The figure shows the structure of each block of the task

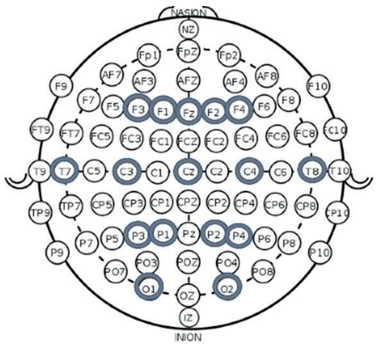

Figure 2. The figure shows the EEG electrode placement in: F3, F1, Fz, F2, F4, T7, C3, Cz, C4, T8, P3, P1, P2, P4, O1, O2

3. Data analysis

Related to EEG dependent measures, two sets of analyses were performed. The first ANOVA applied on raw data of single subject was aimed to test the effect of independent measures on each participants' frequency bands. The second set of analyses considered the intra-brain connectivity calculation for each participant on each frequency band.

In particular, to obtain intra-brain connectivity, the partial correlation coefficient Π_{ij} was computed by normalizing the inverse of the covariance matrix $\Gamma = \Sigma^{-1}$:

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

Then, a second ANOVA was applied to these intra-brain measures.

For ANOVAs, these independent measures were used: Role (encoder/decoder, 2), Valence (positive/negative, 2), Lateralization (left/right, 2), Gesture (social/affective/informative, 3), and ROI (regions of interest, 4). Four ROI were calculated for left/right homologous sides for frontal (F3,F1-F2,F4), central (C3,C4), temporo-parietal (T7,P1-T8,P2), and occipital channels (O1,O2; Balconi & Fronda, 2020a,b, 2021a,b).

For the ANOVAs tests, Greenhouse–Geisser epsilon was used for the correction of freedom degrees.

Post-hoc comparisons (contrast analyses) were applied to the data, and a Bonferroni test was applied for multiple comparisons. In addition, the normality of the data distribution was preliminary tested (kurtosis and asymmetry tests).

The normality assumption of the distribution was supported by these preliminary tests (Balconi & Fronda, 2020a,b, 2021a,b; Balconi et al., 2020, 2021; Fronda & Balconi, 2020).

4. Results

4.1 Brain activity on frequency bands

4.1.1 Delta band

About delta, ANOVA shows a significant Valence X Lateralization X Gesture X ROI interaction effect ($F[6,150] = 11.32$; $p < .001$; $\eta^2 = 0.38$). We only report significant effects for post-hoc analyses. In particular, post-hoc comparisons revealed an increase of delta activity in the frontal area compared to others for affective and social gestures compared to informative gestures (for all post-hoc comparisons $p \leq .001$). Furthermore, an increase of delta activity was observed for positive gestures in the left frontal side compared to the right one ($F[1,26] = 10.34$; $p \leq .001$; $\eta^2 = 0.37$) (Figure 3a).

4.1.2 Theta band

About theta, ANOVA reported a Valence X Lateralization X Gesture X ROI interaction effect ($F[6,150] = 10.78$; $p < .001$; $\eta^2 = 0.37$). Post-hoc comparisons revealed an increase of theta activity in the frontal area compared to others for affective and social gestures compared to informative ones (for all post-hoc comparisons $p \leq .001$). Furthermore, an increase of theta activity was observed in the left frontal side compared to the right one ($F[1,26] = 8.14$; $p < .001$; $\eta^2 = 0.34$) for positive gestures (Figure 3b).

4.1.3 Alpha band

About alpha, as revealed by ANOVA, a Gesture X ROI interaction effect ($F[6,150] = 11.09$; $p < .001$; $\eta^2 = 0.39$) was found. In particular, post-hoc comparisons revealed an increase of alpha brain activity (decrease of alpha power) in the frontal area for affective and social gestures compared to informative gestures (for all post-hoc comparisons p ≤ .001) and in the posterior (temporo-parietal) area for informative gestures compared to affective and social gestures (for all post-hoc comparisons p ≤ .001) (Figure 3c).

4.1.4 Beta band

About the beta band, ANOVA reveals no significant effect.

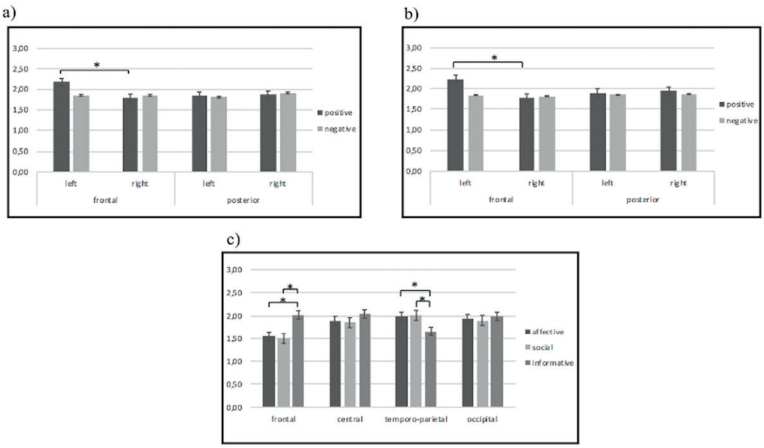

Figure 3. (a, b) Histogram of delta and theta brain activity for positive and negative gestures in frontal and posterior left and right side. (c) Histogram of alpha brain activity for affective, social and informative gestures in frontal, central, temporo-parietal and occipital area. For figures a,b,c bars represent +-1SE. Stars mark statistically significant (p<.05) pairwise comparisons

4.2 Intra-brain connectivity analysis

4.2.1 Delta band

For delta band, ANOVA revealed a significant Gesture X ROI interaction effect (F[6,150] = 9.12; p < .001; η^2 = 0.35). In particular, post-hoc comparisons showed an increase of intra-brain connectivity in frontal areas with respect to others for affective and social gestures and in posterior (temporo-parietal) areas compared to others for informative ones (for all post-hoc comparisons $p \leq .001$) (Figure 4a, d).

4.2.2 Theta band

For theta band, ANOVA shows a significant Gesture X ROI interaction effect ($F[6,154] = 10.78$; $p < .001$; $\eta^2 = 0.37$). Particularly, post-hoc comparisons revealed an increase of intra-brain connectivity in frontal areas compared to other areas for affective and social gestures (for all post-hoc comparisons $p \leq .001$) (Figure 4b, e).

4.2.3 Alpha band

For alpha band, ANOVA shows a Gesture X ROI interaction effect ($F[6,150] = 10.11$; $p < .001$; $\eta^2 = 0.37$). In particular, post-hoc comparisons revealed an increase of intra-brain connectivity in frontal areas with respect to other areas for affective and social gestures, and in posterior areas with respect to others for informative gestures (for all post-hoc comparisons $p \leq .001$) (Figure 4c, f).

4.2.4 Beta band

About the beta band, ANOVA reveals no significant results.

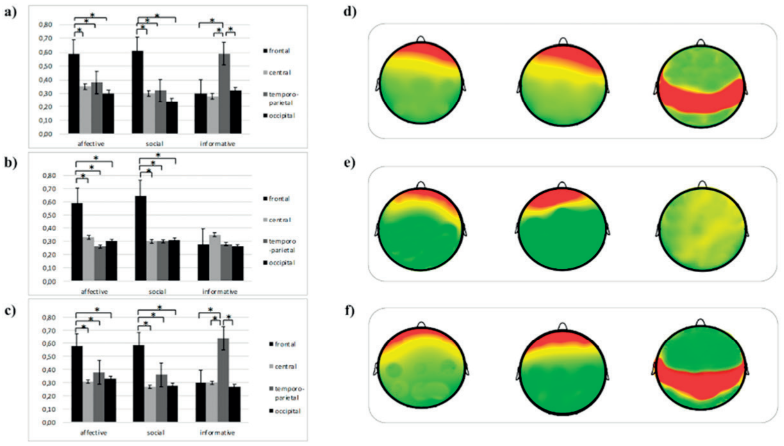

Figure 4. (a, b, c) Histogram of delta, theta and alpha intra-brain connectivity for affective, social and informative gestures in frontal, central, temporo-parietal and occipital areas. For figures a,b,c bars represent ∓1SE. Stars mark statistically significant (p<.05) pairwise comparisons. (d, e, f) Delta, theta and alpha intra-brain connectivity (red area) representation, from left to right, for affective, social and informative gestures

5. Discussion

The present study aimed to investigate the neural mechanisms that underlie the observation of positive and negative affective, social, and informative gestures in both the encoder and decoder.

Specifically, the brain responsiveness and intra-brain connectivity of both individuals were investigated in order to observe possible differences or similar neural mechanisms during the observation of different categories of gestures. In this regard, we expected to observe, firstly, a different modulation of low- and high-frequency bands activity and intra-brain connectivity concerning the category of gestures. Secondly, we expected to find a different cerebral frontal asymmetry according to gestures valence. Finally, we should reveal similar neural responses in frontal and parietal areas during the observation of gestures in both the encoder and decoder, due to the presence of similar mirroring mechanisms in response to the observation task.

Firstly, regarding the results of frequency band analyses, according to the first hypothesis, specific neural responses have emerged during the observation of affective, social, and informative gestures.

In particular, an increase in brain responsiveness for alpha, delta, and theta activity was observed in the frontal region during the observation of affective and social gestures. Regarding this first evidence, the decrease in alpha power in the frontal region for the observation of affective and social gestures could be due to the implementation of sensorimotor processes that are associated with individuals' previous personal experiences with these types of gestures (Balconi & Fronda, 2020b; Mizelle et al., 2010; Puzzo et al., 2011; Quandt et al., 2012; Schneider et al., 2008). Indeed, affective and social gestures, given their more interactional and relational nature, can be more easily connected to the presence of previous personal affective and social experiences.

Instead, the increased activation of delta and theta bands in the frontal area during the observation of affective and social gestures could be related to individuals' abilities to respond emotionally to relational and social situations (Balconi & Bortolotti, 2012, 2013; Balconi & Caldiroli, 2011; Balconi et al., 2011, 2014; Balconi & Fronda 2020a,b; Rameson & Lieberman, 2009), through the use of affective and empathic processes (Balconi & Vanutelli, 2017; Balconi et al., 2015; Mu et al., 2008). Indeed, as revealed by previous research, the increased activation of the frontal area according to affective and social gestures highlighted the involvement of emotional, empathic and mental model processes (Balconi & Fronda, 2020a,b; Balconi & Fronda, 2021a,b; Balconi et al., 2014, 2020, 2021; Fronda & Balconi, 2020; Konvalinka et al., 2014; Rameson & Lieberman, 2009; Rosso et al., 2004). Frontal areas appear to be involved in the regulation of emotional expression and in the understanding of the emotional states of others (Balconi & Fronda, 2020b; Bressem & Müller, 2017; Calbris, 2011; Fragopanagos et al., 2005; Fronda & Balconi, 2020; Kendon, 2017; Liotti & Mayberg, 2001), which are more implicated in this type of gesture. In particular, affective gestures are supported by specific frontal regions, such as the dorsolateral prefrontal cortex (DLPFC), which regulates processes of emotional sharing and mutual intentionality, prosocial, and empathic behavior as well as emotional attunement (Adolphs, 1999; Balconi & Canavesio, 2013, 2014; Balconi et al., 2020, 2021; Greene & Haidt, 2002; Fronda & Balconi, 2020).

Moreover, DLPFC is also involved in the management of the interpersonal relationship and theory of mind processes (Balconi et al., 2017a, 2020, 2021; Fronda & Balconi, 2020; Kalbe et al., 2010; Petrican & Schimmack, 2008).

As affective gestures, social ones result to be mediated by frontal areas, such as the superior frontal gyrus (SFG), that appear to be involved in selfawareness processes and the monitoring of our and others behavior (Balconi et al., 2020, 2021; Crivelli & Balconi, 2017; Fronda & Balconi, 2020; Nakamura et al., 1998; Shima & Tanji, 2000).

Considering, instead, informative gesture observation, aimed at communicating information to direct interlocutor attention towards a specific object in the proximal or distal environment, an increase of alpha brain responsiveness (decrease of alpha power) was observed in temporal-parietal areas. This result could be due to the involvement of individuals' attentional processes (Balconi & Fronda 2020a,b; Posner et al., 1984; Rushworth et al., 2001) required by this category of gestures.

Secondly, considering gesture valence, according to the second hypothesis, a different frontal brain responsiveness for delta and theta bands, that are more involved in emotional processes underlying gesture perception (Balconi & Fronda 2020a,b, 2021a,b; Holle et al., 2012; Knyazev, 2007), has emerged during the observation of positive and negative gestures for all three gestures categories (social, affective, and informative).

This result is supported by the model of double neural signatures of Davidson's emotional experience (Tomarken et al., 1992), also supported by subsequent studies (Balconi & Fronda, 2020a,b, 2021a,b; Balconi et al. 2015, 2020, 2021; Fronda & Balconi, 2020; Wager et al., 2003), that have observed an increase of the left frontal activity for positive emotions and of the right frontal activity for negative ones.

This frontal asymmetry may depend on transient or stable personality traits and the approach or affective avoidance styles (Davidson, 1993; Davidson & Irwin, 1999; Tomarken et al., 1990, 1992; Wager et al., 2003).

Considering, instead, intra-brain connectivity results, according to our hypothesis, an increase of intra-brain connectivity for alpha, delta, and theta bands was observed in the frontal area during the observation of affective and social gestures. Furthermore, an increase of intra-brain connectivity of alpha and delta bands was also observed in temporal-parietal regions during the observation of informative gestures.

The increase of intra-brain connectivity in frontal regions for affective and social gestures and in temporal-parietal regions for informative ones highlights the presence of similar internal connectivity in both the encoder and decoder, who did not differ from each other in their intra-brain connectivity.

In general, the increase of intra-brain connectivity can be considered as advantageous at an evolutionary level because it implies the mediation of different sensorimotor systems and higher cognitive faculties supported by some frontal regions. In particular, the different modulation of cortical activity concerning the category of observed gestures may be due to the involvement of the mirroring processes, supported by specific brain regions, that are involved in perceiving and observing gestures (Balconi & Fronda, 2020a; Rizzolatti et al., 2001; Rizzolatti & Sinigaglia, 2010).

Specifically, these mirroring mechanisms, supported mainly by the frontoparietal circuit, which regulate behavioral and social cognition (Rizzolatti & Sinigaglia, 2010), are implicated in the coupling between action observation and execution (Balconi & Fronda, 2020b; Rizzolatti et al., 1996, 2001), allowing the comprehension of the motor intention underlying actions (Gentilucci et al., 1983). Moreover, mirroring mechanisms, allowing the imitation and the understanding of the interlocutors behaviors (Balconi & Fronda 2020a,b, 2021a; Buccino et al., 2004; Iacoboni et al., 2005; Rizzolatti & Craighero, 2004; Rizzolatti & Luppino, 2001), lead individuals to simulate the others embodied experiences by activating the same neural mechanisms (Balconi & Fronda, 2020a,b, 2021a,b; Buccino et al., 2001; Keysers & Gazzola, 2014; Kohler et al., 2002; Rizzolatti & Sinigaglia, 2010), creating implicit coupling mechanisms between the individuals involved in the interaction (Balconi & Fronda, 2020a,b, 2021a,b; Rizzolatti & Sinigaglia, 2010; Shepherd et al., 2009).

In addition to the presence of mirror mechanisms, the increase of intra-brain connectivity in the frontal and parietal areas could be due to the involvement of these regions in the sensorimotor processes involved in gestures observation (Balconi & Fronda, 2020b; Rizzolatti & Fogassi, 2014; Rizzolatti & Sinigaglia, 2010). Indeed, as demonstrated by previous studies (Balconi et al., 2017; Kasess et al., 2008; Nguyen et al., 2014), frontal regions are more implicated in the processes of gestures imagination and intentionalization, while the parietal ones are more implicated in attentional processes of preparation of movements and imagination of motor actions (Balconi et al., 2017; Balconi & Fronda, 2020a,b; Balconi et al., 2020, 2021; Rushworth et al., 1997).

Finally, regarding this increase of intra-brain connectivity, it has emerged both in the encoder and the decoder underlying how gestures observation represents a common mechanism, regardless of just observation or production.

This result highlights the presence of possible mirroring mechanisms both in the encoder and the decoder, which almost activate specific localized processes in some brain areas during the observation of the different gesture types.

Indeed, as shown by previous studies (Balconi & Fronda, 2020b; Fronda & Balconi, 2020; Holle et al., 2008), the activation of similar brain patterns that support gestures observation occurs during the actions of coding and decoding.

The results of the present study, therefore, show that gestures observation represents a common action among interacting individuals, as evidenced both by the increase of brain responsiveness and intra-brain connectivity in the same brain areas both in the encoder and in the decoder, that underline the presence of mirror, resonant and common mechanisms. These processes turn out to be the basis of social processes, such as empathy (Carr et al., 2003; Molnar-Szakacs et al., 2007), intentionality comprehension and communicative exchanges (Iacoboni et al., 2005; Molnar-Szakacs et al., 2007).

However, despite the potential of this study, some limitations that could be implemented in future studies can be highlighted, such as the sample size, which could be implemented; and a possible consideration about the composition of dyads of different sex, to evaluate any possible differences in individuals' brain responsiveness and intra-brain connectivity. In addition, the use of only EEG to investigate cortical activity could be implemented using a peripheral activity detection tool, as biofeedback. Finally following studies could consider the use of other types of specific gestures, not only affective, social and informative ones.

References

Adolphs, R. (1999). Social cognition and the human brain. *Trends in Cognitive Sciences*, *3*(12), 469-479. https://doi.org/10.1016/s1364-6613(99)01399-6

Balconi, M., Bartolo, A., & Fronda, G. (2021). Social hyperscanning with fNIRS: Intra-brain and inter-brain connectivity for social, affective and informative gestures reproduction. *Gesture*, *19*(2/3), 196-222.

Balconi, M., & Bortolotti, A. (2012). Detection of the facial expression of emotion and self-report measures in empathic situations are influenced by sensorimotor circuit inhibition by low-frequency rTMS. *Brain Stimulation*, *5*(3), 330-336. https://doi.org/10.1016/j.brs.2011.05.004.

Balconi, M., & Bortolotti, A. (2013). Emotional face recognition, empathic trait (BEES), and cortical contribution in response to positive and negative cues. The effect of rTMS on dorsal medial prefrontal cortex. *Cognitive Neurodynamics*, *7*(1), 13-21. https://doi.org/10.1007/s11571-012-9210-4.

Balconi, M., Bortolotti, A., & Gonzaga, L. (2011). Emotional face recognition, EMG response, and medial prefrontal activity in empathic behaviour. *Neuroscience Research*, *71*(3), 251-259. https://doi.org/10.1016/j.neures.2011.07.1833.

Balconi, M., & Caldiroli, C. (2011). Semantic violation effect on object-related action comprehension. N400-like event-related potentials for unusual and incorrect use. *Neuroscience*, *197*, 191-199. https://doi.org/10.1016/j.neuroscience.2011.09.026.

Balconi, M., & Canavesio, Y. (2013). Emotional contagion and trait empathy in prosocial behavior in young people: the contribution of autonomic (facial feedback) and balanced emotional empathy scale (BEES) measures. *Journal of Clinical and Experimental Neuropsychology*, *35*(1), 41-48. https://doi.org/10.1080/13803395.2012.742492.

Balconi, M., & Canavesio, Y. (2014). High-frequency rTMS on DLPFC increases prosocial attitude in case of decision to support people. *Social Neuroscience*, *9*(1), 82-93. https://doi.org/10.1080/17470919.2013.861361.

Balconi, M., Cortesi, L., & Crivelli, D. (2017a). Motor planning and performance in transitive and intransitive gesture execution and imagination: Does EEG (RP) activity predict hemodynamic (fNIRS) response?. *Neuroscience Letters*, *648*, 59-65. https://doi.org/10.1016/j.neulet.2017.03.049.

Balconi, M., Crivelli, D., & Vanutelli, M. E. (2017b). Why to cooperate is better than to compete: brain and personality components. *BMC Neuroscience*, *18*(1), 1-15. https://doi.org/10.1186/s12868-017-0386-8.

Balconi, M., Falbo, L., & Conte, V. A. (2012). BIS and BAS correlates with psychophysiological and cortical response systems during aversive and appetitive emotional stimuli processing. *Motivation and Emotion*, *36*(2), 218-231. https://doi.org/10.1007/s11031-011-9244-7.

Balconi, M., Finocchiaro, R., & Campanella, S. (2014). Reward sensitivity, decisional bias, and metacognitive deficits in cocaine drug addiction. *Journal of Addiction Medicine*, *8*(6), 399-406. https://doi.org/10.1097/ADM.0000000000000065.

Balconi, M., & Fronda, G. (2020a). The use of hyperscanning to investigate the role of social, affective, and informative gestures in non-verbal communication. Electrophysiological (EEG) and inter-brain connectivity evidence. *Brain Sciences*, *10*(1), 29. https://doi.org/10.3390/brainsci10010029

Balconi, M., & Fronda, G. (2020b). Gesture in hyperscanning during observation. Inter-brain connectivity. *Neuropsychological Trends*, *28*, 59-81. http://dx.doi.org/10.7358/neur-2020-028-bal2

Balconi, M., & Fronda, G. (2021a). Intra-brain connectivity vs. inter-brain connectivity in gestures reproduction: What relationship?. *Brain Sciences*, *11*(5), 577. https://doi.org/10.3390/brainsci11050577

Balconi, M., & Fronda, G. (2021b). Inter-brain EEG connectivity in hyperscanning for Italian and French gestures: the culture-related nonverbal language. *Culture and Brain*, 1-22.

Balconi, M., Fronda, G., & Bartolo, A. (2020). Affective, social, and informative gestures reproduction in human interaction: hyperscanning and brain connectivity. *Journal of Motor Behavior*, *53*(3), 296-315. https://doi.org/10.1080/00222895.2020.1774490

Balconi, M., Gatti, L., & Vanutelli, M. E. (2018a). Cooperate or not cooperate EEG, autonomic, and behavioral correlates of ineffective joint strategies. *Brain and Behavior*, *8*(2), e00902. https://doi.org/10.1002/brb3.902.

Balconi, M., Gatti, L., & Vanutelli, M. E. (2018b). When cooperation goes wrong: brain and behavioural correlates of ineffective joint strategies in dyads. International *Journal of Neuroscience*, *128*(2), 155-166. https://doi.org/10.1080/00207454.2017.1379519.

Balconi, M., Grippa, E., & Vanutelli, M. E. (2015). What hemodynamic (fNIRS), electrophysiological (EEG) and autonomic integrated measures can tell us about emotional processing. *Brain and Cognition*, *95*, 67-76. https://doi.org/10.1016/j.bandc.2015.02.001

Balconi, M., & Pagani, S. (2015). Social hierarchies and emotions: cortical prefrontal activity, facial feedback (EMG), and cognitive performance in a dynamic interaction. *Social Neuroscience*, *10*(2), 166-178. https://doi.org/10.1080/17470919.2014.977403.

Balconi, M., & Vanutelli, M. E. (2017). Cooperation and competition with hyperscanning methods: review and future application to emotion domain. *Frontiers in Computational Neuroscience*, *11*, 86. https://doi.org/10.3389/fncom.2017.00086

Bressem, J., & Müller, C. (2017). The "Negative-Assessment-Construction"–A multimodal pattern based on a recurrent gesture?. *Linguistics Vanguard*, *3*(s1). https://doi.org/10.1515/lingvan-2016-0053.

Buccino, G., Binkofski, F., Fink, G. R., Fadiga, L., Fogassi, L., Gallese, V., ... & Freund, H. J. (2001). Action observation activates premotor and parietal areas in a somatotopic manner: an fMRI study. *European Journal of Neuroscience*, *13*(2), 400-404. https://doi.org/10.1046/j.1460-9568.2001.01385.x.

Buccino, G., Vogt, S., Ritzl, A., Fink, G. R., Zilles, K., Freund, H. J., & Rizzolatti, G. (2004). Neural circuits underlying imitation learning of hand actions: an event-related fMRI study. *Neuron*, *42*(2), 323-334. https://doi.org/10.1016/S0896-6273(04)00181-3.

Buzsáki, G., & Draguhn, A. (2004). Neuronal oscillations in cortical networks. *Science, 304*(5679), 1926-1929. https://doi.org/10.1126/science.1099745.

Cabrera, M. E., Novak, K., Foti, D., Voyles, R., & Wachs, J. P. (2017, May). What makes a gesture a gesture? Neural signatures involved in gesture recognition. In 2017 *12th IEEE International Conference on Automatic Face & Gesture Recognition* (FG 2017) (pp. 748-753). IEEE. https://doi.org/10.1109/FG.2017.93.

Cabrera, M. E., Novak, K., Foti, D., Voyles, R., & Wachs, J. P. (2020). Electrophysiological indicators of gesture perception. *Experimental Brain Research*, *238*(3), 537-550. https://doi.org/10.1007/s00221-020-05724-y

Calbris, G. (2011). *Elements of meaning in gesture* (Vol. 5). John Benjamins Publishing.

Carr, L., Iacoboni, M., Dubeau, M. C., Mazziotta, J. C., & Lenzi, G. L. (2003). Neural mechanisms of empathy in humans: a relay from neural systems for imitation to limbic areas. *Proceedings of the national Academy of Sciences*, *100*(9), 5497-5502. https://doi.org/10.1073/pnas.0935845100.

Caspers, S., Zilles, K., Laird, A. R., & Eickhoff, S. B. (2010). ALE meta-analysis of action observation and imitation in the human brain. *Neuroimage*, *50*(3), 1148-1167. https://doi.org/10.1016/j.neuroimage.2009.12.112.

Chaudhary, U., Hall, M., DeCerce, J., Rey, G., & Godavarty, A. (2011). Frontal activation and connectivity using near-infrared spectroscopy: verbal fluency language study. *Brain Research Bulletin*, *84*(3), 197-205. https://doi.org/10.1016/j.brainresbull.2011.01.002.

Chong, T. T. J., Williams, M. A., Cunnington, R., & Mattingley, J. B. (2008). Selective attention modulates inferior frontal gyrus activity during action observation. *Neuroimage*, *40*(1), 298-307. https://doi.org/10.1016/j.neuroimage.2007.11.030.

Costantini, M., Galati, G., Ferretti, A., Caulo, M., Tartaro, A., Romani, G. L., & Aglioti, S. M. (2005). Neural systems underlying observation of humanly impossible movements: an fMRI study. *Cerebral Cortex*, *15*(11), 1761-1767. https://doi.org/10.1093/cercor/bhi053.

Crivelli, D., & Balconi, M. (2017). Agentività e competenze sociali: Riflessioni teoriche e implicazioni per il management. *Ricerche Di Psicologia*, 3, 349-363. https://doi.org/10.3280/rip2017-003006.

Davidson, R. J. (1992). Emotion and affective style: Hemispheric substrates. *Psychological Sciences*, *3*(1), 39-43. https://doi.org/10.1111/j.1467-9280.1992.tb00254.x.

Davidson, R. J. (1993). Parsing affective space: Perspectives from neuropsychology and psychophysiology. *Neuropsychology*, *7*(4), 464. https://doi.org/10.1037/0894-4105.7.4.464.

Davidson, R. J., & Irwin, W. (1999). The functional neuroanatomy of emotion and affective style. *Trends in Cognitive Sciences*, *3*(1), 11-21. https://doi.org/10.1016/S1364-6613(98)01265-0.

De Stefani, E., Innocenti, A., Secchi, C., Papa, V., & Gentilucci, M. (2013). Type of gesture, valence, and gaze modulate the influence of gestures on observer's behaviors. *Frontiers in Human Neuroscience*, *7*, 542. https://doi.org/10.3389/fnhum.2013.00542.

Enfield, N. J., Kita, S., & De Ruiter, J. P. (2007). Primary and secondary pragmatic functions of pointing gestures. *Journal of Pragmatics*, *39*(10), 1722-1741. https://doi.org/10.1016/j.pragma.2007.03.001.

Falk, E. B., & Bassett, D. S. (2017). Brain and social networks: fundamental building blocks of human experience. *Trends in Cognitive Sciences*, *21*(9), 674-690. https://doi.org/10.1016/j.tics.2017.06.009.

Fragopanagos, N., Kockelkoren, S., & Taylor, J. G. (2005). A neurodynamic model of the attentional blink. *Cognitive Brain Research*, *24*(3), 568-586. https://doi.org/10.1016/j.cogbrainres.2005.03.010.

Friston, K. J. (2011). Functional and effective connectivity: A review. *Brain Connectivity*, *1*(1), 13-36. https://doi.org/10.1089/brain.2011.0008.

Fronda, G., & Balconi, M. (2020). The effect of interbrain synchronization in gesture observation: A fNIRS study. *Brain and Behavior*, *10*(7), e01663. https://doi.org/10.1002/brb3.1663

Gentilucci, M., Scandolara, C., Pigarev, I. N., & Rizzolatti, G. (1983). Visual responses in the postarcuate cortex (area 6) of the monkey that are independent of eye position. *Experimental Brain Research*, *50*(2-3), 464-468. https://doi.org/10.1007/BF00239214.

Greene, J., & Haidt, J. (2002). How (and where) does moral judgment work?. *Trends in Cognitive Sciences*, *6*(12), 517-523. https://doi.org/10.1016/S1364-6613(02)02011-9

Hamilton, A., Wolpert, D., & Frith, U. (2004). Your own action influences how you perceive another person's action. *Current Biology*, *14*(6), 493-498. https://doi.org/10.1016/j.cub.2004.03.007.

Hecht, H., Vogt, S., & Prinz, W. (2001). Motor learning enhances perceptual judgment: A case for action-perception transfer. *Psychological Research*, *65*(1), 3-14. https://doi.org/10.1007/s004260000043.

Holle, H., Gunter, T. C., Rüschemeyer, S. A., Hennenlotter, A., & Iacoboni, M. (2008). Neural correlates of the processing of co-speech gestures. *Neuroimage*, *39*(4), 2010-2024. https://doi.org/10.1016/j.neuroimage.2007.10.055.

Holle, H., Obermeier, C., Schmidt-Kassow, M., Friederici, A. D., Ward, J., & Gunter, T. C. (2012). Gesture facilitates the syntactic analysis of speech. *Frontiers in Psychology*, *3*, 74. https://doi.org/10.3389/fpsyg.2012.00074.

Iacoboni, M., Molnar-Szakacs, I., Gallese, V., Buccino, G., Mazziotta, J. C., & Rizzolatti, G. (2005). Grasping the intentions of others with one's own mirror neuron system. *Plos Biology*, *3*(3), e79. https://doi.org/10.1371/journal.pbio.0030079.

Kalbe, E., Schlegel, M., Sack, A. T., Nowak, D. A., Dafotakis, M., Bangard, C., ... & Kessler, J. (2010). Dissociating cognitive from affective theory of mind: a TMS study. *Cortex*, *46*(6), 769-780. https://doi.org/10.1016/j.cortex.2009.07.010.

Kasess, C. H., Windischberger, C., Cunnington, R., Lanzenberger, R., Pezawas, L., & Moser, E. (2008). The suppressive influence of SMA on M1 in motor imagery revealed by fMRI and dynamic causal modeling. *Neuroimage*, *40*(2), 828-837. https://doi.org/10.1016/j.neuroimage.2007.11.040.

Keil, A., Stolarova, M., Heim, S., Gruber, T., & Müller, M. M. (2003). Temporal stability of high-frequency brain oscillations in the human EEG. *Brain Topography*, *16*(2), 101-110. https://doi.org/10.1023/B:BRAT.0000006334.15919.2c.

Kendon, A. (2017). Reflections on the "gesture-first" hypothesis of language origins. Psychonomic *Bulletin & Review*, *24*(1), 163-170. https://doi.org/10.3758/s13423-016-1117-3.

Keysers, C., & Gazzola, V. (2014). Hebbian learning and predictive mirror neurons for actions, sensations and emotions. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *369*(1644), 20130175. https://doi.org/10.1098/rstb.2013.0175.

Kilner, J. M., & Blakemore, S. J. (2007). How does the mirror neuron system change during development?. *Developmental Science*, *10*(5), 524-526. https://doi.org/10.1111/j.1467-7687.2007.00632.x.

Kita, S. (2009). Cross-cultural variation of speech-accompanying gesture: A review. *Language and Cognitive Processes*, *24*(2), 145-167. https://doi.org/10.1080/01690960802586188.

Knyazev, G. G. (2007). Motivation, emotion, and their inhibitory control mirrored in brain oscillations. *Neuroscience & Biobehavioral Reviews*, *31*(3), 377-395. https://doi.org/10.1016/j.neubiorev.2006.10.004.

Kohler, E., Keysers, C., Umilta, M. A., Fogassi, L., Gallese, V., & Rizzolatti, G. (2002). Hearing sounds, understanding actions: action representation in mirror neurons. *Science*, *297*(5582), 846-848. https://doi.org/10.1126/science.1070311.

Koike, T., Tanabe, H. C., & Sadato, N. (2015). Hyperscanning neuroimaging technique to reveal the "two-in-one" system in social interactions. *Neuroscience Research*, *90*, 25-32. https://doi.org/10.1016/j.neures.2014.11.006.

Konvalinka, I., Bauer, M., Stahlhut, C., Hansen, L. K., Roepstorff, A., & Frith, C. D. (2014). Frontal alpha oscillations distinguish leaders from followers: multivariate decoding of mutually interacting brains. *Neuroimage*, *94*, 79-88. https://doi.org/10.1016/j.neuroimage.2014.03.003.

Lindenberger, U., Li, S. C., Gruber, W., & Müller, V. (2009). Brains swinging in concert: cortical phase synchronization while playing guitar. *BMC Neuroscience*, *10*(1), 1-12. https://doi.org/10.1186/1471-2202-10-22.

Liotti, M., & Mayberg, H. S. (2001). The role of functional neuroimaging in the neuropsychology of depression. *Journal of Clinical and Experimental Neuropsychology*, *23*(1), 121-136. https://doi.org/10.1076/jcen.23.1.121.1223.

Liu, T., Saito, H., & Oi, M. (2015). Role of the right inferior frontal gyrus in turn-based cooperation and competition: A near-infrared spectroscopy study. *Brain and Cognition*, *99*, 17-23.

https://doi.org/10.1016/j.bandc.2015.07.001.

Ludwig, K. A., Miriani, R. M., Langhals, N. B., Joseph, M. D., Anderson, D. J., & Kipke, D. R. (2009). Using a common average reference to improve cortical neuron recordings from microelectrode arrays. *Journal of Neurophysiology*, *101*(3), 1679-1689. https://doi.org/10.1152/jn.90989.2008.

McNeill, D. (1992). *Hand and mind: What gestures reveal about thought.* University of Chicago press. https://doi.org/10.2307/1576015.

McNeill, D. (2013). *Gesture and Thought.* University of Chicago Press. https://doi.org/10.7208/chicago/9780226514642.001.0001.

Mizelle, J. C., Forrester, L., Hallett, M., & Wheaton, L. A. (2010). Electroencephalographic reactivity to unimodal and bimodal visual and proprioceptive demands in sensorimotor integration. *Experimental Brain Research*, *203*(4), 659-670. https://doi.org/10.1007/s00221-010-2273-8.

Molenberghs, P., Cunnington, R., & Mattingley, J. B. (2012). Brain regions with mirror properties: A meta-analysis of 125 human fMRI studies. *Neuroscience & Biobehavioral Reviews*, *36*(1), 341-349. https://doi.org/10.1016/j.neubiorev.2011.07.004.

Molnar-Szakacs, I., Wu, A. D., Robles, F. J., & Iacoboni, M. (2007). Do you see what I mean? Corticospinal excitability during observation of culture-specific gestures. *Plos One*, *2*(7), e626. https://doi.org/10.1371/journal.pone.0000626.

Mu, Y., Fan, Y., Mao, L., & Han, S. (2008). Event-related theta and alpha oscillations mediate empathy for pain. *Brain Research*, *1234*, 128-136. https://doi.org/10.1016/j.brainres.2008.07.113.

Muthukumaraswamy, S. D., Johnson, B. W., & McNair, N. A. (2004). Mu rhythm modulation during observation of an object-directed grasp. *Cognitive Brain Research*, *19*(2), 195-201. https://doi.org/10.1016/j.cogbrainres.2003.12.001.

Nakamura, Y., Ohya, Y., Onaka, U., Fujii, K., Abe, I., & Fujishima, M. (1998). Inhibitory action of insulin-sensitizing agents on calcium channels in smooth muscle cells from resistance arteries of guinea-pig. *British Journal of Pharmacology*, *123*(4), 675-682. https://doi.org/10.1038/sj.bjp.0701669.

Nguyen, V. T., Breakspear, M., & Cunnington, R. (2014). Fusing concurrent EEG–fMRI with dynamic causal modeling: Application to effective connectivity during face perception. *Neuroimage*, *102*, 60-70. https://doi.org/10.1016/j.neuroimage.2013.06.083.

Perry, A., Stein, L., & Bentin, S. (2011). Motor and attentional mechanisms involved in social interaction. Evidence from mu and alpha EEG suppression. *Neuroimage*, *58*(3), 895-904. https://doi.org/10.1016/j.neuroimage.2011.06.060.

Petrican, R., & Schimmack, U. (2008). The role of dorsolateral prefrontal function in relationship commitment. *Journal of Research in Personality*, *42*(4), 1130-1135. https://doi.org/10.1016/j.jrp.2008.03.001.

Pineda, J. A. (2005). The functional significance of mu rhythms: translating "seeing" and "hearing" into "doing". *Brain Research Reviews*, *50*(1), 57-68. https://doi.org/10.1016/j.brainresrev.2005.04.005.

Posner, M. I., Walker, J. A., Friedrich, F. J., & Rafal, R. D. (1984). Effects of parietal injury on covert orienting of attention. *Journal of Neuroscience*, *4*(7), 1863-1874. https://doi.org/10.1523/jneurosci.04-07-01863.1984.

Puzzo, I., Cooper, N. R., Cantarella, S., & Russo, R. (2011). Measuring the effects of manipulating stimulus presentation time on sensorimotor alpha and low beta reactivity during hand movement observation. *NeuroImage*, *57*(4), 1358-1363. https://doi.org/10.1016/j.neuroimage.2011.05.071.

Quandt, L. C., Marshall, P. J., Bouquet, C. A., & Shipley, T. F. (2013). Somatosensory experiences with action modulate alpha and beta power during subsequent action observation. *Brain Research*, *1534*, 55-65. https://doi.org/10.1016/j.brainres.2013.08.043.

Quandt, L. C., Marshall, P. J., Shipley, T. F., Beilock, S. L., & Goldin-Meadow, S. (2012). Sensitivity of alpha and beta oscillations to sensorimotor characteristics of action: An EEG study of action production and gesture observation. *Neuropsychologia*, *50*(12), 2745-2751. https://doi.org/10.1016/j.neuropsychologia.2012.08.005.

Rameson, L. T., & Lieberman, M. D. (2009). Empathy: A social cognitive neuroscience approach. *Social and Personality Psychology Compass*, *3*(1), 94-110. https://doi.org/10.1111/j.1751-9004.2008.00154.x.

Rizzolatti, G., & Craighero, L. (2004). The mirror-neuron system. *Annual Review of Neuroscience*, *27*, 169-192. https://doi.org/10.1146/annurev.neuro.27.070203.144230.

Rizzolatti, G., Fadiga, L., Gallese, V., & Fogassi, L. (1996). Premotor cortex and the recognition of motor actions. *Cognitive Brain Research*, *3*(2), 131-141. https://doi.org/10.1016/0926-6410(95)00038-0.

Rizzolatti, G., & Fogassi, L. (2014). The mirror mechanism: recent findings and perspectives. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *369*(1644), 20130420. https://doi.org/10.1098/rstb.2013.0420.

Rizzolatti, G., Fogassi, L., & Gallese, V. (2001). Neurophysiological mechanisms underlying the understanding and imitation of action. *Nature Reviews Neuroscience*, *2*(9), 661-670. https://doi.org/10.1038/35090060.

Rizzolatti, G., & Luppino, G. (2001). The cortical motor system. *Neuron*, *31*(6), 889-901. https://doi.org/10.1016/S0896-6273(01)00423-8.

Rizzolatti, G., & Sinigaglia, C. (2010). The functional role of the parieto-frontal mirror circuit: interpretations and misinterpretations. *Nature Reviews Neuroscience*, *11*(4), 264-274. https://doi.org/10.1038/nrn2805.

Rosso, I. M., Young, A. D., Femia, L. A., & Yurgelun-Todd, D. A. (2004). Cognitive and emotional components of frontal lobe functioning in childhood and adolescence. *Annals-New York Academy of Sciences*, *1021*, 355-362. https://doi.org/10.1196/annals.1308.045.

Ruby, P., & Decety, J. (2004). How would you feel versus how do you think she would feel? A neuroimaging study of perspective-taking with social emotions. *Journal of Cognitive Neuroscience*, *16*(6), 988-999. https://doi.org/10.1162/0898929041502661.

Rushworth, M. F., Krams, M., & Passingham, R. E. (2001). The attentional role of the left parietal cortex: the distinct lateralization and localization of motor attention in the human brain. *Journal of Cognitive Neuroscience*, *13*(5), 698-710. https://doi.org/10.1162/089892901750363244.

Rushworth, M. F. S., Nixon, P. D., & Passingham, R. E. (1997). Parietal cortex and movement II. Spatial representation. *Experimental Brain Research*, *117*(2), 311-323. https://doi.org/10.1007/s002210050225.

Schippers, M. B., Roebroeck, A., Renken, R., Nanetti, L., & Keysers, C. (2010). Mapping the information flow from one brain to another during gestural communication. *Proceedings of the National Academy of Sciences*, *107*(20), 9388-9393. https://doi.org/10.1073/pnas.1001791107.

Schneider, T. R., Debener, S., Oostenveld, R., & Engel, A. K. (2008). Enhanced EEG gamma-band activity reflects multisensory semantic matching in visual-to-auditory object priming. *Neuroimage*, *42*(3), 1244-1254. https://doi.org/10.1016/j.neuroimage.2008.05.033.

Schütz-Bosbach, S., & Prinz, W. (2007). Perceptual resonance: action-induced modulation of perception. *Trends in Cognitive Sciences*, *11*(8), 349-355. https://doi.org/10.1016/j.tics.2007.06.005.

Shepherd, S. V., Klein, J. T., Deaner, R. O., & Platt, M. L. (2009). Mirroring of attention by neurons in macaque parietal cortex. *Proceedings of the National Academy of Sciences*, *106*(23), 9489-9494. https://doi.org/10.1073/pnas.0900419106.

Shima, K., & Tanji, J. (2000). Neuronal activity in the supplementary and presupplementary motor areas for temporal organization of multiple movements. *Journal of Neurophysiology*, *84*(4), 2148-2160. https://doi.org/10.1152/jn.2000.84.4.2148.

Simony, E., Honey, C. J., Chen, J., Lositsky, O., Yeshurun, Y., Wiesel, A., & Hasson, U. (2016). Dynamic reconfiguration of the default mode network during narrative comprehension. *Nature Communications*, *7*(1), 1-13. https://doi.org/10.1038/ncomms12141.

Singer, W. (1999). Neuronal synchrony: a versatile code review for the definition of relations. *Neuron*, *24*(24), 49-64. https://doi.org/10.1016/S0896-6273(00)80821-1.

Stone, D. B., Tamburro, G., Di Fronso, S., Robazza, C., Bertollo, M., & Comani, S. (2019). Hyperscanning of interactive juggling: expertise influence on source level functional connectivity. *Frontiers in Human Neuroscience*, *13*, 321. https://doi.org/10.3389/fnhum.2019.00321.

Tomarken, A. J., Davidson, R. J., & Henriques, J. B. (1990). Resting frontal brain asymmetry predicts affective responses to films. *Journal of Personality and Social Psychology*, *59*(4), 791. https://doi.org/10.1037/0022-3514.59.4.791.

Tomarken, A. J., Davidson, R. J., Wheeler, R. E., & Doss, R. C. (1992). Individual differences in anterior brain asymmetry and fundamental dimensions of emotion. *Journal of Personality and Social Psychology*, *62*(4), 676. https://doi.org/10.1037/0022-3514.62.4.676.

Tomasello, M., Carpenter, M., Call, J., Behne, T., & Moll, H. (2005). Understanding and sharing intentions: The origins of cultural cognition. *Behavioral and Brain Sciences*, *28*(5), 675-691. https://doi.org/10.1017/S0140525X05000129.

Urgen, B. A., Plank, M., Ishiguro, H., Poizner, H., & Saygin, A. P. (2013). EEG theta and Mu oscillations during perception of human and robot actions. *Frontiers in Neurorobotics*, *7*, 19. https://doi.org/10.3389/fnbot.2013.00019.

Van Ede, F., De Lange, F., Jensen, O., & Maris, E. (2011). Orienting attention to an upcoming tactile event involves a spatially and temporally specific modulation of sensorimotor alpha-and beta-band oscillations. *Journal of Neuroscience*, *31*(6), 2016-2024. https://doi.org/10.1523/JNEUROSCI.5630-10.2011.

Vanutelli, M. E., Nandrino, J. L., & Balconi, M. (2016). The boundaries of cooperation: Sharing and coupling from ethology to neuroscience. *Neuropsychological Trends*, *19*, 83-104. https://doi.org/10.7358/neur-2016-019-vanu.

Wager, T. D., Phan, K. L., Liberzon, I., & Taylor, S. F. (2003). Valence, gender, and lateralization of functional brain anatomy in emotion: a meta-analysis of findings from neuroimaging. *Neuroimage*, *19*(3), 513-531. https://doi.org/10.1016/S1053-8119(03)00078-8.

Wriessnegger, S. C., Leeb, R., Kaiser, V., Neuper, C., & Müller-Putz, G. R. (2013). Watching object related movements modulates mirror-like activity in parietal brain regions. *Clinical Neurophysiology*, *124*(8), 1596-1604. https://doi.org/10.1016/j.clinph.2013.02.019.

Yuval-Greenberg, S., & Deouell, L. Y. (2007). What you see is not (always) what you hear: induced gamma band responses reflect cross-modal interactions in familiar object recognition. *Journal of Neuroscience*, *27*(5), 1090-1096. https://doi.org/10.1523/JNEUROSCI.4828-06.2007.

Zhao, X., Xi, Q., Wang, P., Li, C., & He, H. (2014). Altered activity and functional connectivity of superior temporal gyri in anxiety disorders: A functional magnetic resonance imaging study. *Korean Journal of Radiology*, *15*(4), 523-529. https://doi.org/10.3348/kjr.2014.15.4.523.