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# Join actions and the Joint Simon Effect: an ERP and source reconstruction analysis

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# Summary

In the last decades, researchers recognized the importance of studying human cognition in a social context. Indeed, it was demonstrated that the presence of others has a fundamental role in affecting our actions. A growing body of studies suggests that performing a task with a co-agent leads to the formation of co-representations, that ultimately guide our social behavior. Co-representations were investigated distributing a classic cognitive-conflict task, the Simon task, between pairs of participants, thus creating a social version of the task, namely, the Joint Simon Task (JST). Participants' performance is usually affected by the presence of a co-agent as they show to integrate the other's action in their own motor plans even when coordination is not required, as shown by the emergence of the socially induced correspondence effect, the Joint Simon Effect (JSE). Chapter 1 provides a review of the most relevant behavioral studies investigating the processes leading to this effect, explaining the main accounts proposed in the last decades and the social and non-social factors affecting JST performances. Chapter 2 represents an attempt to integrate the results of brain imaging studies investigating the neural mechanisms subserving the JSE and those addressing the brain dynamics related to joint action in general. Neural mechanisms associated to spatial conflict, spatial attention, co-representation, action inhibition and self-other discrimination demonstrates how previous studies employing a JST task reported incomplete and controversial data that need clarification. Chapter 3 describes a study conducted with the aim to investigate and further characterize the behavioral and neural aspects of the JSE. The electroencephalographic (EEG) signal was simultaneously recorded from a large sample of 44 pairs of participants. The simultaneous registration of electrophysiological signals from pairs of participants allowed us to provide replication and systematization of previous contrasting results concerning the event-related potentials usually addressed for the analysis of conflict monitoring and response inhibition processes i.e., N2 and P3 components. Moreover, for the first time, we were able to compute the JSE at a neural level to assess

the alignment of the N2 and P3 between co-agents, demonstrating the occurrence of relevant inter-brain dynamics of participants performing in a JST. Furthermore, an EEG source reconstruction analysis for different frequency bands (theta, alpha, beta and gamma) was implemented with the standardized low-resolution tomography (sLORETA) method to define the brain regions associated with the JSE. Our results revealed the involvement of fronto-parietal networks subserving the resolution of the spatial conflict. More importantly, they showed the recruitment of the medial prefrontal cortex that is known for its role in self-related and social cognition processing. This region was found to be affected by the spatial conflict, suggesting a link between social cognition and spatial coding. Future studies may uncover how this link is characterized by the analysis of intra- and inter-brain connectivity to shed light on the specific neural mechanisms subserving co-representations and joint action.

# Chapter 1

# Joint action and the Joint Simon Task

## 1.1 The Social Brain

As humans, we are constantly surrounded by other humans. The world we live in, from birth until the end of our lives, is social in nature. A newborn cannot survive without someone taking care of her/him, societies and technological advances could not exist without cooperation, and it can be very hard to lift a table without someone helping. Because human brains and minds are deeply shaped both by the presence and the mental representation of others, scientists have been investigating social interactions for decades. Social cognition refers to the complex system of unique processes involved in perceiving and interpreting social information regarding internal body states, intentions, motivations, thoughts and perspectives of others and the interacting self (Amodio & Frith, 2006). With the development of social cognitive neuroscience, scientists started building hypotheses of how the brain processes social information, in terms of which brain regions are responsible for different aspects of social cognition, and how these regions are organized and communicate with each other to support social interactions.

Researchers are trying not only to explain the actual brain structure but also its evolution. The social brain hypothesis (Dunbar, 1998; Dunbar & Shultz, 2007; Frith, 2007), for example, describes the need to deal with an extremely complex social structure, such as that we live in, as one of the main factors influencing the size and the structure of the evolved human brain. Specifically, this theory states that our unusually large and energetically costly brains (compared to non-primate mammals, Dunbar & Shultz, 2007) contain specific areas such as the amygdala, the medial prefrontal cortex, parts of the temporal poles and others, that seem to be specialized for the processing of social information (Adolphs, 2009; Amodio & Frith, 2006; Frith, 2007).

The special properties of our social brain allow us to build a perceptual world impregnated of social cues and shared perspectives that facilitate cooperation and coordination between people; they make it possible for us to interpret thoughts, emotions, intentions of other people, to understand and predict others' actions in order to behave appropriately during interactions.

## 1.2 Joint action and joint attention

One of the main challenges that social interaction poses is the need to coordinate one's actions with those of others. Speaking, dancing, moving a heavy piece of furniture, among the countless actions that can be performed with other individuals, share the need to predict and interpret others' behavior and to appropriately adapt to it. Sebanz and coll. (2006) introduced the term joint action to refer to *"any form of social interaction whereby two or more individuals coordinate their actions in space and time to bring about a change in the environment"* (Sebanz, Bekkering, & Knoblich, 2006, p. 70).

There are several crucial elements for a joint action to be performed. First of all, individuals engaging in joint actions must share a perceptual reality that they can exploit as a reference point, the so-called "perceptual common ground" (Dimitrios Kourtis et al., 2014; Sebanz, Bekkering, et al., 2006). Of course a necessary precondition to create such common ground is attending to the same object or situation at the same time, that is, being engaged in joint attention (Milward & Carpenter, 2018). The literature provides a wide list of definitions of joint attention ranging from those referring to the most basic situation of simply attending to the same object (Butterworth,1995), to the more complex views that also address the case where individuals are aware not only of the attended object but also of the fact that the other person(s) is focusing his/her attention on the same object (Tomasello, 1995). A recent review on the topic by Siposonova & Carpenter (2019) cleverly tried to clarify the concept of joint attention defining it as a complex construct composed by different levels of shared attention. At the bottom of the scale, they define *monitoring attention* as attending the same object that another individual is attending from a third-person perspective. One step higher on the scale, with the same third-person perspective, is *common attention*, which includes both attending to the same object but also acknowledging the other person's focus of attention. The remaining two levels of joint attention are defined by a second-person perspective, where *mutual attention* does not include intentional communication between two or more subjects, while *shared attention* does (Siposova & Carpenter, 2019).

Based on this operationalization of the concept of joint attention, it seems that the minimum level required to perform a joint action would be mutual attention, where individuals depend on each other's attention to create a second-person representation of the other that poses the premises to create the above-mentioned "common ground".

## 1.3 Links between action and perception

Given the sufficient level of joint attention, another issue is how people create functional action plans for successful interactions. At the roots of the relationship between joint attention and joint action is the link between perception and action. On this matter, the common coding hypothesis (Prinz, 1997) maintains the existence of an intimate link between these two functions, postulating that both action and perception rely on the same mental representations of others' actions and that these actions are coded in terms of their goals and perceptual effects (Hommel et al., 2001; Prinz, 1997).

A large body of evidence supports the idea that action and perception have a common representational domain. On a behavioral level, studies on motor and perceptual resonance have demonstrated that action observation can affect action execution either facilitating it (Brass et al., 2000) or interfering with it (Kilner et al., 2003; Stanley et al., 2007) as well as action execution can impair (Zwickel et al., 2007) or guide action perception (Repp & Knoblich, 2007). It has been argued that these bidirectional effects between action and perception would not be possible if a "translation" was necessary from sensory codes to motor codes (Prinz, 1997).

How and which aspects of actions are represented by these codes in the brain in order to move or understand goals and intentions has been the focus of several studies conducted in the last decade supporting a motor theory of social cognition (see Jacob & Jeannerod 2005 for a critique to this approach). One of the main evidence brought to substantiate this theory is the discovery of mirror neurons (Rizzolatti & Craighero, 2004; Rizzolatti & Sinigaglia, 2010). Mirror neurons in the ventral premotor and parietal cortices of macaque monkeys were shown to be active not only during action execution but also during action observation. Moreover, recording the activity of single neurons in the premotor cortex, Fogassi and coll. (2005) found that these neurons were specifically sensitive to the goal of actions: when observing an action (e.g., grasping an object), different neurons fired for different goals (e.g., eat or place). The existence of a mirror-neuron system was demonstrated also in humans, whose bilateral inferior frontal and inferior parietal sites in the brain are similarly active during both action execution and action observation (Buccino et al., 2004; Newman-Norlund et al., 2007; Rizzolatti & Craighero, 2004), this leading to the assumption that actions are not coded in the brain only in terms of the movements needed to perform them, but also as a "motor possibility" for the observing subject (Rizzolatti & Sinigaglia, 2010).

From this point of view, immediate understanding of others' actions in humans would seem to be possible because of individuals mapping observed action in terms of goals and perceptual effects on *their own* motor system.

### 1.4 Shared representations

What happens when we are not only observing an action performed by someone else, but we also have to adjust our own motor planning to that action because we are inter-acting with him/her?

Observing others' actions and mapping them on our motor system might be sufficient for action understanding, but it does not explain many aspects of joint action, for example online coordination, or the fact that we can successfully interact with other people without constantly looking at them (Sebanz & Knoblich, 2009). To efficiently interact with others, we cannot rely only on action *recognition*.

Since people are really fluid in their interaction, it seems like somehow people know what others are doing before they start to move. In fact, researchers started investigating action *prediction.* People seem to be very good at predicting others' behavior (Manera et al., 2013; Verfaillie & Daems, 2002) and also others' behavior outcomes by observation (Aglioti et al., 2008). This predictive ability was also attributed to mirror activity (Blakemore & Frith, 2005; Kilner et al., 2007), nonetheless, the flexibility that action representations need to sustain both action observation and execution cannot be explained by motor contagion alone, raising the question of how the brain differentiates between internally generated and externally triggered motor representations, i.e. the "correspondence" problem (Brass & Heyes, 2005; Schütz-Bosbach et al., 2006). Indeed, prefrontal brain areas associated with self-other differentiation were found to be active during tasks requiring inhibition of imitative response tendencies during action observation (Brass & Heyes, 2005), suggesting a functional link between the brain system supporting mindreading and mental states attribution (e.g. the temporal parietal junction, the medial prefrontal cortex and the precuneus) and the mirror system (e.g. the anterior intraparietal sulcus and the premotor cortex; Van Overwalle & Baetens, 2009). These findings shed light on how the mirror system might maintain both imitative and nonimitative behaviors, through the interaction of mechanisms such as motor contagion, action prediction and self-other discrimination. Unfortunately, the current level of knowledge about these mechanisms still leaves partially unexplained how motor plans are so efficiently adjusted to other during live joint actions.

To address the issue of how people menage to create efficient action plans that take into consideration the ever-changing behavior of others, researchers has resorted to the concept of *shared representations*, also called *co-representations* (Sebanz & Prinz, 2005). Such a concept originates from social and developmental psychology, initially referring to the use of mental representations that allow for social interaction, incorporating both the common coding between action and perception and the differentiation between self and others (Decety & Sommerville, 2003).

With the growing of the scientific interest in joint action, co-representations came to be considered necessary tools for basic coordination (Pezzulo, 2011), representing the key mechanism with which individuals share with others the motor representations of goal-directed actions during interactions. Shared representations allow for the planning, execution and prediction of joint actions through the alignment of cognitive representations between individuals, smoothing social interactions (Sebanz & Prinz, 2005).

In the last few decades social neuroscientists have been trying to explain very complex aspects of social interactions, including mental states attribution, empathy, common decision-making, verbal communication, etc. Some of them though recognized the need to focus their scientific exploration on more basic forms of joint action to pinpoint the building blocks of social interaction. Indeed, because even the most minimal cases of joint action are already quite complex (e.g., passing a glass to somebody), usually involving complementary movements with actors having different perspectives of the same situation, shared representations are not considered as identical representations equally driving the two (or more) agents involved in the interaction. Instead, each individual needs to create her own cognitive representation, consciously or unconsciously (also, automatically) aligning it with that of the other agent, incorporating only those specific aspects of actions that need to be shared to act together.

For the purposes of this dissertation, the terms *shared representation* and *co-representation* will be interchangeably used to refer to the outlined mechanisms of representing actions and intentions, although in the literature they have been used to indicate also more complex forms of social interactions requiring a co-representation of beliefs and feelings (Sebanz et al., 2003). To note, the term *mutual representations* have been proposed to indicate such a more complex version of shared representations employing meta-representations, where people create an internal model of the shared part of the interaction also as being shared (Pezzulo, 2011).

In sum, the concept of shared representation has been demonstrated to be a valuable heuristic to investigate joint action, incorporating fundamental processes such as 1) the creation of a common perceptual ground though joint attention, 2) the intimate link between action and perception, 3) the ability to predict others' actions and intentions independently from action observation, 4) the integration of spatial and temporal features of others' actions with one's own and 5) the necessary differentiation between self and other.

### 1.5 The Joint Simon Task as a tool for investigating joint action

To empirically address the question of how shared representations of joint actions work, Sebanz et al. (2003) developed a paradigm that, since its first application, has been extensively used in studies investigating how the representations of one's own actions interact with the representations of others' actions. This paradigm, known as the Joint Simon Task (JST), is the social version of the individual Simon task (Simon, 1969) which is a classic conflict task in which a single individual is required to respond to a stimulus characterized by a response-relevant dimension, i.e., color (if visual) or pitch (if auditory), and a response-irrelevant one, i.e., stimulus location. In the visual version of the task, for example, the subject might be required to press the left button when the stimulus is red and the right button when the stimulus is green, ignoring its location (left or right). This setting has been repeatedly proven to lead to a spatial correspondence effect (Rubichi et al., 1997; Iani et al., 2021; see Cespón et al., 2020 for an extensive review) where individuals show faster reaction times (RTs) and higher accuracy on trials presenting a match between stimulus and response locations as compared to trials where stimulus and response are on opposite sides. The mechanism underling this correspondence effect was identified as a response conflict due to the automatic activation of the representation of the response corresponding to the side of the stimulus that would compete with the representation of the response dictated by the task rules (Cohen & Donner, 2013; Kornblum et al., 1990). The main account for the spatial correspondence effect observed in the classic version of the Simon task is the dual-route model (Kornblum et al., 1990; Proctor & Vu, 2006), which states that a visuomotor pathway is automatically activated by stimulus presentation, priming the action representation of the response corresponding to the side of stimulus, while at the same time a second, task-related route is triggered depending on the task instructions that allow for the correct response to be performed. In the non-corresponding trials, where the stimulus and the correct response are on opposite sides, a conflict emerges between action representations that needs to be resolved by a top-down cognitive control process that requires time, thus slowing reaction times. On the other hand, on corresponding trials, because the primed response representation is the same as the task-related response, a facilitation effect leads to faster reaction times (Rubichi et al., 1997; Umiltà et al., 1999).

Interestingly, the correspondence effect observed in the individual version of the task also arises when two individuals, sitting one next to the other, are each responsible for only one button press in response to a specific feature of the stimulus (e.g., the left participant responds to the red stimulus, while the right participants respond to green, independently from stimulus location), leading to the so-called Joint Simon Effect (JSE) (Iani et al. 2021; Milanese et al. 2010, 2011; see Dolk et al., 2014 for a review and Karlinsky et al., 2013 for a meta-analysis). The single response required by the JST is similar to the situation created in the *go*/*nogo* version of the task where a single subject is required to respond to only one type of stimulus. In this latter case, because only one response is available and thus represented by the agent, no conflict can emerge, and no correspondence effect is usually recorded (Lugli et al. 2013; Sebanz et al. 2003). Nevertheless, sharing this same task with another person as in the JST, changes subjects' performance, leading to longer reaction times for S-

R non-corresponding trials. The JSE was taken as evidence for the existence of shared representations (Sebanz et al., 2003).

The JSE is typically smaller than the classic Simon effect (Dittrich et al., 2013; Karlinsky et al., 2013), suggesting that different processes might mediate the performance in the two task settings. To support this possibility, Ferraro and coll. (2011) investigated the contribution of facilitation and interference processes in the JST introducing a neutral condition where the stimulus appeared in a central location. The comparison of reaction times for the corresponding trials and the non-corresponding trials to the neutral trials revealed that the JSE mainly arises because of an interference process, since no difference between neutral and corresponding conditions were observed. The possibility that different strategies are employed to perform in the classic and the social version of the task raises the question of which aspects of the task are represented by the agents and, crucially, which features of these representations are shared.

For instance, Lam and Chua (2010) demonstrated that when participants perform the JST with the same stimulus-response assignment, that is, they respond to the same stimulus, no JSE is evident, suggesting that the mere presence of a co-agent is not enough for the JSE to emerge, pointing to the conclusion that the presence of two action alternatives is a necessary condition for triggering action co-representation. Moreover, in a study by Welsh (2009) participants were asked to perform the classic two-choice Simon task and the JST with crossed or uncrossed hands, finding a correspondence effect in all conditions, regardless of the position of the limbs performing the response action. These results were taken as evidence for the assumption that co-agents do not show a JSE simply because of an intra-hemispheric processing advantage due to the lateralized cerebral organization of perceptual and motor systems, nor because the co-agent or the alternative action are used as a mere spatial reference. Instead, authors interpreted their results as confirming the formation of a co-representation of actions bound to the spatial location of response keys (but see Liepelt et al., 2013, for different results and interpretation; Dolk et al., 2014; Welsh, 2009).

## 1.6 Mechanisms underlying the Joint Simon Effect

### 1.6.1 Social accounts

The first report of a JSE was explained by Sebanz and coll. (2003) by hypothesizing that individual represent their own action and the action of a co-agent in a functionally equivalent way. The similarity between these representations would be the cause of the spatial interference effect, that is, because the co-agent's action is somehow included in one's own motor plan (i.e., by the means of a co-representation of the task), responses are coded as left and right similarly to what happens during the classic version of the task, leading to the JSE. The premises for this proposal were the link between action and perception (Hommel et al., 2001; Prinz, 1997), and the role of the mirror system in particular. Because the understanding of actions seems to be achieved by their mapping on one's own motor system (Rizzolatti & Craighero, 2004), it seems plausible that an observed complementary action such as that performed by the co-agent during the JST would be very similar in its neural representation to one's own action. This level of explanation stresses the social nature of the effect. Nonetheless, this first claim did not specify how detailed the representation of the co-agent's action would be and how it would interact with one's own in the formation of a shared representation. Is the participant representing the specific task rules assigned to the co-agent, as well as the specific movements needed to give a response, or a more high-order representation is sufficient to trigger the spatial conflict?

In order to understand which aspects of the joint action performance is co-represented, Sebanz & Prinz (2005) tried to differentiate between *task* co-representation and *action* co-representation. While the first refers to the case where participants represent the specific rule that dictates under which conditions the other agent is required to respond to a stimulus, the latter indicates the mere representation of the action that the co-actor needs to perform without the specifications of what feature triggers the response. The authors hypothesized that these two kinds of representation might be active both separately and at the same time, as they conducted a series of experiments to investigate the specific contribution of *task* and *action* co-representation effects during a joint performance. In a first joint condition, the two participants were given two different tasks, a compatible direction task (i.e., the participant needed to respond when the stimulus was pointing towards her) or a color task (i.e., the participant needed to respond to a specific stimulus color). The second joint condition was the same as the first except for the direction task that was an incompatible direction task (i.e., the participant needed to respond when the stimulus was pointing to the other actor). As a third condition, participant performed the JST. This setting allowed for the separation of task-related conflicts from action-related conflicts. More specifically, taking the point of view of the color-task-participant, when a double-response were required, depending on the direction task, a task-related conflict might manifest itself in association with the action-related conflict or in isolation. In the first case, the participant performing the color task along with someone performing the compatible direction task needs to respond even though the stimulus is pointing towards the other agent, overcoming both the self-relevant S-R mismatch *and* the awareness of the other agent performing a complementary action. In the case of the incompatible direction task, when the target stimulus is pointing towards the participant performing the color task, the action-related conflict is no longer present. Reaction times analyses revealed that all double response trials significantly slowed participants' response compared to the single-trial response, indicating that when the same stimulus required two different actions, participants experienced an influence from the other's action. Nonetheless, participants experiencing both a task and an action conflict were significantly slower than those experiencing only a task conflict, demonstrating that both mechanisms can be active at the same time during a joint performance (Sebanz & Prinz, 2005).

The JSE has been considered as a behavioral marker of how the presence of others inevitably affect our performance increasing response conflict even in situations where coordination is not required. Nevertheless, the effect *per se* doesn't tell us whether this kind of joint action needs "special" socially-dedicated processes or if universal information processing applied to a social situation is sufficient (Dolk et al., 2014) and the controversy is still open.

A few accounts for the JSE points to the special social processes as responsible for the integration of others' behavior. As already mentioned, Sebanz and colleagues (2005, 2006) proposed an *action co-representation account* that hypothesizes that participants co-represent both their own action and also that of their partner in a very detailed way (i.e. with respect to which imperative stimulus has been assigned to the other individual) with the consequential time-consuming conflict during action selection for non-corresponding trials due to the partial overlap of self- and other-action representations (Knoblich & Sebanz, 2006; Sebanz & Prinz, 2005; Tsai et al., 2006; Vesper et al., 2010).

A strong claim following this principle is that if our cognitive system is extremely prone to adapt to the presence of others, even an imaginary co-actor could be a strong enough cue to trigger the social mechanisms that are supposed to elicit the JSE. Tsai and colleagues (2008) tested this hypothesis asking participants to perform a JST either believing to be paired to a non-visible human partner seated in another room, or to a computer that was responsible for the alterative response. They found a JSE only for the "human-belief" condition group, supporting the idea that the processes involved in co-representations alignment are "tuned" to humans. A similar conclusion was drawn by the experiment of Ruys & Aarts (2010) where participants showed a JSE performing the auditory version of the JST with a co-actor sitting in another room. Nevertheless, Sellaro and colleagues (2013) pointed out some limitations in the procedures of these two studies that could have prompted participants to spatially code their response independently of the believed social situation, supporting the findings of a previous study by Welsh et al. (2007) that did not record any interference effect in participants believing to perform the JST with a co-agent situated in another room. By conducting a series of experiments similar to those of Tsai et al. (2008) and Ruys & Aarts (2010) with non-visible partners, but controlling for the confounding factors that may have biased the interpretation of their results, Sellaro et al. (2013) disproved the predictions made by the action co-representation account. Indeed, if the Simon effect is taken as an index of two spatially coded alternative actions, the presence of another person or the mere belief to perform a task with a co-actor were found not to be sufficient nor necessary for the emergence of the spatial coding of responses (Sellaro et al., 2013).

A different but still *social* account of the JSE has been proposed as the *actor* co-representation account proposed by Wenke et al. (2011) in which processes related with the need to determine whose turn to act it is are intertwined with agent identification mechanisms. From this point of view, the conflict underlying the interference effect would emerge because participants mentally represent the presence of another agent responsible for an alternative action, independently from the specific action (and thus the assigned S-R mapping). The social component of the effect would reside in the turn-taking dynamic of the task, where the spatial (non) correspondence conflict would be elicited by a social (non) corresponding conflict (or better, an agent-identification conflict) because spatial information are used to perform the self-other discrimination needed to understand whose turn it is (Ferraro et al., 2011; Philipp & Prinz, 2010; Wenke et al., 2011).

Nevertheless, the actor co-representation account is also incompatible with the results of Welsh and colleagues (2007) who did not find the belief of co-acting to trigger any JSE, or the results by Sellaro and colleagues (2013) where individuals were induced to spatially code responses (presumably) only by the need to use a lateralized button (the right button of the mouse), even when no co-agent was present nor mentioned.

In sum, even if agent-identification is a validate candidate as a factor contributing to joint interference effects, it might be only a part of the explanation.

### 1.6.2 Spatial accounts

Another body of research tried to clarify these incongruities moving a substantial critique to the social accounts, questioning the social nature of the JSE itself and proposing a purely *spatial* interpretation of the phenomenon. For example, Guagnano et al. (2010) introduced the idea of a double source of “sociality” in a JST, addressing both the explicit interactive nature of the task that arises from a turn-taking dynamic, and the mere presence of another individual next to the participant creating a social context. They managed to isolate these two components in a series of experiments (Guagnano et al., 2010) were they manipulated the nature of the task (independent vs. interactive) and the space shared by the co-agents (peripersonal vs extrapersonal). For the independent task, participants performed a JST with the only difference that stimuli appeared at the same time, so that they had to act simultaneously. In this condition, participants showed a JSE. Since the two different tasks assigned to the agents were independent and that the only aspect of the task that was shared between them was the peripersonal space in which they were acting, the authors concluded that no specific action-co-representation is needed for the task to be spatially coded. Instead, they proposed an alternative hypothesis to co-representations, stating that in a JST agents are using the co-actor as a mere reference that leads to a spatially lateralized representation of the response. This interpretation was further supported by the comparison of two similar experiments where co-agents were asked to perform the same independent tasks either sitting one next to each other (peripersonal space) or distant from each other (extrapersonal space). A JSE was only observed in the latter condition, suggesting that the space that is shared between the co-agents is a relevant factor for the spatial coding of actions subserving the S-R correspondence effect (Guagnano et al., 2010; but see Welsh et al., 2013 for a failure in replicating these results).

More recently, a study by Iani et al. (2021) managed to clarify the contrasting results of Guagnano et al. (2010) and Welsh et al. (2013). The authors introduced a new variable affecting the emergence of the JSE, that is, the reachability of response buttons by the participants. In their experiment, they modulated the extention of the extra- and peri-personal space of co-agents by the use of tools, demonstrating that for S-R interference effects to occur the task must not only dictate a turn-taking dynamic, but participants also need to be able to potentially reach the response button of the co-agent. This reachability is what authors interpreted as triggering the representation of the alternative response as a potential action that leads to the spatial interference (Iani et al., 2021). In light of these observations, what impeded the emergence of a JST on the exeriment of Guagnano et al. (2010) might as well have been the possibility for the agents to reach their co-actor's button.

Moreover, not only the shared physical space but also spatial *saliency* appears to be a crucial element determining a spatial coding of responses. It was suggested that when participants are seated next to each other, the presence of the other individual acts as a (social) cue prompting the need for spatial response coding, without the need of the formation of actual action co-representations (Dittrich et al., 2012). If this is the case, other (non-social) factors might also be able to highlight spatial saliency thus leading to interference effects. This possibility was in fact demonstrated by studies that stressed the horizontal spatial arrangement of the alternative responses (see also Sellaro et al., 2013), for example by the use of a joystick that had to be turned left or right during an individual *go*/*nogo* task, which elicited a S-R interference effect even in the absence of a co-actor (Dittrich et al., 2012). In this line of reasoning, both the spatial relation between co-agents (e.g., vertical vs. horizontal) and the spatial alignment of response keys (e.g., vertical vs. horizontal) were shown to affect the joint performance, modulating the JSE.

In summary, independently from the social or spatial source of interference, many factors have already been demonstrated to have a role in the emergence of the JSE: the turn-taking dynamic, the shared physical space, the reachability of the response, and the saliency of the other actor and/or the other response.

### 1.6.3 The referential coding account

A more compelling and comprehensive account for the JSE is represented by the referential coding account (Dolk et al., 2013). Compared to the mentioned theories trying to unfold the mechanism underlying the JSE (e.g., action co-representation, task co-representation, agent co-representation, spatial coding), the referential coding account has the conceptual advantage of ascribing joint-interference processes in the greater context of action-perception mechanisms as interpreted by the ideomotor theory (that assumes a common coding between action and perception; Prinz, 1997) which lays the foundations for the Theory of Event Coding (TEC; Hommel et al., 2001). In this theoretical framework, individuals are thought to code actions in terms of their sensory consequences. Mental representations of actions containing information about the many features of perceivable effects (e.g., spatial location, direction of movement, sounds, effectors, etc.) are assumed to be activated when performing a context-appropriate action and crucially, these mental representations are also thought to be functionally equivalent for own and others' actions. In other words, considering "shared representation" of actions too broadly defined as well as too cognitively demanding, the referential coding advocates for the alternative concept of "event co-representations", addressing more specific and defined features of a joint task.

Applying the TEC logic to the interpretation of the JSE, when participants share a task, they perceive task-related events (e.g., lateralized colored stimuli) that are coded as alternative action events irrespective of the acting agent, in the sense that what matters for the response conflict to arise is the concurrent activation of two action representations independently from the source of activation (Dolk et al., 2014). But why are co-agents activating two action representations in the first place? Referential coding assumes that since the task-relevant dimension (e.g., color) defines typically two kinds of stimuli, each participant is representing both stimuli in terms of their assigned action (mine vs. other's). Hence, what is triggering the spatial coding would be the need to differentiate these two similarly represented action events in the most obvious and efficient way, that is, coding responses as "left" or "right". In the end, the main claim of referential coding is that the JSE is the consequence of a discrimination problem, where the need to differentiate between self- and other-related events relies on a (purely circumstantial) spatial dimension that becomes *salient*, ultimately leading to a spatial conflict ( Dolk et al., 2011, 2013, 2014, 2016).

Several experiments were conducted to support this view, challenging the idea of the social nature of the JSE (Iani, et al., 2011, 2013; Sebanz et al. 2003; Tsai et al., 2008) as the spatial accounts did (e.g., Dittrich et al., 2012; see Dolk et al., 2014 for a review). For instance, non-social events such as the tick of a metronome or the repetitive movements of a Japanese waving cat as well as the presence of an active stroking device were shown to be enough salient events to attract attention during individual *go/nogo* tasks, eliciting an interference effect in the absence of a human co-agent (Dolk et al., 2011, 2013).

Indeed, many contrasting results might be parsimoniously explained by the referential coding view. For example, while some studies found that the belief of acting with a non-visible co-agent is a strong-enough factor to elicit a JSE (e.g., Ruys & Aarts, 2010; Tsai et al., 2008), other studies did not (Sellaro et al., 2013). The referential coding account might resolve this incongruency: depending on the *saliency* of the spatial dimension, participants might or might not have coded responses spatially. That is, different characteristics of the tasks in the experiments by Ruys & Aarts (2010) and Tsai and coll. (2008) might have highlighted the horizontal arrangement of stimuli (and responses) making it a salient dimension to be used for response-coding. For example the turn-taking dynamic emphasized by the task instructions given by Ruys & Aarts (i.e., cooperate vs compete with the co-agent; 2010) and the feedback they provided for the co-actor response (a red light), as well as the mouse-keys arrangement in the study of Tsai and coll. (2008), as suggested by Sellaro and coll. (2010).

The factors listed among those affecting and/or subserving the involuntary spatial correspondence effect in a joint action setting, might though be linked to the changes in the *saliency* of the spatial arrangement of alternative response that help the self-other discrimination problem that is the ultimate source of the interference effect, even when the "other" is not human.

### 1.7 Social or not social?

The greatest challenge that the referential coding account as well as the purely spatial accounts face, is the inclusion in their rationale of the role of social factors mediating the JSE. As a matter of fact, different experiments demonstrated that the manipulation of social variables in the JST are capable to reduce/eliminate or increase the JSE.

Independently from its nature, the JSE is the result of individuals automatically acknowledging the presence of another individual and/or action and it is commonly considered (also by different accounts) a valid measure of self-other integration (Colzato et al., 2013; Liepelt & Raab, 2021). The higher self-other integration, the more individuals might struggle to discriminate their actions from others'. On this premises, individuals showing different levels of self-other integration might also behave differently during joint actions. This prediction  was tested taking into consideration both situationally-manipulated (Colzato et al. 2012a) and trait-related levels of self-other integration (Colzato et al., 2012b). It was demonstrated that people that were primed to think in a "we" logic (versus an "I" logic), as well as people culturally inclined to suppress an independent sense of self (i.e., Buddhists vs atheists), found it harder to discriminate between self- and other-actions during a JST and thus they needed to consistently rely on spatial coding of responses to make this discrimination, as revealed by their higher JSE.

Common sense tells us that people behave differently with other people depending on their mood and also on the behavior of their interacting partner (e.g., friendly/ unpleasant, inclusive/ostracizing). Indeed, in different studies, these variables were found to affect co-representations: induced negative mood (Kuhbandner et al., 2010), an intimidating co-actor (Hommel et al., 2009) and feelings of social exclusion (Costantini & Ferri, 2013) led to the disruption of the formation of co-representations as shown by the absence of a JSE during a JST.

Interestingly, Vlainic et al. (2010)  blindfolded participants during an auditory JST demonstrating that co-actors do not rely on online feedback from the co-actor's action but rather on an *a priori* setting to spatially code their responses (Vlainic et al., 2010). In line with the assumption of a relevance of this *a priori* setting, several studies investigated the consequence of manipulating the relationship between participants by establishing a positive or negative interdependency between co-actors. A negative interdependency is usually defined by a competition setting where participants perform a JST one against the other, knowing that their performance will be compared to their co-actor's to be assigned some sort of a prize in a mutually exclusive dynamic  (but see Ruys & Aarts, 2010 for a broader yet more ambiguous definition), while a positive interdependency is typically defined by co-actors being team-mates pursuing a common goal (Iani et al., 2011, 2014; Liepelt & Raab, 2021; McClung et al., 2013; Mendl et al., 2018; Ruissen & de Bruijn., 2015; Ruys & Aarts, 2010). It appears that competitive settings affect the spontaneous tendency to incorporate the co-actor/ion in one's own by significantly reducing self-other integration as confirmed by a reduced JST. Cooperation, on its side, seems to be the default mode by which participant spontaneously characterize the setting (that *per se* would be neutral), so that highlighting the positive interdependency with specific instructions cannot further modify the setting that is already perceived as shared. The specification of a cooperative setting, though, is powerful enough to re-introduce a blurrier self-other separation when a previous competitive setting was keeping co-actors apart in their action representations leading to a significant JSE after a JST where co-representations were efficiently disrupted (Iani et al., 2014).

While the broader conception of action/task co-representation supported by Sebanz et al. (2003, 2006, 2009) can easily explain these findings by considering co-representations as flexible cognitive entities that are modulated by social factors and self-perception, the referential coding account needs to further specify how and why social factors can so evidently change the degree of spatial coding on which people rely. In particular, the concept of "similarity" (either conceptual and perceptual) is addressed by this view as a variable affecting the degree of difficulty in discriminating between self and other. That is, the more an individual perceive a co-actor as similar to the self, the more the distinction will need to rely on spatial coding (Dolk et al., 2013, 2016; Müller, Brass, et al., 2011; Müller, Kühn, et al., 2011; Stenzel et al., 2012).

In sum, the influence of self-perception, mood, the valence of the relationship, the social status, and the quality of the interdependence between subjects can affect the spatial coding of responses in the JST. This evidence tells us how far our social skills are grounded in low-level representations (Kuhbandner et al., 2010). Nevertheless, whether co-representations concern actions, agents, events, or all of the above, the fact that their formation can be disrupted or impeded by manipulating different aspects of a social situation implies that relying on independent representations (as opposed to co-representations) during joint tasks is possible and that the formation of co-representations during joint action might be automatic in most situations, but not mandatory.

Unfortunately, the evidence collected until now does not tell us whether the JSE is social or spatial in nature, but it suggests that looking for a *purely* social or *purely* spatial explanation might be pointless, since both social and non-social mechanisms subserving the JSE, as joint attention or cognitive control, are continuously interacting during social interactions. Nevertheless, clarifying the specific contribution of the social and spatial components of this experimental paradigm is crucial in order to understand the foundations of social interactions. When and how does spatial coding become social? If the social setting calls for the automatic activation of co-representations (Sebanz et al., 2003), how do individuals manage to act independently from their partner? Do they need to actively inhibit co-representations or the variables that were showed to disrupt the emergence of the JSE prevent their formation? Further studies are necessary to determine how co-representations are formed and exploited to perform joint actions.

### 1.8 Sequential Effects

Another relevant feature of conflict paradigms such as the Simon task, as well the Stroop task and the Flanker task, is trial sequence, that is, the order in which corresponding (C) and non-corresponding trials (NC) are presented. In the individual Simon task, the SE is usually found to be smaller, if not reversed, after non corresponding trials, and greater after corresponding trials. This modulation is called the *sequential effect* or *Gratton effect* (Cespón et al., 2020; Gratton et al., 1992;

Iani et al., 2009). Two main explanations were proposed to explain this effect. The conflict adaptation hypothesis theorizes that experiencing a conflict in a previous trial (N-1) primes top-down control processes that become more efficient during the current trial (N), reducing interference effects (Botvinick et al., 2004). The feature integration theory, on the other hand, accounts for sequential effects hypothesizing that at each trial the task-relevant feature (e.g., color) gets bound to the lateralized motor response in a "event file" that is stored in the working memory and retrieved in subsequent trials. Depending on which stimulus features (e.g., color and/or position) are repeated in a given trial sequence, responses might be facilitated or impeded. Specifically, whenever a complete S-R feature repetition occur from one trial to the other (either c-C or nc-NC sequences[1]), responses are faster because the event file created in the N-1 trial primes the response for the N trial. During partial or null repetitions (c-NC or nc-C), instead, an un-binding process of S-R features must be activated with a cost for behavioral responses (Hommel et al., 2004). A large body of evidence indicate the feature integration theory as the more parsimonious and compelling account, but given the difficulty in designing experiments dissociating features integration and repetition effects, mechanisms related to conflict monitoring processing are not to be excluded (Cespón et al., 2020; Chen & Melara, 2009; Spapé & Hommel, 2014).

Similar low-level trial-to-trial modulations have been observed also in the JST (Liepelt et al., 2011). Addressing the sequential effect in the JST, the main difference with the classic version of the task that must be taken into consideration is the occurrence of *nogo* trials, that adds to the list of possible sequences of trials. The previous trial can be characterized as corresponding or non-corresponding but also as go or *nogo*[2]. Modulation after go trials have been found to mimic the sequential effect of the individual Simon task, with a greater JSE after go-corresponding trials and a

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[1] Correspondence on trial N-1 is always presented with a lowercase while N trials are always indicated with an uppercase.

[2] For the sake of simplicity, throughout this dissertation, correspondence will always refer to the responding subject. For example, in a *nogo* corresponding trial – nogoC- the stimulus is appearing on the opposite side of the person that is withholding the response.

smaller JSE after go-non corresponding trials (Liepelt et al., 2011, 2013; Spapé & Hommel, 2014; Yamaguchi et al., 2018). Interestingly, the same sequential effect is also found in the individual *go/nogo* task, where the magnitude of the SE following go corresponding trials matches the reversed effect after go non-corresponding trials, leading to a null global SE.

Moreover, responses following a *nogo* trial were found to be slower irrespective of correspondence and of the presence of a co-actor, suggesting a strong inhibitory response tag process (Liepelt et al., 2011; Neill et al., 1992) that primes either the position of the response and/or the stimulus with inhibition so that subsequent responses performed on the same side are slowed. These observations point to the conclusion that the individual and the joint *go/nogo* tasks share at least some low-level mechanisms, except for the fact that the presence of a co-actor seems to lead a greater JSE after *go* corresponding trials compared to the individual *go/nogo* task that outgrows the reverse effect after *go* non-corresponding trials. Sequential modulation in the JST were also explained by S-R feature integration mechanisms with the specification that in a joint setting these mechanisms are inevitably interacting with processes of self-other discrimination, so that the S-R binding appears harder to disrupt when stimulus features are not only processed in a “me/not me” logic but also in a “my/other turn” logic (Liepelt et al., 2013).

In line with these observations, sequential modulations were also exploited to infer the extent by which an agent represents the specific S-R mapping assigned to the co-actor. In a study by Yamaguchi et al. (2018), pairs of participants were asked to perform a JST where one of the co-actors was experiencing a unbalance proportion of corresponding and non-corresponding trials, a task characteristic that is known to affect the spatial correspondence effect, where an exceeding number of non-corresponding trials lead to a diminished Simone effect while a greater number of corresponding trials results in a greater Simon effect. The authors reasoned that if participants are representing the specifics of each actor’s task, the agent performing the JST with a balanced number of corresponding and non-corresponding trials (diagnostic actor) should be affected by her co-actor’s task settings (inducer actor). This was not the case, since the diagnostic actor did not show any influence of the inducer actor's trial proportions during *go*-*go* trials. Trials proportion modulations appeared to influence the diagnostic actor only during *nogo*-*go* sequences, pointing again to the conclusion that the characteristics of the co-actor's part of the task are not shared in detail, and that the influence of the co-actor's actions is only evident in trials following a co-actor response (Yamaguchi et al., 2018).

Researchers have been trying to exploit sequential effects evident during JST performance to understand its social aspects, conceptualizing a vicarious conflict adaptation effect (CAE), that would be a consequence of the observing agent experiencing the co-actor's conflict as her own conflict. In other words, the question is whether observing the co-actor responding to a non-corresponding trial can facilitate the resolution of the conflict in the subsequent trial (*nogo*C > *go*NC sequence) (Spapé & Ravaja, 2016). Spapè and Ravaja investigated the role of a virtual vs real co-actor in modulating the vicarious CAE separately for trials following *go* and *nogo* trials, computed as follows:

$$CAE = (cNC - cC) - (ncNC - ncC)$$

The resulting values were tested against 0 in order to quantify not only if the conflict adaptation effect changed (as showed by standard statistical analyses on reaction times) but also to test its magnitude. This way of looking at the sequential modulation has the advantage of directly showing how observing someone experiencing a conflict reduces the behavioral effects of experiencing a conflict in first person, as shown by a reduced JSE after *nogo* corresponding trials. Simply put, this point of view let us clarify if acting with a co-agent leads not only to a co-representation of the task but also to a conflict co-representation. Nevertheless, no differences of vicarious CAE were found comparing co-action with a computer and a human participants, suggesting a subserving mechanism that is bound to low-level rather than high-level/social features (Spapé & Ravaja, 2016).

In sum, different task manipulations investigating sequential effects again point to the conclusion that even though a role of the presence of a co-actor in JST performances is undeniable, as particularly apparent in trials following a co-actor's action, there is no evidence for the formation of detailed co-representations of a co-actor's task.

# Chapter 2

# Neural correlates of joint action: the case of the JST

## 2.1 Neural correlates of joint action

As discussed in Chapter 1, “joint action” is a fuzzy concept, embracing many aspects of human interactions. Studies investigating brain activity associated with joint actions have been focusing on different levels and types of interaction, from simple actions such as grasping or lifting (Kourtis et al., 2013; Kourtis et al., 2014; Miss et al., 2022; Newman-Norlund et al., 2008), to complex music performance (Gugnowska et al., 2022; Novembre et al., 2016), problem solving, and social games (Astolfi et al., 2014; Ciaramidaro et al., 2018; Miss et al., 2022). Each task requires different abilities ranging from basic (involuntary) coordination between individuals (e.g., emergent coordination) that involve simple perceptual and motor mechanisms, to complex interactions that require higher cognitive functions such as the ability to make inferences about the intentions and mental states of others (mindreading, Theory of Mind – ToM) (Knoblich et al., 2011; Miss et al., 2022). Depending on the task, many subprocesses have been listed as supporting joint action: perception of others, action observation, imitation, joint attention, goal representation and monitoring, co-representation, temporal co-ordination, sense of agency, self-other discrimination, among others (Bekkering et al., 2009; Miss et al., 2022; Newman-Norlund et al., 2007b; Sebanz & Knoblich, 2021). The conceptual definition of the specific cognitive mechanisms involved during joint action is a fundamental step toward the understanding of how the brain works during social interactions.

In recent years, researchers adopted experimental tasks designed to tap one or more of these processes in the attempt to isolate and relate them to dedicated brain mechanisms through the help of direct and indirect brain activity recording (e.g., electroencephalography, EEG; functional magnetic resonance, fMRI; functional near-infrared spectroscopy, fNRIS), and /or non-invasive brain stimulation techniques (e.g., transcranial magnetic stimulation- TMS, transcranial direct-current stimulation – tDCS).

Altogether, fMRI studies investigating the localization of brain areas subserving social cognition have allowed to define a network, also called the *social brain,* mainly involving the medial prefrontal areas (mPFC), the anterior cingulate cortex (ACC), the temporo-parietal junction (TPJ), the superior temporal sulcus (STS) and the temporal poles. These areas were demonstrated to be active during different tasks requiring the control and monitoring of own and others' actions and/or outcomes, processes related to self-reflection, person perception, and making inferences about other's intentions, to mention a few (Amodio & Frith, 2006).

Moreover, there is an emerging consensus on the involvement of neurons in the human premotor and parietal cortices with mirror-like properties in processes related to action observation (Iacoboni, 2009; Mukamel et al., 2010), and specifically the understanding of goal-directed actions (Miss et al., 2022; Newman-Norlund et al., 2007b).

Evidence about the distinct brain activity associated with the presence of others compared to individual situations come also from EEG studies which demonstrate that mechanisms of action control and/or inhibition function differently if a task is performed in the presence of another person or individually, as shown by the modulation of event-related potentials (ERP) associated with these mechanisms (mainly the N2 and P3 components; Kourtis et al., 2013; Sebanz et al., 2006; Tsai et al., 2006). Although not intended to be exhaustive, this chapter reports a paradigm-driven review of the studies investigating brain activity related to social interaction with a focus on the Joint Simon Task.

## 2.2 Neural correlates of the Joint Simon Task

As a task designed to investigate joint action, in recent years researchers have tried to pinpoint the neural correlates of the JST (De La Asuncion et al., 2015; Dolk et al., 2012; Humphreys and Bedford, 2011; Liepelt et al., 2016; Michel et al., 2018; Ruissen & de Bruijn, 2015; Sebanz et al., 2007; Tsai et al., 2006, 2008; Wen and Hsieh, 2015). What must be kept in mind in interpreting the results of these studies, is the peculiar point of view that is imposed by the task itself on social interactions. That is, the JST addresses a very specific aspect of joint action, namely the *interference* that the presence of a co-acting individual is supposed exert on the execution of individual actions. As already mentioned in Chapter 1, the most efficient way to perform in a JST would be to ignore the presence of the co-actor. Nevertheless, individuals seem to be unable to do so, experiencing a stimulus-response conflict that influences their performance. This means that whatever brain activity is related to JST performance, it must be interpreted not only in terms of the mechanisms of joint action *per se* (e.g., co-representation, action planning, etc.), but also in terms of the need to differentiate the self from the co-actor.

From the numerous studies investigating co-representations and specifically trying to uncover the processes leading to the JSE, many issues remain unresolved if not controversial (e.g., social vs. not social accounts). Reaction times per se can be hard to interpret because of the slow timing of a motor response compared to the rapid processing of the brain, and conclusions about the specific mechanisms operating during joint performances can be misleading. The advantage of brain imaging and brain recording techniques is the possibility to analyze both covert (i.e., *go* trials) and overt (i.e., *nogo* trials) responses, thus gaining a more comprehensive understanding of the perceptual, motor, and cognitive processes underlying joint actions.

A variety of mechanisms are involved in joint performance and in the JST in particular. For illustrative purposes, we might think of two broad categories of processes subserving JST performances. The first category comprises Simon effect-related processes such as attentional shifts, cognitive control, and action planning, that are likely to emerge both during the standard and the joint version of the Simon task. Furthermore, we might think of a second category including those processes that are more directly linked to the social aspect of the JSE such as action/task/actor co-representation (depending on different interpretations), action inhibition, action monitoring/observation, and self-other discrimination.

## 2.3 Cognitive control, conflict monitoring and attention

The concept of cognitive control refers to the mechanisms that allow for adaptive behavior in an ever-changing environment (Cohen, 2014). It partially overlaps with the concept of executive functions, but in this context the stress goes on the subset of functions that are needed to maintain and shift attention to stimuli carrying conflicting information and the production of an appropriate motor response (i.e., decision making, conflict resolution, error detection, response inhibition, etc.).

The individual Simon task has been largely investigated in the last fifty years or more as a classic paradigm used to investigate cognitive control processes and there is a large consensus about the main processes related to this performance: attention, cognitive control, inhibition and response preparation. It must be kept in mind that in the classic version of the task, each trial is a *go* trial, indicating a response that either spatially correspond or not to the side where the imperative stimulus appears.

What challenges the cognitive control system during a Simon task is the conflict that, in non-corresponding trials, emerges between the response corresponding to the side of the stimulus that is automatically activated and the correct response that is on the opposite side relative to the stimulus.

A large body of evidence shows that the N2, that is a negative ERP component having its peak at fronto-central electrodes around 200 ms after stimulus onset, is associated with mechanisms of response inhibition and conflict monitoring (Bokura et al., 2001; Falkenstein et al., 1995; Lavric et al., 2004). The N2 is particularly evident in *nogo* trials (Bokura et al., 2001) and trials presenting conflicting information (e.g., non-corresponding trials in interference tasks as the Stroop task, Flanker task, Simon task; Falkenstein, 2006) independently from response modality. A greater amplitude (a more negative wave) of the N2 component has been found for non-corresponding trials during the Simon task (Cespón et al., 2020) and it has been interpreted as a consequence of the mental effort necessary to inhibit the automatically activated motor response, although it is thought to reflect the decision process of withholding a response rather than motor inhibition itself (Falkenstein, 2006). Two different sources in the brain have been hypothesized for this component. A first source has been localized in the right ventral and dorsolateral prefrontal cortices (VLPFC / DLPFC), mainly reflecting inhibitory mechanisms, while the second source has been localized in the anterior cingulate cortex (ACC), that is thought to be responsible for conflict monitoring (Bokura et al., 2001; Lavric et al., 2004a). To be noted is also the sensibility of this component to the proportion of trials, where non-corresponding trials appearing less frequently than corresponding trials, elicit a greater N2 in terms of amplitude (Cespón et al., 2020; Falkenstein, 2006).

In most experimental designs addressing the role of social factors in the JST, specific effects of correspondence on the modulation of the N2 have not been directly addressed. Among the few studies investigating the ERP components related to the JST (De La Asuncion et al., 2015; Ruissen & de Bruijn, 2015; Sebanz et al., 2006; Tsai et al., 2006, 2008) only one study indirectly addressed the correspondence effect for N2 amplitudes, reporting no differences between corresponding and non-corresponding trials (Ruissen & Bruijn, 2015). Nonetheless, given that this particular result was not the goal of the study, more focused analyses are needed to draw conclusion about the generalizability of the modulation of the N2 by correspondence from the individual to the joint setting.

Another largely investigated ERP component that has been associated with cognitive control processes is the P3, a positive deflection coming around 300 to 500 ms after stimulus presentation that has its maximum at parietal sites (Kappenman & Luck, 2011). This component was first discovered as a marker for novelty in typical oddball tasks, as it appears to be greater after rare stimuli (Polich & Kok, 1995). This component is sometimes considered as composed of two sub-components, the P3a and the P3b. The first is supposed to arise as a consequence of stimulus-driven frontal attention mechanisms while the latter has been associated to temporal-parietal activity related to attention and memory encoding (Polich, 2007). P3 was originally taken as a perceptual component, and it was considered as the neural marker allowing for distinguishing perceptual processes from response selection mechanisms during the Simon task. Unfortunately, this was disconfirmed, as the P3 has been demonstrated to be sensitive both to stimulus evaluation and response selection, and it has been further characterized in interference tasks as being sensitive also to response inhibition and working memory updating (Cespón et al., 2020). A greater P3 amplitude for corresponding trials and for trials requiring the updating of stimulus-response mappings has been found both in the individual version of the Simon task (Valle-Inclán, 1996; Zhou et al., 2004) and in the JST (Sebanz et al., 2006), although performance in the joint version of the task yielded to contrasting results (Michel et al., 2018; Ruissen & de Bruijn, 2015; Tsai et al., 2006, 2008), suggesting that different processes might be involved in the JSE. Nonetheless, just as highlighted for the N2 component, studies that specifically address the correspondence effects for the P3 component in the JST are lacking, therefore it is not possible to draw a definitive conclusion.

ERP components can be very informative regarding the timing of perceptual processes, but they have also some limits. Being ERPs the mathematical reflection of phase-locked activity (as everything that is not phase-locked is cancelled out in the ERP), the assumption in their use is that the timing of the brain's electrophysiological response is the same on each trial. There is no reason to think that this is always the case in investigating brain activity related to cognitive processes (Cohen & Donner, 2013) . Frequency, and especially time-frequency analyses of the EEG signal have proved to be a useful and complementary tool to characterize brain processes. Indeed, oscillations in the 4-8 Hz range, called the theta band, localized in the medial frontal cortex (MFC) has been associated with effortful mental processes, e.g., working memory, spatial navigation, conflict resolution (Cavanagh

& Cohen, 2022). What has been suggested is that theta activity might be the spectral representation of the N2 component, being generated from the ACC and the midcingulate cortex (MCC) as well, and that it might represents the brain "language" to signal the need of cognitive control to proximate brain regions involved in interference processing (Cohen, 2014, Cavanagh & Cohen, 2022).

In the analysis of individual Simon task performance, a reconstruction of the EEG sources by Cohen and Ridderinkhof (2013) revealed a neural circuit hypothesized to manage the different stages of conflict processing residing in the MFC (i.e., conflict detection, conflict signal transmission to dedicated brain regions, and production of a contextually-adapted behavioral response). In their study, intra-brain connectivity analyses allowed for the description of a complex system subserving these mechanisms, consisting in a theta band activity in the MFC / VLPFC supposedly signaling the increased need for control and recruiting the inferior frontal gyrus (IFG) to inhibit the automatic motor response (Cohen & Ridderinkhof, 2013). Indeed, the emergence of a motor preparation of the automatic (corresponding) response during non-corresponding trials has been measured in several studies using by the emergence of the lateralized readiness potential (LRP) both in the standard Simon task (Stürmer et al., 2002; Valle-Inclán, 1996) and the JST (Holländer et al., 2011; Tsai et al., 2006). The LRP is an increased negativity recorded contralaterally relative to the hand initiating the movement, demonstrating a subthreshold activation of the wrong response that needs to be inhibited (Cespón & Díaz, 2012).

Cognitive-motor skills that are needed to perform in a Simon task such as anticipation, adaptation and attention cannot be easily isolated. Attention, for example, is a notoriously elusive concept that encompasses many different processes, controlled either by top-down and bottom-up factors. A largely accepted model of visual attention by Corbetta and Shulman (2002) postulates the existence of two partially segregated brain networks with specific functions. On one hand, a dorsal (mainly top-down) stream of information has been associated with goal-directed movements, that includes the intraparietal cortex and the superior frontal cortex which are thought to be involved in stimulus evaluation and response selection. On the other hand, the so-called ventral system that encompasses the temporoparietal cortex and the inferior frontal cortex has been proposed to be responsible for the detection of behaviorally relevant stimuli, especially in the occurrence of attention-grabbing events that require a re-orienting of attention in a bottom-up fashion. Given this characterization, it is not surprising that the Simon task elicits activities in many of these brain regions. Different clusters of brain areas have been identified by a meta-analysis of fMRI studies using the Simon task (Cespón et al., 2020), including motor and pre-motor areas in the frontal cortex, the MFC and the cingulate cortex that are thought to be responsible for initiating or selecting action sets and managing response conflict (Nachev et al., 2008; Rushworth et al., 2004), parietal areas as the superior parietal lobe (SPL), the inferior parietal lobule (IPL) and the precuneus that are recruited by spatial attention processes (Molenberghs et al., 2007; Yantis et al., 2002), temporal areas as the middle temporal gyrus, the inferior temporal gyrus and the superior temporal sulcus (STS) that have also been associated with attentional enhancements during interference processing (Xu et al., 2016).

The existence of partially segregated but interacting networks related to visual attention has been also associated with specific EEG oscillations in a study by Fan et al. (2007). For the alerting network, they reported the typical desynchronization in the theta, alpha and beta bands observed after a warning in fronto-parietal areas and the STS, while the gamma band was associated with activity in the orienting network in medial-frontal areas and the fusiform gyrus (Fan et al., 2007).

The description of these attentional networks derives from the observation of individual minds performing a task. What must be acknowledged is that during social interactions these processes are likely to interact with additional mechanisms that support joint attention. As shown by its late development (5 month old), joint attention is very demanding because it requires the involvement of complex abilities such as mentalizing, perspective taking, etc. (Mundy, 2018). The involvement of additional attentional mechanisms during joint action compared to individual performance is supported by the observation of interference effects emerging when two individuals need to attend to the same stimulus but they are instructed to focus on different features (Boeckler et al., 2012). Moreover, perceptual processing of jointly attended objects was demonstrated to be affected by shared attention so that an allocentric perspective is adopted in the presence of another person instead of the default egocentric perspective during a mental rotation task (Böckler et al., 2011) and EEG evidence showed that shared attentional mechanisms are involved in the early stages of action planning during synchronous joint action (Kourtis et al., 2014).

## 2.4 Co-representation and action inhibition

The crucial difference between the standard and the joint version of the Simon task is the presence of a co-actor that imposes a turn-taking dynamic on the task so that trials are no longer only *go* (C or NC) but also *nogo* (C or NC) trials. This means that there are at least two conceptual sources of inhibition that might require an increase of cognitive control in the JST: one being the *spatial* conflict emerging from non-corresponding S-R mappings, and the second being the need to withhold the response during *nogo* trials. The few EEG studies investigating the influence of these cognitive processes on the related ERP components (De La Asuncion et al., 2015; Ruissen & Bruijn, 2015; Sebanz et al., 2006; Tsai et al., 2006) consistently showed that action inhibition for *nogo* trials in the joint task elicits a greater P3 component compared to the same condition in the individual *go*/*nogo* version of the task, hence suggesting that inhibiting a response to a stimulus that calls for the action of a co-agent is more demanding than inhibiting a response in an individual setting. This finding was confirmed also for an imaginary co-actor in a study comparing EEG-ERP activity during a JST performed either with a believed human co-agent or believed computer co-agent, where the sense of agency attributed to the (imaginary) human partner led to a greater P3 component, leading to the assumption that the common coding framework between action and perception that subserves the behavioral JSE would be “tuned” to human agents on a neural level (Tsai et al., 2008). Interestingly, the enhanced inhibition during co-action that modulates P3-related neural activity was not evident in schizophrenic patients who are known for having severe deficits in a wide variety of social cognitive processes (De La Asuncion et al., 2015; Walter et al., 2009), corroborating the idea that the *nogo*-P3 might be a reliable index for action inhibition in social settings.

In line with these observations, a study by de Bruijn et al. (2008) using a competitive *go*/*nogo* task observed the influence of a co-actor simultaneous inhibition (i.e., more inhibition) on the performance of slow responders. That is, only for people that were slower than the co-actor, the need to withhold a response during *nogo* trials was accompanied by an increased P3 when the co-actor was withholding a response as well. These findings raise an important question: were fast responders not affected by the co-actors because they managed to suppress co-representation, thus performing more efficiently, or were they preventing the formation of co-representation in the first place?

What must be noted in trying to answer to this question is that the (hypothesized) effect of co-representation and inhibition mechanisms cannot be disentangled in the JST and similar tasks because they occur simultaneously (Wen & Hsieh, 2015). The modulation of ERP components by the presence of another individual might be exerted by either the need to specifically inhibit the representation of another's action (as suggested by Sebanz et al., 2006) and/or a general increase in cognitive processing demands that is associated with a spatial coding of responses (Dolk et al., 2014; Michel et al., 2018). In this regard, an EEG study investigated the modulation of the LRP in the joint performance showing that vicarious motor preparation occurred in the *nogo* trials (Holländer et al., 2011), and this effect was taken as evidence of the involvement of a co-representation that elicits motor activation. However, Lien et al. (2016), in support of the referential coding interpretation of the JSE, demonstrated that the same modulation of the LRP found by Hollander et al. (2011) was evident also when participants were asked to perform the *go*/*nogo* version of the task with or without a Japanese waving-cat on their side (Lien et al., 2016), thus questioning the interpretation in terms of co-representation.

Despite its pivotal involvement in action inhibition (Bokura et al., 2001; Falkenstein, 2006; Lavric et al., 2004), only two study addressed the modulation of the N2 component in a JST (Ruissen & Bruijn, 2015; Tsai et al., 2006). Interestingly, this component was demonstrated to be sensitive to the social context (vs. nonsocial) for *go* trials (irrespective of correspondence) only in individuals that were administered oxytocin, which is thought to modulate and promote social behaviors (Ruissen & de Bruijn, 2015). Given the sensitivity of the N2 to general inhibition and conflict processes, it might be that this component is not specifically tuned to social aspects, unless these are exacerbated in their neural representation (i.e., by the administration of oxytocin), thus increasing the influence of conflict-related processes that arise when acting in a joint context.

Action inhibition processes during joint action has been demonstrated to be more specific in joint settings in a stop-signal task where participants were slower when asked to stop joint-planned actions compared to individual actions (Cavallo et al., 2014). Indeed, although the understanding of observed actions recruits brain areas involved in the production of those same action (i.e., the mirror system), additional brain areas related to mental state attribution were demonstrated to be active during the prediction of other's actions (Ramnani & Miall, 2004), which might explain the more specific need of inhibition of actions performed in a social context. Following the idea that we map observed actions on our own motor repertoire to understand them, observing someone performing an action also automatically activates the tendency to perform that action (Brass & Heyes, 2005). Given the high relevance of others' action during joint performance, a greater activation of mirror areas is to be expected during joint action compared to individual settings, along with a higher need of inhibition (Newman-Norlund et al., 2007a, 2007b). Indeed, Sebanz and coll. (2007) conducted an fMRI study to investigate the brain networks activated during the JST and found that *nogo* responses elicited a greater activation in parietal cortices and the supplementary motor area (SMA) compared to the individual *go*/*nogo* task. These brain regions have been linked to mirror and inhibitory mechanisms (Buccino et al., 2001; Buccino, Binkofski, et al., 2004), supporting the idea of a greater inhibitory response when a complementary action is performed by a co-actor compared to when no action is performed, in line with the reported ERP evidence about the P3 component (Sebanz, Knoblich, et al., 2006; Tsai et al., 2006, 2008). However, Wen and coll. (2015) found an opposite result in their fMRI study, that is, decreased activity in mirror areas for *nogo* trials during joint performance compared to the individual condition. What must be noted is that in the experiment of Wen and coll. (2015), the co-actor was imaginary, while in the study of Sebanz and coll. (2007) a real human co-actor was sitting outside of the scan. Therefore, even though the belief of a co-actor might be sufficient to elicit a JSE (Tsai et al., 2008), it could be that the presence of a real co-actor induces stronger simulation processes that are reflected in increased mirror activity. In accordance with this view, the degree of similarity between the agent and the observer has been found to play a role in modulating mirror responses (Newman-Norlund et al., 2007a). For example, observing own actions elicits an earlier response in parietal and motor cortices compared to observing others' actions (Grèzes et al., 2004) and motor representations of action performed by conspecifics are stronger than similar actions performed by non-conspecifics (Buccino et al., 2004). In other words, given that humans can understand others' actions either by decoding simple visual properties or by motor simulation depending on various factors (e.g., self-other similarity, expertise, etc; Calvo-merino et al., 2006), it might be that the presence of a conspecific is more likely to activate motor simulation processes than the idea of his/her presence, hence the need for a stronger inhibition to withhold a response. Nevertheless, further studies are needed to understand whether brain networks related to action inhibition and mirror activity are specifically modulated by the co-actor's characteristics during the JST.

The effects of co-representations are more straightforward on tasks explicitly requiring cooperation or synchronization where the need to coordinate with a co-actor performing different actions is not detrimental to the joint performance, for example clinking glasses (Kourtis et al., 2014), passing an object to another person (Kourtis et al., 2013), moving objects to a target in specific orders (Schmitz et al., 2017, 2018). Indeed, EEG data demonstrated that the joint outcomes and own performance are prioritized during joint actions explicitly requiring cooperation, as showed by the larger EEG-ERP responses in cooperative settings (Kourtis et al., 2013; Loehr et al., 2013; Sebanz & Knoblich, 2021).

In sum, the modulation of EEG-ERP components and functional imaging evidence suggest that the inhibition of an action performed in a joint context is affected by social demands, although the exact neural mechanisms remain to be clarified.

## 2.5 Self-other discrimination

If executing and observing an action recruit similar brain circuits, a question arises as to which brain mechanism can discriminate between self-generated and other-generated actions and/or events. Indeed, the medial prefrontal cortex (mPFC) has been associated with this function (Amodio & Frith, 2006; Dolk et al., 2012; Liepelt et al., 2016; Sebanz et al., 2007; Wen & Hsieh, 2015). The mPFC and the TPJ are considered the core regions of a larger mentalizing network that involves frontal, temporal and parietal areas, having a crucial role in social cognition (Van Overwalle, 2009) as demonstrated, for instance, by studies investigating imitative behavior (Brass et al., 2005), ToM abilities (Ciaramidaro et al., 2007), and perspective taking (Kjaer et al., 2002; Northoff & Bermpohl, 2004). Interestingly, a subset of these same brain areas are also associated with the Default Mode Network (DMN), a set of regions that are active during wakeful rest when the individual is not focused on the outside world (Knyazev, 2013; Raichle, 2015; Raichle et al., 2001). This overlapping pattern of activation has been interpreted by considering self-referential thought in the range of mechanisms related to social cognition, which is likely to occur during free mind wandering. The mPFC has been demonstrated to be sensitive to processes related to self-evaluation (Gusnard et al., 2001), communicative intentions oriented to the self (Ciaramidaro et al., 2014) and discrimination of self-relevant stimuli (Northoff & Bermpohl, 2004).

Even though evidence from experiments on infants and non-human primates suggests that high mentalizing abilities are not necessary for the formation of the action co-representations involved in (simple) joint actions (Miss et al., 2022; Sebanz & Knoblich, 2021), the recruitment of the mPFC during JST performance has been reported in two fMRI studies (Sebanz et al., 2007; Wen & Hsieh, 2015), one tDCS study (Liepelt et al., 2016) and one gray matter voxel-based morphometry (VBM) study (Dolk et al., 2012). Given the role of this region in self-related processes, authors interpreted the activity in the mPFC during the JST as contributing to the self-other discrimination that is necessary for the appropriate recognition of self-related stimuli. Indeed, Sebanz and coll. (2007) found increased activity in the mPFC, ACC and frontal eyefield (FEF) during go trials when participants where performing the JST with a co-actor compared to when they were carrying out the individual *go/nogo* tasks, hence supporting the hypothesis of a greater need of self-other discrimination when acting with a co-agent (Sebanz et al., 2007). The same results were found by Wen and coll. (2015) who asked participants to perform the JST either believing to co-act with a human partner or a computer. Even though they found a JSE for both conditions, thus not allowing for the generation of unambiguous assumptions about the social nature of the effect, they observed an increased activity in the mPFC only in the human-belief condition for self-referred stimuli, again suggesting a greater need for self-other discrimination during co-action with a human agent (Wen and Hsieh, 2015). Moreover, the volume of gray matter in the mPFC was negatively correlated to the entity of the JSE in a study by Dolk and coll. (2012), and the inhibition of this same region by means of the tDCS led to a greater JSE in a study by Liepelt and coll. (2016), highlighting a causal link between the mPFC and self-other discrimination processes. Interestingly, in this latter study, the TPJ was also inhibited, but no modulation of the JSE emerged, suggesting that although admitting its role in the formation of co-representation, this specific brain region might not be crucial for the low-level processes of self-other discrimination required in the JST.

Because of the link of self-referential processing and the DMN, most EEG studies found self-related brain activity in the mPFC and other midline structures that have also been linked to the emergence of the P3 component in tasks investigating self-referential processing (Knyazev, 2013). Given the link between the P3 component and the saliency of the stimulus, the reported greater P3 for corresponding trials stimuli in the JST (Sebanz et al., 2006) might be interpreted as a consequence of the greater (self-) relevance of stimuli calling for a response on one’s own side, but more studies are necessary to verify this hypothesis. Moreover, given the association of theta activity and visual self-representations (Miyakoshi et al., 2010), one might speculate that activity in this range of frequencies might be involved in self-other discrimination mechanisms, even though other frequency bands as alpha and gamma have been linked to self-related processes, so that different oscillations might emerge depending on the task and/or other factors (Knyazev, 2013).

# Chapter 3

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# Neural correlates of the Joint Simon Effect: an EEG study

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## 3.1. Overview of the study

The Joint Simon Task has gained large popularity in the last few decades as a task investigating joint action. Its extensive use led researchers to theorize about the different processes causing the conflict that arises in a social situation where people get affected by the presence of a co-actor. As discussed in Chapter 1, the co-representation account (Sebanz et al. 2003) and the referential coding account (Dolk et al. 2014) offer different interpretations of the JSE, and hitherto there is no agreement on which is more plausible. Behavioral studies produced contrasting results about the *social* vs. *spatial* nature of the effect and neuroimaging studies have been conducted to fill this gap. Nonetheless, ERP studies using the JST mainly focused on the comparison between the individual *go/nogo* task and the JST (Sebanz, Knoblich, et al., 2006; Tsai et al., 2006, 2008) or on conditions created to address specific issues (e.g., the role of oxytocin or schizophrenia on the ability to form co-representations; De La Asuncion et al., 2015; Ruissen & de Bruijn, 2015). Moreover, most of these studies analyzed only the amplitude of ERP components, neglecting the temporal aspects (i.e., latency) that are at the core of the JSE.

In sum, the use of different experimental designs and statistical analyses in these studies prevents the formulation of a comprehensive description of how ERP components are associated to the JSE and its specific processes (i.e., the S-R conflict, the turn-taking dynamic and the social context). Moreover, only two fMRI studies tried to uncover the brain areas recruited during performance of a JST (Sebanz et al., 2007; Wen & Hsieh, 2015). Their results revealed the involvement of fronto-parietal networks associated to visual attention, conflict monitoring, and more importantly, self-other discrimination. Nonetheless, limits in the experimental design led to the emergence of a JSE in the control condition of both studies, thus preventing to unambiguously isolate the brain mechanisms related to the social condition.

With a paradigm-driven approach, the present study aimed at investigating joint action by providing a comprehensive description of the processes subserving the JST on a behavioral and neural level. A large sample of eighty-eight participants performed the task in pairs while their brain activity was being simultaneously recorded with a co-registering EEG setup.

On a behavioral level, we expected to replicate the occurrence of a spatial correspondence effect modulated by correspondence sequence. On a neural level, the goal of the study was threefold, specifically it aimed at: 1) providing a detailed description of the ERP components associated with the different conditions of the task. Specifically, we focused on the N2 and P3 components that have been associated with conflict monitoring, inhibition, and response selection processes, thus clarifying previous contrasting results. We expected to find the N2 to be sensitive to conflict-related aspects, and the P3 to be modulated by inhibition and response selection; 2) yielding the first demonstration of an inter-brain synchronization between ERP components during the JST. That is, for the first time we computed the JSE at the EEG level, demonstrating that the EEG-JSE of the acting agent is aligned with the EEG-JSE of the co-agent observing him/her; 3) investigating the cortical sources of the EEG power spectra of cognition-related frequency bands (delta, theta, alpha, beta and gamma) by applying the standardized low-resolution brain electromagnetic tomography method (sLORETA; Pascual-Marqui, 2002) to investigate the brain networks recruited by the JST.

What should be borne in mind is that although our results might provide important insights in the characterization of the JST, it was not the focus of the study to test which theoretical account should be accepted as more reliable. On the contrary, the thorough analysis of the dual-EEG recording of a large sample was intended as a new starting point providing comprehensive and coherent evidence as a guide for future efforts reconciling the existing theories for the understanding of the JST performances and joint action.

## 3.2. Methods

*Participants*. Eighty-eight undergraduates (74 females, Mean Age: 22.43 years; SD: 6.48 years) with normal or corrected-to-normal vision from the University of Modena and Reggio Emilia were recruited. The experiment was conducted in accordance with the ethical standards laid down in the Declaration of Helsinki and was approved by Area Vasta Emilia Nord (AVEN) Ethics Committee (protocol 1070/2019). After written consent was obtained from the participants, an ad-hoc questionnaire was administered to verify if they met the inclusion criteria.

Exclusion criteria were being <18-years-old, left-handed, suffering from psychiatric or neurological disorders, being on drugs that alter cortical excitability (e.g., anti-depressants), having suffered from traumatic brain-injury. Only individuals meeting the inclusion criteria took part in the study and received course credit for their participation. Once selected, participants were asked to fill the Edimburgh Inventory (Oldfield, 1971) for the assessment of handedness as well as the Competitiveness Index (CI) questionnaire (Smither & Houston, 1992) and they were randomly paired with another participant of the same sex.

*Apparatus and Stimuli.* All experimental sessions took place in a noiseless, dimly lit room. The two participants sat one next to the other facing a 27’ screen at a distance of approximately 60 cm. A QWERTY keyboard centrally located with respect to the two participants was provided for key-press responses. The participant sitting on the left was assigned the ‘z’ key, while the ‘underscore’ key was assigned the other participant. The experiment was designed and executed with the E-Prime 3 software. Stimuli consisted in a red or green square presented to the right or left of a fixation cross on a black background.

*Simultaneous multi-subject EEG acquisition.* EEG data were recorded with a 64-channel EEG acquisition system (Brain Product GmbH, Germany - for each subject: 32 EEG channels, online reference at TP10, ground at TP9) with a sampling rate of 250 Hz. Active electrodes were mounted on an elastic cap according to the international 10–20 system. No online filters were applied. Impedances of the electrodes were controlled to be lower than 10 kΩ. The signals of two subjects were recorded as a unique system in order to delete the sources of variance between the two amplifiers. Due to the electrical noise and the electrodes impedance, the same calibration was delivered to all the devices to adjust their sensitivities and to equalize the different gains of the different devices.

*Procedure.* All subjects were required to perform the joint version of the Simon task: each participant was instructed to respond to only one stimulus color, either the green or the red square, as fast and accurate as possible. For half the sample the red square was assigned to the left participant and the green square to the right participant, the other half of subjects experienced the opposite stimulus-response mapping.

Each trial started with the presentation of a white fixation cross at the center of the screen. After 1s, a colored square appeared to the left or the right of the cross for 800 ms or until a response was emitted. Inter-trial interval was fixed at 1s, during which a black screen was presented. After this first session participants performed a second joint Simon task with different instructions as part of a larger research project but analyses about the second part of the experiment are not reported here.

For the first joint Simon task that is the focus of the present dissertation, participants performed 24 practice trials that were not included in the analyses. Practice trials were followed by 256 experimental trials divided in two blocks of 128 trials. In half of the trials, the stimulus appeared on the same side of the response (spatially corresponding trials, hereinafter C), while in the other half, it appeared in the opposite side (spatially non-corresponding trials, hereinafter NC).

After completing the task, participants were asked to rate the experimental situation using a 7-point bipolar semantic differential scale on the following dimensions: easy vs. difficult (1 = easy, 7 = difficult), pleasant vs. unpleasant (1 = pleasant, 7 = unpleasant), positive vs. negative (1 = positive, 7 = negative), and cooperative vs. competitive (1 = cooperative, 7 = competitive). Moreover, participants were asked if they met their pair mate before the experiment and if they did, they had to specify their level of acquaintance (1 = we met once, 2 = we met few times, 3 = we meet very often, 4 = we are colleagues, 5 = we are friends). Finally, they filled out the Inclusion of Other in the Self (IOS) scale, which assesses the perceived inclusion of the other in one's self (Aron et al., 1992). This scale consists of 7 seven pairs of circles with different degrees of overlap with the labels "You" and "Other" that represent the relationship between oneself and another individual. The larger the number of the chosen picture, the more the participant felt interconnected with the co-agent. The complete set of questionnaires with the relative descriptive statistics are reported in the Appendix.

*EEG signal preprocessing*. EEG data were processed offline using BrainVision Analyzer 2 (Brain Product GmbH, Munich, Germany) and Matlab (Mathworks, Natick, Massachusetts, USA). Raw EEG data were filtered differently depending on the type of analysis, to optimize the results as much as possible. Band-pass filters (low-pass and high-pass) for a range of frequencies between 3 Hz and 20 Hz were imposed for ERP analyses, while a range of 1-45 Hz and a notch filter at 50 HZ were applied for the source reconstruction analyses. Ocular correction was performed using the Gratton, Coles, and Donchin (1983) algorithm as implemented in BrainVision Analyzer 2 using the Fpz channel that was removed from the dataset right after the correction. Only for the source reconstruction analysis pipeline, common average referencing (CAR) was introduced.

For analyses in the time domain (ERP), data were then segmented into 1000 ms epochs ranging from -200 to 800 ms around the time of stimulus onset, while an interval from 0 to 800 ms was chosen for the analyses in the frequency domain. An automatic artifact rejection procedure was performed excluding all trials with smaller/greater amplitudes of ±100 µV. For ERP computation, a baseline correction was applied based on the 200 ms pre-stimulus. Epochs were averaged subject-wise according to trial type (*Self* vs. *Other*) and S-R spatial correspondence (C vs. NC)[3]. *Figure 1* depicts all experimental conditions with their labels.

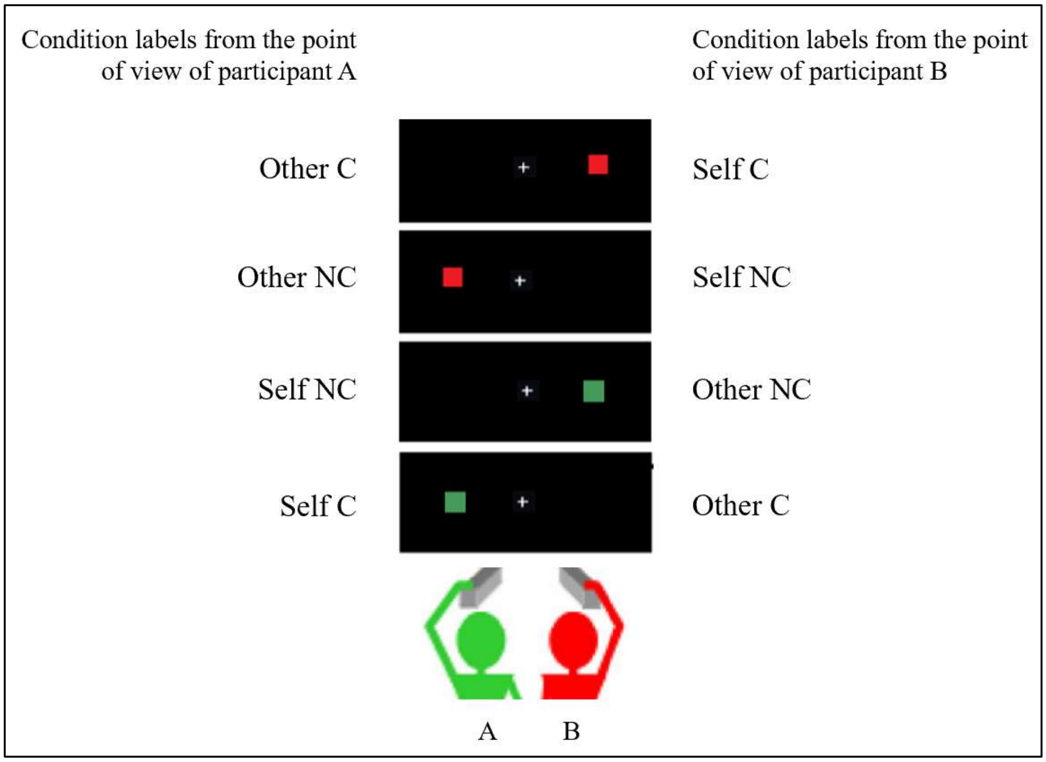

*Figure 1*: Experimental conditions of the Joint Simon Task.

## 3.3. Statistical Analyses

### 3.3.1. Behavioral analyses

Given the very low number of error trials (0.2%), these were removed prior to statistical analyses and not further analyzed. The first trial of each block, trials following errors and trials that

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[3] N.B.: In the analyses, correspondence is always referred to the responding participant (Self).

presented RTs longer than 3 standard deviations below or above the participant's mean were also removed (mean amount of removed trials: 3.9% of corresponding trials and 4.1% for non-corresponding trials)

To assess the emergence of a Simon effect and sequential effects, mean correct RTs were submitted to a 2 x 2 x 2 repeated measures Analysis of Variance (ANOVA) with *Previous actor* (same vs. other actor responding in the previous trial), *Previous correspondence* (c vs. nc, in the previous trial) and *Correspondence* (C vs. NC in the current trial) as within-participant factors. Significant interactions were assessed with appropriate ANOVAs or two-tailed t tests.

Since subjective ratings of the experimental situation were collected to assess the effectiveness of the experimental manipulation introduced in the second session of the experiment that is not reported in this dissertation, no analyses were applied to the first session.

### 3.3.2. ERP analyses

For ERP analyses, the peaks of N2 and P3 components at the electrodes Fz, Cz and Pz were analyzed. Based on visual inspection of the grand average (*Figure* 2), the N2 peak was defined as the most negative peak between 200 and 300 ms, while the P3 peak was defined as the most positive peak in a time window between 300 and 480 ms. Latency and absolute amplitude data were extracted for the peaks of each subject, for each condition, and separately given as an input to a repeated measures ANOVA with *Actor* (*Self* vs *Other*) and *Correspondence* (C vs. NC) as within-participant factors. Separate ANOVAs were conducted for each channel because of the ocular correction applied. Indeed, using the Fpz as EOG channel significantly reduces the amplitudes of surrounding channels, turning channel differences artificial and uninterpretable. Nonetheless, since sufficient evidence has been collected to characterize the topography the N2 and P3 components in the last decades, our main interest was to assess the impact of our experimental manipulation on these components at different brain locations.

*ERP inter-brain synchrony.* To assess the synchronization of the N2 and P3 components between co-agents, we computed the Joint Simon Effect at the neural level as the absolute difference of the latencies for non-corresponding and corresponding trials. This computation was applied separately on *Self* (*Self*-NC – *Self*-C) and *Other* (*Other*-NC – *Other*-C) trials, thus creating a measure of the JSE for the actor and the observer. To statistically assess the alignment of the actor's and the observer's EEG-JSEs, we took the absolute $t$ value as a measure of their distance in time and compared it to the distribution of the same measure computed for random pairs of participants. This distribution was created with a permutation test applied to 500 formal pairs (i.e., who did not perform the task at the same time). We reasoned that if the $t$ value for the comparison of real pairs of participants fell out of the 95% confidence interval of the null-hypothesis distribution, we might consider the EEG-JSE of real pairs as being truly aligned. This procedure was applied separately to N2 and P3 peak latencies measured at each electrode (Fz, Cz and Pz).

### 3.3.3. EEG source reconstruction analyses

We used the standardized low resolution brain electromagnetic tomography (sLORETA), which is a linear inverse algorithm, to localize the sources of the scalp EEG power spectra (Fuchs et al., 2002; Jurcak et al., 2007; Pascual-Marqui, 2002). sLORETA uses a realistic head model based on the MNI152 template (Mazziotta et al., 2001) to compute the 3D source distribution of the EEG signal. This model consists of 6239 voxels at 5 mm spatial resolution (Pascual-Marqui, 2002).

For our purposes, the EEG source analysis was performed in the frequency domain. First, we calculated the average cross-spectral matrices for the epochs (0-800 ms post-stimulus) of each condition for each subject. For this computation, five frequency bands associated with cognition-related activity where defined: delta (1-3 Hz), theta (3.5-7 Hz), alpha (7.5-12 Hz), beta (12.5-30 Hz), gamma (30.5-40 Hz). Second, the cross-spectral matrices were given as input to sLORETA to compute the tomographic images corresponding to the neural sources of brain activity of each frequency. A signal-to-noise ratio of 10 was chosen for the transformation matrix.

For statistical comparisons, the sLORETA images related to each condition (one for each subject) were contrasted in pairs with a nonparametric test applied voxel-by-voxel to the maps of estimated current density for two comparisons: *Self*-NC vs. *Self*-C and *Other*-NC vs. *Other*-C (the significance threshold was based on a permutation test with 5000 permutations (Nichols & Holmes, 2003). As a result, sLORETA statistical contrasts maps were created and plotted on a brain MRI template. For visualization, all non-significant t-values (< 1.67) were converted to zero.

As a region of interest (ROI) for the analysis of the social aspects of the JSE, a direct comparison between the estimated current density for each frequency band in the mPFC of each condition was applied. The absolute power of each band was extracted for each condition from all voxels within a radius of 15 mm in a region centered at ROI coordinates (x = 3; y = 49; z = 10) taken by the fMRI study by Sebanz et al (2007). The obtained values for each frequency band were log-transformed for normality assumption adherence and separately submitted to a repeated measures ANOVA with the within factors *Actor* (*Self* vs. *Other*) and *Correspondence* (C vs. NC).

## 3.4. Results

### 3.4.1. Behavioral results

The 2 x 2 x 2 repeated measures ANOVA revealed a significant main effect of *Correspondence*, $F(1,87) = 58.696$, $p < .000$, $\eta_p^2 = .403$, with faster RTs in C trials (M = 358.5 ms, SD = 52.2) than in NC trials (M = 368.5 ms, SD = 54.6). The main effect of *Previous actor* was also significant, $F(1,87) = 27.246$, $p < .000$, $\eta_p^2 = .238$, showing that participants were faster after *Other* trials (M = 358.4), compared to *Self* trials (M = 368.6) irrespective of the correspondence level of both the current and previous trials. The effect of *Previous correspondence* was modulated both by the *Previous actor* ($F(1,87) = 18.643$, $p < .000$, $\eta_p^2 = .176$) and *Correspondence* ($F(1,87) = 90.588$,

$p < .000$, $\eta_p^2 = .510$) factors. The three-way interaction involving these factors was also significant, $F\ (1,87) = 65.142$, $p < .000$, $\eta_p^2 = .428$. The mean and standard deviations for each condition are reported in Table 1. To further clarify this latter result, two rmANOVAs with the factors *Previous correspondence* and C*orrespondence* were conducted on RTs following *same* vs. *other actor* trials. For responses following *Same actor* trials, the main factors *Previous correspondence* ($F\ (1,87) = 6.345$, $p = .014$, $\eta_p^2 = .068$) and *Correspondence* ($F\ (1,87) = 38.261$, $p < .000$, $\eta_p^2 = .305$) were significant, while the *Previous correspondence* x *Correspondence* interaction did not reach significance ($F\ (1,87) = .911$, $p = .342$, $\eta_p^2 = .010$). For responses following *Other actor* trials, in addition to the main effects of *Previous correspondence* ($F\ (1,87) = 13.497$, $p < .000$, $\eta_p^2 = .134$) and *Correspondence* ($F\ (1,87) = 28.302$, $p < .000$, $\eta_p^2 = .245$), there was a significant two-way interaction, $F\ (1,87) = 160.196$, $p < .000$, $\eta_p^2 = .648$, showing a reversed Simon effect after *Other*-nc trials. The

joint Simon effect as a function of previous actor is depicted in *Figure 2*.

| | Previous actor – *Self* | | Previous actor - *Other* | |
|---|---|---|---|---|
| | *Previous Correspondence* | | *Previous Correspondence* | |
| **Correspondence in the current trial** | *C* | *NC* | *C* | *NC* |
| **C** | 364.65 (59.89) | 361.79 (58.23) | 341.43 (48.83) | 366.15 (49.22) |
| **NC** | 376.86 (62.11) | 370.95 (58.82) | 370.22 (51.41) | 355.96 (53.28) |
| **Joint Simon Effect** | 12,21 | 9,16 | 28,79 | -10,19 |

*Table 1.* Mean RTs and standard deviation (in ms) as a function of *Previous actor*, *Correspondence* and *Previous correspondence*.

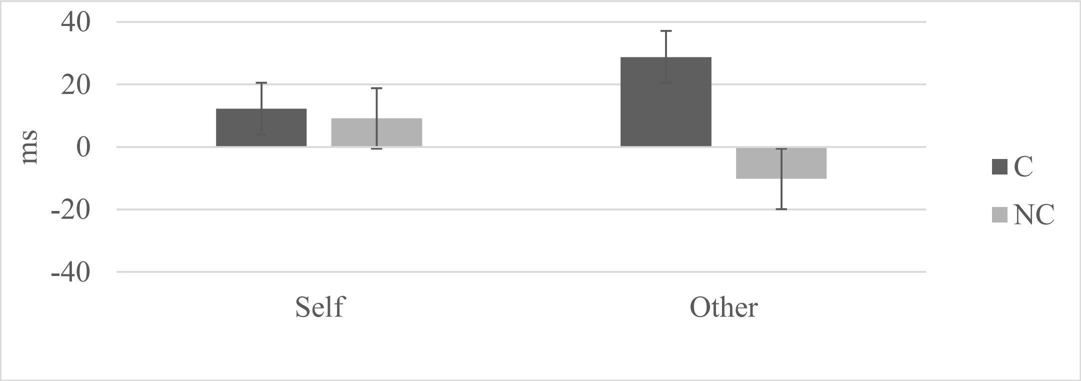

*Figure 2*: Joint Simon effect (NC – C, in ms) as a function of *Previous Actor* and *Previous correspondence*

### 3.4.2. ERP results

Mean values relative to peak latency and amplitude of the N2 and P3 components are reported in *Tables 2* and *3*, respectively. *Figures 3* depicts the grand average for each condition. Given the large number of analyses, an exhaustive report of the results is reported in *Tables 4* and *5*. For easy of clarity, only effects relevant for the purpose of the present dissertation will be discussed.

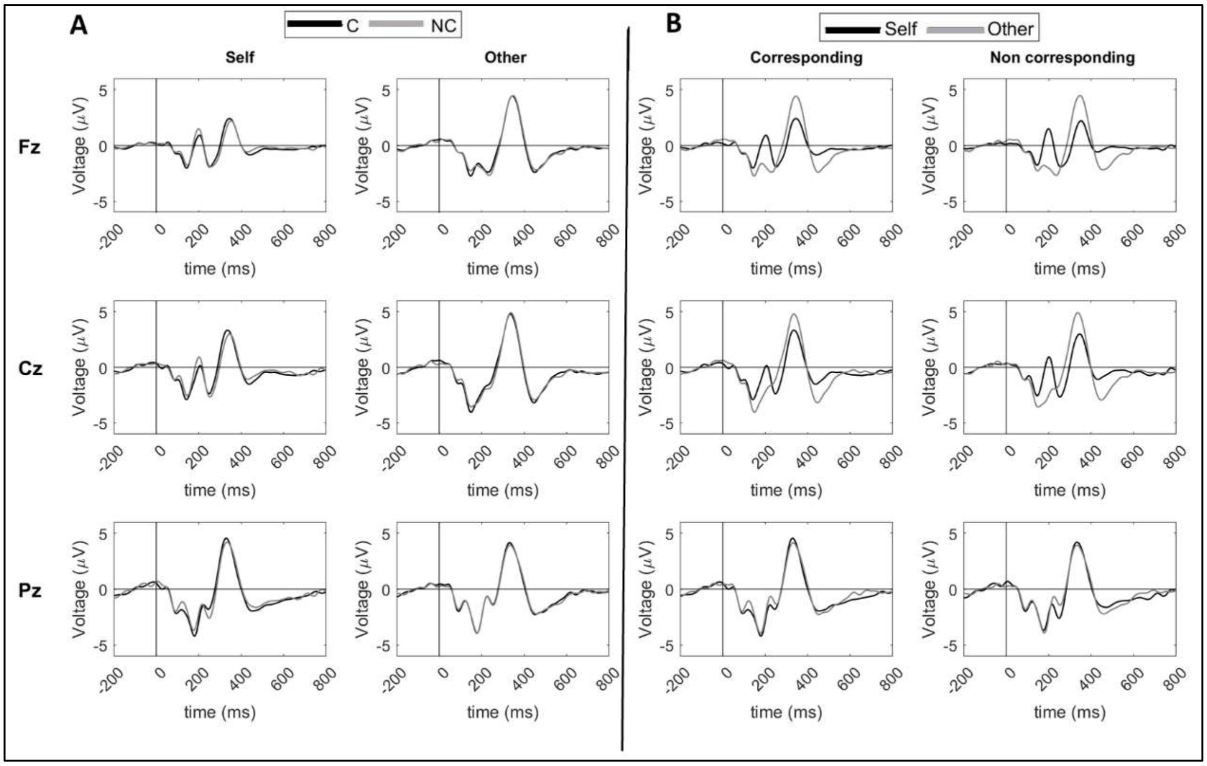

*Figure 3*: Grand average ERPs at Fz, Cz, Pz electrode as a function of A) Correspondence (corresponding, C vs. non-corresponding, NC), for Self and Other trials, separately, and B) Responding agent (Self vs. Other), for corresponding and non-corresponding trials, separately.

| *Actor* | *Correspondence* | **Fz** | **Cz** | **Pz** |
|---|---|---|---|---|
| **N2** | | | | |
| Self | C | 260 (19) | 251 (17) | 245 (15) |
| | NC | 265 (20) | 255 (19) | 254 (14) |
| Other | C | 249 (23) | 250 (25) | 254 (22) |
| | NC | 250 (22) | 248 (25) | 255 (21) |
| **P3** | | | | |
| Self | C | 350 (26) | 342 (26) | 332 (20) |
| | NC | 352 (24) | 348 (27) | 341 (26) |
| Other | C | 345 (19) | 338 (25) | 339 (27) |
| | NC | 346 (24) | 338 (25) | 341 (25) |

*Table 2*: Mean latency and standard deviation (in ms) for the N2 and P3 peaks as a function of Actor and Correspondence

| *Actor* | *Correspondence* | **Fz** | **Cz** | **Pz** |
|---|---|---|---|---|
| **N2** | | | | |
| Self | C | 3.20 (1.55) | 4.28 (2.32) | 3.93 (2.09) |
| | NC | 3.37 (1.54) | 4.52 (2.44) | 4.40 (2.24) |
| Other | C | 3.07 (1.5) | 3.31 (1.96) | 3.61 (1.59) |
| | NC | 3.45 (2.06) | 4.19 (2.22) | 4.02 (1.99) |
| **P3** | | | | |
| Self | C | 3.35 (1.31) | 3.93 (1.70) | 4.66 (1.64) |
| | NC | 3.11 (1.44) | 3.97 (1.70) | 4.79 (1.73) |
| Other | C | 4.37 (2.09) | 4.50 (2.08) | 4.15 (2.09) |
| | NC | 4.52 (2.35) | 4.81 (2.28) | 4.37 (2.32) |

*Table 3*: Mean amplitude and standard deviation (μV) for the N2 and P3 as a function of Actor and Correspondence

*N2 component.* The only significant factor influencing the N2 peak latency appeared to be the factor *Actor* ($p < .000$, $\eta_p^2 = .337$) and only for the electrode Fz, F (1,40 ) = 20.33, $p < .000$, $\eta_p^2 = .337$, with a longer N2 latency in *Self* (M = 262.29 ms) than in *Other* (M = 249.41 ms) trials.. Even though corresponding trials showed a tendency to be slower than non corresponding trials at Fz and Pz electrodes, the main effect of Correspondence was only close to statistical significance ($p = .085$ and $p = .087$, respectively). Relative to peak amplitude, the N2 was larger (more negative, Fz: $p = .036$, $\eta_p^2 = .106$; Cz: $p = .008$, $\eta_p^2 = .184$; Pz: $p = .012$, $\eta_p^2 = .211$) for non-corresponding trials (Fz: M = 3.41 μV; Cz: M = 4.36 μV; Pz: M = 4.21μV) compared to corresponding trials (Fz: M = 3.14 μV; Cz: M = 3.79 μV; Pz: M = 3.77 μV) at all electrodes and irrespective of the responding Actor.

| Electrode | Cases | F test | $p$ | Effect size ($\eta_p^2$) |
|---|---|---|---|---|
| *N2 Latency* | | | | |
| **Fz** | Actor | *F* (1,40) = 20.33 | < .000* | .337 |
| | Correspondence | *F* (1,40) = 3.128 | .085 | .073 |
| | Actor x Correspondence | *F* (1,40) = .650 | .425 | .016 |
| **Cz** | Actor | *F* (1,35) = 1.125 | .296 | .031 |
| | Correspondence | *F* (1,35) = .356 | .555 | .010 |
| | Actor x Correspondence | *F* (1,35) = 2.587 | .117 | .069 |
| **Pz** | Actor | *F* (1,27) = 2.686 | .113 | .090 |
| | Correspondence | *F* (1,27) = 3.148 | .087 | .104 |
| | Actor x Correspondence | *F* (1,27) = 2.612 | .118 | .088 |
| *N2 Amplitude* | | | | |
| **Fz** | Actor | *F* (1,40) = .006 | .940 | . 000 |
| | Correspondence | *F* (1,40) = 4.733 | .036* | .106 |
| | Actor x Correspondence | *F* (1,40) = .737 | .396 | .018 |
| **Cz** | Actor | *F* (1,35) = 2.666 | .112 | .071 |
| | Correspondence | *F* (1,35) = 7.912 | .008* | .184 |
| | Actor x Correspondence | *F* (1,35) = 2.752 | .106 | .073 |
| **Pz** | Actor | *F* (1,27) = .903 | .350 | .032 |
| | Correspondence | *F* (1,27) = 7.225 | .012* | .211 |
| | Actor x Correspondence | *F* (1,27) = .011 | .917 | .000 |

*Table 4:* ANOVA results for peak latency and amplitude of the N2 component at Fz, Cz Pz.

*P3 component.* The analysis on P3 peak latency revealed a significant main effect *Actor* at Fz and Cz electrodes (Fz: $p = .033$, $\eta_p^2 = .071$; Cz: $p = .007$, $\eta_p^2 = .101$) but not at the Pz electrode, showing a slower timing for *Self* trials (Fz: M = 350.73 ms; Cz: M = 345.18 ms) relative to *Other* trials (Fz: M = 345.69 ms; Cz: M = 338.08 ms). At Cz and Pz electrodes, the main effect *Correspondence* (Cz: $p = .016$, $\eta_p^2 = .080$; Pz: $p = .001$, $\eta_p^2 = .148$) was also significant, as P3 peaks were slower at NC trials (Cz: M = 343.21 ms; Pz: M = 340.81 ms) compared to C trials (Cz: M = 340.06 ms; Pz: M = 335.42 ms), irrespective of the responding agent.

Amplitude analyses showed that the P3 was sensitive to response inhibition, since *Other* trials (Fz: M = 4.45 µV; Cz: M = 4.66 µV; Pz: M = 4.26 µV) presented greater amplitude at all electrodes ( Fz: $p < .000$, $\eta_p^2 = .331$; Cz: $p = .002$, $\eta_p^2 = .131$; Pz: $p = .020$, $\eta_p^2 = .077$) compared to *Self* trials (Fz: M = 3.23 µV; Cz: M = 3.95 µV; Pz: M = 4.73 µV. Moreover, at Fz there was a significant *Actor* x *Correspondence interaction, F*(1,62) = 4.580, *p* = .036, $\eta_p^2$ = .069. To further investigate this result, two paired-sample t-test (Bonferroni corrected) were performed to understand whether the difference between non-corresponding and corresponding trials (i.e., the Simon effect) was significant in both *Self* and *Other* trials. These analyses confirmed that P3 amplitude was larger in NC trials (M = 3.45 µV) than in C trials (M = 3.07 µV) for *Other* trials (t (55) = 4.694, *p* < .001, Cohen's d = .627) but not for *Self* trials (t(70) = -1.503, p = .274, Cohen's *d* = -.178).

| **Electrode** | **Cases** | **F test** | ***P*** | **Effect size ($\eta_p^2$)** |
|---|---|---|---|---|
| *P3 Latency* | | | | |
| **Fz** | Actor | F (1,62) = 4.736 | .033* | .071 |
| | Correspondence | F (1,62) = .913 | .343 | .015 |
| | Actor x Correspondence | F (1,62) = .265 | .609 | .004 |
| **Cz** | Actor | F (1,70) = 7.832 | .007* | .101 |
| | Correspondence | F (1,70) = 6.088 | .016* | .080 |
| | Actor x Correspondence | F (1,70) = 3.257 | .075 | .044 |
| **Pz** | Actor | F (1,68) = 1.623 | .207 | .023 |
| | Correspondence | F (1,68) = 11.779 | .001* | .148 |
| | Actor x Correspondence | F (1,68) = 2.177 | .145 | .031 |
| *P3 Amplitude* | | | | |
| **Fz** | Actor | F (1,62) = 30.622 | < .001* | .331 |
| | Correspondence | F (1,62) = .120 | .730 | .002 |
| | Actor x Correspondence | F (1,62) = 4.580 | .036* | .069 |
| **Cz** | Actor | F (1,70) = 10.510 | .002* | .131 |
| | Correspondence | F (1,70) = 2.437 | .123 | .034 |
| | Actor x Correspondence | F (1,70) = 2.227 | .140 | .031 |
| **Pz** | Actor | F (1,68) = 5.681 | .020* | .077 |
| | Correspondence | F (1,68) = .127 | .723 | .002 |
| | Actor x Correspondence | F (1,68) = 1.909 | .172 | .027 |

*Table 5*: ANOVA results for peak latency and amplitude of the P3 component at Fz, Cz, Pz.

*ERP inter-brain synchronization*. The results of the permutation test applied to the co-agents' EEG-JSE revealed an alignment of the N2 component at the Cz electrode and of the P3 component at the Fz electrode as shown in *Figure 4*.

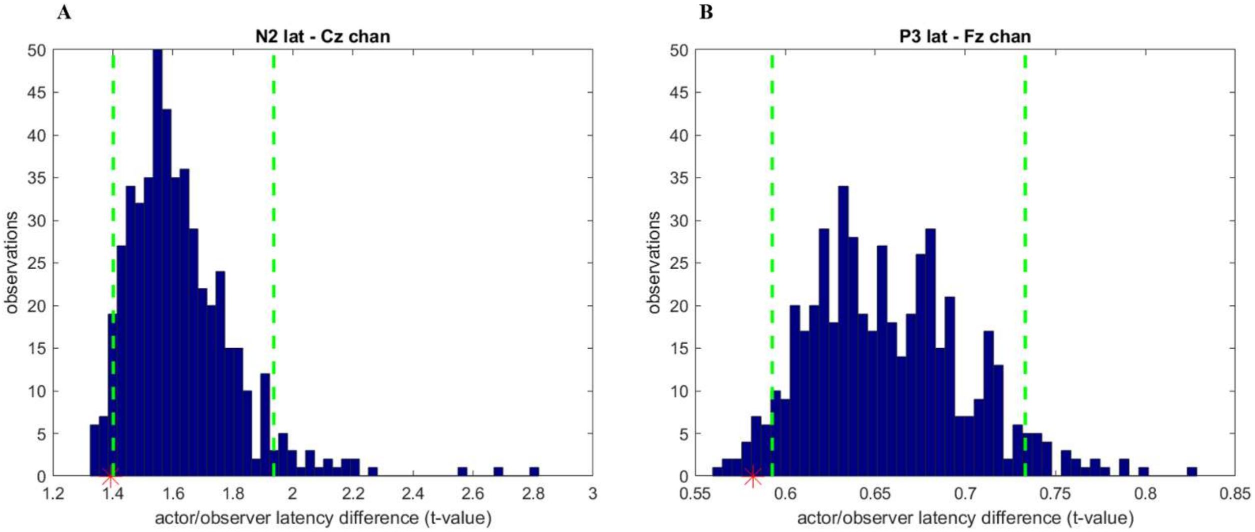

*Figure 4*: Distribution of the *t* values created under the null hypothesis for the (A) P3 and (B) N2 components. Red stars represent the *t* values computed for the real pairs at electrodes Cz and Fz, respectively.

### 3.4.3. EEG source reconstruction results

Extreme significant t values (max/min) resulting from the comparisons of the estimated current density of each condition (*Self*-NC vs. *Self*-C and *Other*-NC vs. *Other*-C) are presented in *Tables 6* and *7*. Both anatomical (MNI) coordinates and Brodmann areas (BA) are reported.

| Frequency band / Brain area | Brodmann | Hemisphere | x | y | z | t min/max |
|---|---|---|---|---|---|---|
| *Delta* | | | | | | |
| Superior Frontal Gyrus | 9 | L | -30 | 20 | 40 | -2.27162 |
| Medial Prefrontal Cortex/ Superior Frontal Cortex | 10 | R | 25 | 60 | 20 | -1.93448 |
| | 10 | R | 10 | 50 | 15 | -1.69469 |
| Anterior Cingulate Cortex | 32 | L | -10 | 25 | 30 | -1.86256 |
| Inferior Occipital Gyrus | 18 | R | 25 | -90 | -15 | -1.84802 |
| *Theta* | | | | | | |
| Medial Temporal Gyrus | 41 | L | -40 | -25 | 10 | -2.43409 |

| | | | | | | |
|---|---|---|---|---|---|---|
| Insula | 13 | L | -40 | -20 | 10 | -2.42612 |
| Medial Prefrontal Cortex/ Superior Frontal Cortex | 10 | R | 25 | 60 | 20 | -2.12352 |
| | 9 | R | 20 | 40 | 20 | -1.98814 |
| | 10 | L | -5 | 55 | 0 | -1.86512 |
| Parahippocampal Gyrus | 28 | L | -20 | -25 | -10 | -2.03404 |
| Anterior Cingulate Cortex | 32 | R | 20 | 40 | 15 | -1.94234 |
| Fusiform Gyrus | 37 | L | -40 | -50 | -25 | -1.85662 |
| Precuneus / Superior Parietal Lobe | 7 | L | -20 | -60 | 65 | 3.23814 |
| | 7 | L | -10 | -65 | 65 | 3.15052 |
| | 7 | R | 0 | -70 | 30 | 2.18526 |
| *Alpha* | | | | | | |
| Lateral Prefrontal Cortex / Superior Frontal Cortex | 9 | R | 55 | 15 | 35 | -2.64487 |
| | 9 | R | 45 | 35 | 35 | -1.75814 |
| Superior temporal Gyrus/ Medial Temporal Gyrus | 21 | R | 70 | -25 | -5 | -2.47681 |
| | 22 | R | 60 | 0 | 5 | -1.74188 |
| Postcentral Gyrus/Inferior Frontal Gyrus | 40 | R | 65 | -20 | 15 | -2.00378 |
| Insula | 13 | R | 40 | 15 | 15 | -1.75075 |
| *Beta* | | | | | | |
| Precuneus / Superior Parietal Lobe | 7 | R | 10 | -45 | 50 | -2.21022 |
| Inferior Parietal Lobe | 40 | L | -45 | -60 | 50 | -1.73764 |
| *Gamma* | | | | | | |
| Precuneus / Superior Parietal Lobe | 40 | L | -50 | -40 | 45 | -1.90345 |
| | 7 | R | 20 | -75 | 50 | -1.86459 |
| Insula | 13 | R | 35 | 5 | 15 | 2.01821 |

*Table 6*: Max/min values for the voxel-by-voxel comparison of the estimated current density in Self-NC vs Self-C conditions

| **Frequency band / Brain area** | **Brodmann** | **Hemisphere** | **x** | **y** | **z** | **t min/max** |
|---|---|---|---|---|---|---|
| *Delta* | | | | | | |
| Postcentral Gyrus/Inferior Frontal Gyrus | 9 | R | 40 | 5 | 30 | 3.43386 |
| | 4 | L | -45 | -20 | 45 | 2.33959 |
| Insula | 13 | R | 35 | 5 | 20 | 3.23965 |
| | 13 | L | -35 | -40 | 20 | 1.82517 |
| Primary Motor Cortex | 43 | R | 60 | -10 | 20 | 2.82868 |
| | 3 | L | -50 | -15 | 50 | 2.33222 |
| Anterior Temporal Pole | 22 | R | 60 | -5 | 10 | 2.43019 |
| Middle Occipital Gyrus | 19 | L | -55 | -70 | -10 | 2.19943 |
| Posterior Temporal Gyrus | 19 | L | -50 | -65 | -5 | 2.19907 |
| Fusiform Gyrus | 37 | L | -50 | -60 | -15 | 2.04887 |
| Cingulate Gyrus | 32 | R | 15 | 15 | 35 | 1.98125 |
| Superior Temporal Gyrus | 41 | L | -40 | -40 | 10 | 1.90813 |

| | | | | | | |
|---|---|---|---|---|---|---|
| Precuneus | 7 | R | 5 | -55 | 65 | 1.88157 |
| Superior Parietal Lobe | 5 | R | 5 | -50 | 65 | 1.83676 |
| | 5 | L | -5 | -50 | 65 | 1.71381 |
| Lingual Gyrus | 19 | L | -25 | -65 | 0 | 1.81793 |
| Inferior Parietal Lobule | 40 | R | 65 | -25 | 25 | 1.70749 |
| *Theta* | | | | | | |
| Supplementary Motor Area | 6 | R | 35 | 0 | 65 | 3.93054 |
| | 6 | L | -20 | 5 | 70 | 2.77964 |
| | 6 | L | -25 | 0 | 65 | 2.73766 |
| Insula | 13 | R | 40 | 5 | 10 | 3.59784 |
| Inferior Frontal Gyrus | 44 | R | 50 | 0 | 20 | 3.54688 |
| Cingulate cortex | 24 | R | 20 | -20 | 45 | 3.23653 |
| Superior Parietal Lobe | 3 | R | 10 | -35 | 70 | 2.79431 |
| | 4 | L | -45 | -20 | 45 | 2.57737 |
| Anterior Temporal Pole | 20 | R | 50 | 0 | -40 | 2.77145 |
| Parahippocampal Gyrus | 34 | R | 30 | 5 | -20 | 2.68105 |
| Precuneus | 7 | R | 5 | -35 | 45 | 2.64796 |
| Orbital Gyrus | 47 | R | 20 | 30 | -30 | 2.14595 |
| Anterior Cingulate Cortex | 25 | R | 5 | 5 | -5 | 2.07722 |
| Medial Temporal Gyrus | 22 | L | -65 | -35 | 0 | 2.05824 |
| Inferior Occipital Gyrus | 19 | R | 45 | -85 | -10 | 1.9961 |
| Posterior Superior Temporal Sulcus / Temporal Parietal Junction | 22 | L | -65 | -45 | 5 | 1.92009 |
| | 40 | L | -60 | -45 | 20 | 1.76882 |
| Fusiform Gyrus | 37 | R | 55 | -60 | -20 | 1.91103 |
| *Alpha* | | | | | | |
| Postcentral Gyrus | 2 | L | -50 | -30 | 60 | -1.77238 |
| Inferior Frontal Gyrus | 45 | R | 60 | 20 | 10 | 2.08724 |
| | 45 | L | -55 | 30 | 5 | 1.85549 |
| Anterior Cingulate Cortex | 33 | L | -5 | 20 | 20 | 1.95846 |
| Medial Temporal Gyrus | 21 | R | 55 | 5 | -35 | 1.83069 |
| Insula | 13 | L | -30 | 20 | 10 | 1.72459 |
| *Beta* | | | | | | |
| Anterior Cingulate Cortex | 32 | R | 0 | 20 | 35 | -2.75121 |
| Supplementary Motor Area | 32 | L | -15 | 10 | 50 | -2.70796 |
| | 6 | R | 5 | 15 | 50 | -2.50447 |
| Anterior Temporal Pole | 22 | L | -50 | 15 | -5 | -1.89018 |
| Inferior Frontal Gyrus | 47 | L | -55 | 20 | 0 | -1.88852 |
| Insula | 13 | L | -45 | 10 | -5 | -1.85458 |
| Precuneus | 31 | R | 15 | -55 | 30 | -1.77566 |
| Posterior Superior Temporal Sulcus / Temporal Parietal Junction | 40 | R | 65 | -50 | 30 | 1.75346 |
| *Gamma* | | | | | | |
| Anterior Temporal Pole | 21 | L | -65 | -15 | -5 | -2.36001 |
| Superior Temporal Gyrus | 22 | L | -60 | -10 | 0 | -2.33498 |
| Insula | 13 | L | -45 | -15 | 0 | -2.09723 |
| Fusiform Gyrus | 20 | L | -55 | -35 | -25 | -1.94281 |

| | | | | | | |
|---|---|---|---|---|---|---|
| Postcentral Gyrus/Inferior Frontal Gyrus | 44 | L | -60 | 5 | 15 | -1.83581 |
| Medial Prefrontal Cortex/ Superior Frontal Cortex | 10 | R | 20 | 60 | 25 | -1.82824 |

*Table 7*: Max/min values for the voxel-by-voxel comparison of the estimated current density in Other-NC vs Other-C conditions

*Self-NC vs Self-C.* From statistical comparison of current density estimates of the *Self*-NC and *Self*-C condition different significant differences emerged for each frequency band. In the delta band, we found a desynchronization in prefrontal areas such as the left superior frontal cortex and the right medial prefrontal cortex, and in the anterior cingulate cortex and occipital areas. For the theta band, we also found a desynchronization in prefrontal areas, specifically in bilateral medial prefrontal and superior frontal cortices, and in the anterior cingulate cortex, along with the left insula, the left medial temporal gyrus, the left parahippocampal gyrus and the left fusiform gyrus. A pattern of synchronization was found for this band in bilateral regions of the precuneus and superior parietal lobe. Alpha oscillations were desynchronized in right prefrontal areas such as the lateral prefrontal cortex and the superior frontal cortex, as well as in right regions of the superior temporal gyrus/medial temporal gyrus, the right postcentral gyrus and the right insula. For the beta band, a desynchronization was observed in the right precuneus/superior parietal lobe and the left inferior parietal lobe. Also, gamma oscillations were desynchronizing in bilateral parietal areas while a synchronization in this frequency band was observed in the right insula.

*Other-NC vs Other-C***.** The comparison of *Other*-NC and *Other*-C conditions led mainly to a pattern of synchronization in the delta, theta, and alpha bands, while the beta and gamma bands appeared to desynchronize. The synchronization in the delta band involved the inferior frontal gyrus, the insula, and the primary motor cortex bilaterally, temporal areas such as the right anterior temporal pole, the left posterior temporal gyrus, and the left superior temporal gyrus, also the left middle occipital gyrus, the left fusiform gyrus, cingulate cortex, the lingual gyrus, and parietal areas as the precuneus, the bilateral superior parietal lobe and the right parietal lobule. Theta synchronization was spread across large clusters. Maximal t values were observed across a large portion of the supplementary motor area bilaterally, including part of the anterior/medial cingulate cortices, right insula and the right inferior frontal gyrus, as well as the bilateral superior parietal lobe and the precuneus. A temporal cluster of synchronization involved the right anterior temporal pole, the left medial temporal gyrus and the left posterior superior temporal sulcus/temporal parietal junction, together with areas in the right parahippocampal gyrus and the right fusiform gyrus. More sparse areas involved the right orbital gyrus and the inferior occipital gyrus. Alpha oscillations were also synchronized bilaterally in the inferior frontal gyrus, in the anterior cingulate cortex, the right medial temporal gyrus, and the left insula, except for a small cluster of desynchronizations in the left postcentral gyrus. The beta band was found to desynchronize in areas of the anterior cingulate cortex, the supplementary motor area in both hemispheres, the left anterior temporal pole, the left inferior frontal gyrus, the left insula, and the right precuneus, while a pattern of synchronization was found in the posterior superior parietal sulcus/temporal parietal junction. A desynchronization in the gamma band was present mainly in the left hemisphere, in temporal areas as the anterior temporal pole and the superior temporal gyrus, the insula, the fusiform gyrus and the inferior frontal gyrus, except for a portion of the medial prefrontal cortex/ superior frontal cortex in the right hemisphere.

*mPFC absolute power*. From the comparison of the estimated current density in the mPFC for the five frequency bands, significant differences emerged only in the theta and beta bands. All results of the ANOVAs are reported in *Table 8*. For the theta band, a significant *Actor* x *Correspondence interaction* revealed different data trends for *Self* and *Other* conditions, where theta desynchronization for the *Self* condition was greater during NC trials (M = 2.442 $\mu V^2$) than during C trials (M = 2.599 $\mu V^2$), while the opposite was true for the *Other* condition (NC: M = 2.511 $\mu V^2$; C: M = 2.406 $\mu V^2$), see *Figure 5*. For the beta band, a main effect of *Actor* emerged, revealing a greater power during *Other* (M = 2.442 $\mu V^2$) trials compared to *Self* trials (M = 3.00 $\mu V^2$).

| Frequency band | Cases | F test | p | Effect size ($\eta_p^2$) |
|---|---|---|---|---|
| Delta | Actor | F(1,85) = 3.275 | .074 | .037 |
| | Correspondence | F(1,85) = 2.688 | .105 | .031 |
| | Actor x Correspondence | F(1,85) = 1.313 | .255 | .015 |
| Theta | Actor | F(1,85) = 1.2 | .276 | .014 |
| | Correspondence | F(1,85) = .162 | .688 | .002 |
| | Actor x Correspondence | F(1,85) = 4.682 | .033* | .052 |
| Alpha | Actor | F(1,85) = .19 | .664 | .002 |
| | Correspondence | F(1,85) = .411 | .523 | .005 |
| | Actor x Correspondence | F(1,85) = 1.379 | .244 | .016 |
| Beta | Actor | F(1,85) = 8.16 | .005* | .088 |
| | Correspondence | F(1,85) = .275 | .601 | .003 |
| | Actor x Correspondence | F(1,85) = .181 | .671 | .002 |
| Gamma | Actor | F(1,85) = .019 | .89 | .000 |
| | Correspondence | F(1,85) = .162 | .689 | .002 |
| | Actor x Correspondence | F(1,85) = .602 | .44 | .007 |

*Table 8*: Results from the ANOVAs applied to the absolute estimated and extracted current density in the mPFC (MNI coordinates 3;49;10) for the five frequency bands (delta, theta, alpha, beta, gamma).

### 3.5. Discussion

The aim of this study was to characterize the behavioral and neural processes related to the JSE at different levels. First, a behavioral analysis was conducted to assess the emergence of the JSE and describe its mechanisms, taking into account the sequential modulations that are known to affect reaction times on a trial-by-trial fashion (Liepelt et al., 2011). Second, the N2 and the P3 components were analyzed to assess the sensitivity of latency- and amplitude- related features to the experimental conditions. More interestingly and for the first time, N2 and P3 peak latencies were used to assess ERP inter-brain synchronization. Ultimately, brain areas related to JST performance were revealed through the standardized low-resolution brain electromagnetic tomography (sLORETA).

Behavioral results revealed a JSE, i.e., faster RTs for corresponding than for non-corresponding trials, replicating the influence of the presence of a co-actor on performance of the JST found in previous studies (e.g., Dolk et al., 2014; Sebanz et al., 2003; Sebanz & Knoblich, 2021). Notably, if responses in NC trials were generally slower than those in corresponding trials, this was not always true when the previous actor (*self* vs. *other*) was considered. Indeed, when the response in the previous trial was assigned to the co-actor, in the following trial the agent's responses were slower when the stimulus appeared in the same location as the previous stimulus to which his/her co-actor responded, this leading to a larger JSE after *Other*-C trials and to a reversed JSE after *Other*-NC. This result is in line with the inhibition tag hypothesis (Liepelt et al., 2011; Neill et al., 1992) which states that in the joint version of the Simon task, when people need to withhold the response during the co-agent's turn, stimulus location might be "tagged with inhibition" (p.368, Liepelt et al., 2011, 2013; Spapé and Hommel, 2014; Yamaguchi et al., 2018). Because of the inhibition tag, a stimulus recurring in the same location in the following trial is slowed down, as already reported by several studies (Liepelt et al., 2011, 2013; Spapé & Hommel, 2014; Yamaguchi et al., 2018).

ERP analyses showed an effect related to motor preparation, as N2 and P3 peak latencies were greater for trials requiring a response, demonstrating that the need to form an action plan is more time-consuming than the inhibition of a motor response. As expected, the N2 component was affected by the spatial S-R conflict but not by motor inhibition in general, as shown by its larger amplitude at the Fz electrode for NC compared to C trials, irrespective of the responding agent. These data suggest that the N2 amplitude is not sensitive to response production during a JST, supporting the idea of the N2 being related to conflict monitoring and/or the decisional processes *in preparation* to motor inhibition (and not motor inhibition itself; Falkenstein, 2006). In line with this logic, P3 latency was found to be affected by correspondence, as NC trials showed a higher latency than C trials at both Fz and Pz electrodes. Given that the P3 component has been associated to processes of stimulus evaluation and response selection (Cespòn et al., 2020), it is reasonable to assume that conflicting information takes longer to be processed. Based on our results, sensitivity to correspondence seemed to emerge more at frontal sites, as expected considering the well-known association between executive functions and frontal/prefrontal areas (Bokura et al., 2001; Lavric et al., 2004b). It must be noted that we did not differentiate between P3a and P3b, so it is possible that differences at more parietal sites were not evident because occurring at different stages of response preparation that were not taken into consideration by our analysis.

Differently from peak latency, P3 amplitude was significantly larger, at all electrodes, when participants needed to withhold a response as compared to when a response was given. In contrast with the results by Sebanz and coll. (2006) and the literature on individual conflict tasks reporting greater amplitude for C relative to NC trials (e.g., Valle-Inclán, 1996; Zhou et al., 2004), but in line with other ERP studies investigating the brain dynamics of the JST (Michel et al., 2018; Ruissen and Bruijn, 2015; Tsai et al., 2006, 2008), we did not find the P3 amplitude to be affected by correspondence. The only exception was the Fz electrode where stimuli requiring response inhibition (*Other* trials) appearing on one's own side showed a larger amplitude compared to stimuli appearing on the other side. This result is easily explained assuming that a stimulus appearing near the participant would require a stronger inhibition as it calls more for action compared to a stimulus appearing on the co-agent's side, in agreement with the evidence showing joint-planned actions to impair action inhibition (Cavallo et al., 2014).

Despite the several studies exploiting the JST to investigate joint action (De La Asuncion et al., 2015; Ruissen & Bruijn, 2015; Sebanz et al., 2006; Tsai et al., 2006, 2008), only the study by Ruissen & Bruijn (2015) directly compared the ERP features of *go* and *nogo* trials, revealing a role of oxytocin in modulating the sensitivity of the N2 to action planning in a social context. Exploring the relationship between *Self* and *Other* trials is important to fully understand the JST dynamics. Indeed, joint actions involve at least two individuals, and it is assumed that when one of these individuals is acting, the other agent is not simply a passive observer. On the contrary, and especially during a JST, participants are constantly immersed in a joint context thus actively inhibiting their own action and monitoring the co-agent in order to adjust future actions coherently.

For the first time to our knowledge, we exploited the simultaneous registration of the EEG signal from pairs of participants to compute a JSE at the neural level in both individuals to further characterize the relationship of the brain dynamics of co-acting agents. As predicted, we found a synchronization between the co-agents at the ERP level, showing that the N2-JSE and the P3-JSE were aligned at the Cz and Fz electrodes, respectively. Again, the significant results at more frontal sites are in line with the idea that these areas are related to cognitive control and social cognition processes, with the specification that these processes might be functionally linked between individuals performing a joint action. A previous fNIRS study co-registering pairs of participants during a JST already demonstrated significant inter-brain neural synchronization in the IPL (Yang et al., 2021), validating the exploration of inter-brain connectivity during this kind of task. Our analyses focused on the Fz, Cz and Pz electrodes where the N2 and P3 components are more evident, thus not allowing us to explore more lateralized parietal areas. Future studies might take into consideration a larger portion of the brain. The EEG-JSE synchronization as described by our analysis cannot highlight a causal link between the cognitive processes of two individuals, and its meaning might be hard to interpret because of the lack of prior studies applying this measure, as pointed out by the only other study measuring P3 synchronization for the investigation of inter-brain dynamics of a dyad performing a Prisoner Dilemma Game (Zhang et al., 2019). Nonetheless, the ANOVA on ERP latencies showed that both N2 and P3 peaks were slower during *Self* trials compared to *Other* trials, revealing that the timing of these components is affected by action planning. It is quite surprising that despite this influence of action planning, the conflict-related brain mechanisms as measured by EEG-JSE in the actor and the observer proved to be aligned, highlighting the relevance of inter-brain dynamics during joint action.

To further understand the mechanisms involved in joint action, we applied an EEG source reconstruction method to reveal which brain regions are recruited during the JST. By contrasting NC to C trials separately for *Self* and *Other* trials we tried to isolate the neural processes related to the experienced and observed JSE. By applying the sLORETA technique (Pascual-Marqui, 2002) for EEG source reconstruction to the whole brain, we expected to reveal different networks subserving different cognitive functions.

Being the JSE an effect related to spatial conflict, we hypothesized to find differences in the estimated current density in areas related to cognitive control and spatial attention. Interestingly, regions in the insula appeared to be relevant for the processing of both experienced and observed conflicts. Even though this observation remains at a qualitative level, it might represent a starting point to further analyze inter-brain dynamics. Activity in the insula for the alpha, theta and gamma band appeared to be significantly different comparing *Self*-NC trials to *Self*-C trials possibly highlighting the role of this area in conflict processing, cognitive control and attentional processes (Menon & Uddin, 2010). This same region showed a significant difference during an observed conflict (*Other*-NC vs. *Other*-C) in the theta beta and gamma band suggesting a functional similarity in the processing of spatially conflicting information for executed and observed action events. A conflict-related network was further characterized by differences in the ACC for the theta band both for experienced and observed conflict. Indeed, this area is well-known for its implication in conflict processing, and it has been hypothesized as the source of the brain markers of cognitive control, i.e., mid-frontal theta and the N2 component (Bokura et al., 2001; Cavanagh and Cohen, 2022; Lavric et al., 2004; Yeung et al., 2004). *Other*-NC trials revealed differences in this area also for the alpha, beta, and delta band, again probably reflecting the greater need for inhibition in response to *Other* stimuli appearing on one's own side. In support for this hypothesis on motor inhibition, in this same condition we also found a large cluster of increased theta activity and reduced beta activity in pre-motor areas (SMA, preSMA, IFG, the primary motor cortex). Given the condition of action observation, it is plausible that mirror activity was embedded in this large cluster, also including the right TPJ, and possibly modulating the degree of inhibition required. Unfortunately, the turn-taking dynamic of the task which makes action inhibition and action observation occurring at the same time does not allow further specifications.

Furthermore, we found differences in the EEG sources in areas dedicated to spatial attention in both *Self* and *Other* contrasts (NC vs C). For the *Self* contrast, a bilateral increase in the theta band and a right decrease in the beta and gamma band were found in the SPL/IPL areas that have been associated to exogenous and endogenous shifts of spatial attention (Molenberghs et al., 2007), as well as a reduction in alpha activity in the right IFG/PMC, a region that has been linked to the detection of stimuli appearing in unexpected locations (Corbetta & Shulman, 2002). Coherently, for the *Other* contrasts, the alpha and theta band were found to behave differently in the IFG, where alpha oscillations increased bilaterally while the theta band was desynchronizing in the left hemisphere, suggesting a differential role of these bands in processes related to spatial attention.

Given the social context characterizing the JST, we expected to find evidence of the involvement of areas of the social brain. Interestingly, significant differences were observed contrasting the current density estimated of the *Self*-NC and *Self*-C in areas that are linked to social processing such as the mPFC, the STS and the precuneus (Hein & Knight, 2008; Van Overwalle & Baetens, 2009), see *Figure 6*.

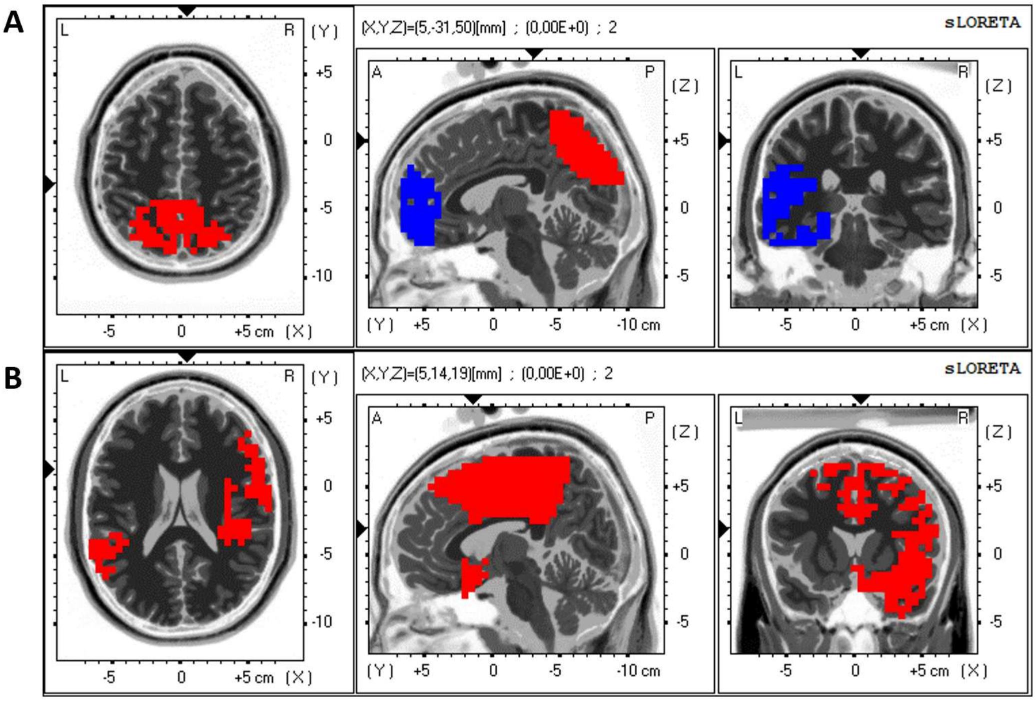

*Figure 6*: The anatomical distribution of significant *t* values in the theta band for A) *Self*-NC vs. *Self*-C and B) *Other*-NC vs. *Other*-C. Blue and red areas represent decreased and increased power, respectively, referred to the first term of comparison of the two contrasts (*Self* NC and *Other* NC, respectively).

Activity in the precuneus and the STS alone might be hard to interpret because of their involvement in different cognitive processes that are not strictly social (Hein & Knight, 2008). Nonetheless, the fact the differences in these regions for the theta band activity are extended to the mPFC supports the interpretation of these differences as being modulated by social factors. Indeed, activity in the mPFC has been consistently associated with the processing of self-relevant stimuli in a variety of tasks (Ciaramidaro et al., 2014; Gusnard et al., 2001; Knyazev, 2013; Northoff & Bermpohl, 2004). Our results confirm these assumptions demonstrating the involvement of brain areas dedicated to social processing, and self-other discrimination, replicating the results of other studies employing the JST finding the activity of the mPFC to be mediated by the spatial coding induced by a social setting (Dolk et al., 2012; Liepelt et al., 2016; Sebanz et al., 2007; Wen & Hsieh, 2015).

Even though our experiment was not designed to support a specific JSE account, it is relevant to note that, to perform a turn-taking task as the JST, brain areas related to social processes should be involved. Indeed, although some of the brain dynamics reflecting cognitive control that are necessary to respond to a spatially conflicting stimulus might be similar in a social and individual setting, the social frame in which participants are embedded during a JST cannot be ignored. In other words, if a parsimonious explanation for the resolution of the *socially* induced spatial conflict would require the involvement of conflict-related areas such as the insula or the ACC (that have been found to be active during the classic Simon task; Cespòn et al. 2020), these areas alone cannot account for the processes related to the acknowledgment of the presence of a co-agent. On the contrary, the desynchronization pattern found in our study for the theta band in the mPFC during *Self*-NC trials provides the evidence for self-related processing being not only mediated by the absence/presence of a co-actor (Sebanz et al., 2007; Wen & Hsieh, 2015), but also by the S-R correspondence of the stimulus. To provide a more detailed description of the modulation of correspondence and agent identification in the mPFC, we looked for differences in the absolute power of the theta band in this area in the four conditions. This explorative analysis revealed that theta desynchronization might be tied to the side of the stimulus, specifically the co-agent's side. One may speculate that since the conflict emerging during the JST is spatial in nature but induced by the social context, the self-other discrimination supported by the mPFC relies on participants mentally "dividing" the space on a self-other logic. As a consequence, the mPFC might be activated differently for what has been tagged by the participant as "my space" relative to "his/her" space. Because non-corresponding stimuli are appearing on "his/her" space, more time is needed to produce a response, as revealed by the JSE found in reaction times.

As previously stated in this Chapter, this conjecture remains speculative, but it might be interisting to consider functional links between the mPFC and socially induced spatial coding, as it would be in line with behavioural studies demonstrating the role of the spatial distance between co-actors and the reachability of a co-actor's response button in the emergence of the JSE (Iani et al., 2021).

In sum, our results confirm that, although detailed brain dynamics are yet to be specified, the presence of a co-actor is sufficient to trigger brain mechanisms related to social cognition. It has been largely stressed that, during a JST, ignoring the co-actor would lead to a better performance. Nonetheless, even if complex mentalizing abilities were demonstrated not to be necessary for the formation of action co-representations (Miss et al., 2022), the presence of a co-actor during a task with a turn-taking dynamic is sufficient to activate the mentalizing circuit. Therefore, it seems plausible that these areas are not *only* involved in performance of theory of mind, perspective taking, etc., which require high-level processes, but also in low-level features of joint action as those leading to the JSE.

### 3.6. Concluding remarks

The ability to coordinate with others is fundamental for joint action and social interactions. The JST has been extensively employed to investigate join action since it leads to implicit coordination. As different accounts of the JSE stress different aspects of the phenomenon (i.e., social or not social), one might integrate these observations by recognizing that even though general processing mechanisms might be a parsimonious explanation for a spatial S-R conflict, this conflict arises in a social context. Cognitive and social factors need to be equally addressed to understand information processing subserving joint action. The co-representation hypothesis proposed by Sebanz and coll. (2003) represented a revolutionary concept in the discovery of the JSE, which triggered a cascade of studies and theories trying to disclose its mechanisms. Nonetheless, if co-representation as a broad concept has proved to be a useful heuristic, direct evidence demonstrating that co-agents represent their co-actor's task rules *literally* "as their own" (Sebanz et al., 2003) is lacking. The referential coding account, on the other side, fits better with the data gathered in the last few decades on joint action and the JSE in particular (Lien et al., 2016; Wen & Hsieh, 2015; Yang et al., 2021) but it seems to underestimate the social context created by the presence of a co-agent.

Our study tried to depict an extensive and coherent picture (although not exhaustive) of the behavioral and neural processes subserving the JSE. The results of the present work replicated the behavioral data reported in the literature and extended the knowledge about EEG activity related to the JST, providing novel insights to the understanding of joint actions. To our knowledge, this study is the first describing both amplitude and latency features of the N2 and P3 components, revealing a delaying effect of action planning both on the N2 and P3 component and confirming their sensitivity to response inhibition and conflict processing.

More interestingly, we described for the first time the alignment of the JSE computed at a neural level between the co-agents. The simultaneous registration of the EEG signal from pairs of participants allowed us to demonstrate that conflict processing might be sustained by similar processes in the agent experiencing the conflict and in the one observing him/her resolving this conflict. Even if ERP synchronization might be hard to interpret, this finding should be seen as the tip of the iceberg of a complex inter-brain dynamic that might be unraveled by future studies investigating how the brains of co-agents are related during the JST. The exploration of inter-brain neural relations brings a new perspective on joint action that can potentially account for the complexity of social interactions, which is not entirely accessible through the investigation of isolated minds (Czeszumski et al., 2020; Konvalinka & Roepstorff, 2012).

Ultimately, we reconstructed the source of the EEG signal to identify the brain circuits related to the processes involved in conflict resolution, spatial attention and self-other discrimination. The main result is the conflict-related modulation of the mPFC which highlights the importance of the social dimension in the JST and demonstrates that activity in this brain region is not only sensitive to the absence/presence of a co-agent but also to the spatial coding of stimuli and responses. Further studies might explore whether and how this brain region specifically interact with the spatial coding of the response induced by the presence of a co-actor.

To conclude, even though the behavioral data accumulated in the last decades do not allow us to resolve the controversy about the “real” nature of the JST, the innovative brain recording tools and analyses recently developed might spread light on the processes subserving the JSE, providing a very detailed description involving both intra- and inter-brain dynamics. It must be recognized that the JST poses some limitations in the investigation of joint action, one above all is the inability to distinguish between action inhibition and action observation, because the moment where participants need to withhold the response coincides with the co-agent’s turn. Nonetheless, it has the crucial advantage to be suitable to isolate and hence study other specific aspects of joint action such as the mere presence of a co-actor, the turn-taking dynamic and the complementary relationship between the co-agents. Overall, the methods applied in this study to investigate the JSE proved to be very useful in the identification of low-level brain processes related to self-other discrimination that is at the basis of joint action and social interactions in general.

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# Appendix : Post performance questionnaire

Partecipante: A B

Sessione:

Conoscevo già la persona con cui ho fatto l'esperimento

- ☐ Si
- ☐ No

Se si, qual è il grado di conoscenza?

- ☐ L'ho vista una volta
- ☐ L'ho vista alcune volte
- ☐ La vedo sempre
- ☐ Siamo compagni di corso
- ☐ Siamo amici

La situazione sperimentale è stata:

Facile ☐ ☐ ☐ ☐ ☐ ☐ ☐ Difficile
Piacevole ☐ ☐ ☐ ☐ ☐ ☐ ☐ Spiacevole
Positiva ☐ ☐ ☐ ☐ ☐ ☐ ☐ Negativa

Competitiva ☐ ☐ ☐ ☐ ☐ ☐ ☐ Non competitiva

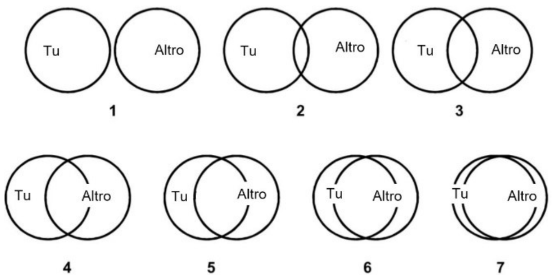
La mia prestazione è stata molto simile a quella della persona con cui ho eseguito il compito:

Completamente d'accordo ☐ ☐ ☐ ☐ ☐ ☐ ☐ Completamente in disaccordo

Se sei in disaccordo, scegli una delle seguenti opzioni:

- ☐ La mia prestazione è stata migliore
- ☐ La mia prestazione è stata peggiore

Quale tra queste immagini descrive meglio la relazione tra te e la persona con cui hai svolto ilcompito?



.

| | **Experimental situation: easy vs difficult** | **Experimental situation: pleasant vs unpleasant** | **Experimental situation: positive vs negative** | **Experimental situation: cooperative vs competitive** |
|---|---|---|---|---|
| Mean | 0.82 | 2.56 | 1.67 | 5.31 |
| Std. Dev. | 0.92 | 1.22 | 0.97 | 1.94 |
| Min | 0 | 1 | 1 | 1 |
| Max | 3 | 6 | 5 | 7 |

Table 9: Descriptive statistics for the subjective ratings of the experimental situation

| | **IOS** | **Competitiveness Index** | **Edinburgh inventory** |
|---|---|---|---|
| Mean | 2.58 | 9.68 | 0.73 |
| Std. Deviation | 1.73 | 2.14 | 0.26 |
| Minimum | 1 | 4 | -0.03 |
| Maximum | 7 | 14 | 1 |

Table 10: Descriptive statistics for the Inclusion of Other in the Self scale, Competitiveness Index and Edinburgh Inventory questionnaires