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Department of Psychology

You are in my plans:

**Neuro-cognitive and social components of dyadic motor interactions
revealed by the kinematics of a joint-grasping task.**

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FINAL DISSERTATION

International Doctor of Philosophy course in
Cognitive Social and Affective Neuroscience

XXVI cycle

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TABLE OF CONTENTS

Preface	5
1. Introduction	8
1.1. “Me and you in the brain”: a history of common coding	10
1.2. “We, together”: a story on joint action	19
1.3. Grasping, the experimental window	29
2. “Take the lead”: signalling, prediction and visuo-motor interference	36
2.1. Aim and hypotheses	36
2.2. Methods	38
2.3. Results	43
2.4. Discussion	54
3. Prejudiced interactions: predictive simulation and racial biases	57
3.1. Aim and hypotheses	57
3.2. Methods	59
3.3. Results	64
3.4. Discussion	73
4. “And yet they grasp together”: free interactions and interpersonal perception	76
4.1. Aim and hypotheses	76
4.2. Methods	78
4.3. Results	85
4.4. Discussion	97

5. Neurocognitive bases of joint action: shared goal coding in left aIPS	101
5.1. Aim and hypotheses	101
5.2. Methods	104
5.3. Results	112
5.4. Discussion	124
6. General discussion	128
References	135
Acknowledgments	153

Preface

We cannot solve our problems with the same thinking we used when we created them

A. Einstein

In the last decade, neuroscience research has begun to explore the neurocognitive bases of social encounters. Despite claiming to investigate the cognitive processes characterizing interacting individuals, most studies have focused on “isolation paradigms” (Becchio et al. 2010) which investigate “offline” social cognition, i.e. social cognition from an observer’s point of view (see Pfeiffer et al. 2013 for critical remarks on this approach). Thus, some authors now call for a Copernican revolution in the field, which would promote the shift from an individual to a “second-person” neuroscience (Schilbach et al. 2013) and validate the idea that – in real life – social interaction is much more than just a concurrent recruitment of the essentially isolated social knowledge of two or many individuals (see also Gallotti and Frith 2013).

One possible way to realize this shift in the frame of reference is moving from the study of single brains to dual brain recording (Hari et al 2013; Hasson et al 2012), an approach assuming that agents’ brain activity becomes coupled during the interaction and that this is what primarily constitutes the interactive experience. Although extremely promising, this research line is still facing a crucial puzzle, which is translating correlations between different brains activity in functional terms: indeed, it still needs to be clarified what psychological function inter-brain correlation is playing, and what is the difference between inter-brain correlations during on-line interactions and the ones reported when individuals share the same physical environment or are individually performing the same cognitive task (see for instance Hasson et al. 2004). However, a parallel (and somehow complementary) approach would be that of maintaining the individual as principal object of analysis, yet i) move to experimental set-ups that allow participants to interact with others during closed-loop processes, e.g. allowing on-line reciprocal mutual adjustments, and

ii) take into account the emotional engagement which characterizes social encounters (Schilbach et al. 2013). By doing so, it becomes possible to study how the emotional “interactive” context and the need to on-line adapt to a partner’s behaviour modulate the individual cognitive system. Eventually, this approach would lead to define what qualify cognitive and emotional processes as strictly “interactive”, providing dual-brain research with a more structured frame of reference.

The present work endorses this latter approach, and it investigates both socio-emotional and cognitive mechanisms which modulate cooperative dyadic interactions. To this aim, a novel interactive scenario was conceived: it requires participants to reciprocally coordinate and synchronize their reach-to-grasp movements during face-to-face interactions, performing on-line mutual adjustments in order to fulfill a common (motor) goal. Thus, our task forces participants to take the partner’s movements into account and to dynamically adapt to them. More specifically, the partner’s movements become part of each agent’s motor plan because they are essential components required to achieve the common goal.

This allows acquiring a “second person” perspective. Indeed, on the one hand, the study of *face-to-face* motor interactions enables to capitalize on evidence emerged from previous literature on action observation, and to directly investigate what characterizes situations wherein people not only observe but observe-to-interact with moving others. Suggestion is made that what characterizes joint action is the presence of a common goal (i.e. the “*shared*” goal) which organizes individuals’ behaviour and channels simulative processes. On the other hand, it provides the opportunity to move forward from investigations of merely cognitive motor processes and explore whether *socio-emotional variables* (e.g. role taking, ethnic stereotypes, or the feeling of not being appreciated) impact the quality of the interaction and modulate co-agents’ overt motor behaviour even when purely “instrumental” movements are required, as it is the case for the reach-to-grasp task adopted here.

Therefore, this work possesses a strong reference to past approaches to “interpersonal” motor representations (e.g. literature on “common coding”, Prinz 1997), but struggles to adopt a

new perspective: it aims to take into account that research on joint action does not deal with a single individual having his or her single brain processing other people's behaviour, but rather with an individual-in-dynamic-relation with others. We suggest this relation is built on the presence of a shared goal, and that it is "socio-emotional" in nature.

1. Introduction

We live our whole life dipped into an interactive social environment where we act in concert with others. From ball tossing to complex surgery operations performed four-hand, from partner-dance to team cooperation during a sport match, any activity dealing with interpersonal coordination implies people synchronizing, adapting to each other movements and communicating their respective intents, often without the need resorting to speech. In their seminal paper, Sebanz and co-authors (2006) define joint actions as activities involving two or more individuals who need to coordinate their actions in time and space in order to intentionally bring about a change in the environment. They suggest success in these activities “depends on the abilities: i) to share representations, ii) to predict others’ actions, and iii) to integrate predicted effects of owns and others actions” (Sebanz et al. 2006). From then on, a new field was born, and several empirical studies have been conducted to investigate the different neurocognitive processes which might be involved in the ability to coordinate one’s own actions with the ones of other people. Merging contributions from different research fields (e.g. dynamic system theory and study of language), several authors now endorse that a variety of processes, ranging from automatic entrainment (Schmidt et al. 2011) to strategic planning (Vesper et al. 2010), play a role during joint actions and are differently recruited depending on task demands and social factors (see Knoblich et al. 2011 for a review). When face-to-face interactions are taken into account, these processes also include diverse simulative mechanisms that previous literature on action observation has largely examined, mostly tackling the topic with classical “mirror neurons inspired” approaches (see Rizzolatti and Craighero 2004).

However, a primary issue in joint action research is the lack of clear definitions: most often, authors discuss their results taking advantage of rather elusive concepts and without providing the appropriate frame of reference; most evident is, in this regard, the use of terms like “shared representations” and “simulation”. Moreover, studies claiming to investigate “interactions” might

not always take into account that different cognitive processes might be involved depending on task constraints.

The aim of this section is to present an overview of cognitive processes relevant to investigations on joint action, in the attempt of providing clear definitions to frame the experimental studies described in chapters two to five. These studies focus on a specific sub-type of joint action: face-to-face motor interactions requiring agents to on-line adapt their movements to the ones of another person who is interacting with them by concurrently performing similar (“imitative”) or different (“complementary”) actions. Thus, reference to previous literature on action observation is crucial, and this section hence starts with an overview of research on “common coding” dealing with simulative processes involved in action perception. Suggestions is made that these simulative mechanisms might be divided between “active” (prediction) and “passive” (action-perception coupling) processes, and that both these sides of simulation are crucial during face-to-face interactions, yet they modulate behaviour at distinct levels of joint action planning and execution. Then, this section clarifies which is the crucial feature that differentiates action observation from joint action, namely the presence of *shared goals*, and description moves to other aspects that literature on joint action takes into account (e.g. *coordination strategies* as effort-distribution and signalling). Finally, it illustrates the general aims and the experimental set-up conceived to investigate face-to-face motor interactions in the studies presented in chapters two to five.

1.1. “Me and you” in the brain: a history of common coding

In science, moreover, the work of the individual is so bound up with that of his scientific predecessors and contemporaries that it appears almost as an impersonal product of his generation

A. Einstein

1.1.1. Visuo-motor interference and action-perception coupling

The “common coding approach” (Prinz 1997) deals with the intuition that perceived events (e.g. coding of observed actions performed by others) and action planning share a common representational domain. This idea can be traced back to the writings of authors in the nineteenth century (e.g. Harless 1861; Lotze 1852), including William James’ milestone *Principle of Psychology* (1890) where the author claims that “every mental representation of a movement awakens to some degree the actual movement which is its object”. This principle - also known as ideomotor theory – thus suggests in its “stronger” formulations that action observation, execution and motor imagery all depend on common mechanisms (see also Jeannerod 2006). More broadly, authors supporting this approach (Hommel et al. 2001; Prinz 1997, 1987; Greenwald 1970) suggested that the traditional stance asserting a complete separation between perception and action was not able to explain experimental evidence from so called induction and interference paradigms, showing that: i) certain stimuli induce certain actions by virtues of similarity, and ii) mutual interference occurs between perception of on-going movements and preparation and control of on-going actions (Prinz 1997). In this regards, prototypical examples are, for instance, studies on **visuo-motor priming** (Craighero et al. 1996), showing that the time needed to plan an action as indexed by reaction times (RTs), e.g. RTs required to grasp a bar oriented either clockwise or counterclockwise, increases if action execution is preceded by the observation of hand pictures which do not match the orientation required by the participant’s action, e.g. observing a hand

matching the posture to grasp the object clockwise when preparing to grasp counterclockwise (Craighero et al. 2002; see also Fischer et al. 2008 and Vogt et al. 2003 for similar experimental paradigms). Similarly, *visuo-motor interference* paradigms show that simple intransitive movements as finger lifting are facilitated (i.e. show faster RTs) when the go-signal is a similar hand action (imitative response) rather than an incongruent one (counter-imitative response, Brass et al. 2001, 2000).

The common coding approach gained tremendous popularity when physiological studies performed with single-cell recording on monkeys provided evidence that specific neurons within the premotor (Rizzolatti et al. 1996a; di Pellegrino et al. 1992) and parietal (Fogassi et al. 2005) areas of macaque brain fire both during execution of specific grasping actions and during the observation of the very same - or similar - actions executed by a different monkey / human agent (so called, respectively, strictly congruent and broadly congruent “mirror neurons”, MNs, see Rizzolatti and Craighero 2004 for a review). In line with these findings, a multitude of neuroimaging studies in humans showed that corresponding neural networks are recruited during action observation and execution (e.g. Grèzes et al. 2003; Decety et al. 1997; Rizzolatti et al. 1996b; see also Caspers et al. 2010 for a review), being recently confirmed by more direct evidence thanks to single-cell recording (Mukamel et al. 2010) and fMRI adaptation paradigms (Kilner et al. 2009; Chong et al. 2008); this led to suggest that a fronto-parietal simulative “mirror” network could be the neural substrate of the action-perception coupling effects shown, for instance, by visuo-motor priming and visuo-motor interference (Blakemore and Frith 2005; Kilner et al. 2003; see also Gallese et al. 1999). However, it is worth noting that most studies investigating visuo-motor interference effects between self-executed actions and those observed in others (Brass et al. 2000, 2001; Kilner et al. 2003) deal with intransitive actions which do not involve any object and have no obvious goal (e.g. finger lifting or aspecific linear arm movements), whereas “mirror neuron” inspired experimental paradigms usually regard goal-directed grasping actions. Notably, moreover, further studies applying both visuo-motor priming and interference paradigms demonstrated that

multiple factors (e.g. visual salience, object-directedness, stimulus-response compatibility, see for instance Jansson et al. 2007; movement direction, see for instance Tschentscher and Fischer 2008; and training, Borghi et al. 2007) need to be taken into account to explain these “visuo-motor” attentional effects.

1.1.2. “Mirroring” goals and intentions

Distinction between transitive (i.e. goal-directed) and intransitive (i.e. not goal-directed) actions becomes particularly relevant considering that studies investigating the functional role of the recruitment of motor areas within the fronto-parietal network during action observation (also referred to as *motor resonance*) show monkey MNs in premotor area F5 code the *action goal*. Indeed, they discharge only when grasping actions are aimed to specific objects (while not for hand movements or objects alone), and even if the final part of the action is occluded, provided the object to be grasped was previously shown in the occluded area (Umiltà et al. 2001). Moreover, MNs also discharge for action effects, e.g. when the monkey only hear the sound of action (Kohler et al. 2002), indicating both actions and their effects in the environment are coded in motor terms within the same neural substrate. Finally, MNs re-map tool-assisted goal-directed action (e.g. grasping an object using pliers) depending on the type of action (e.g. grasping an object) independently from movement kinematics (e.g. regardless the pliers imply flexing the finger – regular plier - or extending the finger - as in the case of inverse pliers -, Umiltà et al. 2008). Moreover, MNs in parietal area AIP seem to code the *intention* of the action, here defined as the “higher level” or “ultimate” goal of an action planned by an individual, e.g. they differentiate their response on the basis of whether the grasping action is aimed to place or to eat the grasped object (Fogassi et al. 2005). This evidence led to hypothesize MNs support “action understanding” (Rizzolatti et al. 2001): although largely criticized (see for instance Cook et al. in press), this term refers to the idea “mirror” simulation captures the action “semantics” (e.g. “grasping an object”) regardless (some) physical details of the movement involved, as in the inverse-pliers experiment (Cattaneo et al. 2009;

Umiltà et al. 2008; see also Prinz 2006). Namely, these neurons might support *perceptual discrimination* of an action by coding it in general motor terms, i.e. directly into the motor experience of the observer, without context-specific details. Remarkably, this claim is supported by a chain model of action organization (Chersi et al. 2011; Rizzolatti et al. 2006), suggesting MNs might support “action understanding” (or, in other words, perceptual discrimination of action based on action goals) thanks to the fact actions are organized in chains of motor acts (see also Fogassi and Luppino 2005). Within this framework, an action (e.g. eating a piece of food placed on the table) has an “intention” (i.e. eating the piece of food) which requires a chain of several goal-directed motor acts to be achieved (e.g. reach-to-grasp the food, grasp the food, bring the food to the mouth), each one possessing its own sub-goal; thus, MNs would simply code the goal of each motor act yet, being organized in chains which are co-activated during action observation, they would also automatically support recognition of the supra-ordinate action intention (see also Bonini et al. 2013).

Studies on humans support these claims. For instance, Transcranial Magnetic Stimulation (TMS) studies measuring cortico-spinal facilitation evoked by single-pulse TMS on primary motor cortex during action observation (Fadiga et al. 1995) show simulation is somatotopic, since actions are mirrored in a body-centered frame of reference (Urgesi et al. 2006a), and codes the final posture of the observed movement (also referred to as the “action goal”, Cattaneo et al. 2013, 2009; Jacquet and Avenanti 2013; Urgesi 2010, 2006b); these studies also show that ventral premotor cortex (vPM), the homologous of monkey area F5, is responsible for this facilitation (Avenanti et al. 2013a; Cattaneo et al. 2010), and that this area also supports action discrimination during perceptual tasks (Jacquet and Avenanti 2013; Avenanti et al. 2013b; Candidi et al. 2008; Urgesi et al. 2007). Finally, the amount of previous experience acquired with the observed action modulates motor resonance (Loula et al. 2005; Calvo-Merino et al. 2005; Repp and Knoblich 2004; Knoblich and Flach 2003), supporting the notion “mirror” simulation codes the perceived action directly into the

observer's motor repertoire. Neuropsychological reports also supported these findings (Moro et al. 2008; Pazzaglia et al. 2008).

1.1.3. Prediction and emulation

All the above mentioned literature refers to tasks when monkey or human participants are required to passively observe actions performed by others or, if participants are moving as in visuo-motor interference paradigms, the observed action is irrelevant to the task. Thus, the action-perception coupling leading to visuo-motor interference effects as well as motor resonance evoked by the observation of others' actions might be regarded as "**passive**" **simulative mechanisms**. However, as suggested by Roger Sperry in 1952: "*Perception is basically an implicit preparation to respond*. Its function is to prepare the organism for adaptive action. The problem of what occurs in the brain during perception can be tackled much more effectively once this basic principle is recognized". The ideomotor principle at the basis of common coding was itself grounded in two conditions (see Elsner and Hommel 2001): i) it is required that movements and their ensuing effects become associated, so that, given a movement, it is possible to predict its effect, and ii) this association is required to be bidirectional, so that it becomes possible to predict the required movement given the anticipatory representation of the intended effect (see also "forward" models and "inverse" models, respectively, in computational modeling, e.g. Wolpert et al. 2003). As a matter of fact, evidence of goal coding in F5/vPM might also be interpreted as evidence that sensorimotor simulative mechanisms are anticipatory in nature, since the motor system simulate future postural states along movements' path during others' action observation (Urgesi et al. 2010, 2006b; Umiltà et al. 2001), thus allowing the monitoring of their deployment in time (Candidi et al. 2012; Aglioti et al. 2008). Moreover, the motor system is already pre-activated when we expect others to act (Kilner et al. 2004), and during observation of others' hand actions the observer's gaze precedes the action on the object ("goal") and predicts the forthcoming grip, just like it happens during action execution (Flanagan and Johansson 2003).

Several accounts have theoretically framed this notion as **“active” anticipatory simulation**. For instance, Grafton and Hamilton (2007) suggested that action observation can be considered in terms of *hierarchical inference*; namely, they suggest a distributed fronto-parietal network might code actions in terms of the link between “motor intentions” (i.e. action goals) and their proprioceptive and/or exteroceptive (e.g. visual) consequences, independently from whether the network was activated during action planning or action observation (i.e. independently from agency). Similarly, the *chain model of action organization* (Chersi et al. 2011; Fogassi and Luppino 2005) suggests that the activation of a motor act in a given context (e.g. grasping a piece of food) would anticipatorily activate a neuronal chain associated to a specific motor intention (e.g. grasping-to-eat, see also Bonini et al. 2013). Moreover, *emulation theory of representation* (Grush 2004) postulates that internal models developed during the interaction between the body and the environment may be run off-line in order to permit the estimation of the outcome of observed actions. Finally, Friston and colleagues (2011) have applied a broader theory of brain functioning based on Bayesian inference (“Free energy principle”, Friston et al. 2006) to the case of action observation and suggested that mirror neurons allow for *predictive coding* of others’ action in terms of their consequences in the environment in order to minimize sensory (e.g. visual or proprioceptive) “surprise”, which corresponds to prediction error; this would ultimately optimize the ability to anticipatorily adapt to a constantly changing world (Kilner et al. 2007). In short, these approaches share the intuition that i) others’ actions might trigger predictions about the outcomes of the observed movements, and ii) this does not necessarily require simulation of the movement itself, e.g. this does not require a one-to-one matching at the kinematic level. In a similar vein, studies on imitational learning in children (see Wohlschläger et al. 2003; Bekkering et al. 2000) suggest actions might be imitated (i.e. overtly simulated) disregarding the means by which they are accomplished and purely focusing on the “final result” (i.e. the ultimate goal), which can also be considered as what allows “making sense” of actions performed by others (“teleological reasoning”, Gergely and Csibra 2003), e.g. the

experimenter performs unusual head movements on a box in order to open it, and the child imitates the action by just opening the box with his or her hand (see also Csibra 2008).

Crucially, all evidence referring to *anticipatory simulation of action goals* (i.e. prediction) deal with the observation of goal-directed actions. This remark might seem trivial, as no goal could be anticipated in case the action implied no goal. However, it underlies a crucial difference between this literature and studies on pure visuo-motor interference due to action-perception coupling (which all imply actions with no obvious goal), and suggests “active” and “passive” sides of action simulation might be distinct (although strictly interconnected) processes.

1.1.4. Good reasons why this concerns joint action

Now a crucial question might arise: why is this literature on action observation relevant to research on joint action? Although “joint action” might refer to almost any interactive activity, when face-to-face motor interactions are taken into account we handle situations requiring agents to on-line adapt their movements to the ones of another person who is concurrently performing a different action in front of them. Thus, agents are moving while simultaneously observing another moving agent. As a consequence, in line with literature on action observation, it is likely that some sort of simulative mechanisms are recruited in interactive contexts. However, what still needs to be established is which kind of simulation plays a role during joint action planning and execution. See Figure 1.1.

Action-perception coupling mechanisms might be relevant in joint action since they might help to establish a common ground allowing agents to be “on the same page” without the need of symbolic communication. For instance, automatic coupling between interactive agents leads to behavioural phenomena as involuntary mimicry and synchronization (see paragraph 1.2.2.). Crucially, “subjective” familiarity with the observed model plays a crucial role. For instance, racial bias simply induced by a model’s skin-colour may strongly modulate sensorimotor mirroring of observed neutral actions and emotive states (Gutsell and Inzlicht 2010; Molnar-Szakacs et al. 2007; Désy and Theoret 2007) and somatomotor inhibition associated to observation of painful

stimulation (Azevedo et al. 2012; Avenanti et al. 2010). Moreover, ethnic categorization modulates the recruitment of the fronto-parietal simulative network during intention understanding (Liew et al. 2011) and imitation (Earls et al 2013; but see also Losin et al. 2012). Thus, it seems that although humans are prone to automatically resonate with others, this happens less readily when they classify other people as “out-group” members or unfamiliar individuals. This might have an impact on the quality of interaction as well, because it might mine the procedural common ground which allows partners’ alignment on the same page.

However, joint action is not just acting *while* another individual is moving as well. Joint actions deal with *moving together*. This has at least two main consequences. Firstly, interaction cannot rely on purely “passive” simulative processes. Indeed, far from passively reacting to the others’ behaviour, individuals involved in joint actions need to make reliable predictions about the outcomes of others’ movements in order to efficiently and prospectively adapt their behaviour accordingly (Sebanz and Knoblich 2009; Keller et al. 2007; Sebanz et al. 2006; Wilson and Knoblich 2005; Knoblich and Jordan 2003). As a consequence, ***prediction*** becomes crucial. In keeping, it has been shown that in the absence of on-line sensorimotor feedback about a partner’s movements, individuals achieve good temporal coordination on the basis of internal motor predictions (Vesper et al. 2013). Secondly, agents voluntarily taking part to an interaction have a minimal degree of awareness that the task requires the partner’s contribution to be accomplished, e.g. if I ask someone else to help me moving a big table, I know the other person has to lift and move one of the table sides. Namely, agents have a minimal degree of awareness that i) they are sharing a *common goal* (see paragraph 1.2.1.), and ii) the achievement of this common goal requires both partners’ contribution, iii) which might be distributed according to some task constrains; as a consequence, others’ action deployment might be guessed on the basis of these task constrains. More precisely, *task sharing*, i.e. partner’s reciprocal knowledge regarding stimuli and constrains under which the joint action will be accomplished, might guide predictions. Therefore, minimal motor cues from the partner’s actions might deal to clear predictions about the action outcomes,

thanks to a reduction of degrees of freedom. The extreme consequence of task sharing is that a partner’s action might be predicted (and simulated) even when no physical action is observed (see for instance Vesper et al. 2013; Ramnani and Miall 2004).

	<u>Observation</u>	<u>Observation + Execution</u>
PASSIVE PROCESSES movement level (spatial features)	Motor resonance	Visuo-motor interference (motor contagion)
ACTIVE PROCESSES action level (goals)	Anticipatory simulation Other’s error monitoring	Joint action <i>common goals and task-sharing</i>

Action-perception coupling

Action-discrimination

Prediction

Figure 1.1. Simulative processes classified according to a “passive” and “active” criterion.

To conclude, while predictions during passive observation are simple and immediate, predictions during joint action can be based on structured models about the link between others’ movements and task constrains: this allows preparing an adaptive motor response a considerable time ahead. Moreover, while both “passive” (i.e. action-perception coupling) and “active” (i.e. prediction) sides of simulation might modulate the ability to interact with others, they might tackle two different levels of the planning process. Empirical investigations need to take into account these distinctions and clearly define which level they refer to.

1.2. “We, together”: a story on joint action

*All of science is nothing more
than the refinement of everyday thinking*

A. Einstein

Imagine Anne and John need to move their brand new crystal table from the living-room to the kitchen, since their son Mat has invited his 10-year old friends for his birthday party and Anne does not want the table to be used as goal post for the indoor football match the kids will most likely decide to organize last minute. The crystal table has a huge flower vase on it, and Anne decides it is handier to leave it there (“not to risk ruining those gorgeous lilies”) and move the all stuff at once. Since the table is quite big, John decides to help her. Thus, they place themselves at the opposite sides of the tables, facing each other, and synchronously lift the ensemble. They actually must be very synchronous; otherwise the vase will roll down. Yet, they do not even need to speak to coordinate: at the right moment, John emphasizes bending his legs and Anne knows is the right moment to pull her side of the table up. Then, they start walking towards the kitchen: since they’re facing each other, Anne is walking onwards pushing the table, while John is walking backwards pulling it. When approaching the kitchen door, troubles begin: since the room is long and narrow, they need to turn as the jamb is passed to have enough space to bring the table in. Nevertheless, they succeed: as soon as John enters the room - pulling and walking backwards -, he pushes slightly on his right to help Anne passing; she (pushing the table onwards) then turns her side on the opposite direction, and the hindrance is easily overcome. While doing this, Anne tilts a bit the table on one side...you could already see the vase slowly taking its way to the edge...but John perceives the tilting and put it back without even realizing it. Forty seconds, and the table is safe in the kitchen; it took much longer for the reader to have a glance at this paragraph than have this done for them.

Lifting and moving a table together is one of the easiest every-day life examples to explain what joint actions are. Basically all people have tried to do this at least once, typically succeeding, without even realizing how many computations their brain was dealing with: indeed, this task requires to synchronize but also adapt to the partner's movements, to predict his or her next step but also to signal (often through purely motor cues) the next step we intend to take. Sebanz and co-authors (2006) suggest success in these activities “depends on the abilities: i) to share representations, ii) to predict actions, and iii) to integrate predicted effects of own and others actions” (Sebanz et al 2006). Trying to describe what “prediction” means has been the aim of the previous section. This part will focus on describing how “shared representations” have been defined and how the integration between predicted effects of one's own and others' actions might be realised. Moreover, other processes possibly involved in joint action, i.e. entrainment (Schmidt et al. 2011; Marsh et al 2009) and signalling (Pezzulo and Dindo 2011), will also be addressed.

1.2.1. “*Philosophy phirts*”: shared goals

Philosophical investigations on joint action aim to identify features of some or all of these cases in virtue of which human activities count as joint actions. One philosophical account most influential in psychology is Michael Bratman's one, which postulates joint actions are ‘shared intentional activities’, which means activities explainable by *shared intentions* (Bratman 1999, 1992). To illustrate what shared intentions are, Bratman explains their functional role is to: (i) coordinate activities; (ii) coordinate planning; and (iii) provide a framework to structure bargaining. In other words, if, for instance, we share the intention of cooking dinner together, this shared intention will allow us to structure negotiations to decide what to cook or how to cook it, assuming that we are going to cook it together (“structure bargaining”); coordinate our planning by each bringing complementary ingredients and tools, and coordinate our activities by preparing the ingredients in the right order. Moreover, Bratman's definition also suffices to rule out certain cases where,

intuitively, there is no shared intention, e.g. the case where we each intend to cook dinner, but you want to cook your fish and I want to make my cake.

This definition of shared intentionality has inspired interpretations of empirically-oriented research. For instance, Tomasello et al. (2005) argue that developmental studies on cooperation in children show that what characterizes human cognition is precisely the ability to share intentions between individuals, namely shared intentionality.

However, these accounts refer to activities which go far beyond immediate *hic et nunc* on-line coordination between agents. For instance, the example of “cooking dinner together” rather implies a long sequence of both joint and individual actions, e.g. from phone up your friend and invite him for dinner to pour the soup in his dish when it is ready. Thus, they rather refer to what Searle (1983) defines “prior intentions”, namely the initial representation of the action goal prior to the actual initiation of the action. Depending on the level of abstraction, this might also refer to an intention which will generate an action after a considerable amount of time, e.g. the intention to pass the exam makes we study the whole night. On the contrary, the focus of this work is on a rather different sub-type of joint actions, namely face-to-face motor interactions requiring agents to on-line adapt to each other movements. Thus, assuming such detailed and “abstract” representations as the one postulated by the philosophical accounts described above (Tomasello et al. 2005; Bratman 1999, 1992) seems unnecessarily restrictive. On the other hand, these approaches undeniably highlight that when two or more people need to coordinate their behaviour, “something” is needed to support this coordination. This is the reason why *shared goals* have been call into play (Butterfill 2012). With regard to the aims of the present work, three features of shared goals are crucial:

- i) *one goal, two or more agents*: there is a single goal, G, to which each agent’s actions are (or will be) individually directed;
- ii) *expectations about goal-directed actions*: each agent expects each of the other agents to perform an action directed to the shared goal;

- iii) *expectations about a common effect*: each agent expects this goal to occur as a common effect of all actions directed toward it, i.e. both his or her own and the partner's ones.

Framing research on joint action as “research on actions involving two or more agents *sharing a common goal*” implies being able to explain (at least at the theoretical level) what might support agents' ability to “integrate predicted effects of owns and others actions” (Sebanz et al. 2006). Namely, postulating joint actions are characterised by the presence of a common goal explains why predictions about the partner's action effects are included in the agent's motor plan: indeed, if Anne and John want to lift and move their table from the living room to the kitchen, and this is their common goal, they both know that, in order to have the table moved, each of them needs to lift and move his or her own table side, and that –given some task constrains- Anne has to push while John has to pull. Thus, “John pulling” is already within Anne's motor plan when she decides to push her side of the table; more precisely, she would not even push the table if she did not predict John would pull his side, and she can predict John would pull his side since she knows they both share the common goal of moving the table to the kitchen. In other words, having a common goal allows agents to coordinate their interactions by representing the others' actions as part of the joint action planning, in purely motor terms, without the need of any “abstract” form of intention sharing.

It is worth noting that the definition of shared goals provided above might partly overlap with what some authors have defined *task sharing* (see Sebanz et al. 2006 for a review): indeed, stating Anne and John share the common goal of moving the table to the kitchen might be the same as stating Anne and John share the task of moving the table to the kitchen. However, shared goals do not overlap with *task co-representations* (or simply “shared representations”) as they have been defined by studies on joint attention (Atmaca et al. 2008; Tsai et al. 2008; Sebanz et al. 2007, 2005, 2003; see also Wenke et al. 2011 for a critical review), because these latter studies address situations in which no shared goal is provided. Indeed, this research line typically investigates situations in which one binary choice task with two competitive target stimuli (e.g. paradigms leading to Simon effect, Tsai et al. 2008, Flanker effect, Atmaca et al. 2011, and SNARC effect,

Atmaca et al. 2008) is split between two participants, with each participant responding to only one of the targets in turn-taking, i.e. each participant's turn is defined according to which target is presented, since each participant has "his or her own target" to respond to. These "joint" conditions are then compared to i) individual conditions in which participants perform the same single go/no-go task alone, i.e. they are required to respond to one target only and to ignore the other, and ii) individual conditions in which participants perform the whole binary choice task alone, i.e. they have to provide different responses according to which target stimulus is presented. These studies consistently showed that, although in principle performance in the joint condition should resemble the individual go/no-go one (since in both cases participants have to attend to one target stimulus only and to ignore the other), yet it instead parallels performance in the individual binary choice condition: namely, participants involuntarily take the co-actor's task into account in the joint condition as they had to respond to both target stimuli, albeit they are explicitly instructed to respond to their target stimulus only and to ignore the other. To sum up, these results show humans have a tendency to form "task co-representations" which specify not only one's own but also a co-actor's task, even if the co-actor's task is irrelevant to (or even interfering with) one's own task fulfillment. Thus, these studies conceptually resemble, within a different domain, interference effects showed by studies on action-perception coupling. Namely, they refer to incidental and automatic (i.e. "passive") processes recruited when agents act side-by-side. Just as visuo-motor interference has its "active" counterpart in anticipatory simulation (i.e. prediction) during joint action, shared goals are "active" ingredients of joint action planning, and turn the attentional interference generated by involuntary task co-representation into an active tool to integrate predicted effects of the partner's action within the agent's motor plan.

1.2.2. From entrainment to communication: an emergent-planned continuum

In the attempt to classify the several processes involved in joint action, Knoblich et al. (2011) have suggested they might be arranged along an emergent-planned continuum (see Figure 1.2.).

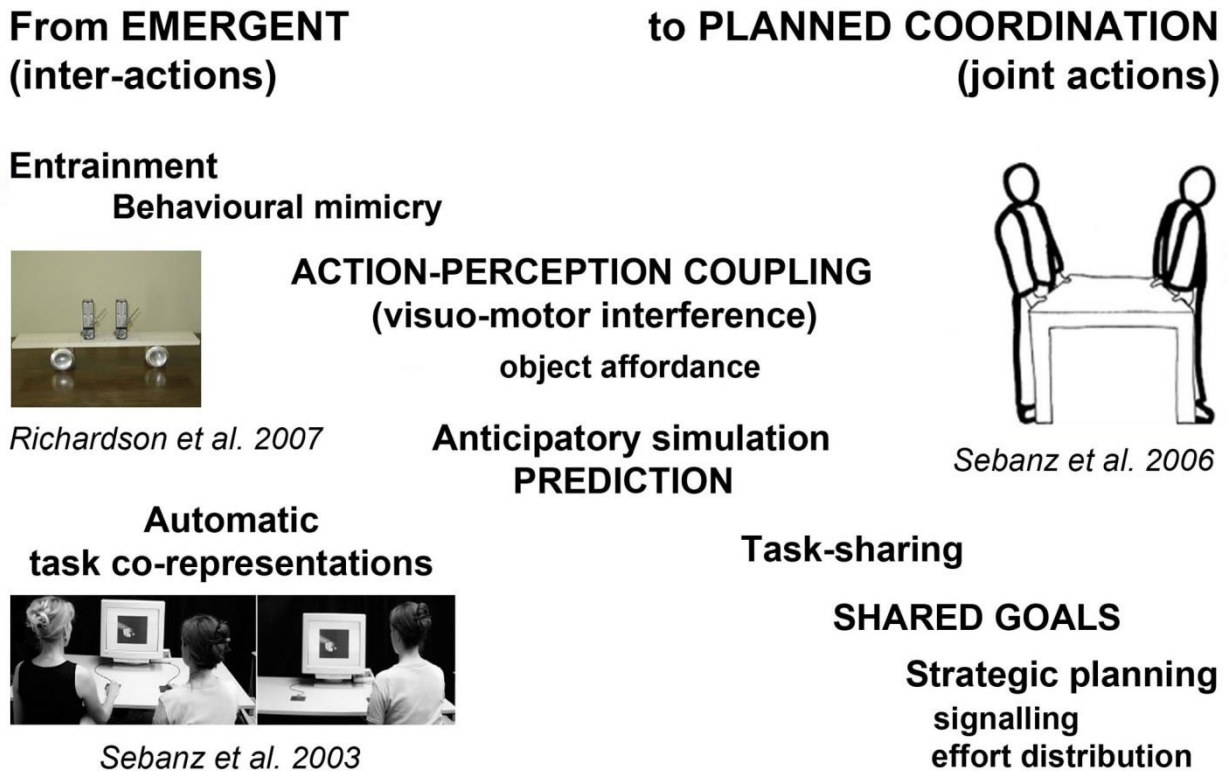


Figure 1.2. Classification of motor processes investigated by literature on joint action arranged according to an emergent-planned continuum, as proposed by Knoblich et al. (2011). Suggestion is made that the emergence of automatic task co-representations shown by studies on joint attention differs from task-sharing emerging during joint actions due to the lack of a shared goal linking co-agents.

At the very left side of this continuum, studies on spontaneous temporal synchrony and *entrainment* mechanisms (Schmidt et al. 2011; Marsh et al 2009) are placed. In physics, entrainment has been used to refer to the process whereby two interacting oscillating systems, which have different periods when they function independently, assume a common period (usually falling into synchrony, but other phase relationships are also possible). The concept was introduced by the pendulum clock inventor, the Dutch physicist Christian Huygens, who noticed, in 1666, that the pendulums of two clocks mounted on a common board gained synchronized oscillations; in

keeping, ecological psychologists have used the term to describe evidence that people end up spontaneously synchronizing even when they are not explicitly planning to act in concert: people placed side by side fall into the same walking patterns (Van Ulzen et al 2008) and tend to coordinate the swinging of hand-held pendulums (Schmidt and O'Brien 1997), clapping (Neda et al. 2000), tapping (Oullier et al. 2008) and rocking chairs frequency (Richardson et al. 2007, 2005); these effects resemble the ones occurring in mechanical and biological systems, although human partners are not mechanically coupled. This “behavioural dynamic perspective” (Schmidt et al. 2011) is worth taking into account for at least three main reasons: i) it helps explaining what supports temporal coordination during the interaction; ii) it provides new hints to explain why multiple individuals gathered in the same place (e.g. the audience of a crowded arena) tend to act in a similar way although being completely unaware of this; iii) suggests at least some aspects of interpersonal coordination can be explained only if separate agents are considered as a single coordinated entity (Marsh et al 2009; Spivey et al. 2007): recent studies on brain-to-brain coupling (see for instance Hasson et al. 2012 for a review) actually capitalise on this intuition.

However, suggestions have been made that “communication” (either eye-contact or being involved in conversation) is what creates the link necessarily to bond the interactive agents and create entrainment between humans. This suggests other processes rather than pure physical oscillatory coupling might be the sources of involuntary temporal coordination between interactive agents. For instance, it may be due to the fact individuals are acting in the same environment and thus follow the same environmental motor cues (affordances) and/or are influenced by similar action-perception coupling mechanisms (Brass and Heyes 2005).

Finally, the other facet of spontaneous interpersonal coordination is *behavioural mimicry*, i.e. the spontaneous reciprocal imitation of gestures, postures, mannerisms, and other motor acts in interacting individuals, e.g. during conversation (Chartrand and Bargh 1999). The relation between interactional synchrony and mimicry is quite complex (see Chartrand and Lakin 2013 for a review), because whereas behavioural mimicry always yields behaviours that are similar in form and close in

timing, interactional synchrony may or may not yield behaviours that are similar in form; moreover, mimicry might result in synchronicity, yet synchronicity might support mimicry. Further research is needed to clarify this issue. However, what it is worth noting here is that although all the above mentioned processes are considered “emergent” as they spontaneously arise without conscious awareness, they –by definition- emerge during voluntary coordination as well. Thus, studies on voluntary coordination during face-to-face interactions ought to take them into account. This becomes particularly relevant when considering both spontaneous synchronization and mimicry have been shown to be profoundly modulated by social factors. For instance, it has been shown that being involved in synchronous interactions promotes perceived similarity with others and improves cooperation and altruistic behaviour (Valdesolo et al. 2011, 2010; Wiltermuth and Heath 2009) and that –from the opposite perspective- affiliation promotes mimicry as often mimicry promotes affiliation (Van Baaren et al. 2009; Chartrand and Bargh 1999). As a consequence, social factors might have an impact on the ability to interact with others (also) since they modulate these emergent processes, which in turn might constitute the building bricks to establish a social/emotional bond between interacting agents.

At the opposite side of the emergent-planned continuum are situations where individuals voluntarily plan to work together. In these cases, explicit shared goals are at play. As described in the previous paragraph (1.2.1), the term task co-representation (or simply “shared representations”) has also been used in the attempt to explain evidence that individuals tend to take other people’s task instructions into account even if they are irrelevant to their own task. Nevertheless, in most cases humans overtly plan to cooperate: thus, task co-representations become explicit *task sharing* (and linked to *shared goals*). Namely, these interactions require a minimal degree of awareness not only of the fact that a co-agent X is there acting with me (Wenke et al. 2011), but also that intended outcomes can only be achieved thanks to his or her support (“Me + X” representation, Vesper et al. 2010). As a consequence, individuals might apply specific *strategies* to achieve coordination. For instance, it has been shown individuals *reduce temporal variability* of their own movements to

become predictable as an effective strategy to support temporal coordination in the absence of visual feedback about the partner's performance (Vesper et al. 2011; Konvalinka et al. 2010). Moreover, *effort distribution* based on task constraints also plays a role: when partners aim to achieve coordination but need to do so accomplishing different sub-task which imply different levels of complexity, the partner with the easier task adapt to the other's constraints (e.g. slows down his or her own movements) to achieve synchronicity (Vesper et al. 2013). Finally, *signalling* strategies have also been described (Pezzulo and Dindo 2011): if asymmetry of information is present between partners, i.e. if one partner's task requires him or her to guide the other agent towards the achievement of the common goal, then individuals tend to reduce movement variability and amplify movement features to help the partner disambiguating their own actions and intentions (see also van der Wel et al. 2011; Sartori et al. 2009), paralleling some sort of strategies that have been described in the verbal communication domain (Clark 2002, 1996). It is worth noting that these strategies all imply the presence of task sharing and shared goals: indeed, partners apply strategies to coordinate (e.g. signalling their intentions to the partner) only if they are aware of the partner's task-constraints, and thus chose to support their partner's task achievement in the service of the shared goal fulfilment.

With regard to both "active" and "passive" simulative processes (i.e. action-perception coupling and prediction), they are placed somewhere in between the emergent/planned extremes of the continuum. Indeed, while action-perception coupling is a rather involuntary process and might even be considered the mechanism at the basis of behavioural mimicry and motor contagion (Blakemore and Frith 2005), emulation and prediction might be described as key-processes supporting joint action motor planning. However, the distinction between emergent and planned processes might be misleading, because agents might voluntary choose to become predictable in order to synchronise as a results of an explicit coordination strategy (Vesper et al. 2011), while "task co-representations" spontaneously emerge when agents are not required to coordinate at all (see Wenke et la. 2011), and are modulated by social variable just as behavioural mimicry and

synchronicity (Iani et al. 2011, Hommel et al. 2009). In a similar vein, the shift from “passive” (visuo-motor matching) to “active” (prediction and emulation) simulative processes is neither an all-or-none event (the processes might interact each other) nor under the agent’s control, being rather task dependent. Thus, the classification is not meant to define different “kinds of interaction”, whereas it is a useful tool to remember *any interaction* might be studied at different levels, depending on the experimental questions. The following paragraph provides an overview of which aspects have been addressed by the empirical section (chapters 2 to 5) of the present work.

1.3. Grasping, the experimental window

The hand is the visible part of the brain

I. Kant

The difference between a helping hand and an outstretched palm is a twist of the wrist

L. Leamer

1.3.1. General aims

The present work had the primary aim to develop a novel interactive scenario able to investigate realistic face-to-face dyadic interactions within a naturalistic and yet controlled experimental environment. Indeed, the present work was meant to support investigations of closed loop processes requiring pairs of naive individuals to learn how to reciprocally adapt their movements on-line, and to allow studying the impact of “interpersonal” socio/emotional reactions realistically induced in the participants on individuals’ motor behaviour. To this aim, a new experimental paradigm was conceived: it requires participants to reciprocally coordinate their reach-to-grasp movements towards two bottle-shaped objects in order to be as synchronous as possible and thus maximize their common pay-off (see Figure 1.3. and paragraph 1.3.2 below for a detailed description).

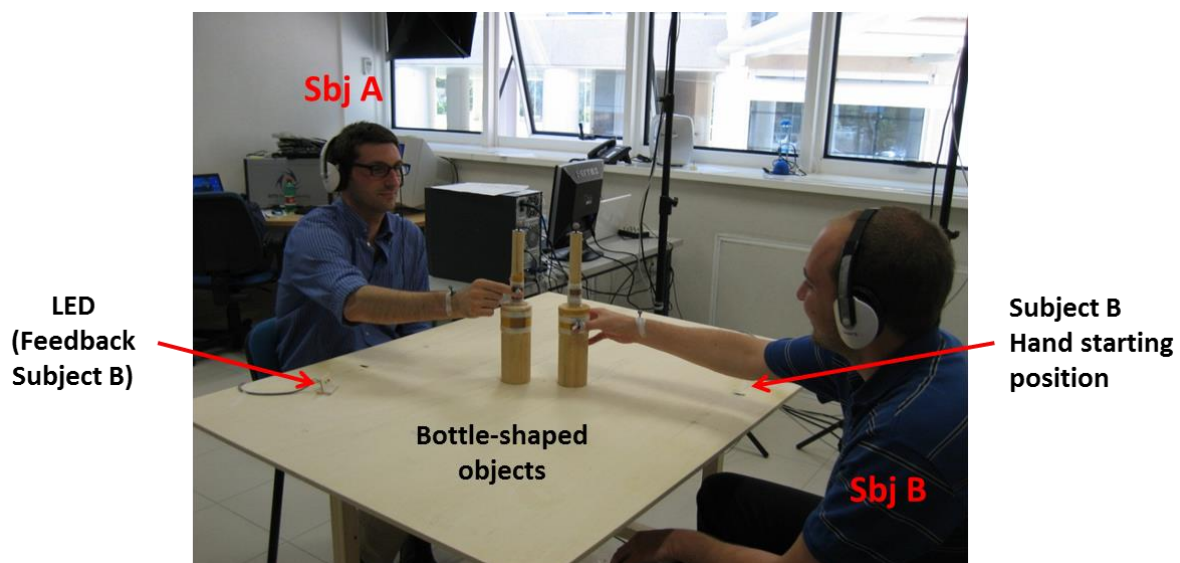


Figure 1.3. The experimental set-up.

Four crucial features of this paradigm are worth taking into account: participants were instructed to perform with a partner a face-to-face motor task which i) implied a *common goal* (i.e. being synchronous) that - in order to be fulfilled - required participants to achieve each one his or her own motor sub-goals (i.e. required them to grasp each one his or her own bottle-shaped object), but ii) each participant's motor sub-goal depended on the partner's action (i.e. the task required *mutual adjustments*); moreover, in different experimental conditions, the task required iii) participants to perform either *imitative* or *complementary* movements with respect to their partner's one, and iv) to adjust to the partner's movements either in *time* only (being synchronous) or in *time and space*. As a consequence, we have been able to explore the impact of different simulative mechanisms when participants not only observe but observe-to-interact-with moving others. Indeed, the comparison between imitative and complementary movements indicates whether simulation of the movements observed in the partner influences participant's action execution; yet, while visuo-motor interference would emerge in complementary actions independently from the experimental condition, anticipatory simulation would emerge only when predicting the partner's movement is relevant to the participant's task fulfillment (i.e. only when prediction and adjustments in space are required). Besides, our task enables to analyze correlations between partners' motor behaviours, thus allowing to investigate the emergence of automatic entrainment; finally, the analysis of which strategies participants apply to maximize their synchronicity (and, consequently, their common pay-off) consents to make inferences on the presence/absence of task sharing during the experiment. We investigated whether the above mentioned processes are modulated by the following socio-emotional variable:

- Role-taking (chapter 2),
- Ethnic biases (chapter 3),
- Interpersonal perception and feeling of not being appreciated by the partner (chapter 4).

We selected reach-to-grasp movements to explore this issue since grasping movements have been largely described both in terms of their kinematic features (Jeannerod 1984, 1981) and in terms of their neural bases (see Castiello 2005 for a review), thus becoming an “experimental test-case” for the study of goal directed actions (Grafton 2010). For instance, it has been shown that specific kinematic parameters (e.g. grip aperture and reaching trajectory) are modulated not only by object features (Mark et al. 1997; Goodale et al. 1994) and by the agent’s action goals (Ansuini et al. 2008, 2006) but also by social factors as an agent’s cooperative or competitive intention (Becchio et al. 2008a, 2008b; Georgiou et al. 2007, see also Becchio et al. 2012 for a review). Moreover, grasping neurophysiology has been largely explored in human and non-human primates both during action observation and execution (see Grafton 2010; Castiello 2005; Rizzolatti and Craighero 2004 for a review), providing a well-established neuro-cognitive model which links different neural substrates with the ability to perform grasping in different conditions. It is thus possible to selectively manipulate the contribution of these neural substrates (and, consequently, of their related motor/cognitive functions) during interaction with others by means of Transcranial Magnetic Stimulation (TMS). More specifically, we aimed to identify a possible neural substrate of shared goal representation because this is –in our view – the crucial feature which differentiates joint actions from individual actions performed synchronously with another individual. To this aim, we applied an inhibitory TMS protocol to investigate whether inhibition of different brain areas within the grasping network impairs coordination during complementary joint actions (chapter 5).

1.3.2. The interactive task

Experimental set-up

The experimental set-up retained similar features in all studies. Participants were comfortably seated at the working surface, a rectangular table of 120 x 100 cm. They were required to reach and grasp a bottle-shaped object (30 cm total height) constituted by two superimposed cylinders with different diameters (small, 2.5 cm; large, 7.0 cm) and placed next to centre of the working surface,

45 cm away from the participant and 5 cm on the right of the midline. The bottle-shaped object dimensions were designed to prompt a particular type of grip: namely, while grasping the small cylinder (i.e. the higher part of the bottle) would elicit a precision grip, grasping the large one (i.e. the lower part of the bottle) would elicit a power grip. In order to record participants' touch-time on the bottle, two pairs of touch-sensitive copper plates (one per each cylinder) were placed at 15 cm and 23 cm of the total height of the object. Before each trial, participants positioned their right hand on a start-button placed at a distance of 40 cm from the bottle-shaped object and 10 cm on the right of the midline, with their index finger and thumb gently opposed. When the study involved two participants who needed to synchronize and adapt to each other's movements (chapter 2 and 4), they were seated opposite each other in front of the working surface and the set-up configuration was equivalent for both of them, allowing each one to reach and grasp his or her own bottle-shaped object (see Figure 1.4, panel a). When the study involved one participant interacting with a virtual partner (chapter 3 and 5), participants watched a 1024x768 resolution LCD monitor placed on the table at a distance of approximately 60 cm from their eyes (see Figure 1.4, panel b).

Participants' task depended on the study; however, it always included the instruction of being *as synchronous as possible* with the (virtual/human) partner in grasping the bottle-shaped object. The action was considered synchronous when the time-delay between the participant's and the partner's index-thumb contact-times on their bottle fell within a given time-window which was narrowed or enlarged on a trial by trial basis according to a stair-case procedure: the time-window became shorter as participants got better in the task and longer if they failed in three consecutive trials. This procedure allowed case-by-case tailoring the time-window to assess synchronicity on participants' skills. In order to motivate the individual commitment during the task, participants knew their monetary reward would depend on the number of wins accumulated during the experimental sessions. A win trial needed that participants followed their auditory instructions (different depending on the study) and achieved synchronicity with the human/virtual partner in grasping the bottle-shaped objects. At the end of each trial, participants received a feedback (a

green/red LED turned on) about their performance (win/loss trial). As synchronicity with the partner was participants' ultimate purpose, Grasping Asynchronicity (GAsynchr) was always assessed as the critical dependent variable indexing the success of interpersonal coordination. GAsynchr was computed as the absolute time-delay between participants' (or participant's and avatar's) touch-times on the bottle, i.e. $[\text{abs}(\text{sbjA's touch-time on the bottle} - \text{sbjB's touch-time on the bottle})]$. Please note that "touch-time" is defined as the time-delay from each trial onset-time to the instant the touch-sensitive copper plates recorded the touch on the bottle-shaped object.

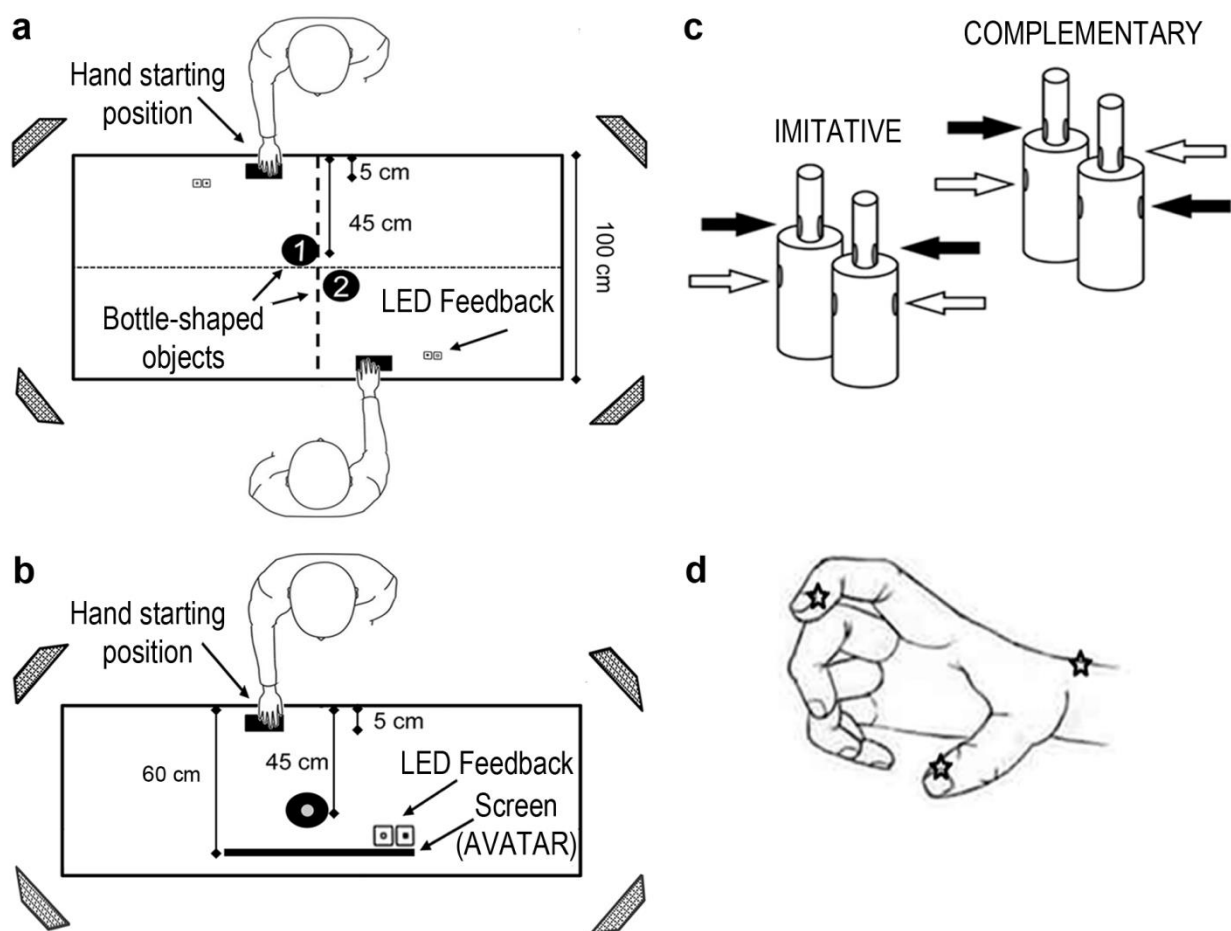


Figure 1.4. On the left, top-view of the experimental set-up used (a) in studies involving two participants, and (b) involving one participant interacting with a virtual avatar. On the right, (c) schematic representation of the action-types (complementary/imitative) that participants were required to perform, and (d) position of the infrared reflective markers on the participants' right hand.

All studies also comprised the instruction of performing complementary/imitative actions, namely the opposite/same movement with respect to the partner's one. Given the bottle-shape of the object,

an imitative action would imply that, for instance, if the partner grasped the upper part of the object (thus performing a precision grip), the participant would also grasp the upper part (thus performing a precision grip); on the contrary, in order to perform a complementary action in this example the participant would grasp the lower part of the object, thus performing a power grip (see Figure 1.4, panel c).

Kinematics recording

In all studies, participants' kinematics was monitored during the interactive task using a SMART-D motion capture system (Bioengineering Technology & Systems [B|T|S]) and stored for off-line processing. Four infrared cameras with wide-angle lens (sampling rate 100 Hz) placed about 100 cm away from each of the four corners of the table captured the movements of infrared reflective markers (5 mm diameter) in 3D space. The standard deviation of the reconstruction error was always lower than 0.5 mm for the three axes.

Infrared reflective markers were attached to participants' right upper limb on the following points: i) thumb, ulnar side of the nail; ii) index finger, radial side of the nail, and iii) wrist, dorso-distal aspect of the radial styloid process (see Figure 1.4, panel d).

The SMART-D software package (B|T|S) was also used to provide a 3-D reconstruction of the marker positions as a function of time and to analyse data. The times of participants' start-button hand release and index-thumb contact-times on the bottle were used to subdivide the kinematics recording with the aim of analysing only the reach-to-grasp phase, i.e. (when two participants were involved) from the instant the hand of the quickest participant released the start-button to the instant the hand of the slowest participant touched the bottle.

With regard to the reaching component (reported by studies described in chapter 2 and 5 only), we analysed wrist trajectory as indexed by the maximum peak of wrist height on the vertical plane (maxH), while for the grasping component (reported in all studies) we analysed maximum grip

aperture (maxAp), i.e. the maximum peak of index-thumb 3D Euclidean distance. When two participants were involved, kinematics were computed for both participants at the same time.

2. “Take the lead”:

signalling, prediction and visuo-motor interference

The art of being wise

is the art of knowing what to overlook

W. James

2.1. Aim and hypotheses

Pair dancing implies two individuals dancing together but with different roles. Typically, the Leader is responsible for initiating appropriate steps to suit the music and guiding the partner via hand pressure and other body signals. In contrast, the Follower complements with the movements he/she has been prompted to make and thus ensures that smoothly synchronised and coordinated choreographies are created. Role taking in complementary motor behaviours may be considered to be a general mechanism at the basis of human coordination in joint actions. Such complementary interactions generalize to what happens in linguistic communication, where production and comprehension never occur in isolation: rather, the speaker’s production unfolds while the listener tries to comprehend the message most probably via interactive alignment (Pickering and Garrod 2013; Menenti et al. 2012; Garrod and Pickering 2009; Brennan and Hanna 2009). However, individuals’ roles in everyday life interactions might not be as well defined as during verbal communication. In particular, coordinating in a complementary fashion requires partners to agree on a common strategy. The fact that humans are able to solve coordination problems without resorting to speech suggests that motor interaction also implies a form of communication, as demonstrated by the emergence of signalling strategies (Pezzulo and Dindo 2011) both in the verbal (Clark 2002, 1996) and motor (Sartori et al. 2009) domains.

It is worth noting, however, that in pair dancing the Leader's signalling prompts optimal coordination only if the Follower is able to use these signals to predict what the Leader is about to

do. Indeed, far from passively reacting to others' behaviour, partners involved in joint actions try to make reliable predictions about the outcome of others' movements and thus efficiently and prospectively adapt their behaviour (Sebanz and Knoblich 2009; Keller et al. 2007; Sebanz et al. 2006; Knoblich and Jordan 2003). When visual information on a partner's movements is available, action-perception coupling mechanisms triggered by action observation might be called into play as well. However, prediction and action-perception coupling might be more relevant for the Follower (who needs to adapt to the partner's movements) than for the Leader (who rather need to disambiguate his own movements in order to facilitate the Follower's task). Although evidence of effort distribution depending on task demands have been provided (Vesper et al. 2013), investigations on whether different neurocognitive processes (e.g. signalling, prediction and action-perception coupling) are variously recruited according to task demands are lacking. Similarly, it is unknown which interactive conditions imply the dominance of one process over the others and in which cases they sustain or hamper efficient interpersonal coordination.

In the present study we address these issues by investigating whether the kinematics of a joint grasping task is modulated by the interactional role played by each partner. We asked pairs of same-gender participants who did not previously know each other to grasp as synchronously as possible a bottle-shaped object placed in front of them using either a power or precision grip and performing either imitative or complementary actions. Participants received asymmetric auditory instructions, so that in each trial they performed the task acting either as i) Leader, being directly instructed on which part of the bottle-shaped object they had to grasp (i.e. on whether performing a power or a precision grip), or ii) Follower, being instructed to perform imitative or complementary actions with respect to their partner's ones. Thus, asymmetric information was provided to the pair, because in each trial only one participant (Leader) knew in advance where to actually grasp the object while the other participant had to on-line adapt to his or her movements in order to perform an imitative/complementary action. It is important to note that whatever the instruction and role, each participant had to take the partner's movements into account in order to achieve temporal

coordination, since partners shared the common goal of grasping each one his or her bottle-shaped objects as synchronously as possible.

We hypothesized that participants would modulate their kinematics according to their interactional role even if no role had been explicitly assigned. Specifically, when acting as Leaders, participants might easily realize that they were the only person aware of the message to be conveyed. Thus, leading would require the recruitment of signalling strategies to make movements as informative as possible, e.g. bringing forward the instant in which kinematic peaks are reached, boosting movement features and reducing movement variability. In contrast, following was expected to require predictive strategies in order to “comprehend” the Leader’s message. Remarkably, acting as Follower might also have the effect of triggering visuo-motor interference of the partner’s movements when a complementary action is required: this effect was expected to be detrimental to the pair’s performance. In sum, we expected 1) the recruitment of signalling and predictive simulation to be modulated by task demands and 2) the emergence of visuo-motor interference (when acting as Follower) to be detrimental to the joint performance.

2.2. Methods

2.2.1. Participants

Fourteen participants (8 males, average age 24.8 +/- 3.9) took part in the experiment and were assigned to 7 same-gender pairs. All participants were right-handed, as confirmed by the Standard Handedness Inventory (Briggs and Nebes 1975), reported normal or corrected-to-normal vision and were naive as to the purpose of the experiment.

The experimental protocol was approved by the ethics committee of the Fondazione Santa Lucia and was carried out in accordance with the ethical standards of the 1964 Declaration of Helsinki. Participants gave their written informed consent to take part in the study, received reimbursement

for their participation and were debriefed on the purpose of the experiment at the end of the experimental procedure.

2.2.2. Stimuli and procedure

Individual auditory instructions regarding the movements to be performed were administered simultaneously to both participants via headphones. Instructions consisted of two different sounds (*Leader instructions*; duration = 500 ms, intensity 4.5 db, frequency 1378 and 215 Hz) according to the type of grip (precision or power, respectively), and two words (*Follower instructions*; “Opposite” or “Same”, duration 700 ms) according to the type of action to be executed.

Paired participants were seated opposite each other in front of the working surface (see Figure 1.4., panel a). The GO signal, in addition to the feedback signal, was provided by means of a green/red LED placed near each participant next to the starting position of their hands.

Participants received written instructions concerning the overall experimental procedure. They were told that their task was to grasp the bottle-shaped object in front of them synchronously with their partner, executing different individual movements according to auditory instructions. The instructions could either be: i) a sound (*Leader instructions*), specifying which part of the object they would have to grasp (low-pitched sound meaning “grasp the lower part”, high-pitched sound meaning “grasp the upper part”); or ii) a word (*Follower instruction*), specifying whether they had to do an imitative (“same”) or complementary (“opposite”) movement with respect to their partner. Participants were not explicitly informed about their partner’s instructions nor were they told about the different roles depending on the auditory-cues - they only knew that there were two different kinds of cue and that, whatever the condition, they always had to try to grasp the object as synchronously as possible. Moreover, auditory instructions regarding the movement to be performed by each individual were simultaneously administered to both participants. No explicit leader/follower role was thus assigned to the participants.

At the beginning of each trial, participants heard their auditory cue, then, 1000 ms after the onset of the instruction, the LED placed in front of each participant was turned off (GO-signal); in this way, the GO-signal was not affected by the difference in duration of Leader's and Follower's auditory instructions. Trials in which one of the participants released the Start-button before receiving the GO-signal were considered "false-starts" and discarded from the analysis. At the end of each trial, participants received feedback (by means of the green/red LED) about their performance as a couple (win/lose trial). They won when they both respected their own instructions and achieved good synchronicity in grasping the object. Throughout the experiment, participants were instructed not to talk to each other and the experimenter checked to make sure they did not convey any verbal or facial information.

Participants performed four 24-trial sessions comprising 2 blocks each. In each session, the Leader/Follower order was counterbalanced, so that in block 1 one participant (*Leader*) received 6 high- plus 6 low-pitched sounds (in randomized order) while the partner (*Follower*) received 6 "opposite" plus 6 "same" instructions (in randomized order), and the role would then be reversed in block 2. Stimulus presentation and randomization were controlled by E-Prime1 software (Psychology Software Tools Inc., Pittsburgh, PA).

Before recording the motor task, participants listened to the auditory instructions as long as they needed in order to achieve an errorless association of high-pitched/low-pitched sounds (Leader's instructions) and opposite/same instructions (Follower) with the correct movement; moreover, a preliminary block consisting of 8 trials was provided; in this block, each participant performed 2 trials per condition, i.e. 2 trials x 2 Roles (Leader/Follower) x 2 Action-type (Imitative/Complementary) x 2 Movement-type (Power/Precision grip).

2.2.3. Data handling and design

Only correct trials (i.e. trials in which both participants respected their instructions and did not make a false start, mean accuracy = 94.46 %) were analysed.

We considered as *behavioural measures*: i) Grasping Asynchronicity (GAsynchr), and ii) Reaction Times (RTs), i.e. time from the GO-signal to the instant of Start-button release.

We analysed *kinematic measures* associated with both the reaching and the pre-shaping component of the reach-to-grasp movement (Jeannerod 1984, 1981). Namely, for the reaching component we analysed peak wrist velocity on the median plane (V) and wrist trajectory (indexed by the peak of wrist height on the vertical plane, H), while for the grasping component we analysed maximum grip aperture (Ap, i.e. the peak of index-thumb 3D Euclidean distance). For each of these kinematic parameters we extracted two variables, namely the maximum peak amplitude (maxV, maxH and maxAp) and the instant at which this peak was reached (T-maxV, T-maxH and T-maxAp). Trial-by-trial instants of peaks (T-maxV, T-maxH and T-maxAp) were normalized on movement time (final measures expressed in percentage). Moreover, with regard to the spatial variables (H and Ap), we also measured peak wrist height and maximum grip aperture mean standard deviations (SD_maxH and SD_maxAp) as indices of movement noise in each condition, i.e., these were considered indices of how variable participants' movements were in space. As a result, we extracted three dependent variables from Ap, three from H and two from V. While the dependent variables extracted from V were selected to examine the temporal features of the movement, variables referring to H and Ap were necessary to describe spatial features, respectively of the reaching (H) and grasping (Ap) components of the reach-to-grasp movement.

Behavioral or kinematic values that fell 2.5 SDs above or below each individual mean for each experimental condition were excluded as outlier values (on average, 0.54% of total, namely 0.52 ± 0.89 trials). At the group level, participants with an individual mean 2.5 SDs above or below the group mean would be excluded from the analyses; however, no outlier participant was found according to this criterion.

With regard to mean *Grasping Asynchronicity*, we first tested the presence of a learning curve throughout the session with a one-way ANOVA. Then, we compared participants' synchronicity in different conditions. However, since GAsynchr is a variable pertaining to couples

(i.e. having one value per trial per each pair of participants), Action-type (Complementary/Imitative) was the only within-couple factor to be analysed; indeed, since in each trial one participant was playing Leader and the other Follower and (in complementary actions) one participant was performing a movement type (precision/power grip) while the other was performing the opposite, it was not possible to associate trials with Leader/Follower and Power/Precision grip labels for couples; as a consequence, these factors were left out from the analysis and we directly compared pair performance in Imitative vs Complementary actions by means of a paired t-test. All the other variables (single-subject variables) were analysed with a repeated-measure ANOVA with Role (Leader/Follower) x Action-type (Complementary/Imitative) x Movement-type (Power/Precision grip) as within-subject factors. Since we extracted more than one variable from the same kinematic parameter (i.e. peak amplitude, instant of peak and – for H and Ap - SD of peak), a MANOVA was first performed by pooling together all variables (mean peak amplitude, mean time of peak and standard deviation of mean peak) linked to the same kinematic parameter (V, H, Ap) in order to protect the analyses from family-wise error inflation. Then, post-hoc ANOVAs were performed on significant effects. All tests of significance were based upon an α level of 0.05. Where appropriate, post-hoc tests were performed using the Newman-Keuls method. We expected partners in the role of Leader to increase their signalling by increasing the difference between movement maximum spatial peaks (H and Ap) in power vs precision grips and bringing forward the time of their wrist maximum velocity peaks (T-maxV) and reducing movement variability (i.e. reduction of H and Ap standard deviations). Conversely, we expected the movements of Followers to show an increase in visuo-motor interference in complementary trials, i.e. that kinematics (maximum H and/or Ap) would differ between imitative and complementary trials only when participants were acting as Followers, due to the tendency to involuntarily mimic a partner even in complementary movements.

2.3. Results

2.3.1. Grasping Asynchronicity (GAsynchr) and Reaction Times (RTs)

GAsynchr showed a significant main effect of Session ($F(3,18) = 3.70, p = .03$), suggesting the presence of a learning effect throughout the experiment. The analyses on GAsynchr showed that the performance of each pair did not differ in Complementary as compared to Imitative trials (Complementary = 112.22 ± 37.24 ms, Imitative 103.32 ± 34.38 ; $t(8) = 1.42, p = .19$, see also Table 2.1.). This result was further supported by the analysis on single-subject behavioral performance in terms of Reaction Times (RTs). Indeed, RTs showed neither a main effect of Action-type ($p = .95$) nor a significant Role x Action-type interaction ($p = .3$), indicating that overall Imitative and Complementary trials were equivalent in terms of computational cost during movement preparation. These results indicate that complementary movements were equivalent to imitative ones with regard to movement preparation and the behavioural performance of the pairs of participants. However, RTs showed a significant main effect of Role ($F(1,13) = 29.51, p < .001$), a Role x Movement-type significant interaction ($F(1,13) = 7.89, p = .015$) and a Role x Action-type x Movement-type significant interaction ($F(1,13) = 6.36, p = .025$), indicating that while participants always showed longer reaction times when following as compared to when leading, the longest movement preparations were shown before performing Precision grips ($p = .02$) and particularly before Complementary Precision grips ($p = .03$).

Table 2.1. Absence of main effect of Action-type in GAsynchr and RTs, both expressed in ms.

	Complementary	Imitative	P
Grasping Asynchronicity	112.22 ± 37.24	103.32 ± 34.38	.19
Reaction Times	472.11 ± 82.79	471.79 ± 81.31	.95

2.3.2. Kinematic Data

All significant effects are summarized in Table 2.2.

Wrist velocity peak (V)

The MANOVA on mean peak and time of wrist velocity peak on the x axis (maxV and T-maxV) showed a significant main effect of Role ($F(2,12) = 19.47, p < .001$) and a significant Action-type x Movement-type interaction ($F(2,12) = 7.83, p = .007$). With regard to the latter interaction, post-hoc ANOVAs showed that - regardless of the Role - Imitative actions differed from Complementary ones only in Power grips (maxV, Action-type x Movement-type $F(1,13) = 8.82, p = .011$; T-maxV, $F(1,13) = 14.34, p = .002$, respectively), where participants were faster ($p = .04$) and showed a shorter deceleration time ($p = .03$). More importantly, with regard to the comparison between Leader and Follower roles, T-maxV showed a significant main effect of Role ($F(1,13) = 37.46, p < .001$) indicating that, when leading, participants brought forward the instant in which they reached wrist peak velocity; this was possibly done in order to prolong the deceleration phase and provide the partner with more time to disambiguate their movements.

Wrist height peak (H)

The MANOVA on mean peak (maxH), time of wrist height peak on the y axis (T-maxH) and peak SDs (SD_maxH) showed significant main effects of Action-type ($F(3,11) = 28.7, p < .001$) and Movement-type ($F(3,11) = 352.8, p < .001$) and a significant Action-type x Movement-type interaction ($F(3,11) = 32.0, p < .001$). Moreover, the MANOVA showed Role x Action-type ($F(3,11) = 30.4, p < .001$), Role x Movement-type ($F(3,11) = 7.2, p = .006$) and Role x Action-type x Movement-type ($F(3,11) = 19.2, p < .001$) to be significant interactions.

A post-hoc ANOVA on maxH revealed all the significant effects described above (see Table 2.2.). These effects were all explained by the triple Role x Action-type x Movement-type significant interaction ($F(1,13) = 30.36, p < .001$), which indicated that subjects emphasized their movements

overall when leading as compared to when following (Role x Movement-type, $F(1,13) = 17.69$, $p = .001$), since they reached a higher wrist maxH when grasping the upper cylinder with a Precision grip ($p < .001$) and followed a lower trajectory when grasping the lower cylinder with a Power grip ($p < .001$) regardless of the Action-type (Complementary/Imitative) they were performing (see Figure 2.1, left panel).

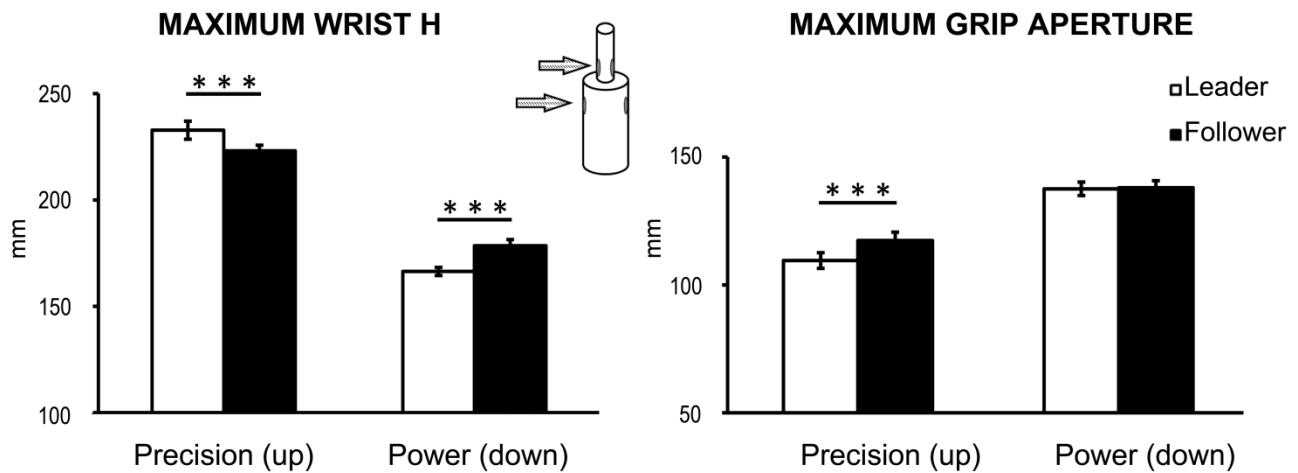


Figure 2.1. “Signaling” strategies applied by Leaders; data on maxH and maxAp. The graphs show the significant Role x Movement-type interaction for both maxH ($F(1,13) = 17.69$, $p = .001$; $p < .001$) and maxAp ($F(1,13) = 45.18$, $p < .001$; $p < .001$). These effects indicate that when participants acted as Leaders they significantly emphasized the features of their movements in order to make their behaviour easier to disambiguate. With regard to maxH (on the left), their wrist followed an higher trajectory when grasping the upper part of the bottle and a lower trajectory when grasping the bottom part when they were leading as compared to when they were following. With regard to maxAp (on the right), they showed a smaller grip aperture when grasping the smaller part of the object. It is worth noting the absence of a significant difference between Complementary and Imitative actions shown by Leaders, which indicates that they did not show visuo-motor interference induced by the observation of the partner’s action. The fact that a significant effect of maxAp was found only in Precision grips may be due to both the fact that the features of the recorded parameter (peak Ap) imply a ceiling effect in Power grips and to the more accurate nature of the planning for Precision grips.

Error bars indicate s.e.m., (***) $p < .001$

On the contrary, when following participants behaved differently in Complementary as compared to Imitative actions, i.e. they were influenced by their partner’s movement during complementary

actions. Indeed, when grasping the lower cylinder with a Power grip, participants followed a higher trajectory in Complementary than in Imitative trials, namely in those trials in which the partner was grasping the upper cylinder (all $ps < .001$, See Figure 2.2., left panel). In this condition participants displayed imitative behaviour even if they were not required to do this (i.e. when the task required a complementary action). This effect emerged only when participants were acting as Followers and may have been the consequence of visuo-motor interference between self-executed actions and those observed in their partner. We expected this visuo-motor interference to emerge also in the complementary condition when participants grasped the upper part of the object (i.e. while their partner was grasping the lower part); however, the small variation of peak MaxH when participants were grasping the upper part of the object may have concealed the effect in the Complementary-Precision grip condition. In these trials, participants may have followed a lower trajectory (as they might have been visuo-motor interference the movement of the Leader) but the need to reach the upper part of the bottle could have induced a correction that made the wrist height peak identical during complementary and imitative conditions.

A post-hoc ANOVA on SD_maxH again showed all the above listed significant effects. Indeed, although overall Complementary actions were more variable than Imitative ones (Main effect of Action-type $F(1,13) = 28.64$, $p < .001$), this was true only when subjects were acting as Follower (Role x Action-type, $F(1,13) = 9.35$, $p = .009$; $p < .001$) and performing a Power grip on the lower cylinder (Role x Action-type x Movement-type, $F(1,13) = 18.47$, $p < .001$; all $ps < .001$; see Figure 2.2., right panel).

Finally, the ANOVA on T-maxH showed a significant main effect of Action-type ($F(1,13) = 6.66$, $p = .02$) which was further explained by the Role x Action-type ($F(1,13) = 7.64$, $p = .016$) significant interaction. Indeed, the latter indicated that while participants did not change their behaviour in Complementary as compared to Imitative movements when acting as Leader ($p = .9$), they reached their height peaks later in Imitative movements as Follower ($p = .001$). Moreover, results showed that height peaks were always reached later when participants performed Precision grips on the

upper cylinder (main effect of Movement-type $F(1,13) = 63.57, p < .001$), as might be expected given the longer trajectory implied by this condition); however, the Role x Movement-type ($F(1,13) = 16.49, p = .001$) significant interaction indicated that when acting as Leader (as compared to when acting as Follower, $p = .003$) participants brought forward the instant at which they reached the peak in wrist height, in order to provide the partner with more time to disambiguate their movements.

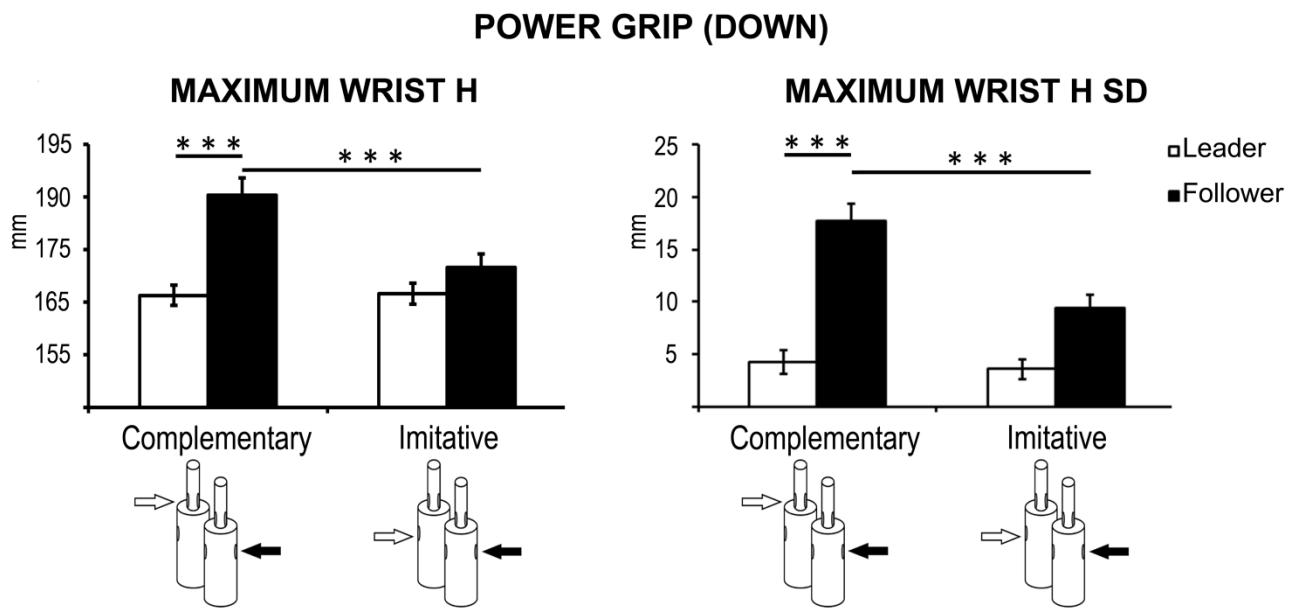


Figure 2.2. Visuo-motor interference between self-executed actions and those observed in partners when participants were acting as Followers. The graphs illustrate the significant interaction between Role x Action-type x Movement-type as shown by both maxH ($F(1,13) = 30.36, p < .001$; all $ps < .001$) and SD_maxH ($F(1,13) = 18.47, p < .001$; all $ps < .001$) and report data on mean maximum wrist height (maxH, on the left) and mean standard deviation (SD_maxH, on the right) in Power grips only. These effects suggest that the comparable level of GAsynchr in Complementary as compared to Imitative actions was achieved by pairs at the expense of the Follower's individual effort to deal with an automatic tendency to imitate the partner's movements in complementary trials (action-perception coupling effect). The fact that a significant effect was more evident when participants were grasping the lower part of the bottle-shaped object is likely due to the features of the recorded parameter (peak H), which imply a ceiling effect when participants correctly grasp the upper cylinder with a precision grip. Error bars indicate s.e.m., (***) $p < .001$

Grip Aperture (Ap)

The MANOVA on mean peak (maxAp), time of grip aperture peak (T-maxAp) and on peak SDs (SD_maxAp) showed significant main effects of Role ($F(3,11) = 23.2, p < .001$) and Movement-type ($F(3,11) = 109.4, p < .001$), and a significant interaction between Role x Movement-type ($F(3,11) = 22.6, p < .001$). Post-hoc ANOVAs on maxAp and SD_maxAp both showed the significant main effect of Role ($F(1,13) = 31.1, p < .001$ and $F(1,13) = 21.19, p < .001$, respectively), indicating that, when leading, individuals had a smaller grip aperture which was much less variable. Moreover, the Role x Movement-type significant interaction ($F(1,13) = 45.18, p < .001$ and $F(1,13) = 39.11, p < .001$, respectively) demonstrated that, although overall Precision grips implied a smaller grip aperture which was more variable as indicated by the main effect of Movement-type on maxAp ($F(1,13) = 229.66, p < .001$) and on SD_maxAp ($F(1,13) = 167.11, p < .001$), Leaders emphasized their movements performing smaller Precision grips ($p < .001$, see Figure 2.1, right panel) which were significantly less variable ($p < .001$).

Finally, the post-hoc ANOVA on T-maxAp showed a significant main effect of Movement-type ($F(1,13) = 21.50, p < .001$) and a significant interaction between Role x Movement-type ($F(1,13) = 23.36, p < .001$), indicating that although it took more time for subjects to reach the maximum grip aperture in Power grips, when leading (as compared to when following, $p < .001$) participants brought forward the instant in which they reached maximum grip aperture in order to provide the partner with more time to disambiguate their movements.

2.3.3. The dark side of interactions

Given the results described above, we further analysed our data in order to verify whether the enhancement of wrist maxH of participants in Complementary as compared to Imitative actions when they were acting as Follower [i.e. maxH Role x Action-type x Movement-type significant interaction ($F(1,13) = 30.36, p < .001$, all $ps < .001$)] was actually due to detrimental interference effects (Kilner et al. 2003) between the self-executed actions and those observed in their partner.

Indeed, it has to be noted that behavioural studies (Ocampo and Kritikos 2010; Poljiac et al. 2009; van Schie et al. 2008) have reported the absence of visuo-motor interference in joint-like contexts, which some authors associate with the presence of an integrated representation of both participants' actions in a shared motor plan (Sebanz et al. 2006). Thus, the presence of visuo-motor interference is probably the result of an un-integrated representation of the task during planning which in turn has a negative impact on joint performance.

To this aim, we analysed the trials with reference to pair performance (i.e. GAsynchr) and collated the data from the 25% best and 25% worst trials for each couple; thus, we were able to compare the kinematics of “effective” interactions (i.e. the trials showing the highest degree of synchronicity) directly with “ineffective” interactions (i.e. the trials with the lowest degree of synchronicity) by means of between group t-tests per each condition corrected for multiple comparisons (final threshold $p_{\text{corr}} = 0.05/8 = .006$). Results showed that the only condition in which the maxH data significantly differed between effective and ineffective interactions was in Complementary-Power grips when subjects were following [$t(81) = -3.01$; $p_{\text{corr}} < .02$]; see Figure 2.3., left panel]. In other words, only the least coordinated interactions (i.e. the ones in which participants did not achieve good synchronicity) were characterized by detrimental imitative behaviour in Followers, while the best synchronized interactions were characterized by the absence of the visuo-motor interference.

Finally, in the light of this evidence, we applied a correlational approach to further explore the relation between the “interference effect” and the joint performance emerged from the analyses reported above along the continuum of participants' joint behaviour. In order to be able to collate the data pertaining to all the participants and to correlate a “pure” measure of the interference effect in pair performance, we performed a Z-transformation of GAsynchr in the condition of interest (i.e. Follower-Complementary-Power grip) and reversed the sign (i.e. reported the opposite value) so that higher values indicated higher synchronicity:

$$\frac{(single\ trial - individual\ average\ value\ of\ the\ condition)}{individual\ SD\ of\ the\ condition}$$

Then, we correlated these values trial-by-trial with the index of visuo-motor interference in maxH in this condition (namely, the ratio between maxH in each Follower-Complementary- Power grip trial and the mean participant's maxH in the Follower-Imitative- Power grip condition).

$$\frac{single\ trial\ maxH\ in\ Follow\ Complementary\ Power\ grip}{individual\ mean\ maxH\ in\ Follow\ Imitative\ Power\ grip}$$

Results showed a highly significant negative correlation between these indices ($r = -.29, p < .001$; Figure 2.3., right panel), indicating that the higher the interference effect in the Follower, the poorer the joint performance was.

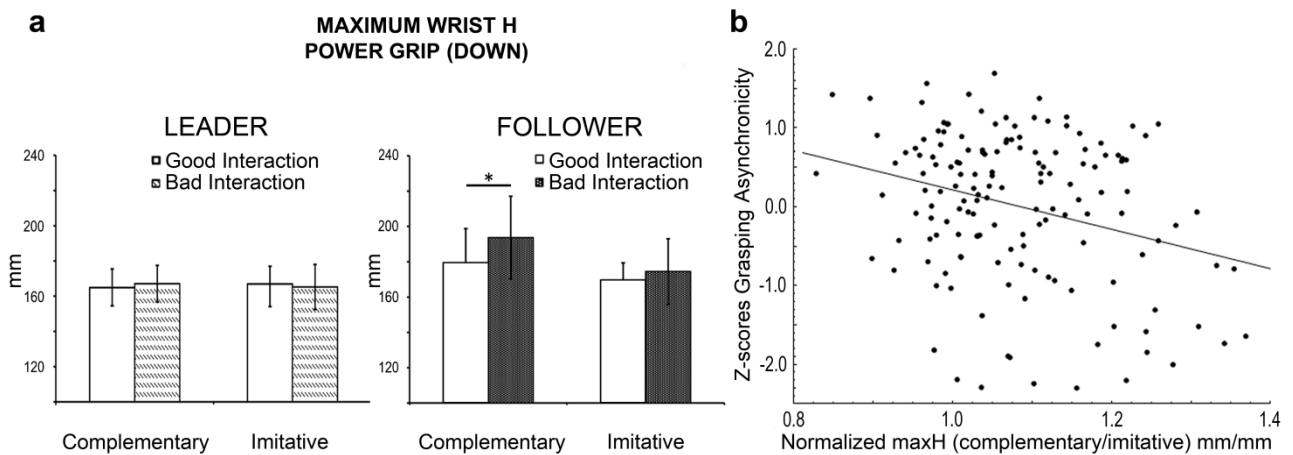


Figure 2.3. The graphs illustrate the results of the analysis of the link between visuo-motor interference and joint performance. On the left (**a**), the histograms illustrate the results of the between-group t-tests comparing maxH data in trials showing the 25% best/worst performances in terms of GAsynchr for each couple. On the right (**b**), the graph shows a significant correlation ($r = -.29, p < .001$) between visuo-motor interference shown by Followers maxH in complementary movements and joint performance. Note that on the y axis GAsynchr z-scores have been reported with the opposite sign, so that higher Z-scores correspond to better performance. Error bars indicate SDs, (*) $p < .05$.

Thus, although several factors may play a role in determining trial-by-trial joint performance, visuo-motor interference between self-executed actions and those observed in their partner emerged when participants acted as Followers was linked to worse coordination within the pair. Taken as a whole, these results suggest that although “simulation” seems to be linked to prediction (because action-perception coupling is shown only when participants act as Followers, namely only when they need to predict the partner’s movements in order to adapt their own behaviour accordingly), in our joint task visuo-motor interference constitutes a marker of the least coordinated interactions.

Table 2.2. All significant effects on kinematics. *F* statistics in MANOVA are calculated according to Wilky's Lambda. Results from the MANOVAs on wrist Velocity on the median plane (V), wrist Height on the vertical plane (H) and absolute grip Aperture (Ap) are separately reported as well as all the post-hoc ANOVAs on Velocity, wrist Height and grip Aperture maximum peaks (maxV, maxH and maxAp) and instants (Time, T) of maximum peaks (T-maxV, T-maxH and T-maxAp) and – for the spatial parameters - mean Standard Deviations (SD_maxH and SD_maxAp). See main text for a detailed description. (*) = $p < .05$; (**) = $p < .01$; (***) = $p < .001$

MANOVA on V			
	Effect	F	Df
	Main effect of Role	19.47***	2, 12
	Action-type x Movement-type	7.83**	2, 12
ANOVAs on V			
Parameter	Effect	F	Df
MaxV	Action-type x Movement-type	8.82**	1, 13
T-maxV	Main effect of Role	37.46***	1, 13
	Action-type x Movement-type	14.34**	1, 13
MANOVA on H			
	Effect	F	Df
	Main effect of Action-type	28.7***	3, 11
	Main effect of Movement-type	352.8***	3, 11
	Action-type x Movement-type	32.0***	3, 11
	Role x Action-type	30.4***	3, 11
	Role x Movement-type	7.2**	3, 11
	Role x Action-type x Movement-type	19.2***	3, 11
ANOVAs on H			
Parameter	Effect	F	Df
MaxH	Main effect of Action-type	53.97***	1, 13
	Main effect of Movement-type	408.71***	1, 13
	Action-type x Movement-type	24.28***	1, 13
	Role x Action-type	95.24***	1, 13

ANOVAs on H (follows from previous page)			
Parameter	Effect	F	Df
MaxH	Role x Movement-type	17.69***	1, 13
	Role x Action-type x Movement-type	30.36***	1, 13
SD_maxH	Main effect of Action-type	28.64***	1, 13
	Main effect of Movement-type	5.3*	1, 13
	Action-type x Movement-type	88.71***	1, 13
	Role x Action-type	9.35**	1, 13
	Role x Movement-type	10.03**	1, 13
	Role x Action-type x Movement-type	18.47***	1, 13
	T-maxH	Main effect of Action-type	6.66*
	Main effect of Movement-type	63.57***	1, 13
	Role x Action-type	7.64*	1, 13
	Role x Movement-type	16.49***	1, 13
MANOVA on Ap			
	Effect	F	Df
	Main effect of Role	23.2***	3, 11
	Main effect of Movement-type	109.4***	3, 11
	Role x Movement-type	22.6***	3, 11
ANOVAs on Ap			
Parameter	Effect	F	Df
MaxAp	Main effect of Role	31.1***	1, 13
	Main effect of Movement-type	229.66***	1, 13
	Role x Movement-type	45.18***	1, 13
SD_maxAp	Main effect of Role	21.19***	1, 13
	Main effect of Movement-type	167.11***	1, 13
	Role x Movement-type	39.11***	1, 13
T-maxAp	Main effect of Movement-type	21.5***	1, 13
	Role x Movement-type	23.36***	1, 13

2.4. Discussion

In the present study we sought to determine whether and how the kinematics of a joint grasping task is modulated by the participants' interactional roles (Leader/Follower) when no explicit instruction on how to coordinate their movements is provided. The results showed that the employment of visuo-motor interference, prediction and signalling (three neurocognitive processes which are crucially involved in joint actions) is profoundly influenced by the interactional role of each partner. Remarkably, the specific signatures of each of these processes are reflected in participants' kinematics depending on the specific role played by them. Our results showed that i) when acting as Leader, participants tried to make their kinematics more "communicative" by using signalling strategies (Pezzulo and Dindo 2011) to increase the predictability of their movements, and that ii) only when acting in as Follower did participants recruit simulative processes tending to imitate the Leader in complementary actions, but when visuo-motor interference emerged it had a negative impact on joint performance.

Paralleling previous findings in both the verbal (Clark 2002, 1996) and motor communication (Sartori et al. 2009) domains, kinematic cues provided by leaders allowed partners to have more time and to more easily interpret where leaders' movements aimed to. For instance, leaders bring forward the instant in which maximal wrist velocity, maximum grip aperture and maximum wrist height are reached in order to provide the partner with more time to disambiguate the intended movement; they enhance the difference between the grip aperture and the wrist trajectory of precision and power grips; they reduce movement variability. It is worth noting that our participants were not explicitly instructed to "communicate" anything to their partner. Rather, leaders were simply told which part of the object they had to grasp, and they shared with the partner the common goal of being as synchronous as possible. Thus, our study shows that during motor interaction individuals not only take the partner's task into account (Sebanz et al. 2007, 2005, 2003; Tsai et al. 2008; Atmaca et al. 2008, 2003), but, as indexed by the implementation of signalling,

they implicitly take on a specific role according to both their own and their partner's instructions (sub-goal distribution in the light of the shared goal); indeed, they would not have needed to "signal" (i.e. communicate) their intent if they did not represent both their own and their partner's task realizing that their partner would more easily adapt to their movements if they made them more predictable. Our study also expands previous findings on planning strategies used during pure temporal or haptic coordination (Vesper et al. 2013; van der Wel et al. 2011; Vesper et al. 2011) by showing that the same principle of predictability plays a role during face-to-face dyadic interactions requiring coordination in both space and time. Significantly, our study demonstrates that predictability becomes a strategy to create a purely motor form of shared language which allows participants to achieve a common goal. This would be in line with evolutionary theories suggesting that the use of ostensive signals and the ability to learn from them is typically human (Csibra and Gergely 2011), and that "intentionality" might have been one of the key features that allowed the development of a "proto-language" deriving from the primate ability to imitate manual gestures (Arbib 2005).

In keeping with previous findings (van Schie et al. 2008), we show that performing complementary movements in joint contexts does not imply any additional cost at a behavioural level. Indeed, results from the analyses of Grasping Asynchronicity and movement preparation (as indexed by the length of RTs) showed no differences between Imitative and Complementary trials. Nevertheless, kinematic data indicate that the kinematics of participants acting as Followers were subjected to interference when they had to perform movements which were incongruent with (i.e. complementary to) those of the Leader. Indeed, Followers displayed signs of visuo-motor interference in the reaching component (wrist height on the y axis, maxH and SD_maxH). Thus, it might be that the comparable level of synchronicity reached in Complementary as compared to Imitative actions was achieved at the expense of the Follower's individual effort to deal with an automatic tendency to imitate his or her partner's movements (i.e. action-perception coupling

dealing to visuo-motor interference effects). Evidence that visuo-motor interference only emerged when participants acted as Follower - i.e. when they needed to predict their partner's motor goals and to adapt to them - highlights the close link between "simulation" and prediction and the fact these motor processes are differently recruited according to task demands (Vesper et al. 2013).

However, our results also show that higher visuo-motor interference was associated with worse joint performance (i.e. it reduced synchronicity between partners). This parallels a comparable detrimental effect of action-perception coupling which has been noted in strategic contexts in which it reduces payoff (Cook et al. 2012). Thus, results are in line with evidence that distinct (and more "active") simulative processes rather than action-perception coupling (e.g. emulation, Grush 2004, Knoblich and Jordan 2003; and Bayesian inference, Kilner et al. 2007) are likely to be recruited to achieve successful temporal and spatial predictions of a partner's actions, which are necessary in our task when participants act as Followers.

To sum up, our study further expands previous research on face-to-face interactions by proving that during a realistic joint grasping task not only participants' prior intentions (Becchio et al. 2010; Sartori et al. 2009; Becchio et al. 2008a, 2008b; Georgiou et al. 2007) but also the actual "interactive roles" taken on by each individual modulate the joint action kinematic features. In particular, being the Leader of an interaction implies the (intentional) recruitment of communicative behaviours (e.g. signalling) in order to convey essential information to the interacting partner. Acting as Follower implies adaptation to the partner's movements on the basis of good predictive abilities; this predictions, likely supported by the presence of a shared goal, are linked but differ from pure action-perception coupling, because when the recruitment of simulation leads to visuo-motor interference it has a detrimental impact on the pair performance. Overall, this supports the notion that joint actions imply a form of communication during which smooth coordination is achieved only when partners effectively send motor signals and are prompt to interpret them. As in pair dancing, only when both Leader and Follower efficiently do their job might a synchronised complementary choreography be obtained.

3. Prejudices interactions: predictive simulation and racial biases

Belief creates the actual fact

W. James

3.1. Aim and hypotheses

As the racial composition of the population changes, intergroup interactions are increasingly common. However, although it has been shown that implicit in-group preferences emerge in early childhood (Dunham et al. 2008), and affect social categorization and evaluations even when processed subliminally (Maister et al. 2013; Peck et al. 2013; Ito and Bartholow 2009; Amodio 2008), little is known about whether racial biases change the features of face-to-face motor interactions.

Social neuroscience is beginning to unravel the ways in which inter-individual differences and cultural factors shape neural and behavioural responses in realistic social contexts (Kubota et al. 2012). Recent findings show that even basic forms of neurophysiological responses to interpersonal situations such as those typically attributed to simulative mechanisms are modulated by high-level cognitive and cultural influences. In particular, it has been shown that racial biases simply induced by a model's skin-colour modulate mirroring of observed neutral actions and emotive states (Molnar-Szakacs et al. 2007; Désy and Theoret 2007; Gutsell et al. 2010) and somato-motor inhibition associated to observation of painful stimulation (Azevedo et al. 2012; Avenanti et al. 2010); moreover, racial biases also affect the recruitment of the fronto-parietal "simulative" neural during intention understanding (Liew et al. 2011) and imitation (Earls et al. 2013; but see also Losin et al. 2012). Finally, bodily illusions (Maister et al. 2013; Peck et al. 2013) and social attention as indexed by gaze-mediated orienting (Pavan et al. 2011) may be influenced by group membership. Thus, it seems that although humans are prone to automatically resonate with others (Rizzolatti and Craighero 2004), this happens less readily when people classify other individuals as "out-group"

members. Tellingly, modulation of embodied resonance induced by in-group biases occurs as a function of culturally-learned racial prejudice (Chiao and Mathur 2010). Indeed, they are more prominent in high-prejudice participants and might even disappear in unbiased ones (Azevedo et al. 2012; Gutsell and Inzlicht 2010; Avenanti et al. 2010).

Crucially, however, no study has so far tested whether group biases also modulate face-to-face motor interactions requiring individual to mutually adjust their movements on-line. Since in these situations not only participants execute an action while concurrently observing the partner performing a different one, but they also need to predict the other's movement in order to adapt their behaviour accordingly, both "passive" automatic action-perception coupling (leading to mimicry, Chartrand and Bargh 1999, and/or visuo-motor interference, Kilner et al. 2003) and "active" predictions of others' action deployment in time (Urgesi et al. 2010, 2006; Kilner et al. 2007; Knoblich and Jordan 2003) may occur and be influenced by the social categorization of the partner as an in-group/out-group individual.

Here we sought to determine whether movement kinematics and individuals' ability to coordinate with in-group/out-group avatars during realistic motor interactions are modulated by individuals' implicit in-group preferences. To this aim, we asked a group of Caucasian participants to coordinate their reach-to-grasp movements with two different in-group (Caucasian) or out-group (African) virtual partners that moved with identical (previously recorded) real human kinematics. The task included two interacting conditions requiring participants to either synchronize with (Temporal interactions) or to synchronise with plus on-line adapt to the avatar's movement (Adaptive interactions) performing imitative/complementary actions with respect to the avatar's ones. We expected racial biases would modulate simulative mechanisms, as inferred from the comparison between complementary and imitative actions, and that this modulation would not be aspecific (i.e. the result of a broad action-perception coupling) but rather linked to motor prediction, i.e. it was expected to emerge during Adaptive interaction only, when participants are asked to predict the partner's movements in order to adapt to them.

3.2. Methods

3.2.1. Participants

Fourteen Caucasian participants (9 males, age 23 ± 2.96) took part in the experiment. The experimental protocol was approved by the ethics committee of the Fondazione Santa Lucia and was carried out in accordance with the ethical standards of the 1964 Declaration of Helsinki. All participants were right-handed as confirmed by the Standard Handedness Inventory (Briggs and Nebes 1975), reported normal or corrected-to-normal vision and were naive as to the purpose of the experiment; they gave their written informed consent to take part in the study, received reimbursement for their participation and were debriefed on the purpose of the experiment at the end of the experimental procedure.

3.2.2. Stimuli and procedure

Participants were comfortably seated in front the monitor where clips of the virtual partner's movements were shown (see Figure 1.4., panel b). Auditory instructions concerning the movement to be executed were delivered to participants prior each trial via headphones. They consisted in three sounds having the same intensity (4 db) and duration (200 ms) but different frequency: i) "high-pitched", 1479 Hz, ii) "low-pitched", 115.5 Hz, iii) "whistle", 787.5 Hz. Feedback signals about participants' performance were provided via a green/red LED placed next to the left corner of the screen.

The kinematics of the virtual partners was based on human participants performing grasping movements within the experimental set-up of the present study (see Figure 3.1.). Each clip showed only the upper body of the avatar from the shoulders to hips, without the neck and the head, and included the avatar's bottle-shaped object. Both the in-group (Caucasian) and the out-group (African) avatar performed the same 12 power and 12 precision grips towards the bottle-shaped object. Crucially, in 33% of the trials, the video included an on-line correction, i.e. the avatar

switched from a power to a precision grip (or vice-versa) during the reaching phase. Kinematics of the virtual partners were recorded using a Vicon MX optical tracking system (Vicon Motion Systems, Oxford, UK) with 10 infrared light emitting cameras. 3D positions of 37 passive reflecting markers, attached to the subject's complete upper body (pelvis, chest, head, left and right arm, right hand) were recorded with a spatial error below 1.5 mm and at a temporal resolution of 120 Hz. Raw data were processed offline using commercial Vicon software and the final processed trajectories were animated using commercial software (Autodesk, Motion Builder).



Figure 3.1. The figure illustrates how avatars' movements were created from real human kinematics.

The experiment was divided in three phases: i) the Implicit Association Test (IAT), ii) the human-avatar motor interaction, and iii) the Manipulation-check.

Implicit Association Test (IAT). Participants completed a computerized version of the two-category skin-colour IAT (Greenwald et al. 2003, 1998) in order to evaluate their implicit race-related attitude as measured by IAT D-score. See Table 3.1. for individual results.

Cover-story and human-avatar motor interaction. Firstly, participants were given the cover story and told they would perform the task with two different partners whose kinematics had been previously recorded. Written instructions specified participants would watch clips showing kinematics recorded from two male participants performing reach-to-grasp movements towards a bottle-shaped object identical to participants' one; they were shown a (fake) picture of these two participants – with covered eyes and a neutral facial expression - who resembled an Italian (“Luca”) and African (“Ibrahim”) student who attended the university in the city where participants lived

(Rome); they were told that Ibrahim's and Luca's movements had been implemented in the virtual character in order to control for differences in the body shape, but that they could recognize the two participants from the avatar's skin colour (white for the Italian student, and black the African one).

Participants were required to grasp the bottle-shaped object placed in front of them as synchronously as possible with their virtual partner, during two interactive conditions: i) in *Temporal interactions*, a high-/low-pitched sound would specify which part of the object they had to grasp (low-pitched meaning "grasp the lower part" performing a power grip, high-pitched sound meaning "grasp the upper part" performing a precision grip), so that participants had to focus on synchronizing with the avatar only; instead, during ii) *Adaptive interactions*, participants heard the whistle - indicating they had to on-line adapt to the partner's movements without knowing in advance where to grasp the object - and to perform, in different sessions (i.e. *Complementary/Imitative*), opposite/same movements with respect to their virtual partner. Thus, during Adaptive interactions they were both required to coordinate in time (being synchronous) and on-line adapt in space (performing complementary/imitative movements).

The trial time-line was as following. First, a fixation cross placed on the region of the screen where the avatar's hand would appear alerted participants about the impending trial. Then, participants heard auditory instructions (i.e. high/low-pitched sound or whistle), and after 300 ms the clip started. Upon receiving the auditory instruction participants could release the Start-button and reach-to-grasp the object. In the case participants started before hearing the instruction, the trial was classified as false-start and discarded from the analyses. At the end of each trial, participants received a feedback (a green/red LED) about their performance (win/loss trial). A win trial implied that participants followed their instructions and achieved synchronicity with the avatar. Note the avatar's index-thumb contact-times were measured trial-by-trial by a photodiode placed on the screen that sent a TTL signal which was recorded by E-Prime2 software (Psychology Software Tools Inc., Pittsburgh, PA). The photodiode was triggered by a black dot (not visible to the participants) placed on the screen on the frame of the clip corresponding to the moment at which the

avatar grasped his virtual object. Previous to any recording of the motor task, participants could listen to the auditory instructions as long as they needed to achieve an errorless association of whistle/high-pitched/low-pitched sounds with the correct instruction; no familiarization block was provided.

Participants performed six Complementary/Imitative sessions (counterbalanced order between participants), each comprising four 24-trial blocks. In each block, auditory instructions lead participants to perform 12 times a Temporal and 12 times an Adaptive interaction (counterbalanced between participants). The Complementary/Imitative instruction to be followed during Adaptive interaction was given at the beginning of each session. Unbeknownst to the participants, this instruction implied consistent imitative or complementary actions also during Temporal interaction. Within each session, participants interacted both with the in-group and out-group partner in different blocks (in-group/out-group block order was counterbalanced between participants), and watched four times the same 24 clips (depicting actions performed twice by the in-group and twice the out-group partner during Adaptive/Temporal interaction). Half of trials required participants performing a precision/power grip. In 33% of the clips, the avatar performed a movement correction ("Correction" clips). Stimuli presentation and randomization were controlled by E-Prime2 software (Psychology Software Tools Inc., Pittsburgh, PA).

Manipulation-check. At the end of the experiment, participants were asked to rate on a series of Visual Analogue Scales (VAS, 100 mm) a series of questions aimed to verify whether participants believed the cover story. Participants rated: i) how good they considered the performance achieved during the interaction with the in-group (In-group PERFORMANCE) and ii) with the out-group (Out-group PERFORMANCE) partner, and iii) how much realistic they rated the movement reconstruction (REALISM); finally, they were asked iv) whether they doubted the movements had been recorded from two different people and not from a single person (DOUBT).

3.2.3. Data handling and design

Only correct trials were entered in the behavioural and kinematics analyses, i.e. we excluded from the analyses trials in which participants i) missed the touch-sensitive copper-plates and response was thus not recorded, ii) made false-starts, or iii) did not respect their auditory instructions (excluded trials = 9.5 ± 4.5 %).

We considered as behavioural measures:

1. Accuracy, i.e. number of movements executed according to the trial instructions;
2. Reaction Times (RTs), i.e. time from the instant when the clip started to the instant of participants' start-button hand release;
3. Grasping Asynchronicity (GAsynchr).

With regard to movement kinematics, we analyzed kinematics of maximum grip aperture (maxAp), i.e. the peak of index-thumb 3D Euclidean distance, during the reach-to-grasp phase. We selected maximum grip aperture kinematics because it has been shown to be sensitive to the ultimate goal of grasping actions and to the social context (Becchio et al. 2010; Grafton 2010; Castiello 2005).

For each of the above-mentioned measures we calculated the individual mean in each condition, excluding each value that fell 2.5 SDs above or below each individual mean for each experimental condition as outlier value (on average, 0.6 ± 0.5 % of total, namely 3.5 ± 3.2 trials). Individual means were entered in separate within-subject ANOVA having Partner (In-group/Out-group) x Action-type (Complementary/Imitative) x Clip-type (Correction/No-correction) x Interaction-type (Temporal/Adaptive interaction) x Movement-type (Power/Precision grip) as within subjects factors. Finally, we planned to verify by means of a correlational approach whether any in-group/out-group effects showed by the ANOVA would depend on the individual implicit in-group preference as measured by the IAT D-Score. The α level of significance was set a $p = 0.05$. When appropriate, post-hoc tests were performed using Newman-Keuls method.

3.3. Results

3.3.1. Manipulation-check

Firstly, we verified whether participants believed the cover story.

Results from a single-sample t-tests corrected per multiple comparisons (final threshold, $p = .025$) showed participants' judgments were significantly higher (REALISM) and lower (DOUBT) than 50% (which would correspond to an intermediate/medium judgment, 50 mm; $mREALISM = 68.9 \pm 24.6$ mm, $t(1,13) = 2.87$, $p_{corr} = .026$; $mDOUBT = 8.00 \pm 21.5$ mm, $t(1,13) = -7.30$, $p_{corr} < .001$), indicating participants perceived the avatars' movements as realistic and wrongly perceived as different the In-group/Out-group kinematics which were identical instead. With regard to judgments on In-group/Out-group PERFORMANCE, results from a dependent-sample t-test showed they did not differ ($mIn\text{-}group\text{ PERFORMANCE} = 50.79 \pm 19.13$ mm, $mOut\text{-}group\text{ PERFORMANCE} = 56.50 \pm 22.89$ mm; $t(1,13) = -1.07$, $p = .30$), indicating that –at an explicit level- participants did not feel their performance depended on the partner's racial belonging. See also Table 3.1.

Table 3.1. Individual IAT D-Scores and VASs judgements. Note explicit judgements on REALISM, DOUBT, In-group/Out-group PERFORMANCE were measured on separate Visual Analogue Scales from 0-100 mm.

Participant	IAT D-Score	REALISM	DOUBT	In-group PERFORMANCE	Out-group PERFORMANCE
1	0.47	84	74	61	80
2	0.87	81	0	64	54
3	0.67	31	38	29	25
4	0.92	97	0	40	73
5	0.83	96	0	73	69
6	0.42	24	0	29	67
7	0.22	59	0	40	54
8	0.85	71	0	26	4
9	0.49	62	0	83	91
10	0.34	100	0	55	65
11	0.16	78	0	34	37
12	0.76	80	0	74	43
13	0.49	34	0	39	66
14	0.80	68	0	64	63

The above mentioned results confirmed participants believed the cover story and perceived the (identical) kinematics of the In-group/Out-group partners as belonging from two (real) different people. Thus, we considered the clips and the cover story validated and analyzed data from the human-avatar interaction as described in the paragraph 2.4. Namely, we included Partner (In-group/Out-group) as with-in subject factor in the ANOVA.

3.3.2. Human-avatar interaction

For the sake of clarity, we separate here significant results linked to in-group/out-group effects (paragraph 3.3.2.2) from purely motor significant effects which did not include the factor Partner and were thus not linked to in-group/out-group effects but rather depended on task constrains (paragraph 3.3.2.1). With regard to Grasping Asynchronicity (GAsynchr) and maximum grip aperture (maxAp), all significant results are reported in Table 3.2. and Table 3.3. and described below with reference to the significance of each post-hoc test.

3.3.2.1. Purely motor effects.

Accuracy. Overall, participants were highly accurate in performing the task (mean Accuracy = 95% \pm 2.3). Since one experimental condition (i.e. Out-group–Complementary–NoCorrection–Adaptive–PowerGrip) was at ceiling data did not allow for a factorial ANOVA. However, In-group vs. Out-group participants' mean accuracy was not statistically different (dependent-samples t-test: mIN-GROUP = 95.2 \pm 2.4 %, mOUT-GROUP = 95.87 \pm 2.3 %, $t(1,13) = -1.90$, $p = .078$).

Reaction Times. The ANOVA on RTs showed a significant main effect of Interaction-type ($F(1,13) = 55.09$, $p < .001$, $\eta_p^2 = .8$), indicating Adaptive interaction required longer RTs than Temporal interaction. The Interaction-type x Clip-type was also significant ($F(1,13) = 5.04$, $p = .043$, $\eta_p^2 = .28$), since RTs in Temporal interaction were significantly faster during observation of a Correction than a No-correction clip ($p = .03$). Importantly, RTs did not show any main effect or significant

interaction with Partner, indicating movement preparation prior to the proper joint-execution was not influenced by the avatar’s group membership.

GAsynchr. See Table 3.2. for a description of all significant effects. The ANOVA on *GAsynchr* showed a significant main effect of Clip-type, indicating it was easier for participants to synchronize with the avatars in No-correction clips. Moreover, the Action-type x Clip-type and Action-type x Clip-type x Movement-type significant interactions showed that, regardless the Partner, synchronization in Correction clips was more difficult in Complementary compared to Imitative Action (Correction-Complementary vs. Correction-Imitative, $p = .001$) and that this effect was significant only when participants had to change from a precision to a power grip (Complementary-Correction-Power grip vs. Imitative-Correction-Power grip, $p = .016$). The Action-type x Clip-type x Movement-type significant interaction showed that during No-Correction *GAsynchr* was better during Complementary compared to Imitative Power grips ($p = .022$).

Table 3.2. All significant effects emerged from the ANOVA on *GAsynchr*. **In bold**, significant interactions with the within-factor Partner, i.e. In-group/Out-group effects.

Grasping Asynchronicity				
Effect	df	F	<i>p</i>	<i>Partial Eta-Squared</i>
Main effect of Clip-type	1,13	60.09	< .001	.82
Interaction-type x Clip-type	1,13	6.12	.028	.32
Action-type x Clip-type	1,13	10.55	.006	.44
Action-type x Clip-type x Movement-type	1,13	15.07	.002	.54
Partner x Interaction-type x Clip-type	1,13	4.93	.045	.27
Partner x Interaction-type x Clip-type x Movement-type	1,13	4.74	.048	.27

MaxAp. See Table 3.3. for a description of all significant effects. The ANOVA on *maxAp* showed a significant main effect of Movement-type indicating that, as expected, *maxAp* was larger in Power compared to Precision grips. Moreover, it showed two significant main effects of Clip-type and Interaction-type, indicating that *maxAp* was larger in Correction compared to No-corrections and during Adaptive compared to Temporal interaction, probably reflecting participants' attempt to increase the safety margin in Corrections and in Adaptive interactions. Post-hoc tests on the two-way Interaction-type x Clip-type, Clip-type x Movement-type and Interaction-type x Movement-type significant interactions further specified that: i) *maxAp* in Corrections was larger than in No-corrections only during Adaptive interactions ($p < .001$), ii) *maxAp* in Corrections was larger than in No-corrections only for Precision ($p < .001$), and iii) *maxAp* during Adaptive interactions was larger than during Temporal interactions only for Precision grips ($p < .001$). Finally, the three-way Interaction-type x Clip-type x Movement-type additionally clarified these effects showing that, in Precision grips only, *maxAp* was larger in Corrections compared to No-corrections both during Adaptive interactions ($p < .001$) and during Temporal interaction ($p = .024$).

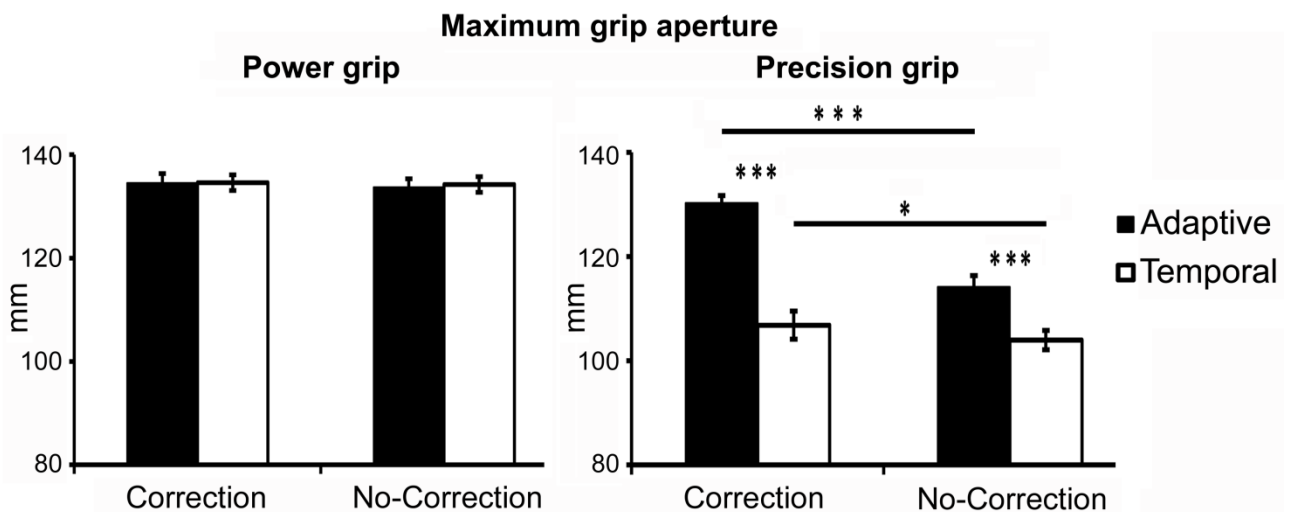


Figure 3.2. The figure illustrates the significant interaction between Interaction-type x Clip-type x Movement-type ($F(1,13) = 31.6, p < .001$) relative to *maxAp*. For the sake of simplicity, we did not report the significance of the comparison between Power grip and Precision grip in all conditions (all $ps < .001$ except for Adaptive-Corrections where Precision vs. Power grips difference was reduced, $p = .012$). Error bars indicate s.e.m., (***) $p < .001$, (**) $p < .01$, (*) $p < .05$.

As shown by Figure 3.2., the above mentioned effects demonstrates that participants actually performed movement corrections in response to the avatars' correction, since in this condition their maxAp in Precision grips gets closer to the maxAp typical of Power grips. This modulation was found in Precision grips only probably due to the more accurate nature of the precision grip planning (Castiello 2005).

Lastly, Action-type x Interaction-type significant interaction showed that, overall, maxAp in Complementary actions was smaller than in Imitative actions only during Temporal interactions ($p = .006$), but not during Adaptive interactions. This effect was strongly modulated by the Partner.

3.3.2.2. In-group/out-group effects.

Accuracy and Reaction Times. No ingroup-out-group significant effect emerged.

GA_{synchr}. See Table 3.2. for a description of all significant effects. The Partner x Interaction-type x Clip-type significant interaction showed GA_{synchr} in Correction tended to be better during Adaptive as compared to Temporal interaction only when interacting with the In-group partner ($p = .008$, $d = .61$, see Figure 3.3.). The Partner x Interaction-type x Clip-type x Movement-type significant interaction suggested this facilitation in Adaptive Corrections with the In-group was stronger during Power grips (In-group–Adaptive–Correction–Power grip vs. In-group–Temporal–Correction–Power grip $p = .048$, $d = .64$). Crucially, this different performance in Corrections during Adaptive as compared to Temporal interaction was not present during interactions with the Out-group ($p = .579$).

Grasping Asynchronicity

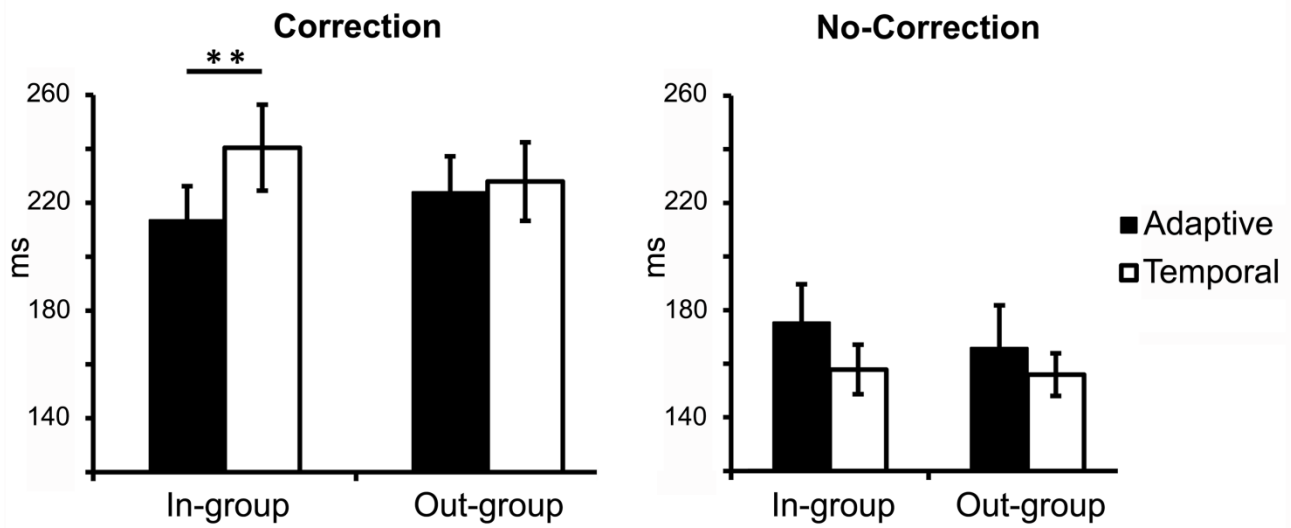


Figure 3.3. The figure illustrates the interaction between Partner x Interaction-type x Clip-type ($F(1,13) = 4.93, p = .045$) showed by data on GAsynchr. For the sake of simplicity, we did not explicitly report in the figure the significance of the comparison between Correction and No-correction ($ps < .001$ in all conditions, as also suggested by the significant main effect). Error bars indicate s.e.m., (**) = $p < .01$.

MaxAp. See Table 3.3. for a description of all significant effects. The ANOVA on *maxAp* showed a significant main effect of Partner, suggesting participants' *maxAp* was generally larger when they interacted with the Out-group partner. This effect was explained by the four-way Partner x Action-type x Interaction-type x Movement-type significant interaction, showing that: i) participants' *maxAp* during interaction with the In-group partner was significantly smaller than with the Out-group ($p = .001, d = .35$) during Imitative–Adaptive–Precision grips; and, crucially, ii) during interactions with the In-group partner only, *maxAp* was significantly larger in Complementary as compared to Imitative actions during Adaptive interactions (Precision grips only, $p < .001, d = .45$), and significantly smaller in Complementary compared to Imitative actions during Temporal interaction (Precision grips only, $p = .043, d = .19$). Thus, the avatar's movements influenced participants' kinematics only when interacting with the In-group.

In order to make this four-way effect on *maxAp* easier to interpret, we performed an additional analysis normalising (dividing) the kinematics data of Complementary actions on those of Imitative

ones. Namely, we wanted to directly test the impact of simulation of the partner’s movements mediated by Partner in-group/out-group membership controlling for movement and task constrains. [design: Partner (In-group/Out-group) x Clip-type (Correction/No-correction) x Interaction-type (Temporal/Adaptive) x Movement-type (Power/Precision) as within subjects ANOVA; since it was the second time we tested the same dataset (data on maxAp), we corrected for multiple comparisons (final threshold $p = 0.05/2 = 0.025$), see Table 3.3., most right column]. The Partner x Interaction-type x Movement-type significant interaction ($F(1,13) = 8.8$, $p_{\text{corr}} = .022$, $\eta_p^2 = .40$) showed that visuo-motor interference emerged only in Adaptive interaction and only when interacting with the In-group (all $ps \leq .001$; Adaptive interaction–Precision grip–In-group VS Adaptive interaction – Precision grip – On-group $d = .78$). As a matter of fact, In-group–Adaptive–Precision grip was the only condition showing a Complementary/Imitative ratio higher than 1 (single-sample one-tailed t-test, $p = .009$, see Figure 3.4., left panel).

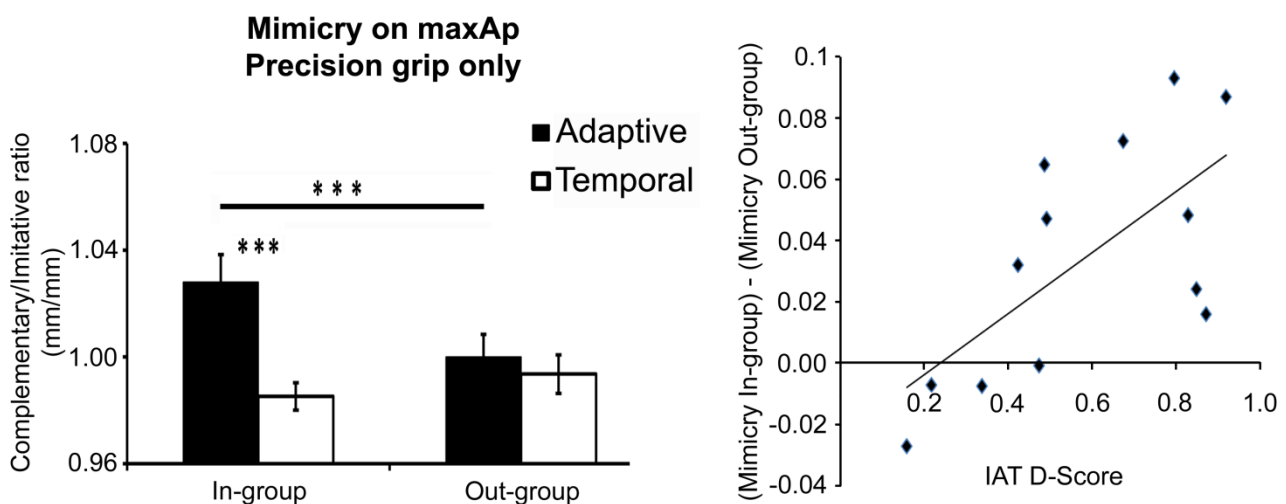


Figure 3.4. Analyses of “Mimicry” on maxAp data. On the left panel, the Partner x Interaction-type x Movement-type significant interaction ($F(1,13) = 8.8$, $p_{\text{corr}} = .022$) indicating mimicry effects emerged only in Precision grips during Adaptive interactions with the In-group. The fact this modulation was found in Precision grip only might be due to the more accurate nature of the precision grip planning. On the right panel, the highly significant positive correlation ($r = .67$, $p = .012$) indicates that the difference between visuo-motor interference (Complementary/Imitative maxAp, mm/mm) emerged with the In-group as compared to with the Out-group partner [(Mimicry In-group) – (Mimicry Out-group)] was higher in more highly biased participants. Error bars indicate s.e.m., (***) $p < .001$.

Finally, in order to test whether the modulation of visuo-motor interference described below was linked to individual racial prejudices, we extracted from the analysis below an index of the difference in visuo-motor interference with the In-group vs. Out-group partner and correlated it with the individual IAT D-score, as follows. We separately selected In-Group and Out-group data on Adaptive–PrecisionGrip and participant-by-participant averaged this “index of Mimicry” (i.e. Complementary/Imitative ratio) between Corrections and No-corrections (note that this index follows the significant interaction showed by the ANOVA on the Complementary/Imitative ratio, and reflects visuo-motor interference emerged during the complementary condition). Then, we subtracted (Mimicry In-group) minus (Mimicry Out-group) and correlated these values with the individual IAT D-scores.

The analysis showed a highly significant positive correlation ($r = .67, p = .012$; see Figure 3.4., right panel), indicating the higher the IAT D-score, the greater was the difference between Mimicry with the In-group partner as compared with the Out-group one. This suggests that the categorization of the partner as an In-group/Out-group individual had an impact on Mimicry according to the strengths of the individual implicit in-group preference, being maximal in high-prejudice participants and minimal in unbiased ones. Note that analysis of Cook’s distances revealed one subject as an outlier. Thus, the correlation analyses were performed on 13 out of the 14 participants.

Table 3.3. All significant effects on maximum grip aperture. Since we tested twice the same experimental hypothesis on the same set of data, both corrected and uncorrected p-values are reported. In *Italics*, the effects which did not survive the correction for multiple comparisons. In **bold**, significant effects including the within factor Partner, i.e. In-group/Out-group effects.

Maximum grip aperture					
Effect	df	F	<i>p</i>	<i>Partial Eta-Squared</i>	<i>p_{uncorr}</i>
Main effect of Clip-type	1,13	75.0	<.001	.85	<.001
Main effect of Interaction-type	1,13	61.8	<.001	.83	<.001
Main effect of Movement-type	1,13	149.1	<.001	.91	<.001
Interaction-type x Clip-type	1,13	37.8	<.001	.74	<.001
Interaction-type x Movement-type	1,13	105.8	<.001	.89	<.001
Clip-type x Movement-type	1,13	60.5	<.001	.82	<.001
Interaction-type x Clip-type x Movement-type	1,13	31.6	<.001	.70	<.001
Action-type x Interaction-type	1,13	13.3	.006	.50	.003
<i>Main effect of Partner</i>	<i>1,13</i>	<i>5.1</i>	<i>.084</i>	<i>.28</i>	<i>.042</i>
Partner x Action-type x Interaction-type x Movement-type	1,13	8.5	.024	.39	.012
Normalised data on maxAp (Complementary/Imitative)					
Main effect of Interaction-type	1,13	14.41	.004	.52	.002
Interaction-type x Movement-type	1,13	6.76	.044	.34	.022
<i>Partner x Interaction-type</i>	<i>1,13</i>	<i>5.21</i>	<i>.08</i>	<i>.28</i>	<i>.040</i>
Partner x Interaction-type x Movement-type	1,13	8.8	.022	.40	.011

3.4. Discussion

Humans are extremely prone to divide others in an “Us vs. Them” fashion (Amodio 2008; Tajfel 1981) according to socially relevant categories (such as race, age or gender) which represent powerful cues to group membership, especially in the absence of other affiliation factors. In the present study, we demonstrate for the first time that during face-to-face motor interactions the social categorisation of virtual partners as in-group/out-group individuals modulates the i) ability to achieve interpersonal coordination and ii) mimicry of the partner’s movements, in terms of visuo-motor interference between self-executed actions and those observed in the partner. Tellingly the mimicry reduction strongly correlated with the individual degree of implicit in-group preference as indexed by the Implicit Association Test.

Results on Grasping Asynchronicity showed that, overall, participants achieved similar performance with the In-group and the Out-group partner. Yet, the need to predict the partner’s movement during Adaptive interaction facilitated participants’ adjustments to the avatar’s movement corrections only during interactions with the In-group avatar. Since results on Accuracy and RTs showed the absence of any significant in-group/out-group effect, we exclude results shown by GAsynchr could be either linked to non-specific perceptual/attentional factors or to speed-accuracy trade-off. Instead, these are in line with studies showing that a negative interdependence between partners (e.g. a competitive context, Hommel et al. 2009) as the categorisation of the partner as an “out-group” (Muller et al. 2013) strongly reduces the emergence of incidental task co-representations during attentional tasks. Our results expand this knowledge showing that in “challenging” situations (as during partner’s movement corrections) the need to predict and adapt to the partner’s movement (which is facilitated by the presence of task sharing and of a shared goal which allows including the partner’s movements within one’s own motor plan) facilitates coordination with an In-group partner, while the Out-group partner does not benefit from this integration.

Results on maximum grip aperture showed mimicry (in terms of visuo-motor interference) emerged only during Adaptive interactions, and, crucially, only when interacting with the In-group avatar. The absence of visuo-motor interference (Kilner et al. 2003) between self-executed actions and those observed in the partner during Temporal interaction highlights the close link between action simulation and action prediction (Candidi et al. 2012; Aglioti et al. 2008): indeed, mimicry arose only when participants needed to predict the partner's movements in order to adapt to them. However, being involved in complementary actions influenced participants' movement execution only during interactions with the In-group. Thus, the emergence of automatic action-perception coupling might constitute the marker of perceived affiliation between interactive partners. Accordingly, unconscious mimicry of others' postures and mannerisms during interaction (Chartrand and Bargh 1999) may have the social outcome of promoting affiliation (van Baaren et al. 2009, 2004; Lakin and Chartrand 2003) and voluntary mimicry of out-group members may reduce racial biases (Inzlicht et al. 2012). Further research is needed to investigate whether the reinforcement of social bonds that arise during motor interactions might exert the same powerful modulation.

To conclude, this study demonstrates for the first time that during joint action action-perception coupling between one's own and others' movements is recruited only when the partner is coded as an in-group individual. Even more importantly, our results suggest this modulation is shaped by cultural inter-individual differences (Azevedo et al. 2012; Chiao and Mathur 2010; Avenanti et al. 2010), since the in-group/out-group modulation of interactive kinematics is observed only in biased participants with implicit positive bias towards in-group individuals. Although the absence of visuo-motor interference during interactions with the Out-group is reminiscent of the influence exerted by racial biases on mirror-like responses to others' action and pain observation (Gutshell and Inzlicht 2010; Molnar-Szakacs et al. 2007; Désy and Theoret 2007; Avenanti et al. 2010; Azevedo et al. 2012), results showed that in our task mimicry-like responses (and,

consequently, their in-group/out-group modulation) arose only when participants needed to predict the partner's movements in order to adapt to them. Thus, this study expands previous literature on the impact of social variables on joint action kinematics (see Becchio et al. 2010 for a review) by highlighting: i) the close link between action-perception coupling and action prediction during joint action; ii) that the recruitment of simulative mechanisms during social interaction depends on the degree of the partners' interdependence called for by the interaction itself.

4. “And yet they grasp together”:

free interactions and interpersonal perception

The deepest principle in human nature

is the craving to be appreciated

W. James

4.1. Aim and hypotheses

Contradicting the adagio “if you want something done right, do it yourself”, we are constantly asked to interact with others in social contexts where our behavior is influenced by first sight impressions, social categorizations and stereotypes which automatically and unavoidably arise during interactions (Degner and Wentura 2010; Cosmides et al. 2003). On the one hand, somatomotor- and affective- simulative neural responses evoked by the observation of others’ actions and emotions are modulated by the perception of others’ status, group membership and similarity (Losin et al. 2012; Liuzza et al. 2011; Pavan et al. 2011; Avenanti et al. 2010; Serino et al. 2009; Désy and Théoret 2007; Molnar-Szakacs et al. 2007; Singer et al. 2006), suggesting observed states of others may be mapped onto our own sensorimotor system according to the degree of affiliation with the observed person; moreover, studies on joint attention have shown that social and emotional factors modulate the emergence of task co-representations, preventing “joint” attentional effects (e.g. the joint Simon effect) when the partner is perceived as non-cooperative and unfriendly or when the task requires limited interdependence between participants (Iani et al. 2011; Hommel et al. 2009). On the other hand, mimicry as well as interpersonal synchrony reduce racial biases (Inzlicht et al. 2012) and promote cooperation (Wiltermuth and Heath 2009; Van Baaren et al. 2009, 2004; Valdesolo et al. 2011, 2010). Nevertheless, the bidirectional impact of interpersonal coding on dyadic motor interactions has never been directly investigated.

These aspects are crucial since interacting with others may be difficult because of the complexity of aligning oneself with others on a common ground. Indeed, dual coordination is only achieved if both subjects act in conjunction instead of following their own strategy and “mutually adjust” at some level of the planning process (intention, action plans and movement, Vesper et al. 2010, see also Clark 1996; Pezzulo and Dindo 2011; Braun et al. 2011). Nevertheless, most studies on joint action investigate joint-like contexts where participants observe and subsequently/on-line execute their own action rather than coordinate themselves with an on-line responsive partner (van Schie et al. 2008; Polijac et al. 2009; Newman Norlund et al. 2007; Kokal et al. 2009) or – when investigating mutual adjustments - selectively focus on the temporal aspect of the interaction (Vesper et al. 2013, 2011; Konvalinka et al. 2010; van der Wel et al. 2011; Noy et al. 2011). As a consequence, studies in which two people have to mutually adjust in time and space choosing between different individual sub-goals is lacking, as well as investigations concerning the mechanisms which allow a person to adapt his or her behaviour to another co-agent who is concurrently trying to adapt to the partner as well (social “closed loop processes”, Frith 2007).

Thus, in the present study we aimed to investigate whether the ability to coordinate with a partner and the kinematics of a joint reach-to-grasp action are modulated by co-agents’ reciprocal interpersonal perception. We studied the ability of two individuals who did not know each other in advance to learn how to achieve a *shared goal*: namely, synchronising their reach-to-grasp movements by synchronously grasping a bottle-shaped objects either via *imitative* or *complementary* actions.

Two different interactive conditions were investigated, namely i) *Guided interactions*, requiring partners’ reciprocal adjustments in time only: each individual was informed on what part of the object he had to grasp being thus only required to adjust his movement velocity to synchronize with the partner’s grasping time, and ii) *Free interactions*, requiring both time and space adjustments: participants were required not only to synchronize but also to re-model their individual movements (i.e. on-line decide which part of the object to grasp) in order to perform imitative/complementary

movements with respect to their partner's ones. Further, in two different groups of participants, interpersonal perception was either left neutral or negatively biased.

We specifically hypothesized that inducing a negative interpersonal perception would differently affect co-agents' coordination in Free and Guided interactions and that this would also be reflected in movement kinematics. Specifically, the analysis of kinematics differences between imitative and complementary actions allowed us to investigate the presence of visuo-motor interference (Kilner et al. 2003) between co-agents' movements, which we expected to be absent in neutral conditions on the basis of previous literature (Ocampo and Kritikos 2010; van Schie et al. 2008). Importantly, the behavioural and kinematic analyses of the joint-grasping task were performed after having assessed the reliability of the interpersonal perception manipulation.

4.2. Methods

4.2.1. Participants

Twenty-eight male participants took part in the experiment and were randomly assigned to two groups (each made of seven pairs), i.e. "Neutral group" (NG), age 24.2 ± 2.9 ; "Manipulated group" (MG), age 23.7 ± 4.5 . Based on previous findings indicating that the impact of an unfair partner's behaviour is stronger in men compared to women (Singer et al. 2006), only male participants were selected. All participants except one per group were right-handed as confirmed by the Standard Handedness Inventory (Briggs and Nebes 1975). All participants reported normal or corrected-to-normal vision and were naive as to the purpose of the experiment. Participants gave their written informed consent to take part in the study, received a reimbursement for their participation and received a debriefing on the purpose of the experiment at the end of the experimental procedure. The experimental protocol was approved by the ethics committee of the Fondazione Santa Lucia and was carried out in accordance with the ethical standards of the 1964 Declaration of Helsinki.

4.2.2. Stimuli and procedure

Auditory instructions concerning the movement to be executed were contemporarily delivered to both participants via headphones. The instructions consisted in three sounds having the same intensity (4 db) and duration (200 ms) but different frequency: i) “high-pitch”, 1479 Hz, ii) “low-pitch”, 115.5 Hz, iii) “whistle”, 787.5 Hz.

In order to make the social manipulation reliable, participants were told they would take part in two separate experiments on: i) “verbal and non-verbal communication” (“Experiment 1”, i.e. Interpersonal Manipulation); and ii) “motor interaction” (“Experiment 2”, i.e. Joint grasping Task). Participants were told (as covert story) that the first experiment was aimed to study the correlation between personality traits and communication-styles used applied by people to describe themselves, while the second experiment investigated motor coordination learning. Importantly, participants were led to believe the two experiments were not linked to each other (see Figure 4.1.).

Interpersonal Manipulation. Participants were asked to complete a series of personality tests: a 125-item version of the Temperament and Character Inventory (TCI, Cloninger 1994); the Reading the Mind in the Eyes Test (Baron-Cohen et al. 2001); the Personal Norm Reciprocity (PNR, Perugini et al. 2003); a test on Leadership (scale created from the International Personality Item Pool, IPIP Goldberg et al. 2006); and a pen-and-pencil questionnaire in which they were asked to describe their personal background (e.g. family, childhood, education), future perspectives (e.g. their plans within three years), hobbies and personality (e.g. “list three of your gifts and flaws”). Once they had finished compiling these tests, participants were given the partner’s questionnaire and were asked to read through it and judge through Visual Analogue Scales (VAS1, Judgments on partner personality – Pre-interaction): (i) several traits of their partner’s personality (i.e. “Based on your impressions, how much do you rate your partner a self-confident/ easy/ friendly/ original/ mature/ intelligent/ calm/ agreeable/ sincere person?”), (ii) the perceived similarity with the partner, and (iii) the level of cooperation quality they expected to reach if asked to interact with him. In addition, participants

completed a 25-items self-referred version of the BIG-5 personality questionnaire (De Digman 1990; Caprara and Perugini 1994) and a modified version of the same questionnaire referred to their perception of the partner (BIG-5 Other-Pre).

After having completed the personality testing, half of the sample (the Manipulated group, MG) received a negative “false-feedback” about the partner’s judgements (see Figure 4.1.). More specifically, MG participants were led to believe their partner did not esteem their interests and personality (“self-esteem threatening manipulation” procedure, Caprara et al. 1987). Immediately after this manipulation, participants were asked to assess along VASs the subjective impact of the false-feedback (VAS2 - Reaction to manipulation): VAS2 included a key-question concerning a re-rating of the level of cooperation quality they expected to reach if asked to interact with their partner. No feedback was given to the Neutral group.

Joint grasping Task. During the whole experiment, participants’ task was to grasp as *synchronously as possible* the bottle-shaped object in front of them, executing different individual movements according to auditory instructions. Instruction could either be: i) a whistle, implying they would have to perform a *Free interaction*; or ii) a high- or low-pitch sound, implying they would have to perform a *Guided Interaction*. In Guided interactions the sound would specify which part of the object they had to grasp: a low-pitched sound would mean “grasp the lower part” (i.e. perform a power grip), while a high-pitched sound would mean “grasp the upper part” (i.e. perform a precision grip). Conversely, during the Free interaction condition, both partners were free to grasp either the upper or the lower part at will. However, in different blocks (i.e. “Complementary” or “Imitative”), each participant had to do the opposite/same movement with respect to his partner; the opposite/same instruction to be followed in the free interaction condition was given at the beginning of each block. We monitored the movements to ensure that partners did not implicitly agree on a consistent strategy (e.g. one always grasping the top and the other the bottom).

On each trial, the LED visible to each participant was turned off to alert about the impending whistle/sound instruction go-signal. Upon receiving the synchronous auditory instruction participants could release the start-button and reach-to-grasp the object. Given the simultaneous delivery of the auditory instruction, no explicit leader/follower role was induced. Thus, each participant had to monitor the partner's movement and adapt to it accordingly. Participants knew they would always receive the same kind of instruction (sound/whistle to both) and that in Guided interactions same or different sounds could be randomly delivered to them. At the end of each trial, participants received a feedback (the green/red LED turned on) about their performance as a couple (win/loss trial). A win trial needed that both participants followed their own instructions and achieved synchronicity in grasping the objects. Previous to any recording of the motor task, participants practiced the task as long as they needed to achieve an errorless association of whistle/high-pitched/low-pitched sounds with the correct instruction; a preliminary familiarization block constituted by 10 whistles and 12 sounds (requiring either imitative or complementary response, counterbalanced between pairs) was also provided. Then, participants performed two sessions, each comprising one Complementary and one Imitative block delivered in counterbalanced order in the different couples. Each block consisted of 66 trials divided in 3 sub-blocks of 10 Free interaction (whistle) plus 12 Guided interaction (sounds) trials. The order of Free and Guided instructions was counterbalanced in the different couples. In the Free interaction conditions, the instruction to perform imitative or complementary actions was given at the beginning of the block. Unbeknownst to the participants, this instruction implied consistent imitative or complementary actions also in the guided interaction condition in 10 out of 12 sounds for each sub-block. In the 2 additional Guided trials for each sub-block, the sounds instructed each member of the couple to perform a type of action (complementary or imitative) non consistent with the rest of the block: these two "odd trials" aimed at making the partner's movements less predictable and were excluded from the analyses. Stimulus presentation and randomization were controlled by E-Prime1 software (Psychology Software Tools Inc., Pittsburgh, PA).

Manipulation-check and debriefing. At the very end of the experiment, all couples completed again the VAS ratings regarding judgements on partner's personality (VAS3 - Judgments on partner personality – Post-interaction) and the BIG-5 personality questionnaire referred to the partner (BIG-5 Other-Post). Finally, participants in the MG were explicitly asked whether they believed or not that the false-feedback was actually given by their partner (manipulation-check procedure). At the end of all experimental procedures, all participants were debriefed.

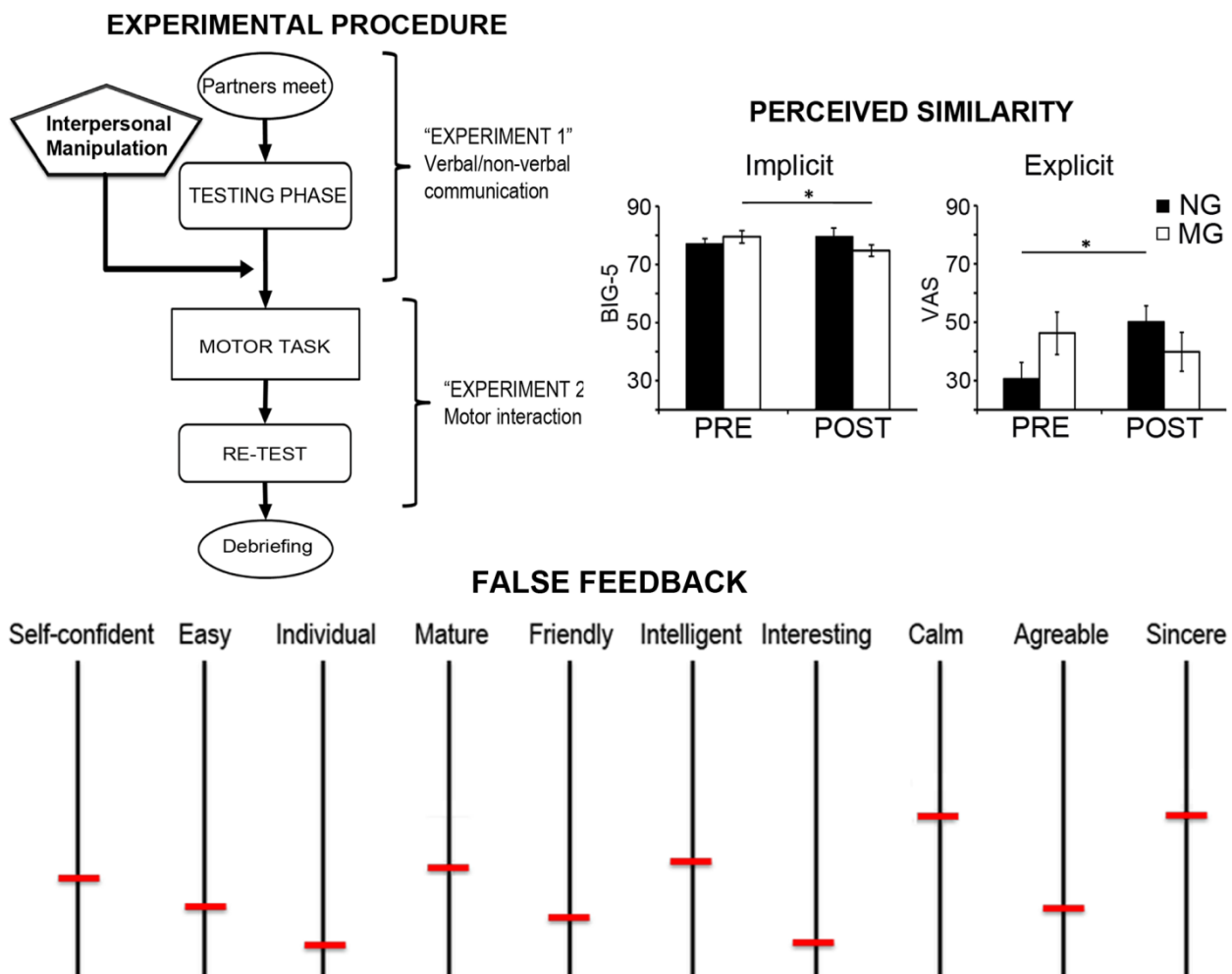


Figure 4.1. On the left, the experimental procedure; importantly, participants were led to believe the two experiments were not linked to each other. On the bottom, the false-feedback provided to participants in the Manipulated Group. On the right, data indicate the interpersonal manipulation was indeed effective (see main text). Error bars indicate s.e.m., (*) = $p < .05$.

4.2.3. Data handling and design

Only correct trials were entered in the behavioural and kinematics analyses.

We considered as behavioural measures:

1. Reaction Times (RTs), i.e., time from the instant at which participants received the auditory instruction to Start-button hand release, as measures of movement preparation timings;
2. Grasping Asynchronicity (GAsynchr);
3. Accuracy, i.e., number of movements executed according to participants' instructions;
4. Wins, i.e., number of correct trials where GAsynchr was below the time-threshold (corresponding to the amount of money earned at the end of the experiment).

For each of the above mentioned behavioural measures we calculated the individual mean in each condition. These values were entered in a mixed ANOVA (see below). With regard to RTs, we calculated individual mean and individual variance of the RTs recorded for each condition, the latter being considered an index of movement preparation variability. Moreover, we calculated the trial-by-trial time-delay between partners' Reaction Times (Start Synchronicity, "Diff_RT"); this analysis aimed to test whether participants would end up automatically synchronizing ("entrain") their RTs (i.e. their movement preparation timings) although not explicitly asked to do so.

As *kinematic measures* we focused on the pre-shaping components of the reach-to-grasp (Jeannerod et al. 1995; Jeannerod 1981) and analysed:

1. the index-thumb maximum 3-D Euclidean distance (maximum grip aperture, maxAp);
2. its variance (Var_maxAp), as an index of variability in following the typical pre-shaping pathway of each individual.

We selected maximum grip aperture kinematics because it has been shown to be an index sensitive to the ultimate goal of the grasping and to the social context (see Graton et al. 2010; Becchio et al. 2010; Castiello 2005 for a review).

Each behavioural and kinematic value that fell 2.5 SDs above or below each individual mean for each experimental condition was excluded as outlier value (on average, 1.4% of total in NG and

1.2% of total in MG, namely 3.8 +/- 0.9 trials in NG and 3.1 +/- 0.9 trials in MG). No participant exhibited behavioural or kinematics values 2.5 SDs above or below the group mean.

Interpersonal manipulation. We verified the reliability and efficacy of our social manipulation, as following. With regards to Visual Analogue Scales (VAS), (i) we firstly checked whether MG participants' answers to VAS2 - Reaction to manipulation confirmed our manipulation had been effective: we checked the presence of a drop-off in the expected level of cooperation quality with respect to the one rated in VAS1 - Judgments on partner personality – Pre-interaction (paired t-test VAS1-VAS2). Then, (ii) we compared data collected before and after the interaction regarding the VAS scores referred to the partner's personality and the explicit perceived similarity (i.e. two Mixed ANOVAs on Judgments on partner personality with factors Pre/Post x Neutral/Manipulated Group); the same was done on (iii) the index of implicit perceived similarity (see Caprara et al. 2007 for a detailed description of the procedure) extracted from the comparison between the self-referred BIG-5 questionnaire and the Big-5 Other-Pre and -Post (i.e. Mixed ANOVA on Implicit perceived similarity with factors Pre/Post x Neutral/Manipulated Group). After having assessed the reliability of our Interpersonal Manipulation with the analyses described above, we analysed behavioural and kinematic data from the Joint grasping Task considering “neutral” and “manipulated” couples as two separate groups. With reference to personality tests, we controlled that the two groups did not differ for baseline inter-individual differences (between-sample t-tests).

Joint grasping Task. Each behavioural index linked to performance at a couple-level (Accuracy, Wins and GAsynchr and Start Synchronicity) was entered in a separate factorial analysis of variance (ANOVA) with Session (Session1/Session2) x Action-type (Complementary/Imitative) x Interaction-type (Free/Guided) as within-factors and Group (NG/MG) as between-factor. Concerning reaction times and maximum grip aperture (RTs, RTs Variance, maxAp, Var_maxAp), we run separate factorial ANOVAs with Session (Session1/Session2) x Action-type

(Complementary/Imitative) x Interaction-type (Free/Guided) x Movement-type (Power/Precision grip) as within-subjects and Group (NG/MG) as between-subjects factor. All tests of significance were based upon an α level of 0.05. When appropriate, post-hoc tests were performed using Newman-Keuls method.

4.3. Results

One pair of participants from the MG did not believe the Interpersonal Manipulation (as assessed by the manipulation-check procedure) and kinematic data of one pair of participants from the NG was not recorded due to technical problems. Thus, these two couples were not included in the analyses. The final sample comprised 6 pairs from the NG (12 participants) and 6 pairs from the MG (12 participants).

4.3.1. Interpersonal Manipulation

The effectiveness of the social manipulation was indexed by checking several properties of the interaction:

i) Expected cooperation.

The comparison between the quality of the expected cooperation with the partner provided by MG participants (along VAS) before and after the “false-feedback exchange” (VAS1-2) showed a significant decrease in expected cooperation (paired t-test, $t(11) = -3.65$, $p = .003$; $mPre = 71.7 \pm 8.4$ mm, $mPost = 46.9 \pm 18.1$ mm), which indicates the participants in the MG developed a negative disposition towards their mate as consequence of the negative feedback provided by him.

ii) *Judgments on partner personality and explicit perceived similarity.*

Between samples t-tests on the ten adjectives describing the partner's personality before the interaction (and the interpersonal manipulation) confirmed that the Groups did not differ in their judgements at the beginning of the experiment (all $p > .1_{\text{uncorr}}$). On the contrary, Pre-Post x Group interaction on the mean judgement about partner's personality was significant ($F(1, 22) = 13.33, p = .001$) because MG participants significantly worsened their evaluations of partner's personality ($p < .001$); this indicates they had changed their first-sight impression. Moreover, concerning the crucial question about perceived similarity ("How much do you think your partner is similar to you?"), we found a significant Pre-Post x Group interaction ($F(1,22) = 7.38, p = .012$) showing that explicit perceived similarity significantly increased ($p = .039$) only in NG (see Figure 4.1. on the right).

iii) *Implicit perceived similarity (BIG-5 Other -Pre and -Post).*

The analysis of implicit perceived similarity extracted from the 25-item BIG-5 personality questionnaire complemented the explicit judgement results. Indeed, we found a significant Pre-Post x Group interaction ($F(1,22) = 11.55, p = .002$) which was accounted for by a significant reduction of implicit perceived similarity after the interaction in MG ($p = .027$) but not in NG (see Figure 4.1. on the right).

Neither the enhancement of explicit or implicit perceived similarity correlated (Pearson's r) with the behavioural performance or amount of won trials at couple level (all $ps > .3$), thus ruling out the possibility that post-interaction changes in perceived similarity were influenced by the amount of won money. Importantly, t-test on the results of each personality measure (subscales in TCI, 25-item BIG-5 personality questionnaire, Eye-Test, PNR, Leadership) confirmed that group differences in Perceived Similarity ratings were not due to differences in personality traits (all $ps > .1$).

4.3.2. Joint grasping Task

Results from the Interpersonal Manipulation procedure confirmed our social manipulation was effective and had an impact on reciprocal interpersonal perception in MG participants. Thus, we analysed behavioural and kinematic data collected during the motor task focussing on Groups' difference. Due to the high number of factors in the experimental design and the critical role of the Interpersonal Manipulation for our purposes, we extensively describe in the main text only the between factor Group significant interactions. All the other significant effects are reported in Table 4.1, Table 4.2. and Table 4.3.

4.3.2.1. Joint-coordination performance

Results related to Accuracy, Grasping Asynchronicity and Wins are reported in Table 4.1.

Grasping Asynchronicity, Wins and Accuracy (as well as Start Synchronicity, see below) are all parameters calculated at the couple-level (one value per each pair of participants) and thus the factors of the design consisted in Session x Interaction-type x Action-type x Group; indeed, the factor "Movement-type" was left outside the analysis as it was not possible to associate Power and Precision grip labels at couple-level in complementary movements, since in this condition one partner was performing a movement-type while the other was performing the opposite. As a consequence, we decided not to take the factor Movement-type into account.

Accuracy. No significant result emerged from the ANOVA on pairs' accuracy. Importantly, the two groups did not differ in their overall accuracy (Main effect of Group $p > .4$).

Grasping Asynchronicity. Although the overall performance was comparable in the two groups (Main effect of Group $p > .9$), and regardless the general improvement over sessions (Main effect of Session $F(1,10) = 5.45$, $p = .042$), the learning profiles of the two types of interaction (Free vs Guided) differed between the two groups as showed by the Session x Interaction-type x Group

significant interaction ($F(1,10) = 8.59, p = .015$, see Figure 4.2.). Indeed, participants in NG showed a comparable level of performance in GAsynchr between Free and Guided interaction during the first session of the motor task (as shown by the absence of any significant difference in GAsynchr in these two conditions in Session 1, $p > .7$); moreover, they improved their GAsynchr in the Guided condition throughout Session 1 and Session 2 ($p = .02$). In contrast, for MG participants the Guided interaction was easier than the Free one in Session1 ($p = .01$); crucially, this difference vanished in Session2 due to an improvement in Free interactions ($p = .048$).

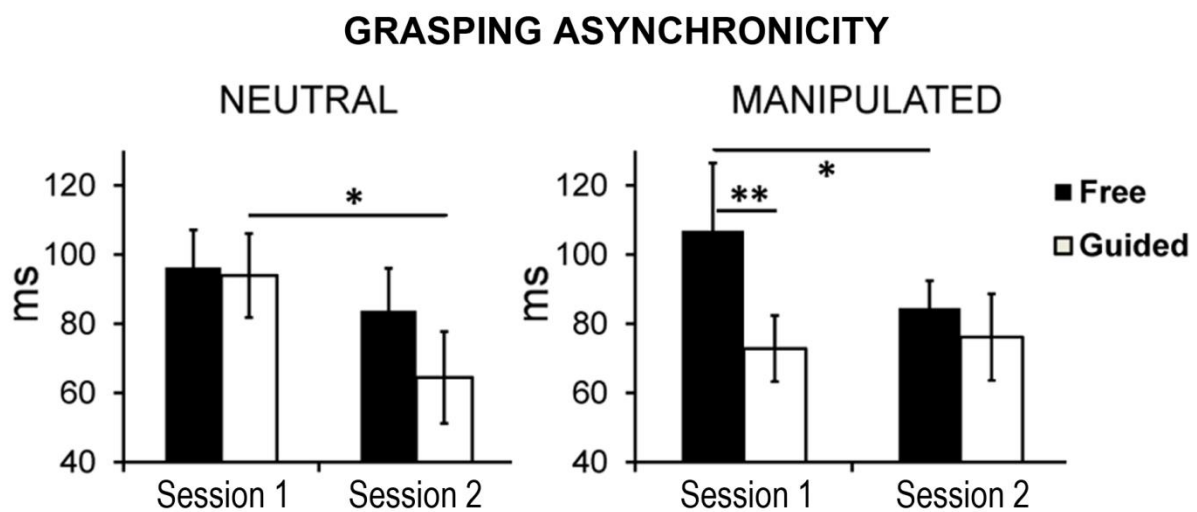


Figure 4.2. The figure illustrates that although the overall performance was comparable in the two groups (absence of main effect), their learning profiles throughout sessions differed in the Free vs Guided interaction (significant Session \times Interaction-type \times Group interaction). Indeed, while NG participants improved their GAsynchr in the Guided condition, MG participants improved in the Free condition. It is worth noting that only for MG participants Free interactions were more difficult than Guided ones in Session1. Error bars indicate s.e.m., (*) $p < .05$, (**) $p < .01$.

Wins. Despite differences in GAsynchr, the two Groups did not differ in terms of amount of won trials and consequently in the amount of money participants earned at the end of the experiment (Main effect of Group $p > .4$). Moreover, Wins did not show any significant interaction with the between-subjects factor Group. This was due to the wanted effect of the stair-case procedure, which let us personalize the task difficulty (i.e. the width of the tolerance time-window to assess

synchronicity) to the ability in synchronising typical of each couple. As a consequence, on average, the couples of the two groups earned the same amount of money at the end of the experiment despite their performance was very dissimilar in terms of grasping synchronicity; thus, we excluded any of the reported effect could be accounted for by a systematic different level of reward.

Table 4.1. All significant results on Accuracy, Grasping Asynchronicity and Wins. Design: Session x Interaction-type x Action-type x Group. In **bold** and *italics*, significant effects with Group described in the main text. (*) $p < .05$, (**) $p < .01$, (***) $p < .001$.

Parameter	Effect	F	Df
Accuracy	<i>-No significant effect-</i>	-	-
GAsynchr	Main effect of Session	5.45 *	1,10
	<i>Session*Interaction-type*Group</i>	8.59 *	1,10
Wins	Main effect of Interaction-type	15.88 **	1,10
Start Synchronicity	Main effect of Session	9.59 *	1,10
	Main effect of Interaction-type	34.04 ***	1,10
	Main effect of Action-type	8.88 *	1,10
	<i>Session *Action-type *Group (p = .072)</i>	4.05	1,10
	<i>Session*Interaction-type*Action-type*Group</i>	6.83 *	1,10

Reaction Times (RTs). The ANOVA on Reaction Times (RTs) did not show any significant interaction with the between-subjects factor Group, although the Session x Group interaction approached significance ($F(1,22) = 3.67, p = .069$). This trend was explained by the fact RTs in NG in Session 1 tended to be longer than both NG's RTs in Session 2 ($p < .001$) and MG's ones in Session 1 ($p = .02$), suggesting NG participants were initially trying to coordinating their movement preparation with the partner's one and then chose to become more predictable as a coordination strategy. Results on RTs Variance are coherent with this interpretation (see Table 4.2 for a detailed description).

Start Synchronicity (Absolute difference in Reaction Times, Diff_RT). See Table 4.1., lower panel, for a description of all significant results emerging from the ANOVA on Start synchronicity, i.e. on the absolute difference between partners' RTs (Diff_RT). The ANOVA showed a significant main effect of Session, Action-type and Interaction-type. Namely, trial-per-trial time-delay between participants' RTs was longer in Complementary with respect to Imitative actions ($p = .014$), was longer in Free with respect to Guided interaction ($p < .001$) and significantly decreased from Session 1 to Session 2 ($p = .011$) in both groups. However, the partners' synchronization in RTs followed different patterns in the Manipulated with respect to the Neutral group. Indeed, Diff_RT showed a trend towards significance of the Session x Action-type x Group interaction ($F(1,10) = 4.05, p = .072$). This indicates that while NG participants tended to increase their RTs synchronicity from Session 1 to Session 2 only in the Imitative condition, MG participants exhibited this tendency only in the Complementary condition. Note that the significant Session x Interaction-type x Action-type x Group quadruple interaction ($F(1,10) = 6.83, p = .026$) further specified that the reduction of Diff_RT found in the Imitative condition in NG partners was significant in both Free ($p = .001$) and Guided ($p = .01$) interaction-types. In contrast, the reduction of Diff_RT found in the Complementary condition in MG participants was significant only in Complementary-Free interactions ($p < .001$), which in this group was also the condition that in Session 1 showed the maximum Diff_RT with respect to the other conditions (all $ps < .001$).

4.3.2.2. Kinematics data

All significant results on maximum grip aperture (maxAp) and maximum grip aperture variance (Var_maxAp) are reported in Table 4.3.

Maximum grip aperture (maxAp). The ANOVA on maxAp showed that, in general, Power grips implied a larger grip aperture with respect to Precision grips (main effect of Movement-type, $p < .001$) as it was expected given the different dimensions of the lower/upper parts of the bottle-shaped

object (7 cm vs 2.5 cm of diameter). Moreover, this analysis also showed a significant main effect of Interaction-type ($F(1,22) = 6.9, p = .016$) and a significant Interaction-type x Movement-type interaction ($F(1,22) = 17.7, p < .001$; all $ps < .001$). These effects indicate that participants increased their maxAp during Free interactions possibly to enhance the communicative value of their movements (as it has been showed by previous studies, see for instance Sartori et al. 2009), and that this was the case for Precision grips only, as expected given this movement implies a more careful planning and execution and on the basis of previous studies showing that Precision grip is more affected by cognitive variables such as movement goals (see Graton 2010, Castiello 2005 for a review).

Finally, this analysis showed three significant four-way interactions: Session x Interaction-type x Movement-type x Group interaction ($F(1,22) = 5.6, p = .027$), Session x Action-type x Movement-type x Group interaction ($F(1,22) = 10.2, p = .004$), and Interaction-type x Action-type x Movement-type x Group interaction ($F(1,22) = 4.4, p = .048$). Since we expected only Precision grips to be modulated by the experimental conditions (see above) and following the main effect of Movement-type, we performed two separated ANOVAs for Power and Precision grip in order to make the four-way effects easier to interpret (see Table 4.3.). As expected, the ANOVA on Power grips showed no significant main effect or interaction (all $ps > .1$). On the contrary, the ANOVA on Precision grips showed again a significant main effect of Interaction-type ($F(1,22) = 12.0, p = .002$) and a significant Session x Action-type x Group interaction ($F(1,22) = 8.45, p = .008$). Post-hoc tests indicated that only in MG maxAp in Complementary actions tended to increase in Session2 with respect to Session1 ($p = .06$), so that the two Action-type (complementary/imitative), that were identical at the beginning of the experiment ($p = .5$), diverged in Session2 ($p = .02$). This was not the case in the NG. This result also explains the two-way significant Action-type x Movement-type interaction ($F(1,22) = 10.3, p = .004$) found in the general ANOVA. Therefore it seems that Complementary actions lead participants to increase their maxAp with respect to in Imitative ones in Precision grips ($p < .001$), and this effect seems to be a likely consequence of interference effects

between self-executed and observed actions (indeed, in Complementary Precision grips participants were performing a precision grip while observing the partner performing a power grip). However, the higher level interaction indicates this effect was present only in MG and only in Session 2 (see Figure 4.3.).

We suggest these results hint at the possibility that participants who underwent the interpersonal manipulation (MG), stopped being able to “ignore” the partner’s movements as the interaction developed in time. As a consequence, participants started to be influenced by the partner at the expense of their individual movement execution. Notably, this visuo-motor interference was not found in NG participants.

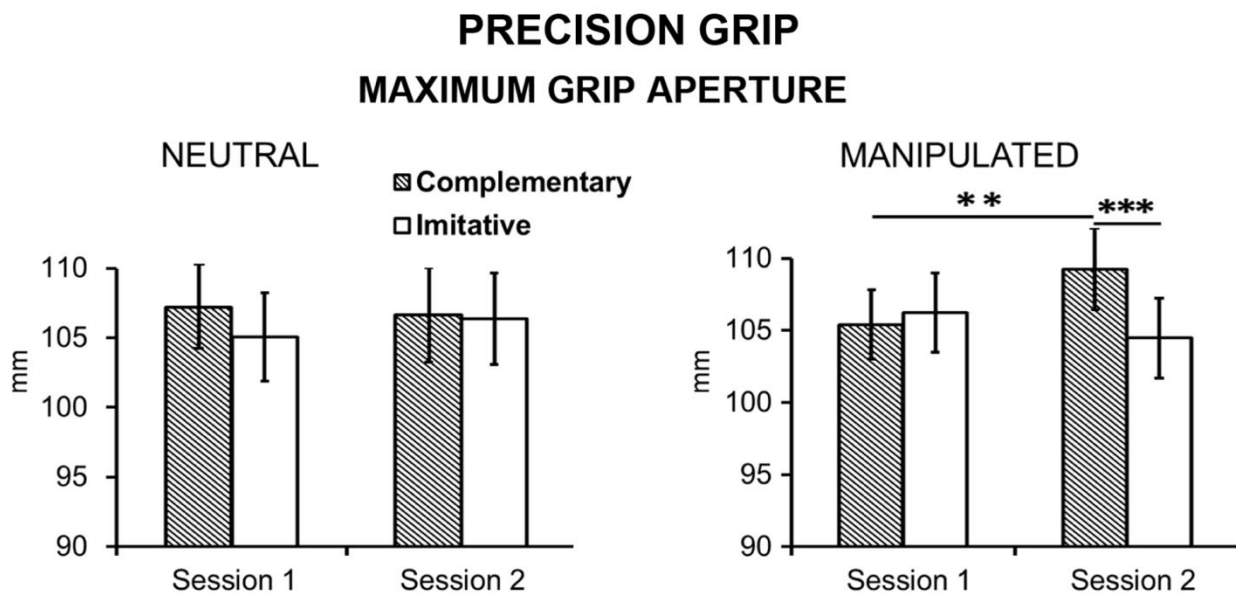


Figure 4.3. The figure illustrates the four-level Session x Action-type x Movement-type x Group significant interaction shown by the general ANOVA on Maximum grip aperture (maxAp). Data on Precision grip only are reported. Results indicate that, only in MG, maxAp changed over sessions according to Action-type; indeed, only in this group, maxAp in Complementary trials increased in Session 2 with respect to Session 1 ($p = .006$), so that the two Action-types (complementary/imitative), which were identical in Session 1 ($p = .4$), diverged in Session2 ($p = .001$). These results suggest that in MG visuo-motor interference induced by the observation of an incongruent movement performed by the partner increased over time. Error bars indicate s.e.m., (**) $p < .01$, (***) $p < .001$.

Maximum grip aperture variance (*Var_maxAp*). ANOVA on *Var_maxAp* showed significant main effects of Interaction-type and Movement-type (respectively $F(1,22) = 13.9, p < .001$; and $F(1,22) = 32.42, p < .001$) and the significance of Interaction-type x Movement-type interaction ($F(1,22) = 15.46, p = .001$; all $ps < .001$) indicating that, overall, *Var_maxAp* (only in Precision grips) was higher during Free interactions when compared with Guided ones. Moreover, the significant Session x Interaction-type x Movement-type x Group interaction ($F(1,22) = 4.48, p = .046$) suggested that, during Precision grips in Free interaction, *Var_maxAp* significantly decreased from Session1 to Session2 in the NG ($p < .001$), while it significantly increased in the MG ($p < .001$). See Figure 4.4.

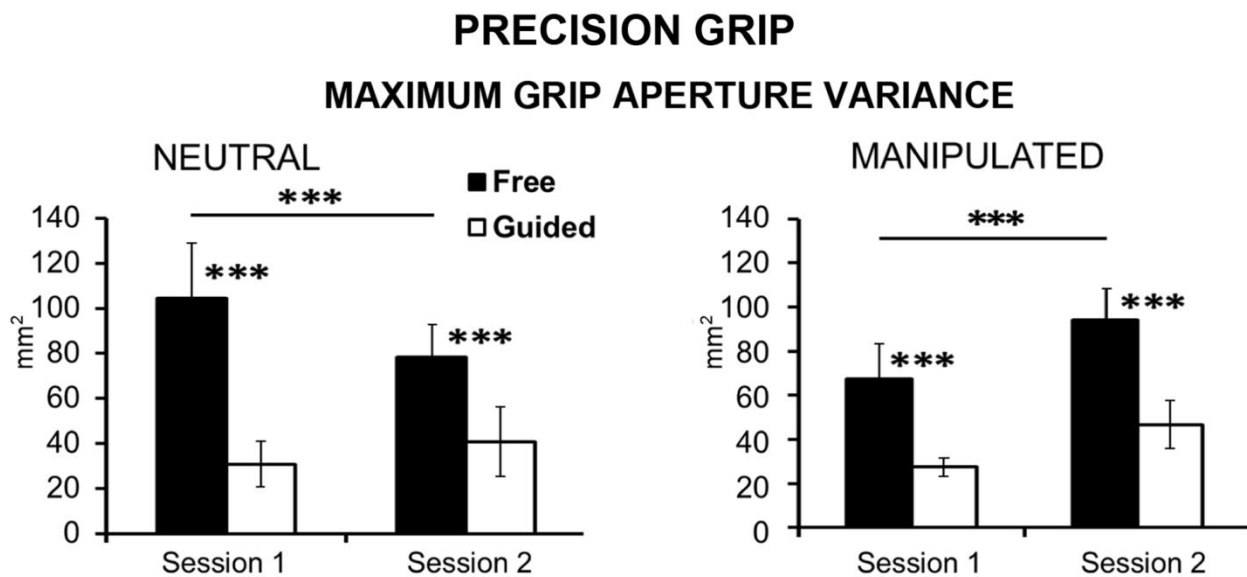


Figure 4.4. The figure illustrates the Session x Interaction-type x Movement-type x Group significant interaction emerged from the general ANOVA on maximum grip aperture variance (*Var_maxAp*). Data on Precision grip only are reported. The grip aperture variance in Precision grips significantly decreased in NG while it significantly increased in MG throughout sessions. This pattern suggests that while individuals in the NG learned how to coordinate without being influenced by the partner's movement, participants in the MG became more mutually responsive over time, suggesting an enhancement of reciprocal responsiveness between partners in the MG in terms of both involuntary visuo-motor interference (action-perception coupling effect) and increased number of movement corrections. That these effects were found in Precision grip only is likely to be due to the more sensitive feature of this movement-type to action goals. Error bars indicate s.e.m., (*) $p < .05$, (**) $p < .01$, (***) $p < .001$.

As previously described for maxAp, we divided the analysis into two separated follow-up ANOVAs for Power and Precision grips to further specify the 4-way significant effect (see Table 4.3.). Again, results showed the absence of any significant effect in Power grips (all $ps > .1$); on the contrary, the ANOVA on Precision grips showed a significant main effect of Interaction-type ($F(1,22) = 15.09, p = .001$) and a significant Session x Interaction-type x Group interaction ($F(1,22) = 4.7, p = .041$). These effects confirmed that: i) overall, Var_maxAp in Precision grips was higher during Free interactions when compared with Guided ones; and that ii) in NG Var_maxAp in Free interactions was significantly reduced from Session 1 to Session 2 ($p = .04$), while it significantly enhanced from Session 1 to Session 2 in MG ($p = .04$).

These results suggest that while individuals in the NG learned how to improve their joint-coordination and then reduced the need of performing many individual movement corrections, MG participants increased the number of movement corrections from Session1 to Session2. This effect may index that mutual responsiveness increased over time for MG participants.

Table 4.2. Results on RTs (ms) and RTs Variance (ms²).

Parameter	Effect	F	Df
RTs	Main effect of Session	37.08****	1,22
	Main effect of Interaction-type	7.5*	1,22
	Main effect of Action-type	4,66*	1,22
	Session*Interaction-type	12.5**	1,22
	<i>Session * Group (p = .069)</i>	3.67	1,22
RTs variance	Main effect of Session	6.69*	1,22
	Main effect of Interaction-type	15.31****	1,22
	Session*Interaction-type	4.49*	1,22
	Interaction-type*Action-type*Movement-type*Group	5.22*	1,22
	<i>Session*Group</i>	6.11*	1,22

The ANOVA on RTs Variance showed a significant Session x Group interaction ($F(1,22) = 6.11$; $p = .022$) which was accounted for by the fact that RTs Variance was higher in NG with respect to MG in Session 1 (RTs Variance in Session 1, NG vs MG, $p = .009$) and then significantly reduced from Session 1 to Session 2 (RTs Variance in NG in Session 1 vs Session 2, $p = .008$).

As a reduction of variance of a behavioural parameter is considered to be an index of its increased predictability (Vesper et al. 2011), these results suggest that NG increased the predictability of their RTs from Session 1 to Session 2 while, on the contrary, the MG did not show such a trend. We suggest the between group difference in RT variability time-patterns (i.e. from Session 1 to Session 2) might be due to the fact that only NG participants were sensitive to the partner's movements in Session 1 and tried to coordinate their RTs with a consequent enhancement of RT variability. On the contrary, MG participants disregarded the partner's movements and adhered to their own idiosyncratic movement preparation timing, and this kept low the RTs variability in MG in the first session. Coherently, RT variance was higher in Free vs Guided interaction only in NG, supporting the hypothesis that the increase in RT variance reflected the attempt to coordinate (Interaction-type*Action-type*Movement-type*Group). Crucially, it has to be noted that the higher RTs variability found in NG in Session 1 was not due to an unspecific between-group difference in RT variability since the two groups did not differ on mean RT variance (main effect of Group, $p > .1$). These results on RT Variance were coherent with the trend emerged from the analysis of mean RTs, which showed that the Session x Group interaction approached significance ($p = .069$, see main text).

Table 4.3. All significant results on maximum grip aperture (MaxAp) and maximum grip aperture variance (Var_maxAp).

Parameter	Effect	F	Df
maxAp	Main effect of Interaction-type	6.9 *	1,22
	Main effect of Movement-type	650 ***	1,22
	Interaction-type*Movement-type	17.7 ***	1,22
	Action-type*Movement-type	10.3 **	1,22
	<i>Interaction-type*Action-type*Movement-type*Group</i>	4.4 *	1,22
	<i>Session*Interaction-type*Movement-type*Group</i>	5.6 *	1,22
	<i>Session*Action-type*Movement-type*Group</i>	10.2 **	1,22
Precision grip only	Main effect of Interaction-type	12.0 **	1,22
	<i>Session*Action-type*Group</i>	8.45 **	1,22
Power grip only	-No significant effect-	-	-
Var_maxAp	Main effect of Interaction-type	13.9 ***	2,22
	Main effect of Movement-type	32.42 ***	2,22
	Interaction-type*Movement-type	15.46 ***	2,22
	<i>Session*Interaction-type*Movement-type*Group</i>	4.48 *	2,22
	Precision grip only	Main effect of Interaction-type	15.09 ***
<i>Session*Interaction-type*Group</i>		4.7 *	1,22
Power grip only	-No significant effect-	-	-

Design: Session x Interaction-type x Action-type x Movement-type x Group. In **bold** and *italics*, significant effects with Group described in the main text. (*) $p < .05$, (**) $p < .01$, (***) $p < .001$.

4.4. Discussion

In the present study we demonstrate for the first time that during face-to-face interactions the mutual interpersonal perception heavily influences motor behaviour of individuals involved in a joint-grasping task.

Behavioural performance profiles showed that in neutral situation (NG) free and guided interactions were equally challenging for participants. This might seem surprising, since guided interactions might have been expected to be much easier as compared to free interactions, because they required only temporal vs. temporal plus spatial mutual adjustments. We suggest this was the case since NG participants represented the task and its goal in a “highly integrated” manner (what Vesper et al. 2010 suggest to define a “Me + X” mode): namely, they were aware that the task goal (i.e. be synchronous) could only be achieved thanks to the partner’s support (i.e. they represented the task in terms of *shared goals*). Thus, when planning their own action they took into account the partner’s movement, despite the initial cost paid for monitoring the partner’s movements in the guided condition. This “integration” of partner’s movements in the agent’s motor planning is reflected in kinematics data: indeed, NG participants initially showed high movement variability, suggesting they performed several movement corrections during the reach-to-grasp (as in the attempt to adapt to the partner’s movements). Over time, they developed a strategy to improve performance (e.g. by reducing their RTs variability) and ended up entraining their movement preparation timings; as a consequence, they could also reduce the number of movement corrections (as shown by reduction in maxAp variability in Session 2). Finally, they never showed visuo-motor interference between self-executed actions and those observed in the partners during complementary actions.

On the contrary, with regard to participants sharing a negative interpersonal relationship (MG), achieving coordination in “self-organized” free interactive grasping was more demanding as compared to in guided interactions. Since MG participants’ impairment in free interactions was

paralleled by: i) good performance in pure temporal coordination, which would benefit from neglecting the spatial features of the partner's movements, and ii) very low RT and movement execution variability, altogether data indicate that the partners in the MG were impervious to mutual influence and tended to ignore each other, performing the task "each one on his own". This might have led to the poor performance in free interactions. These results are in line with evidence that a negative interdependence between partners (e.g. a competitive context) strongly reduces the emergence of automatic task co-representations (Iani et al. 2011, Hommel et al. 2009). We suggest that in our study the manipulation of interpersonal perceptions had instead a direct impact on the efficacy of interpersonal coordination because it prevented participant from representing the task in terms of shared goals.

Our results also showed that the need to fulfil the common goal (and thus maximize the individual pay-off) promoted the improvement of reciprocal adjustments in MG. Indeed, the improvement in free interactions synchronicity was paralleled by an enhancement of maximum grip aperture variance in this condition, suggesting the behavioural improvement was supported by an enhancement of movement corrections. Finally, the enhancement of movement corrections in Session 2 was matched with the emergence of visuo-motor interference between the self-executed movements and those observed in the partner in complementary actions. Altogether, the emergence of visuo-motor interference and the enhancement of movement variability in free interactions indicate that co-agents enhanced social responsiveness in the second session. Importantly, the temporal changes of participants' behaviour are unlikely due to a decrease of the manipulation effect since post-interaction implicit and explicit judgements showed that the negative interpersonal effect had not faded away. Rather, these results suggest that the interaction did not change the perception of the mate at an explicit "cognitive" level; instead, the time course of the interference effect indicates that motor interaction per se promotes social bonds at an implicit, sensorimotor level.

Our results and experimental set-up proved adept at acquiring a bi-personal perspective. Indeed, the manipulation of the agents' *reciprocal* interpersonal perception had an impact on *both* co-agents. In view of this, we analysed the time-course of automatic entrainment as a process that should consider the two partners as part of a unique dynamic system (Schmidt et al. 2011). Given the sharing of the same environmental cues, we expected participants to synchronize also the behavioural parameters which were not strictly relevant to the task (Marsh et al. 2009), e.g. not only grasping-times but also RTs. This is what we found in both groups as shown by the main effect of Session in the analysis of Start synchronicity. Tellingly, however, the partners' synchronization in RTs followed different patterns in the manipulated with respect to the neutral group. In particular, NG partners enhanced the synchronisation of their movement preparation timings both in free and guided interaction in the imitative condition, while MG participants did so only in the free-complementary condition. If any "entrainment" effect was to be found, it was expected to emerge in our motor task regardless the Interaction-type (i.e. both in guided and free interactions). Moreover, entrainment should be more prominent in imitative as compared to complementary actions given in the first case participants follow exactly the same trajectory and share the same environmental motor cues in terms of object affordances (i.e. their grasps are aiming at the same part of the object). Thus, the selectivity of the effect found in NG (i.e. entrainment only in imitative actions) is easy to interpret. On the contrary, the effect found in MG (i.e. entrainment only in free-complementary actions) is unexpected and difficult to be explained just in terms of "entrainment" processes. Finally, the enhancement of RTs synchronisation found between NG partners together with evidence that only NG participants enhanced their explicit judgments about their perceived similarity with the partner is reminiscent of the influence of synchrony (Valdesolo et al. 2011, 2010; Wiltermuth and Heath 2009) and involuntary mimicry (Van Baaren et al. 2009; Chartrand and Bargh 1999) in social contexts.

To conclude, we showed that in neutral realistic interactive situations (NG) two strangers are able to gradually learn how to coordinate their actions both in space and time. Moreover, when the “social bond” is disrupted by the belief the partner has mined one’s own self-esteem (MG), participants have difficulties in mutually adapt to each other movements: suggestion is made that this impairment is due to the lack of establishment of a shared goal between partners in the MG group, which results in more problems in predicting the partner’s actions in order to anticipatorily adapt to them. This is not likely to be due to attentional factors since negatively biased participants achieved high-level performance when only temporal coordination was required (i.e. in guided interactions). Thus, that NG initially performed free and guided interactions achieving the same level of performance while MG participants did not is likely due to differences in the motor planning strategies applied at the beginning of the joint-task, i.e. “Me + X” mode vs. “everyone on his own” strategies. Thus, the possibility to establish task sharing and represent shared goals to support interpersonal coordination during motor interaction is not independent from the interpersonal relation linking co-agents, proving the partner is not a “neutral” stimulus each agent needs to adapt to.

5. Neurocognitive bases of joint action:

shared goal coding in left aIPS

*If you care enough for a result
you will most certainly attain it*

W. James

5.1. Aim and hypotheses

The attempt to study individual neural activity in socially ecological, interactive and dynamic experimental set-ups (Schilbach et al. 2013; Gallotti and Frith 2013) imposes a shift of perspective from studying the neural correlates of imitative behaviour to non-imitative one, as in every-day dyadic encounters we usually interact with others in non-imitative fashions. On top of that, the beauty of partner-dance, or the ability to win a sport competition, rather arises from individuals' ability to adequately complement each other's gestures more than from plain synchronized imitation. Yet, the purported automaticity of simulative imitation mechanisms in sensorimotor regions (Rizzolatti and Craighero 2004) advocated by animal and human neurophysiology (Mukamel et al. 2010; Fadiga et al. 2005; Di Pellegrino et al. 1992), neuropsychology (Fontana et al. 2012; Pazzaglia et al. 2008; Moro et al. 2008; Saygin et al. 2007), behavioural (Kilner et al. 2003; Brass et al. 2001, 2000) and imaging studies (Kilner et al. 2009; Chong et al. 2008) seems at odds with the ease with which we entertain efficient non-imitative motor interactions (Sacheli et al. 2013, 2012; Ocampo Kritikos 2010; van Schie et al. 2008). Neuroimaging studies (Kokal et al. 2009; Newman-Norlund et al. 2008, 2007) have suggested simulative processes occurring in the fronto-parietal network might play a role in supporting both imitative and non-imitative (i.e. complementary) actions. However, no study has clarified yet which could be then the critical neural substrate causally mediating complementary motor interactions as compared to imitative ones. Here, we used repetitive Transcranial Magnetic Stimulation to tackle this issue.

Studying imitative and complementary interactions in the form of joint actions allows dissociating two crucial aspects of human motor behaviour: prediction of others' movement and shared goal representation. Indeed, while during synchronous imitation the agent's and partner's motor features overlap (from a motor point of view), complementary joint actions require by definition a mismatch between self-executed movements (and one's own motor sub-goal) and those observed in the partner (and the partner's sub-goal) in order to fulfil a shared goal. For instance, lifting and moving a table together (complementary action) require a mismatch between self-executed movements (e.g. pushing the table, one's own motor sub-goal) and those observed in the partner (e.g. pulling the table, the partner's sub-goal) in order to have the table moved from the kitchen to the living room (shared goal). Thus, while imitative interactions might also be achieved through pure anticipatory simulation, complementarity heavily dissociate individuals' roles and calls for substrates to link and integrate one's own and others' movements within a unique motor plan: namely, complementary actions require a neural substrate for *shared goal* motor coding (Butterfill 2012; Sebanz et al. 2006). What lacks is the description of which brain areas may causally support shared goal implementation during motor planning and on-line execution of realistic dyadic motor interactions.

That premotor and parietal regions engaged in sensorimotor simulative mechanisms are anticipatory in nature has been largely suggested (Kilner et al. 2007; Knoblich and Jordan 2003; Wolpert et al. 2003). In particular, the left anterior intra-parietal sulcus (aIPS) has been specifically ascribed the role of predictively coding other people's goals and intentions (Fogassi et al. 2005; Fogassi and Luppino 2005; Hamilton and Grafton 2006). This region, involved in visuo-motor transformations within the "expanded" dorsal visual stream (McIntosh and Schenk 2009; Goodale and Milner 1992), integrates objects' spatial and perceptual features during grasping (Verhagen et al. 2012), and it seems to be at play when agents need to control individual reach-to-grasp movements implementing intended goals (Tunik et al. 2005; Andersen and Burneo 2002; Binkofski et al. 1998), as well as when they need to abstract goal-related information from others' object-

directed movements (Fontana et al. 2012; Hamilton and Grafton 2006; Fogassi et al. 2005; Freund 2001; see also Tunik et al. 2007 for a review). As such, the left aIPS might be a good candidate as neural substrate taking part to the representation of shared goals (i.e. of the integration between one's own and his or her partner's action sub-goals) in the domain of imitative and non-imitative motor interactions.

In order to investigate this issue, in two experiments we examined the causal role of left aIPS in realistic imitative and non-imitative reach-to-grasp interactions with a virtual partner by temporarily inhibiting the neural activity of this region through repetitive Transcranial Magnetic Stimulation.

Participants were asked to grasp a bottle-shaped object placed in front of them via either a precision or a power grip (i.e. grasping the upper or the lower part of the bottle, respectively) *synchronously* with a virtual partner shown on a screen in front of them. They did not know in advance which action they needed to perform: in fact, in separated blocks, they were required to on-line adapt to the avatar's movements performing either the opposite (complementary) or the same (imitative) action with respect to its one. To foster participants' need for on-line adaptation, in half of the trials the virtual partner performed a movement correction during the reaching phase, shifting from power to precision grip (or vice-versa). Individuals' Accuracy (Acc) and Grasping Asynchronicity (GAsynchr) were assessed as critical dependent variables indexing the success of interpersonal coordination. Kinematics of both the reaching (wrist trajectory indexed by wrist height) and pre-shaping (grip aperture indexed by index-thumb 3D distance) components of participant's hand movements were monitored via infra-red cameras during the interaction to verify whether participants were actually adapting to the avatar's movements. In different sessions, the joint-grasping task was preceded by a 20 seconds off-line inhibitory continuous Theta Burst Stimulation (cTBS) on either the left aIPS or the vertex as a control site (experiment 1, see Figure 5.1., right panel). In experiment 2, cTBS was applied over left aIPS, left vPM, or as sham

stimulation. Using identical hand-object comparison between performance in the imitative vs. complementary condition allows disentangling the role of object affordances and shared goal implementation. Indeed, finding the effect of aIPS in complementary but not imitative actions independently from the type of movement performed (precision/power grip) would show that the integration of individual' and partner' goals was tackled more than individual's action type *per se*. Furthermore, finding impairments in the ability to coordinate (but not in kinematics) in both precision and power grips during complementary actions after inhibition of left aIPS suggest that the effects are not due to changes in the ability to perform the two types of movement *per se*, but that the impairment rather regards the integration of one's own goal with that of the partner (i.e. the shared goal coding).

5.2. Methods

5.2.1. Participants

Twenty-six participants took part in the study (experiment 1: 12 participants, 4 males, age 24.5 ± 4.3 ; experiment 2: 14 participants, 2 males, age 24.6 ± 4.0). All participants were right-handed as confirmed by the Standard Handedness Inventory (Briggs and Nebes 1975), reported normal or corrected-to-normal vision and were naive as to the purpose of the experiment.

The experimental protocol was approved by the ethics committee of the Fondazione Santa Lucia and was carried out in accordance with the ethical standards of the 1964 Declaration of Helsinki.

None of the participants had neurological, psychiatric, or other medical problems or any contraindication for TMS (Wasserman 1998). Participants gave their written informed consent to take part in the study, received a reimbursement for their participation and were debriefed on the purpose of the experiment at the end of the experimental procedure. No discomfort or adverse effects were reported or noticed in any of the participants.

5.2.2. Stimuli and procedure

Experimental stimuli, task instructions and procedures during the interactive task were identical in experiment 1 and experiment 2. Participants were comfortably seated in front of a rectangular table and watched a monitor where virtual partner's movements were shown (see Figure 1.4., panel b). The go-signal was delivered to participants via headphones (a whistle 4db and 787.5 Hz). The feedback signals about participants' performance were provided via a green/red LED placed next to the left corner of the screen.

Virtual partner. The kinematics of the virtual interaction partner were based on the movements of human participants actually performing different grasping movements (see Figure 3.1.; in the present experiment, only the Caucasian avatar was used). These grasping movements were performed with the right dominant hand and recorded using 3D motion capture. Motion capture was performed using a Vicon MX optical tracking system (Vicon Motion Systems, Oxford, UK) with 10 infrared light emitting cameras. 3D positions of 37 passive reflecting markers, attached to the participant's complete upper body (pelvis, chest, head, left and right arm, right hand) were recorded with a spatial error below 1.5 mm and at a temporal resolution of 120 Hz. Raw data were processed offline using commercial Vicon software to reconstruct and label the markers and to interpolate short missing parts of the trajectories. The final processed trajectories were animated using commercial software (Autodesk, Motion Builder) in the appearances of a Caucasian male character. Since we wanted the participants to ignore facial expressions, the final video stimuli contained only the upper body down from the shoulders, without the neck and the head.

The complete sample of clips comprised 16 different grasping movements. Half of those movements ended at the top position of the bottle-shaped graspable object (thus being precision grips) while the other half of the movements ended at the bottom position (being power grips). Moreover, in 50% of the trials, the grasps included an on-line correction, i.e. the avatar performed a movement correction switching from a precision to a power grip (or vice versa) during the reaching

phase. Thus, the 16 clips could be divided in four conditions (Correction/No-correction x Power/Precision grip) each comprising 4 different variants of the movement.

Previous recording the interactive task, a pilot study was conducted in order to validate the movements of virtual character. 12 participants were asked to rate on visual analogue scales ranging from 0-100 “how much natural and realistic” they perceived the avatar’s movements. Participants’ rating showed the movements were perceived as realistic (63.8+/- 24.4). More importantly, a two-way repeated-measure ANOVA on the different types of clip (Correction/No-Correction x Precision/Power grip) showed judgments did not differ between types of clip (no significant effect, all $ps > .2$).

Interactive Task. Participants were required to perform the grasping task interacting with their virtual partner. Namely, they had to reach and grasp with their right dominant hand the bottle-shaped object placed in front of them as synchronously as possible with their virtual partner. At each trial, participants had to adapt to the virtual partner’s movement without knowing in advance where to grasp the object: in different blocks (i.e. “Complementary” or “Imitative”), they had to perform opposite/same movement with respect to their virtual partner, e.g. in Imitative block, if the avatar was grasping the upper part of the object they also had to grasp the upper part, while in Complementary blocks they had to perform the opposite movement (in this example, grasping the lower part of the object). Both the participants’ and the avatar’s movements were performed with the right dominant hand. Whatever the condition (Imitative/Complementary) they always had to grasp the object as synchronous as possible with the avatar. Thus, they were required to coordinate with him both in time (being synchronous) and space (doing complementary/imitative movements). The “opposite/same movement” instruction to be followed was provided on the screen at the beginning of each block.

The trial time-line was as following (see Figure 5.1, left panel). The presentation of each clip was preceded by a fixation cross placed on the region of the screen where the avatar’s hand

would appear. The cross had the purpose of alerting participants about the impending trial. Then, participants heard an auditory go-signal and (after 300 ms) the clip started. Upon receiving the auditory instruction participants could release the Start-button and reach-to-grasp the object. In case participants started before hearing the instruction, the trial was classified as false-start and discarded from the analyses. At the end of each trial, participants received a feedback (a green/red LED turned on) about their performance (win/loss trial). A win trial needed that participants followed their auditory instructions (i.e. correctly performed complementary/imitative movements with respect to the avatar's ones) and achieved synchronicity with the avatar in grasping the objects. Note that the avatar's index-thumb contact-times were measured trial-by-trial by a photodiode placed on the screen which sent a TTL signal recorded by E-Prime2 software (Psychology Software Tools Inc., Pittsburgh, PA). The photodiode was triggered by a black dot (not visible to the participants) placed on the screen on the frame of the clip corresponding to the moment at which the avatar grasped his virtual object. Previous to any brain stimulation and recording of the motor task, a familiarization block was provided: it comprehended 4 imitative and 4 complementary movements.

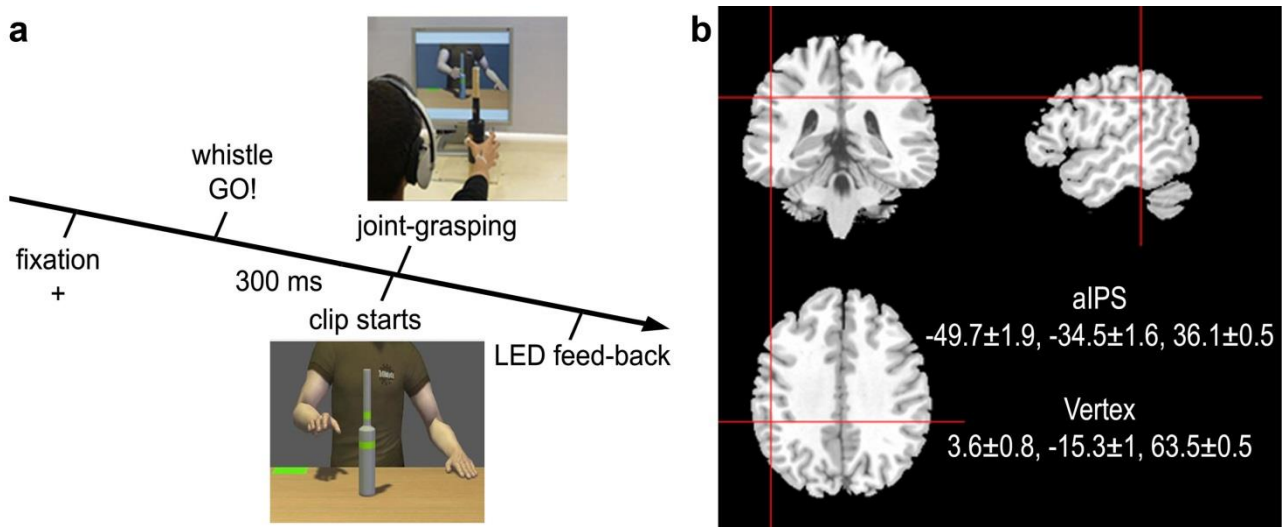


Figure 5.1. On the left (**a**), the trial time-line of the interactive task. On the right (**b**), mean stimulation site for aIPS in experiment 1, Talairach coordinates (*Tal*). 20 s off-line inhibitory continuous Theta Burst Stimulation was applied on either the left aIPS or the Vertex as a control site. In experiment 2, cTBS was applied over left aIPS (-48.7±1.08, -34.5±1.27, 36.3±0.5 *Tal*), the ventral premotor cortex (vPM, -52.1±1.0, 10.12±1.6, 23.5±0.6 *Tal*), or as sham stimulation.

Per each session (after cTBS), participants performed four 28-trials Complementary / Imitative blocks (in a counterbalanced order between participants). Since the clip sample comprised 16 clips divided in four conditions (Correction/No-correction x Power/Precision grip, each including 4 different variants of the movement), in each block, out of 4 item per condition, 3 items were repeated (final block-sample = 7 item per condition, presented in randomized order). Both the Imitative and Complementary blocks were performed twice in a session. Thus, in each four-block session participants performed 14 trials per condition (Complementary/Imitative x Correction/No-Correction x Power/Precision grip). Crucially, in Imitative and Complementary blocks participants watched and adapted to exactly the same avatar's movements. Stimuli presentation and randomization were controlled by E-Prime2 software (Psychology Software Tools Inc., Pittsburgh, PA).

5.2.3. Transcranial Magnetic Stimulation

The intensity of stimulation was determined for each participant relative to the participant's resting motor threshold (rMT). Participants wore a tightly fitting bathing cap on which scalp stimulation points were marked. Motor evoked potentials (MEPs) were recorded from the first dorsal interosseous (FDI) muscle of the right hand. Surface Ag/AgCl electrodes were placed in a belly-tendon montage with the active electrode placed over the motor point and the reference over the interphalangeal joint. Electromyographic (EMG) recording was performed with a Viking IV (Nicolet Biomedical) electromyograph. The resting motor threshold, defined as the lowest intensity able to evoke 5 of 10 MEPs with an amplitude of at least 50 μ V, was determined by holding the stimulation coil over the optimal scalp position (OSP). The OSP for inducing MEPs in the right FDI muscle was found by moving the coil in steps of 1 cm over the left primary motor cortex until the largest MEPs were found and then marked with a pen on a bathing cap worn by participants. Mean rMT were 59 % \pm 7 % of the stimulator output in experiment 1 and 57.6 % \pm 7.9 % of the stimulator output in experiment 2.

Stimulation sites were identified on each participant's scalp with SofTaxic Navigator system (EMS). Skull landmarks (nasion, inion, and two preauricular points) and 64 points providing a uniform representation of the scalp were digitized by means of a Polaris Vicra Optical Tracking System (NDI). Coordinates in Talairach space (Talairach and Tournoux 1988) were automatically estimated by the SofTaxic Navigator from an MRI-constructed stereotaxic template using an individualized probabilistic head model computation. This individualized head model preserves the anatomical scalp–brain correlates of a mean MR template, providing an accurate set of estimated MRI data, specific for the participant under examination. TMS was performed using a 70-mm figure-of-eight coil connected to a Magstim Super Rapid Transcranial Magnetic Stimulator (The Magstim Company) applying 20 seconds of continuous Theta-Burst stimulation paradigm similar to Huang et al. (2005): trains of three pulses at 50 Hz were delivered every 200 ms (i.e. at 5 Hz) for 20 s (300 pulses in total). cTBS was applied at 80% of the resting motor threshold (experiment 1, mean $47\% \pm 4.6\%$ of the stimulator output; experiment 2, mean $46.2\% \pm 4.7\%$ of the stimulator output). After the cTBS participants rested for 5 minutes with their right arm relaxed on the side, then they started the interactive task. The task never lasted more than 10 minutes, so that the inhibitory time-window was never exceeded.

Experiment 1. The scalp locations that allowed the best stimulation of left aIPS (as reported by Hamilton and Grafton 2006, *Tal* -47, -34, 37) and Vertex coordinates (*Tal* 0, -17, 63, Okamoto et al. 2004) were identified and stored by the SofTaxic Navigator system (EMS). Mean stimulation sites were -49.7 ± 1.9 , -34.5 ± 1.6 , 36.1 ± 0.5 for left aIPS and 3.6 ± 0.8 , -15.3 ± 1 , 63.5 ± 0.5 for the Vertex, Talairach coordinates (see Figure 5.1., right panel). Thanks to coil calibration, the system allowed the overlapping of the coil focus with these coordinates and monitoring on-line any movement of the coil during the 20 s cTBS. Displacements from the optimal individual scalp locations for aIPS/Vertex stimulation never exceeded 2 mm in the three axes. aIPS/Vertex stimulation was counterbalanced between participants. Transcranial Magnetic Stimulation has a

spatial resolution that might tackle regions of IPS involved in both hand shape and reaching control (Gallese et al. 1994; MacKay et al. 1992)

Experiment 2. The scalp locations that allowed the best stimulation of left aIPS (as reported in experiment 1) and vPM (*Tal* -52, 10, 24, Avenanti et al. 2013a) were identified and stored by the SofTaxic Navigator system (EMS). Mean stimulation sites were -48.7 ± 1.08 , -34.5 ± 1.27 , 36.3 ± 0.5 for left aIPS and -52.1 ± 1.0 , 10.12 ± 1.6 , 23.5 ± 0.6 for left vPM (Talairach coordinates). During sham stimulation, TBS was delivered on a 3-cm-thick wooden rectangular-shaped object placed on the vertex of participants' head. Displacements from the optimal individual scalp locations for aIPS/vPM stimulation never exceeded 2 mm in the three axes. aIPS/vPM/Sham stimulation was counterbalanced between participants.

5.2.4. Data handling and design

Only correct trials were entered in the behavioural and kinematics analyses, i.e. we excluded from the analyses trials in which participants i) missed the touch-sensitive copper-plates and response was thus not recorded, ii) made false-starts, or iii) did not respect their complementary/imitative instructions. We considered as crucial behavioural measures:

- i) Accuracy, i.e. number of movements executed according to participants' instructions (false-starts were also considered as errors);
- ii) Reaction Times (RTs), i.e. time from the go-signal to the instant of participants' Start-button hand release;
- iii) Movement Times (MTs), i.e. time from the instant of participants' Start-button hand release to the participant's index-thumb contact-time on the bottle;
- iv) Grasping Asynchronicity.

For each of the above-mentioned behavioural measures we calculated the individual mean in each condition. These values were entered in a within-subject ANOVA (see below).

Moreover, we analyzed kinematics associated to the reaching and pre-shaping component of the reach-to-grasp movement (Jeannerod 1984, 1981). This was done in order to monitor participants' motor execution during the task. Indeed, the left aIPS was found to be involved in the on-line monitoring of grasping (Tunik et al. 2005). Thus, we aimed to control results in Accuracy and Grasping Asynchronicity could not be accounted for by i) deficit in motor execution, or ii) the fact participants did not properly perform the task, i.e. we monitored that participants truly tried to adapt to the avatar's movements during the reach-to-grasp.

The SMART-D software package (B|T|S|) was used to analyze data and provide a 3-D reconstruction of the marker positions as a function of time. The times of participants' Start-button hand release and index-thumb contact-times on the bottle were used to subdivide the kinematics recording with the aim of analyzing only the reach-to-grasp phase. With regard to the reaching component, we analyzed wrist trajectory as indexed by the maximum peak of wrist height on the vertical plane (maxH), while for the grasping component we analyzed maximum grip aperture (maxAp, i.e. the maximum peak of index-thumb 3D Euclidean distance).

Each behavioural or kinematics value that fell 2.5 SDs above or below each individual mean for each experimental condition was excluded as outlier value. At the group level, participants with an individual mean 2.5 SDs above or below the group mean was be excluded from the analyses; one participant in experiment 1 was an outlier on Grasping Asynchronicity according to this criterion. Thus, she was excluded from the analyses and replaced (final sample 12 participants).

Each behavioural and kinematics dependent measure was then normalized on the individual grand-mean and SD (Z-transformation) and entered separate analyses of variance (ANOVAs). In experiment 1, the ANOVAs had stimulation Site (aIPS/Vertex) x Action-type (Complementary/Imitative) x Clip-type (Correction/No-correction) x Movement-type (Power/Precision grip) as within subjects factors (i.e. 2x2x2x2 within-subject design). In experiment 1, the ANOVAs had stimulation Site (aIPS/Vertex/Sham) x Action-type (Complementary/Imitative) x Clip-type (Correction/No-correction) x Movement-type

(Power/Precision grip) as within subjects factors (i.e. 3x2x2x2 within-subject design). With regard to accuracy, it was not possible to run an ANOVA since some conditions had showed no variance, namely aIPS-Complementary-NoCorrection-Power grip, aIPS-Imitative-NoCorrection-Power and –Precision grips and Vertex-Imitative-NoCorrection-Power grips in experiment 1, aIPS-Complementary-NoCorrection-Power grip, aIPS-Imitative-NoCorrection-Power and –Precision grips and vPM-Complementary-NoCorrection-Power and –Precision grips in experiment 2. Thus, we verified the absence of speed-accuracy trade-offs with GASynchr by means of non-parametric tests on the condition of interests, i.e. the Site x Action-type significant interaction. We calculated the individual difference between individual mean accuracy in Complementary minus Imitative action per each stimulation site and applied a Wilcoxon matched pair test in experiment 1, aIPS(Complementary-Imitative) vs. Vertex(Complementary-Imitative), and a Friedman ANOVA in experiment 2, aIPS(Complementary-Imitative) vs. vPM(Complementary-Imitative) vs. Sham(Complementary-Imitative). All tests of significance were based upon an α level of 0.05. When appropriate, post-hoc tests were performed using Newman-Keuls method.

5.3. Results

5.3.1. Experiment 1: aIPS vs Vertex

All significant results are reported in Table 5.1.

Movement kinematic results. Kinematics results demonstrated participants took into account the movements of the avatar replicating findings on human-human interaction in a similar task (Sacheli et al. 2013, 2012). Indeed, they on-line corrected their movement trajectory when the avatar made a movement correction during the reaching phase. More importantly, participants showed automatic mimicry of the avatar movements, as shown by the interference between self-executed actions and those observed in the avatar in the Complementary condition, i.e. when the avatar's movements are

incongruent with the participant's ones. This suggests that in order to coordinate with the virtual partner they recruited somatomotor simulative resources as illustrated by the significant Clip-type x Action-type x Movement-type interaction ($F(1,11) = 11.6, p = .006$, see Figure 5.2, left panel) shown by the ANOVA on maximum grip aperture (maxAp). Namely, maxAp in Precision grip was significantly larger in Correction as compared to No-Correction both in Imitative and Complementary actions (all $ps < .001$, see also the highly significant Clip-type x Movement-type interaction ($F(1,11) = 175.7, p < .001$, all post-hoc tests $ps < .001$), indicating that when participants watched the avatar performing a correction they opened the grip more as to perform a Power grip and then corrected to a Precision grip, factually adapting to the avatar's movements. Moreover, the same Clip-type x Action-type x Movement-type significant interaction also demonstrated that maxAp in No-corrections-Precision grips during Complementary actions was significantly larger than during Imitative actions ($p = .001$), namely it was larger when participants interacted with the avatar performing a Power grip. Note the inverse effect is absent in Power-grip because the distance between index-thumb reaches its maximum when grasping the lower part of the bottle thus masking the tendency to mimic the other's precision grip. This suggests participants automatically imitate the virtual partner's movement.

Consistent effects were shown by the ANOVA on maximum wrist height (maxH, Action-type x Clip-type x Movement-type significant interaction, $F(1,11) = 5.56, p = .038$, see Figure 5.2., right panel). Indeed, maxH results showed that Power grips (i.e. the condition when participants grasped the lower part of the bottle-shaped object) showed a significantly lower trajectory than Precision grips (i.e. the condition when participants grasped the upper part of the bottle-shaped object) in No-corrections (all $ps < .001$), while Correction-Power and Correction-Precision grip did not differ ($p = .1$ and $.2$ in Complementary and Imitative actions respectively). This shows that during Correction-Power grips participants were truly performing a movement correction, changing trajectory from a higher (i.e. Precision grip position) to a lower one (i.e. Power grip position) during the reaching phase. Moreover, with regards to No-correction, Complementary-Power and Imitative-Power grips

significantly differed ($p = .002$), indicating participants wrist trajectory was influenced by the virtual partner's one. The fact that these significant effects were more evident when participants were grasping the lower part of the bottle-shaped object (i.e. in Power grips) is due to the features of the recorded parameter (peak H), which imply a ceiling effect when participants correctly grasp the upper cylinder with a precision grip.

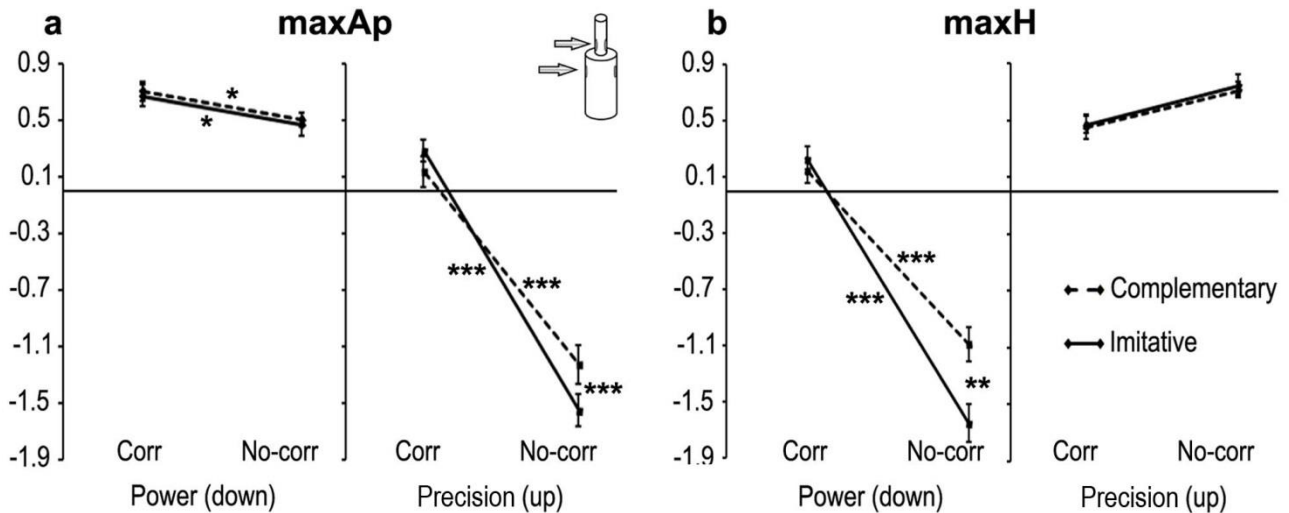


Figure 5.2. Kinematics data from experiment 1. On the y-axis, Z-scores of (a) maximum grip aperture and (b) maximum wrist height. The figure reports results from the Action-type x Clip-type x Movement-type significant interaction (maxAp, $F(1,11) = 5.6$, $p = .038$; maxH, $F(1,11) = 5.6$, $p = .038$). Crucially, these results showed that i) participants were performing on-line movement corrections when they observed the avatar performing movement corrections, suggesting they were truly adapting to the avatar's movements, and ii) participants recruited somatomotor simulative processes during the interaction in a similar vein as it happens with human partners, since they showed visuo-motor interference due to the observation of the avatar's movements in complementary actions. For the sake of simplicity, we did not explicitly report in the figure the significance of the comparison between Power and Precision grip in all conditions (all $ps \leq .001$, as also suggested by the significant main effects, See Table 5.1.). "Corr" = Corrections; "No-corr" = No-corrections. Error bars indicate s.e.m. (***) $p < .001$, (**) $p < .01$, (*) $p < .05$. Similar results were found in experiment 2 (see main text).

Overall, these results indicate movement corrections and somatomotor simulation involved both the grasping and the reaching component of the reach-to-grasp movement. Thus, results suggest processes recruited during human-human interaction (i.e. mutual adjustment and somatomotor

simulation) in a similar task (Sacheli et al. 2013, 2012) are also recruited when participants interact with virtual characters if the action goal cannot be accomplished without taking into account the virtual partner's movements and adapting to them. None of these effects showed significant interactions with stimulation Site (all p s > .4 in maxAp and all p s > .6 in maxH), indicating aIPS stimulation did not imply impairment of motor execution kinematics.

Joint-coordination performance. The ANOVA on Grasping Asynchronicity (GAsynchr) showed a significant main effect of Clip-type ($F(1,11) = 14.69, p = .003$) indicating that coordinating with the avatar during Corrections was overall more difficult than during trials in which the virtual partner did not correct his movements on-line. The higher-order Action-type x Clip-type x Movement-type significant interaction ($F(1,11) = 6.14, p = .031$) indicated that the only significant difference in GAsynchr between Correction and No-correction was found during Imitative – PrecisionGrip ($p = .049$). These effects were not modulated by stimulation Site.

Regardless the role of corrections, the ANOVA on GAsynchr showed a stimulation Site (aIPS/Vertex) x Action-type (Complementary/Imitative) significant interaction ($F(1,11) = 7.54, p = .02$; see Figure 5.3., left panel). Post-hoc tests showed that stimulation of left aIPS caused a selective decay of performance in complementary actions so that joint-coordination was significantly lower during complementary as compared to imitative actions ($p = .02$) and tended to be so also with respect to complementary actions after Vertex stimulation ($p = .06$). On the contrary, complementary and imitative actions achieved an equal level of joint synchronicity after cTBS on the control site (Vertex), thus showing to be similar in terms of overall difficulty in line with previous literature (van Schie et al. 2008; Sacheli et al 2013). This also makes it unlikely that inhibition of aIPS disrupted complementary action performance because of baseline difference in the complexity of this condition with respect to imitative interactions.

With regard to accuracy, Wilcoxon matched pair test gave no significant results in the comparison of interest ($z = .88, p = .37$) indicating the lack of speed-accuracy trade-offs.

The absence of significant interaction with stimulation Site in reaction times and movement times (see Table 5.1.) excludes the effect described above were due to attentional factors or non-selective impairment in movement execution.

5.3.2. Experiment 2: aIPS vs vPM vs Sham

All significant results are reported in Table 5.2.

Movement kinematic results. Kinematics results confirmed that participants realistically interacted with the avatar and on-line adapted to its movements recruiting somatomotor simulative processes, as shown by experiment 1. Indeed, data on both maxAp and maxH showed a triple Action-type x Clip-type x Movement-type significant interaction ($F(1,13) = 19.9, p < .001$, and $F(1,13) = 10.9, p = .006$ respectively), indicating kinematics was modulated both by the need to on-line correct one's own movements when the avatar performed a correction and by automatic mimicry triggered by the actions observed in the avatar (see Table 5.2.). As in experiment 1, none of these effects was modulated by stimulation Site.

Joint-coordination performance. The ANOVA on GASynchr showed a significant main effect of Action-type ($F(1,13) = 11.88, p = .004$), which apparently suggests that complementary interactions were more difficult than imitative ones. Conversely, this effect was entirely accounted for by the stimulation Site (Action-type x Site, $F(1,13) = 5.37, p = .011$; see Figure 5.3., right panel). Indeed, GASynchr in complementary interactions indicated worse performance (i.e. higher Grasping Asynchronicity) as compared to imitative ones only after inhibition of aIPS ($p < .001$) and not after vPM or sham stimulation ($p = .14$ and $p = .63$ respectively). Moreover, performance in

complementary interactions after aIPS inhibition was significantly lower than in all other conditions (all $ps < .015$). As for Experiment 1, this indicates disruption of the ability to synchronize with the partner during complementary interactions induced by aIPS inhibition was not due to baseline differences in the complexity of this condition with respect to imitative interactions, since neither after stimulation of any of the control sites (Vertex, Exp 1, or vPM, Exp 2) nor after sham stimulation complementary and imitative interactions significantly differed in terms of performance.

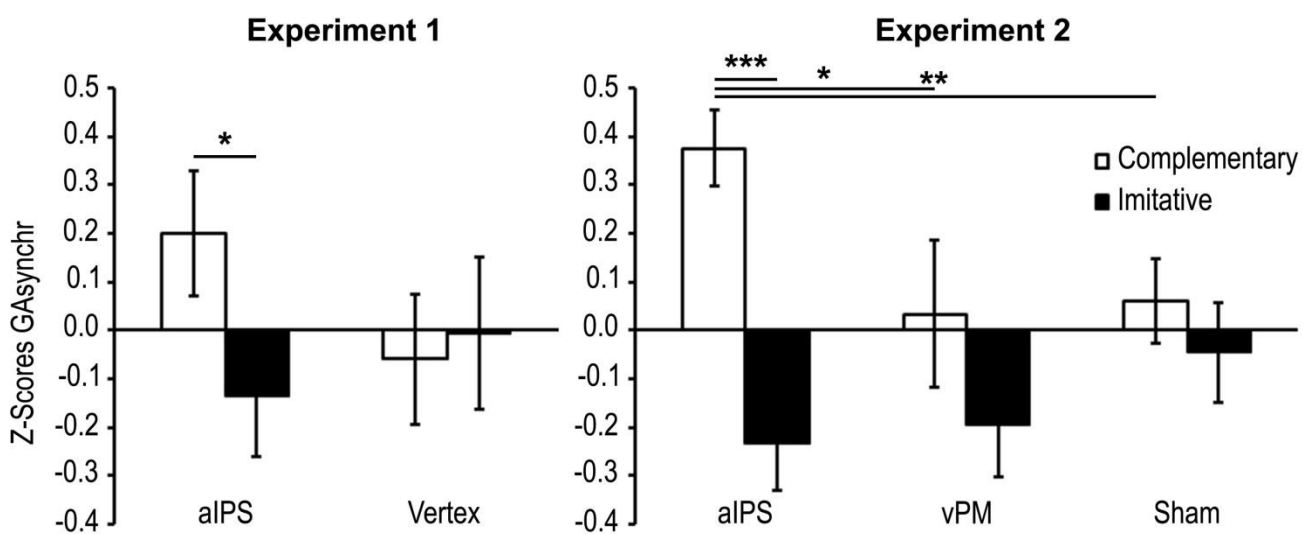


Figure 5.3. Joint-coordination performance after cTBS stimulation. In line with previous studies, participants achieved equally proficient performance in Complementary and Imitative actions in all control conditions (vertex and left vPM stimulation and sham stimulation). On the contrary, performance dissociated after left aIPS inhibition. **(a)** The figure illustrates the Site (aIPS/Vertex) x Action-type (Complementary/Imitative) significant interaction ($F(1,11) = 7.54, p = .02$) showed by the ANOVA *GAsynchr* z-scores in experiment 1. **(b)** The figure illustrates the stimulation Site (aIPS/vPM/Sham) x Action-type (Complementary/Imitative) significant interaction ($F(1,13) = 5.37, p = .011$) showed by the ANOVA on *GAsynchr* z-scores in experiment 2.

Finally, the ANOVA on *GAsynchr* also showed a triple Action-type x Clip-type x Movement-type significant interactions ($F(1,13) = 89.37, p < .001$). This interaction specified that Imitative-NoCorrection-Precision grip was the condition in which participants achieved a significantly higher level of performance with respect to all other conditions (all $ps < .003$), while Imitative-

NoCorrections Power grips showed the opposite trend (significantly lowest performance, all $ps < .05$ except as compared to Complementary-NoCorrection-Precision grips). Moreover, during Complementary-Corrections participants achieved lower performance as compared to Complementary-NoCorrections during Power grips, and better performance during Precision grips. These effects show that the relative complexity of Complementary vs. Imitative interactions depended on the combination with other conditions and did not reflect a general feature of the task. Crucially, these effects were not modulated by the stimulation Site (Site x Action-type x Clip-type x Movement-type, $p = .7$) and thus cannot account for results showed by the Site x Action-type significant interaction.

With regard to the accuracy of the performance, Friedman ANOVA gave no significant results in the comparison of interest ($\chi^2(2) = 2.97, p = .22$) indicating lack of speed-accuracy trade-offs. Moreover, the absence of significant interaction with stimulation Site in movement times excludes the effect described above could be due to non-selective impairment in movement execution (see Table 5.2).

Finally, reaction times showed significant interactions between Site and Action-type ($F(1,13) = 3.5, p = .045$) and Site and Movement-type ($F(1,13) = 3.8, p = .036$); post-hoc tests on the latter interaction revealed reaction times after aIPS inhibition were faster than in all other conditions (all $ps < .025$), yet this effect did not interact with Action-type (Site x Action-type x Movement-type, ($F(1,13) = 2.19, p = .13$) and could thus not explain the significant effect on GAsynchr. Moreover, post-hoc tests on the Site x Action-type significant interaction showed no significant results (all $ps > .16$) and specifically indicated the absence of significant difference in reaction times between Complementary and Imitative actions after aIPS inhibition ($p = .77$). This pattern of results suggests the significant effect on GAsynchr could not be due to either a modulation of efficiency in movement preparation (i.e. motor planning) or attentional factors.

Altogether, the results from experiment 1 and experiment 2 converged in showing that aIPS is causally involved in scaffolding on-line non-imitative motor interactions, while vPM was shown not to play a comparable crucial role in this condition, although – similarly to aIPS – it is a key-node of the fronto-parietal network involved in grasping planning and despite being constantly recruited during action observation. That aIPS inhibition interfered with performance synchronicity in complementary interactions regardless the specific movement features (either precision or power grip), while it did not impair imitative interactions (i.e. actions where the agent's and partner's action goals do not differ), suggests the interference occurred at a high-level of action programming/representation, namely shared-goal coding, rather than at the level of movement programming/control.

Table 5.1. The table reports all significant effects in experiment 1 showed by the ANOVAs on Z-scores of Grasping Asynchronicity, Reaction Times, Movement Times and wrist and pre-shaping kinematics (maxH and maxAp), having stimulation Site (aIPS/Vertex) x Action-type (Complementary/Imitative) x Clip-type (Correction/No-correction) x Movement-type (Power/Precision grip) as within-subject factors. In **bold**, the significant interaction between Action-type x stimulation Site on Grasping Asynchronicity described in the main text. All but this latter effect are due to the physical constraints of the set-up.

GRASPING ASYNCHRONICITY				
Effect	F	df	p	η^2
Main effect of Clip-type	14.69	1,11	.003	.572
Site x Action-type	7.54	1,11	.019	.407
Action-type x Clip-type x Movement-type	6.14	1,11	.031	.358
REACTION TIMES				
Effect	F	df	p	η^2
<i>No significant effect</i>				
MOVEMENT TIMES				
Effect	F	df	p	η^2
Main effect of Clip-type	266.4	1,11	< .001	.960
Action-type x Movement-type	1264	1,11	< .001	.991
Action-type x Clip-type x Movement-type	62.94	1,11	< .001	.851
MAXIMUM WRIST HEIGHT (maxH)				
Effect	F	df	p	η^2
Main effect of Clip-type	297.9	1,11	< .001	.964
Main effect of Movement-type	213.4	1,11	< .001	.950
Action-type x Clip-type	13.2	1,11	.004	.546
Clip-type x Movement-type	240.9	1,11	< .001	.956
Action-type x Clip-type x Movement-type	5.6	1,11	.038	.336

MAXIMUM GRIP APERTURE (maxAp) (follows from previous page)				
Effect	F	df	<i>p</i>	η^2
Main effect of Clip-type	296.9	1,11	< .001	.964
Main effect of Movement-type	269.1	1,11	< .001	.960
Action-type x Clip-type	5.6	1,11	.037	.338
Clip-type x Movement-type	175.7	1,11	< .001	.941
Clip-type x Action-type x Movement-type	11.6	1,11	.006	.512

Table 5.2. The table reports all significant effects showed in experiment 2 by the ANOVAs on Z-scores of GAsynchr, Reaction Times, Movement Times, wrist and pre-shaping kinematics (maxH and maxAp), having stimulation Site (aIPS/Vertex/Sham) x Action-type (Complementary/Imitative) x Clip-type (Correction/No-correction) x Movement-type (Power/Precision grip) as within-subject factors. In **bold**, the Action-type x stimulation Site significant interactions described in the main text. All but these latter effects are due to the physical constraints of the set-up.

GRASPING ASYNCHRONICITY				
Effect	F	df	p	η^2
Main effect of Action-type	11.88	1,13	.004	.477
Main effect of Movement-type	8.46	1,13	.012	.394
Action-type x Movement-type	35.81	1,13	.000	.734
Action-type x Clip-type x Movement-type	89.37	1,13	.001	.873
<i>Site x Action-type</i>	5.37	1,13	.011	.292
REACTION TIMES				
Effect	F	df	p	η^2
Action-type x Clip-type	5.49	1,13	.036	.297
<i>Site x Action-type</i>	3.5	1,13	.045	.212
<i>Site x Movement-type</i>	3.8	1,13	.036	.226
MOVEMENT TIMES				
Effect	F	df	p	η^2
Main effect of Clip-type	255	1,13	< .001	.951
Action-type x Movement-type	2560	1,13	< .001	.995
Action-type x Clip-type x Movement-type	1131	1,13	< .001	.989
MAXIMUM WRIST HEIGHT (maxH)				
Effect	F	df	p	η^2
Main effect of Clip-type	97.5	1,13	< .001	.882
Main effect of Movement-type	139.1	1,13	< .001	.914
Action-type x Clip-type	10.9	1,13	.006	.456

MAXIMUM WRIST HEIGHT (maxH) (follows from previous page)				
Effect	F	df	<i>p</i>	η^2
Action-type x Movement-type	13.3	1,13	.003	.505
Clip-type x Movement-type	105.8	1,13	< .001	.890
Action-type x Clip-type x Movement-type	10.9	1,13	.006	.456
MAXIMUM GRIP APERTURE (maxAp)				
Effect	F	df	<i>p</i>	η^2
Main effect of Clip-type	350.4	1,13	< .001	.964
Main effect of Movement-type	316.6	1,13	< .001	.960
Action-type x Clip-type	16.1	1,13	< .001	.553
Clip-type x Movement-type	118.4	1,13	< .001	.901
Clip-type x Action-type x Movement-type	19.9	1,13	< .001	.605

5.4. Discussion

Behavioural results from experiment 1 and experiment 2 converged in showing that only inhibition of aIPS selectively reduces the ability to synchronize with the partner during complementary joint actions, while leaving specific movement features (either precision or power grip kinematics) and imitative action performance unchanged. On the contrary, vPM was shown not to play a comparable crucial role in the complementary condition, although – similarly to aIPS – it is a key-node of the fronto-parietal network involved in grasping planning and despite being constantly recruited during action observation. This evidence suggests aIPS causally scaffolds the integration of one's own and others' movement goals during non-imitative joint action and highlight that segregated neural substrates are crucial for the execution of imitative vs. complementary interactions.

Previous research on joint action has shown several processes - ranging from automatic entrainment to high-level planning processes (e.g. perspective-taking) - play a role in supporting the deceptively simple human ability to coordinate with others (Knoblich et al. 2011), possibly with the involvement of somatomotor simulation in the putative MNs (Kokal et al. 2010, 2009; Newman-Norlund et al. 2007, see also Sartori et al. 2013, 2012). Yet, the neural code of realistic complementary interactions remains unexplored; namely, no hint has been given on which neural basis causally supports the ability to “go from predicting another's action to choosing an appropriate complementary action at an appropriate time” (Sebanz et al. 2006).

We selected reach-to-grasp movements to explore this issue since their neurophysiological bases have been largely explored in both monkeys and humans during actual movement execution (Castiello 2005) and observation (Rizzolatti and Craighero 2004). Both vPM and aIPS (as their homologues in monkeys, F5 and AIP) perform visuo-motor transformations and have been described as the main cortical regions involved in grasping planning and execution together with the primary motor area (Jeannerod et al. 1995); moreover, they are both consistently activated during observation of grasping actions (Rizzolatti and Craighero 2004). In particular, neurophysiological

and TMS studies have shown that left vPM is responsible for anticipatory simulation during the observation of others' actions (Avenanti et al. 2013b; Urgesi et al. 2010, 2006; Umiltà et al. 2001). Recent TMS studies have also described its role in coding the “goal” of passively observed actions during action recognition (Avenanti et al. 2013a; Jacquet and Avenanti 2013; Cattaneo et al. 2010). Crucially however, these latter studies asked participants to discriminate images of hand postures without performing any action, being thus more concerned on the role of aIPS and vPM in perceptual tasks. Finding no involvement of aIPS in these perceptual tasks suggests that our result mainly deals with the role of aIPS in the actual performance of on-line joint action rather than with the observation of others' movements. All the same, left aIPS has been consistently shown to discharge ahead of a planned hand action so as to take part in the motor implementation of action intentions (Andersen and Burneo 2002) and to code both relevant environmental (i.e. object-related) information for sensorimotor integration during pre-shaping planning (Binkofski et al. 1998) and observed action goals in terms of their outcomes in the environment (Bonini et al. 2013, 2010; Chersi et al. 2011; Jastorff et al. 2010; Ramsey and Hamilton 2010; Hamilton and Grafton 2006; Fogassi et al. 2005). In particular, Freund (2001) has suggested that while vPM is undoubtedly recruited during action observation, “parietal cortex is also recruited whenever an action involves objects. This emphasizes the significance of parietal cortex for goal-directed motor behavior”. Moreover, parietal but not premotor damage has been shown to reduce anticipatory action preparation preceding others' actions observation, supporting the claim parietal activity involves anticipatory processes related to other's actions (Fontana et al. 2012). Finally, aIPS is also involved in monitoring on-going action execution through feed-forward processing of visuo-motor information (Tunik et al. 2005). Given aIPS is anatomically (Bonini et al. 2010; Schmahmann et al. 2007) and functionally (Davare et al. 2011; Caminiti et al. 2010; Fogassi and Luppino 2005) strictly interconnected with vPM, it thus becomes a good candidate for integrating information about the physical environment with “motor predictions” forwarded by premotor areas both during planning of individual motor execution and during others' actions observation (Tunik et al. 2007). This might

be crucial for joint action: indeed, the time-constraints to achieve on-line interpersonal coordination prevents agents from just passively reacting to others' behavior and thus require reliable predictions about the outcome of others' movements in order to efficiently adapt one's own behavior accordingly (Knoblich and Jordan 2003). These predictions regarding the outcome of the partner's actions (i.e. about the partner's sub-goals) become beneficial to the joint action fulfillment only when integrated in the agent's motor plan, i.e. only when they are bounded to the agent's own sub-goals to represent the interaction shared goal (Sebanz et al. 2006). In this regard, complementary joint actions crucially differ from imitation since in the latter case "self" and "other" movements need less effort in order to be integrated as their motor features overlap. Indeed, synchronous imitation might also be achieved thanks to pure anticipatory action-perception matching. On the contrary, during complementary joint actions, cues regarding the partner's kinematics are misleading (since the agent observes a movement but is required to perform an incongruent one), and the individual thus needs an effort to focus specifically on the action sub-goal (i.e. in our experiment, the object the partner is going to grasp) in order to plan his own movement accordingly. Besides, both the partner's and the agent's action sub-goals (in terms of objects to be grasped) might be coded in aIPS and are strictly interrelated, because the individual plans his own action sub-goal on the basis of the partner's one. As a consequence, aIPS becomes the most likely neural substrate to code the partner's goals as integrated within the same motor representation used to plan his or her own actions (and his or her own goals): namely, to code the joint action shared goal.

In line with this interpretation, studies directly testing the neural underpinnings of "low-level" and "high-level" action goal representations in non-human primates showed that the majority of neurons in the parietal cortex (PFG and AIP) are tuned to higher-order action goal coding (Bonini et al. 2013, 2010). This supports the idea that these regions might be crucial when asking individuals to combine executed and observed action goals in "higher order" shared-goals. Moreover, previous fMRI studies (Egetemeir et al. 2012; Kokal et al. 2010, 2009; Newman-Norlund et al. 2008, 2007) have consistently reported aIPS recruitment during both imitative and

complementary actions. However, the correlational nature of previous studies did not allow making inferences about the functional significance of these activations. On the contrary, the present study provides for the first time evidence that aIPS temporal inhibition causally and selectively affects the ability to coordinate with others during complementary interactions.

6. General discussion

Propose theories which can be criticized.

Think about possible decisive falsifying experiments—crucial experiments

But do not give up your theories too easily—not, at any rate,

before you have critically examined your criticism

K. R. Popper

The present work had the primary aim to develop a novel interactive scenario able to investigate face-to-face dyadic interactions within a naturalistic and yet controlled experimental environment. Our purpose was to acquire a “second-person” perspective (Schilbach et al. 2013), designing a task which allowed the emergence of both closed-loop processes (i.e. partners’ reciprocal adjustments) and socio-emotional bonds between interacting participants. To this aim, a new experimental paradigm was conceived: it requires pairs of participants to reciprocally coordinate their reach-to-grasp movements and perform on-line mutual adjustments in time and space in order to fulfill a common (motor) goal. This allows a direct comparison between pure temporal synchronization and more complex coordination in space and time controlling for low-level movement constraints (i.e. the ones required to perform precision vs. power grip), and provides a naturalistic scenario where, similarly to real-life situations, “mutual adjustments” (Sebanz et al 2006) and predictions on both “what” the partner is doing and “when” he is going to act (Sebanz and Knoblich 2009) are crucial. Thanks to this scenario, we have been able to investigate how social, emotional, and cognitive processes modulate “interactive” overt motor behaviour.

Firstly, a review of the literature on the various cognitive processes called into play by joint actions has been provided (chapter 1). For classificatory purposes, these processes have been described along an “emergent-planned continuum” (see Knoblich et al. 2011, see Figure 1.2.), from

spontaneous behavioural mimicry and synchronization (“entrainment”) to strategic signalling and effort-distribution promoted by task-sharing. This review also includes diverse sub-types of “simulative” processes typically investigated by literature on action perception. Suggestions is made that these simulative mechanisms might be divided between “active” (prediction) and “passive” (action-perception coupling) processes (see Figure 1.1.), and that both these sides of simulation are crucial during face-to-face interaction, yet they modulate behaviour at distinct levels of joint action planning and execution. In particular, the presence of *task-sharing* and *shared goals*, which is unique of joint action, might channel predictions, while the socio-emotional context strongly modulates the degree of action-perception coupling between interactive partners.

Given these premises, we investigated whether all the above mentioned processes are modulated by socio-emotional variables as: role- taking (chapter 2), ethnic biases (chapter 3), and a negative interpersonal perception caused by the feeling of not being appreciated by the partner (chapter 4). In particular, we assumed that the socio-emotional context is part of the interaction itself, and that the direct impact of its modulation on individuals’ overt motor behaviour would be the litmus test of its role in supporting the cognitive and motor processes which underlie agents’ “interactive” behaviour.

In chapter two, we hypothesized that participants would modulate their kinematics according to the interactional role played during the joint-grasping task, even if no role had been explicitly assigned but just on the basis of an asymmetric allocation of information. Results demonstrate that when acting as Leaders, participants carry out communicative behaviours (*signalling*) in order to convey essential information to the interacting partner. On the contrary, acting as Followers implies adaptation to the partner’s movements based on predictive abilities; these predictions, likely facilitated by the presence of the shared goal, differ from pure action-perception coupling, because while prediction is needed to synchronize with the partner’s movement, when the recruitment of simulation leads to visuo-motor interference (i.e. action-

perception coupling effect) it has a detrimental impact on the pair performance. Overall, this study demonstrates that signalling, predictive simulation and action-perception coupling are modulated by the interactive role played by each agent involved in the interaction. Moreover, it supports the hypothesis of an *effort-distribution* during the interaction sustained by the presence of the shared goal. Indeed, when leading, participants would not have needed to “signal” (i.e. communicate) their intended movements to the partner if they did not represent both their own and the partner’s task and realize that the partner (i.e. the follower) would more easily adapt to their own movements if they made them more predictable: thus, leaders implicitly take on a specific role according to both their own and the partner’s instructions in order to maximize the common pay-off, which indicates effort distribution in the light of the shared goal.

In chapter three, we sought to determine whether movement kinematics and individuals’ ability to coordinate with in-group/out-group avatars during realistic motor interactions are modulated by individuals’ implicit in-group preferences. We demonstrate that the social categorization of virtual partners as in-group/out-group individuals modulates i) the ability to achieve interpersonal coordination (based on *prediction*), and ii) mimicry of the partner’s movements, as indexed by visuo-motor interference between self-executed actions and those observed in the partner (*action-perception coupling* effect). Tellingly, mimicry-like responses (and, consequently, their in-group/out-group modulation) arose only when participants needed to predict the partner’s movements in order to adapt to them. This highlights the close link between action-perception coupling and action prediction during joint action; namely, although being different subtypes of simulation (see chapter 2), yet some degree of action-perception coupling might be the building brick to generate predictions, and the lack of coupling due to in-group/out-group biases might then reduce the ability to make fast on-line predictions because of the lack of a “procedural” common ground. Crucially, the mimicry reduction strongly correlated with the individual degree of implicit in-group preference as indexed by the Implicit Association Test, suggesting the

establishment of such common ground depends on the degree of “social interdependence” with the partner subjectively perceived by agents themselves.

In chapter four, we hypothesized that inducing a negative interpersonal perception (caused by the subjective feeling of not being appreciated by the partner) would affect co-agents’ interpersonal coordination during “free” interactions requiring on-line mutual adjustments, and that this would also be reflected in movement kinematics. To the best of our knowledge, this is the first study enabling to investigate the impact of interpersonal perception on *reciprocity* between interactive agents (Frith and Frith 2010): when we properly work in concert, we adapt our behaviour to the one of another agent who is also concurrently adapting to us; this implies the ability to predict how one’s own action will induce changes in the partner’s behaviour, and how to adapt to these changes in turn (“influence learning model”, Hampton et al. 2008). We hypothesised that the negative interpersonal perception would specifically impair these “closed loop” interactions. As a matter of fact, results showed that while in neutral interactive situations (Neutral group) two strangers are able to gradually learn how to coordinate their actions both in space and time, on the contrary, when co-agents try to act “each one on his own” (as it is the case in the Manipulated group, MG), they are not able to fulfill smooth closed-loop coordination during Free interactions. We suggest this might be due to differences in the way the task is “represented” by partners in the two groups. While NG participants rely on shared goals and include the partner’s movements within their own motor plans (“Me + X” mode, Vesper et al. 2010), on the contrary, when the social bond between partners is disrupted by the belief the partner has mined one’s own self-esteem (MG), participants have difficulties in mutually adapting to each other movements. Suggestion is made that this impairment in MG is due to the lack of the establishment of a shared goal between partners, which results in more problems in predicting the partner’s actions in order to anticipatorily adapt to them. Thus, both the degree of action-perception coupling between interactive agents (chapter 3) and the possibility to establish *task sharing* and represent *shared goals*

to support interpersonal coordination (chapter 4) are not independent from the interpersonal relation linking co-agents, proving the partner is not a “neutral” stimulus each agent needs to adapt to.

Overall, the novelty of the studies presented in chapter two, three and four is investigating how socio-emotional variables modulate joint actions by postulating joint actions crucially rely on the presence of shared goals. In chapter five we more closely focused on this assumption, and we investigated which neuro-cognitive processes might support shared goal coding; by doing so, we also aimed to indirectly prove shared goal coding is crucial in interactive contexts. We tackled this issue by applying an inhibitory TMS protocol over two main fronto-parietal regions supporting grasping planning and execution, namely the left ventral premotor cortex (vPM) and the left anterior intra-parietal sulcus (aIPS). Results suggest that aIPS causally scaffolds the integration of one’s own and others’ movement goals (i.e. shared goal coding) during non-imitative joint actions, and they highlight that segregated neural substrates might be crucial for the execution of imitative vs. complementary interactions. We expected left aIPS to be involved in shared goal coding for several reasons. Firstly, it is highly interconnected with vPM and it might thus receive predictions about others’ action deployment in time (Davare et al. 2011; Caminiti et al. 2010; Tunik et al. 2007; Fogassi and Luppino 2005); secondly, previous studies showed it monitors both goal-based on-line corrections during movement execution (Tunik et al. 2005) and goal-based coding of others’ actions (Hamilton and Grafton 2006); finally, it represent “high level” action goals (Bonini et al. 2013, 2010; Fogassi et al. 2005). Thus, the crucial role of aIPS in complementary joint actions suggest they rely on goal-based “higher level” motor representations grounded in the integration of (predictions about) one’s own and the partner’s actions, which are here defined shared goals (see also Butterfill 2013; Sebanz et al. 2006).

At last remark, it is worth noting that recent TMS studies have tried to address the issue of whether mirror-like resonant systems are involved in simulating motor responses which are not only

congruent but also incongruent with respect to an observed movement (Cavallo et al. 2013; Barchiesi and Cattaneo 2013). In line with the **associative learning** account (Heyes 2010; Catmur et al. 2009; Brass and Heyes 2005), some authors showed that cortico-spinal facilitation for observed movements induced by single-pulse TMS over M1 (Fadiga et al. 1995) might be reversed by means of counter-mirror visuo-motor training (Catmur et al. 2007), and that both mirror and counter-mirror simulation are boosted by triggering activity in ventral and dorsal premotor cortices (Catmur et al. 2011). This led to suggest both congruent and incongruent responses to observed movements might be planned within the premotor cortex (see also Newman-Norlund et al. 2007) as both might be supported by associative learning (Catmur et al. 2009; Brass and Heyes 2005). Other experimental evidence supports an intermediate perspective, suggesting action observation constantly and automatically leads to imitative simulation, while an incongruent response might be subsequently planned as a result of the inhibition of this early and automatic imitative simulation (Barchiesi and Cattaneo 2013; Sartori et al. 2013, 2012, 2011) with the likely recruitment of brain regions supporting higher-order cognitive control or mental state attributions (Ubaldi et al. 2013; Spengler et al. 2010, 2009; Wang et al. 2011).

In apparent contrast with these accounts, our study showed inhibition of vPM does not affect performance in either imitative or complementary joint actions. We believe this discrepancy in results highlights the crucial difference between studies investigating visuo-motor interference induced by motor resonance to *incongruent* movements and investigations on *complementary* joint actions, namely the presence of shared goals. We reckon research on joint action deals with participants who do not just observe or react to others' movements, but who include others' movements in their own motor plan thanks to the presence of a shared goal. Accordingly, our experimental paradigm not only forced participants to take the (virtual or human) partner's actions into account in order to plan their own motor responses accordingly, it also implied the partner's movements become part of a shared joint action goal (i.e. "be synchronous" plus "perform complementary/imitative actions"). Coming back to our story on joint action (chapter 1), Anne and

John would never manage to coordinate while moving their crystal table from the living room to the kitchen if they did not both want to have it moved there. More precisely, the shared goal is what links partners' actions during the interaction: for instance, John pulls and Anne pushes the table *because* they both want the table moved. Moreover, modulations of the establishment of task sharing and shared goals induced by socio-emotional variables (chapter two, three and four) highlight the *genuinely interpersonal and interactive nature* of such representations. Thus, social neuroscience research on the neuro-cognitive bases of joint action requires to move forward from investigations on pure sensory-motor coupling, on the one hand, and inhibition of automatic imitation on the other, and take into account moving *together* is much more than just “I move while I see you moving at the same time”. Considering these situations naturally occur in everyday life since young childhood (Brownell et al. 1992), it might be likely they do not require higher level cognitive control or mental state attributions (Ubaldi et al. 2013; Spengler et al. 2010, 2009; Wang et al. 2011) but rather rely on goal-directed motor processes (Butterfill 2012), as the shared goal coding in left aIPS.

To conclude, the present work might provide hints to answer a crucial question: *what is so special about face-to-face motor interactions?* By showing that modulation of socio-emotional variables and of available neural resources coding shared goals (e.g. left aIPS) affects the ability to coordinate with others, results from the studies presented here indirectly support the assumption that sharing a socio-emotional context and a common goal is indeed what characterizes interactive contexts and singles out research on joint actions with respect to previous approaches (e.g. the so called “isolation paradigms”, Becchio et al. 2010). More specifically, we suggest that it is the presence of shared goals and socio-emotional contexts which allow defining individuals' behaviour as “interactive”. This is just one possible answer to the question, yet it is the one we adopted here; in fact, this work is not a piece of research on interaction in general, but our story on cooperative joint actions.

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Acknowledgements

*La posta in gioco qui è produrre pensiero nuovo, qualcosa che prima non c'era,
qualcosa che all'inizio non aveva neppure un nome
E che a un certo punto comincia ad esistere
e a un certo punto si comincia persino a sapere come chiamarla*

S. M. Aglioti

Ringrazio il Prof Aglioti per la sua inesauribile capacità umana e professionale. Perché ha una fiducia smisurata nei suoi studenti; perché nei momenti cruciali sa chiarirti le idee quando tutto sembrava confuso, e scambussolarle completamente quando pensavi di averle chiare; perché prova a insegnarci lo sguardo di chi sa guardare oltre.

Ringrazio Matteo, perché mi ha insegnato questo lavoro, e da lui non smetterò mai di imparare. Perché da quel giorno a Chieti, oltre al resto, c'è voluta sicuramente anche molta pazienza per lavorare con me. Perché, anche se non ama ammetterlo, dalla prima all'ultima sillaba questo lavoro non sarebbe mai esistito senza di lui.

Ringrazio Enea, per il suo aiuto onnipresente, anche a centinaia di chilometri di distanza; gli devo ancora una mucca frisona. Grazie ad Emmanuele e ai suoi consigli un po' folli, perché sono esattamente quello che serve all'inizio per cominciare.

Grazie ad Arianna, Vanessa e Marco. Senza saperlo, mi hanno insegnato molto mentre pensavano di dover imparare da me.

Grazie a Giusi, la mia compagna di merende; a Katha, Giulia, Giulia, Brittany e Biljana che a volte quelle merende le hanno condivise con noi. Grazie a Serena, Marco, Ila1, Ila2, Elia, per me resteranno sempre i “grandi” da cui imparare. Grazie a Paola, perché ha una pazienza infinita; Irene è una bambina fortunata. Grazie a Lore, Francesca, Ale, Luigi, Ruben, Vanda, Patrizia, Giorgia, Valentina, al LAB passato presente e futuro: tutti voi siete stati, a turno, compagni di banco e di

viaggio, con cui ridere e con cui arrabbiarsi, da cui imparare e a cui insegnare qualcosa...sicuramente persone che stimo tanto, e con cui condividere una grande passione.

Grazie ad Anna, Maria, Silvia, Paolo e Terry, la mia famiglia romana. Grazie alla Città Eterna, che nel suo sole mi ha accolto come una mamma e mi ha aiutato a crescere.

Grazie ad Harold Bekkering, che con nonchalance mi ha dato quella turning-point opportunity di cui tutti scrivono nelle application senza sapere cosa sia, finchè qualcuno non te la regala. Grazie a Sabine e al suo specialissimo Babylab, a Marlene perché è una delle persone più acute che io conosca, a Johanna, Ricarda, Sarah e Claire perché mi hanno fatto compagnia. Grazie a Birgit, perché di fatto mi ha dato una mano enorme. Grazie al Free energy principle e al principio per cui si può sopravvivere anche arrivando ogni giorno in laboratorio fradici di pioggia e stanchezza, se ne vale la pena.

Grazie a chi ha reso possibile tutto questo. Ai miei genitori, per avermi insegnato che crescere non è rinunciare ai propri sogni, ma trovare il coraggio di crederci tanto da realizzarli, e mi hanno dato una spinta in più quando quel coraggio da sola non l'avrei trovato. Grazie alla mia sorellina, che in questi anni mi è un po' mancata anche se nei momenti importanti c'è e c'è sempre stata. Le voglio così bene che c'è poco da dire, se non che non saprei come fare senza di lei.

Grazie alla nonna Cicci, che fa sempre il tifo per me. Alla nonna Carla, agli zii, ai cugini, "la mia meravigliosa e squinternata famiglia" perché una definizione migliore non la troverò mai. Grazie agli amici vicini e lontani che mi sono venuti a trovare oppure no, mi hanno sostenuto e incoraggiato, e mi hanno perdonato quando non sempre in questi anni romani ci sono stata per loro.

Grazie a Guido, perché all'inizio di tutto questo mi hai preso per mano, e hai deciso di camminare con me. Se è vero che Amore e Ricerca hanno in comune di non essere una meta da raggiungere ma una strada da percorrere, gambe in spalla, perché siamo solo all'inizio.

Learn from yesterday, live for today, hope for tomorrow.

The important thing is not to stop questioning.

A. Einstein