SCUOLA DI DOTTORATO
UNIVERSITÀ DEGLI STUDI DI MILANO-BICOCCA

Department of Psychology

PhD program in Experimental Psychology, Linguistics and Cognitive Neuroscience
XXX Cycle
Mind, Brain, and Behavior Curriculum

TMS-induced motor evoked potentials as a measure of human behavior: feasibility and pitfalls

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ACADEMIC YEAR 2016/2017

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Overview

The combination of Transcranial Magnetic Stimulation and Electromiography (TMS-EMG) to induce and record motor evoked potentials (MEPs) is a well-known and broadly used paradigm in neuroscience, for both clinical and research purposes. When applying a single TMS pulse over the primary motor cortex a muscle twitch over the contralateral peripheral muscle is induced, which can be amplified and recorded by means of an EMG apparatus. MEPs can be considered a hallmark to non-invasively quantify corticospinal and, indirectly, cortical excitability. Typically, TMS is applied over the hand knob and the muscle contraction is recorded from the contralateral hand. Due to the great spatial focality of TMS, specific muscle within the hand can be targeted, such as the first dorsal interosseous (FDI), the abductor digiti minimi (ADM) or the opponens pollicis (OP). Aside the hand, also other limb and body muscle are often targeted (e.g. Perez et al., 2004, for the leg; Fadiga et al., 2002 for the tongue). One of the main use of MEP measurement is clinical, such as assessing the state of the motor system and the integrity of corticospinal motor pathway. In neuroscientific research MEPs have been massively used to explore motor functions properties, connectivity and state-changes in the cortical motor system during simple task or decision-making (Barker et al., 1986; Rossini & Rossi, 1998; Kobayashi & Pascual-Leone, 2003; Fadiga et al., 2005; Koch et al., 2006; Klein-Flügge et al., 2013). MEP measurement gained new interest around 20 years ago, when Fadiga and co-workers (1995) showed the possibility to investigate through this technique the properties and functioning of the human mirror system (HMs).

HMs is a neural network which is activated not only during action execution but also during action observation (Di Pellegrino et al., 1992), leading to an effect known as *motor facilitation* or *motor resonance* (Fadiga et al., 1995) which has been investigated to evaluate action intention, preparation and to understand the influence of context over action perception (Iacoboni et al., 2005; Wurm & Schubotz, 2012).

The main theme of the present thesis is providing some examples and critical discussion on how TMS-induced MEPs, as a measure of corticospinal excitability modulations, can be used beyond the assessment of motor functions, to explore action understanding and higher cognitive functions.

The appropriateness of the conclusions drawn from human MEP measurements relies on an accurate understanding of the complex nature of their physiological underpinnings. For this reason, the first chapter of the present work will address the physiological basis and the compound nature of MEPs, characterized by many generators and components. This complexity can render MEPs a sneaky measure, hence all the variables that need to be taken into account when deciding to design a study employing this measure will be reviewed.

In the second and third chapters a set of studies will be presented where MEPs are used to investigate how human mirror activity is affected by the context in which actions are embedded. Specifically, in the second chapter a set of neuroeconomics studies will be illustrated, exploring whether the same observed action, conveying different economic outcomes within an economic game, modulates corticospinal excitability as a function of several features, independently from the intrinsic properties of the action, and foreseen by models accounting for human behaviour during economic interactions. The third chapter contains a study aiming at investigating whether motor resonance can be affected also by contextual cues with a social connotation, such as the stereotypic perception of the agent.

In the fourth chapter the conclusions from all the studies on motor resonance taken together will be drawn, outlining our contribute to this field of research. Moreover, the open questions on the neural networks involved in action observation and comprehension will be briefly discussed and the future direction to deeper investigate this issue will be presented.

The fifth chapter will provide an example of another type of use of MEP measure, employed in this case to explore more a complex phenomenon in the field of embodied cognition. In particular, we tracked the influence of a peculiar emotional state, such that induced by power experience, over own body schema and surrounding space perception.

In the last chapter, the overall conclusions from studies' results will be drawn and discussed in relation to the specific topic of the comparability across studies and in the broader sense of the potentialities and limits of using MEPs measure to understand more complex behaviour.

1. The physiological underpinnings of the motor-evoked potentials and their use for understanding human behaviour

1.1 Physiological underpinnings and compound nature of MEPs

Motor evoked potentials (MEPs) are one of the few quantifiable indices of brain activity providing an online and measurable, although indirect, read-out of corticomotor pathway (Barker et al., 1985; Rothwell et al., 1987; Day et al., 1987) in both physiologic and pathologic conditions (Barker et al., 1986; Rossini & Rossi, 1998; Kobayashi & Pascual-Leone, 2003).

When transcranial magnetic stimulation (TMS) pulses are delivered over the primary motor cortex (M1) they elicit a quantifiable contraction in contralateral muscles which can be recorded through electromyography (EMG) with surface electrodes.

From an historical perspective, the corticospinal pathway has been studied at first in animals, by giving an electrical stimulus to the motor cortex and recording its output by placing electrodes on different parts of the bulbar region: the pyramidal tract of the medulla (Adrian & Moruzzi, 1939); the bulbar pyramids and the lateral column of the cervical spinal cord (Patton & Amassian, 1954); the dorsolateral surface of the cervical spinal cord (Kernell & Chien-Ping, 1967). These studies shed light on the central excitatory pathway, which precedes the final motor output and recorded a series of high-frequency waves (about 600 Hz).

The earliest wave recorded in animals is called direct (D-) wave (Patton & Amassian, 1954) and is evoked from the direct activation of the initial axonal segments of fast-conducting pyramidal tract neurons. D-waves are relatively resistant to changes in cortical excitability: they persist, for example, after cortical depression and cortical ablation, suggesting that they depend from the activation of corticospinal axons in the subcortical white matter.

Subsequent waves require instead the integrity of cortical grey matter and are thought to originate from indirect and trans-synaptic (intra- and trans-cortical) activation of the pyramidal tract neurons and are called indirect (I-) waves (Patton & Amassian, 1954).

The first studies recording corticospinal volleys in humans were performed on anaesthetized patients during surgery, applying transcranial electrical stimulation (TES) or TMS (Boyd et al., 1986; Berardelli et al., 1990; Thompson et al., 1991; Burke et al., 1993). The main limit of this procedure was that anesthesia influenced the recruitment of descending ways for both type of stimulation.

Recordings from conscious humans were performed some years later (Kaneko et al., 1996; Nakamura et al., 1996; Di Lazzaro et al., 1999) by using implanted epidural electrodes. These studies showed that TES activated the motor cortex recruiting D-waves, while TMS usually evoked I-waves and recruits D-waves only at higher intensities.

I-waves origin and nature is complex and not entirely understood (Di Lazzaro et al., 2008; Rusu et al., 2014, Di Lazzaro and Ziemann, 2013). Taken together, I-waves have different generators and involve different descending volleys, occurring at latencies between 2.4 and 7 ms after the D-wave. I-waves can be distinguished in early (I1) and late I-waves (I2, I3, I4) (Amassian et al., 1987; Boyd et al., 1986; Di Lazzaro & Ziemann, 2013; Di Lazzaro et al., 2004, 2012).

I1 waves are induced by indirect activation of corticospinal cells, while late I-waves originate from a separate and more complex circuit composed of a chain of cortical interneurons whose activation produces a repetitive discharge of corticospinal cells (Di Lazzaro et al., 2008).

Early and late I-waves also differ to their sensitivity to GABAa receptors (Paulus et al., 2008): benzodiazepins, for example, produce a selective suppression of late I-waves with no effect on the I1 (Di Lazzaro et al., 2000).

MEPs are then a compound signal in which cortical and spinal-segmental contributions are combined to determine MEPs amplitude (Bestmann & Krakauer, 2015), which quantifies the level of corticospinal excitability (Barker et al., 1985; Rothwell et al., 1987; Day et al., 1987).

MEPs’ latency, instead, reflects the time needed for neural impulses to reach peripheral muscles and rely upon the speed of the corticospinal projections, the summation of descending volleys at the spinal motor-neuron level and the conduction time along peripheral motor neurons (Bestmann & Krakauer, 2015).

MEPs size and shape are influenced by technical and physiological factors. Among technical parameters there are the target muscle, TMS stimulation intensity, coil placement and shape and pulse waveform; therefore, all these parameters should be considered when planning an experiment (Kiers et al., 1993; Dunnewold et al., 1998; Julkunen et al., 2009). Typically, in studies where TMS-elicited MEPs are measured, the figure-of-eight coils are used since they are more focal than circle ones (Di Lazzaro & Ziemann, 2013); moreover, biphasic waveform seems to be more effective in eliciting MEPs (Kammer et al., 2001). Concerning coil orientation, a position tangential to the scalp with the handle pointing backward and laterally at 45° angle away from the mid-sagittal axis of participant’s head induces an electric current flowing in the brain in a posterior-anterior direction, which is perpendicular to the central sulcus. This current direction can induce trans-synaptic activation of the corticospinal pathways, and is considered the optimal orientation to trigger and record MEPs (Brasil-Neto et al., 1992; Mills et al., 1992).

In many cases, measuring MEPs is an unavoidable prerequisite for running TMS studies. Stimulation intensity, indeed, is often based on the individual motor threshold, defined as the lowest intensity of the stimulator output that elicits MEPs with an amplitude of at least 50 μV in the contralateral FDI muscle with a 50% probability when the subject kept the muscle relaxed (Rossini et al., 1994). It is important to assess this threshold for each participant: while this parameter has a relatively constant value within a subject, it varies greatly between individuals (Wassermann, 2002; Danner et al., 2008, 2012; Säisänen et al., 2008).

On the other side, also some physiological factors, such as muscle activity, alertness, medication, age and physiologic fluctuations at the cortical and spinal level (Kiers et al., 1993; Thickbroom et al., 1999; Magistris et al., 1998) are able to affect MEPs (Pitcher et al., 2003; Darling et al., 2006; Hess et al., 1987; Paulus et al., 2008; De Gennaro et al., 2007) and need to be kept into consideration when designing experiments and when comparing studies.

These caveats do not hinder the usefulness of MEPs as a measure of state changes in the human motor system. Rather, these findings suggest caution against drawing fast conclusion about motor excitability absolute values, and can help in taking care of all the parameters able to influence MEPs properties when designing an experiment.

1.2 The use of MEPs: from the motor function per se to motor resonance and affordance

Thanks to the relative easiness of recording, MEPs were largely used since the very first years of TMS research to tap M1 excitability fluctuations in relation to motor functioning, with different purposes.

First, from a clinical point of view MEPs are a valuable method to assess the motor system state and the integrity of the corticospinal pathway. This measure, indeed, is often recorded in clinical settings to monitor and diagnose different diseases involving motor dysfunctions, such as multiple sclerosis, amyotrophic lateral sclerosis, stroke, movement disorders, disorders affecting the spinal cord, facial and other cranial nerves (Rossini & Rossi, 2007; Groppa et al., 2012; Rossini et al., 2015; Menon et al., 2015).

Furthermore, MEPs have been used to investigate online the effects (e.g. duration, dose dependent responses) and offline aftereffects of non-invasive brain stimulation neuro-modulatory techniques, such as tDCS (e.g. Pellicciari et al., 2013; Nitsche & Paulus 2000) or rTMS (e.g. Maeda et al., 2000).

Although MEP recordings were originally designed to test the integrity of the motor system and to monitor changes in M1 during and following motor learning (Bagce et al., 2013; Todd et al., 2009; Gelli et al., 2007) and performance (Lemon et al., 1995), MEPs gained new interest after the mirror system discovery. Mirror neuron system was first discovered in the ventral premotor cortex (PMv; area F5) of the macaque monkey and was shown to fire both while the animal was executing a specific action and when it was observing the same action performed by others (Di Pellegrino et al., 1992; Fadiga et al., 1995; Fadiga et al., 2005; Rizzolatti et al., 1996; Rizzolatti & Craighero, 2004).

Identifying human MNs (HMs) counterpart became immediately a prolific challenge (Gallese et al., 2011), getting lots of researchers involved with a variety of neuroimaging and neurophysiological paradigms and techniques. HMs is a complex network which involves, ventral and dorsal premotor cortices, the supplementary motor area, the primary motor and the inferior parietal regions (see for neuroimaging meta-analyses Caspers et al., 2010; Molenberghs et al., 2012).

The specific role of HMs has been largely debated, while some authors stressed its role in action understanding and anticipation (Gallese & Goldman, 1998.; Michael et al., 2014; Stadler et al., 2012), highlighting its potential role in social–cognitive development and imitation in children (Marshall & Meltzoff, 2014), others doubted about its origins and functions (Hickok & Hauser, 2010; Hickok, 2009; Heyes, 2010).

In particular, one of the most well studied phenomenon attributed to the HMs is motor facilitation or motor resonance (Fadiga et al., 1995), a modulation of corticospinal excitability due to the observation of an action. This modulation can be investigated through the application of TMS over M1. Specifically, MEPs are greater when the participant observes a movement involving the recorded muscle. This was first demonstrated in a pioneering work by Fadiga and co-authors (1995), where TMS single pulses were delivered over left M1 to elicit MEPs in two hand muscles, FDI and OP, plus two muscles in the forearm, while participants watched an experimenter performing grasping movements or arm movements. EMG activity revealed a corticospinal facilitation in all four muscles during the grasping movement, while in the arm movement all muscle but the OP showed a facilitation, compared to a baseline condition in which participants observed a static hand or a dimming light. This was a first evidence that the observation of a movement modulated the same muscles recruited during action execution.

Since then, motor resonance has become one the most well-studied phenomenon attributed to the HMs. A large number of studies focused on which action features and parameters were able to influence motor resonance. Critically motor facilitation is specific for the muscles involved in performing the observed action (Fadiga et al., 1995; Strafella & Paus, 2000; Romani et al., 2005; Alaerts et al., 2009; Gangitano et al., 2001; Valchev et al., 2015; Urgesi et al., 2006), is time-locked with its specific kinematics (Alaerts et al., 2012; Borroni et al., 2011, Gangitano et al., 2001, 2004; Urgesi et al., 2010) and is sensitive to the perspective from which the action is observed (Maeda et al., 2002).

Interestingly other researchers highlighted that motor facilitation can be also influenced by a series of non-motor directly linked features, such as action’s goals (Cattaneo and Rizzolatti, 2009; Cavallo et al., 2012; Iacoboni, 2005; Umiltà et al., 2001), action meanings (Liuzza et al., 2014) and social variables such as the performer’s ethnicity (Avenanti et al., 2010).

A growing body of evidence, indeed, indicates that this measure of HMs activation can be modulated by top-down influences, modifying its amplitude according to action meaning or goals (Iacoboni et al., 2005).

Iacoboni et al. (2005), for example, demonstrated that the same grasping action embedded in different contexts (i.e. grasping a bottle to drink vs grasping a bottle to clean) modulated activity in pre-motor areas, thus highlighting the role of the HMs in coding agent's intentions. Similarly, greater HMs activations were recorded during meaningful compared to meaningless actions (Newman-Norlund et al., 2010).

Recently, researches focused also on the social value assumed by an action during interpersonal interaction, which is one of the most ecological sets in which the HMs is supposed to play a relevant role (Hogeveen and Obhi, 2012). In particular, HMs involvement seems greater for actions performed in interaction contexts as compared to the same actions performed in isolation, suggesting a sensitivity to social situations. Accordingly, an increase in contingent negative variation ERP component (Kourtis et al., 2010), as well as an increment in motor facilitation (Sartori et al., 2011, 2012), occurred when the observed action could elicit a complementary response compared to when it did not imply any active response. Similarly, the observation of grasping movements performed with social intent (as to build a tower together with a partner) engenders a stronger activation within the HMs as compared to isolated single movements (Becchio et al., 2012). Finally, Bucchioni et al. (2013) compared two kinematically identical actions which could imply or not a social interaction (e.g. throwing a ball to a partner vs throwing a ball against the wall). They found a significant increase in MEPs amplitude during the observation of a social rather than an individual movement. Crucially, in this experiment, participant's involvement in the action was not requested or even suggested, highlighting that the mere presence of a social context is able to influence motor resonance.

Another research field, in which MEPs have been largely employed as a measure to explore more complex phenomena, taking advantage of their measurability and implicitness, regards the notion of affordance. Forty years ago, in his ecological approach to vision, Gibson (1977, 1979) first introduced the concept of affordance, referring to the idea that the visual perception of an object automatically generates a set of possible actions we can perform on and with it. Affordances are automatically triggered by object's sight even if there is no explicit intention to interact with it and are limited by the observer's action abilities and possibilities.

The first neurophysiological support to Gibson's idea came from animals' studies with single neurons recordings. Rizzolatti and colleagues (1988) firstly described a neuron population in macaque monkeys' premotor area F5, which selectively discharged during goal-directed actions, such as grasping or manipulating objects. The 20% of these neurons showed object-related visuo-motor properties, firing not only when animals grasped an object, but also when they simply looked at a similar object without making any action on it (Murata et al., 1997).

This neuronal population has been called canonical neurons (Rizzolatti & Fadiga, 1998) to differentiate them from the more popular mirror neurons discovered in the same area, but activated from action's execution and observation (Di Pellegrino et al., 1992; Gallese et al., 1996).

Subsequent studies deeply investigated the existence of a cortico-cortical network, composed of ventral and dorsal premotor cortices (Raos et al., 2004; Raos et al., 2006) intraparietal and posterior parietal regions (Murata et al., 2000; Rozzi et al., 2008), involved in transforming object's visual information in grasping actions.

Consistent with single cell recordings in monkeys, behavioural and neurophysiological findings in humans confirmed that the mere vision of an objects elicits in the observer the motor programs necessary to interact with it, even without any explicit intention to act (Craighero et al., 1999; Tucker & Ellis, 1998).

Usually, behavioural studies investigated affordances by using the so-called compatibility effect (Tucker & Ellis, 2001; Tucker & Ellis, 2004): in this paradigm participants have to respond to objects' features, for example to classify them as natural vs artifact, by producing a motor action. Results show that even if objects' features are not relevant for the task, they interfere with performance by increasing reaction times required to answer.

Crucially, neuroimaging studies consistently suggested that the simple observation of common objects or pictures of objects triggers an automatic recruitment of parieto-frontal regions. In particular, activation in response to action observation of the premotor and posterior parietal cortices, even in absence of motor outputs (Grafton et al., 1997; Grèzes et al., 2003; Chao & Martin, 2000) suggested that the dorsal visual stream might constitute the neural underpinning for the concept of affordance, as originally hypothesized by Gibson. This network might be the responsible for transforming visual object's information, such as size and orientation, into the appropriate hand motor programs necessary to grasp it (Jeannerod et al., 1995).

Furthermore, neurophysiological studies on corticospinal excitability highlighted that object presentation elicited higher MEPs as compared to a non-object condition.

In a study from Franca and colleagues (2012), for example, participants observed small-size objects (i.e. a lipstick, a penknife, a lighter), easily graspable with a precision grip involving thumb and index fingers. In the experiment all objects were in the peripersonal – reachable space, 40 cm from the participant and placed in a box illuminated for 300 ms, with TMS pulses delivered 120, 150, 180 ms after object's presentation. Results showed that M1 excitability automatically increased within a small time interval after the observation of graspable objects, only for muscles involved in the grasping movement, that is OP and FDI muscles, as compared to muscles not activated during grasping as ADM.Further studies suggested that corticospinal modulation might depend on different object's properties or features.

Object’s ease-to-grasp, for example, is a variable able to influence corticospinal excitability: Cardellicchio and coworkers (2011) suggested that a graspable object, for example a mug, can induce higher MEPs as compared to a cube. In the same vein, the sight of a mug with a handle located to the right side increase MEPs sight as compared to the same handle located to the left (Buccino et al., 2009).

In the same study Buccino and colleagues (2009) highlighted that also structural object’s features are able to influence MEPs size: the sight of a virtual mug with an intact handle elicited higher MEPs as compared to the same object presented with a broken handle.

Another important variable able to affect motor excitability is the object’s location in the space: Cardellicchio and colleagues (2011), for example, showed that when a virtual object is presented in the near – reachable space MEPs are higher as compared when the same object is in the far – unreachable space.

In conclusion, MEPs can be and have been used to assess more complex phenomena of human behaviour than motor function, for instance in the field of motor resonance, to explore HMs activity, and in the domain of embodied cognition, being an easy and direct measure of motor excitability modulation induced by affordances.

Aims of the present thesis

Motor system’s primary role is to control body parts movement (Tomasino & Gremese, 2016) however studies with animals (Ashe et al., 1993; Pellizzer, 1996; Carpenter et al., 1999; Wise & Murray, 2000) and humans applying neuroimaging (Grafton et al., 1995; Porro et al., 1996; Honda et al., 1998; Karni et al., 1998) and brain stimulation (Ganis et al., 2000; Tomasino et al., 2005; 2008) techniques supported the idea that the motor cortex (M1) is involved in higher motor functions.

In a recent meta-analysis Tomasino & Gremese (2016) analyzed data from 126 neuroimaging (PET or fMRI) experiments on healthy participants which reported M1 activation on different cognitive categories. Their analyses suggested that the left motor cortex, and specifically area 4a (the rostral part of M1), seems to be involved in different cognitive functions namely motor imagery, working memory, emotion/empathy and language.

In the same vein, we applied a different method to test whether also corticospinal excitability is sensible to higher cognitive features and is not only influenced by the action parameters which characterized the observed movement such as muscle involved, kinematics and observer's point of view.

To deeper investigate this hypothesis, we used MEPs in four different experiments in which we tested theories and previsions by playing on instrinsic properties of the corticospinal excitability.

In a first study we used MEPs in a neuroeconomic paradigm exploring whether the same observed action, characterized by exactly the same action properties in terms of kinematics, muscle involved and observer's point of view, but conveying different economic outcomes within an economic game. We found a modulation of corticospinal excitability due to the context in which the action was performed, thus suggesting that the corticospinal excitability is sensible to the semantic meaning of an action (Iacoboni et al., 2005).

Given the fact that MEPs are also influenced by non-motor properties of an action, it is possible to use them to analyse contextual and social properties in which an action is embedded. With this main idea on mind we applied this method to study whether the contextual frame of an action is able to influence corticospinal excitability.

Specifically we used MEPs to test the veridicity of a famous economic theory, that is the Regulatory Focus Theory, by creating different conditions within this framework and measuring how they impacted on MEPs amplitude.

In a similar vein we investigated whether manipulating contextual cues was able to influence the perception of the social threat induced by an outgroup member. Specifically we measured whether inducing social menace through external sounds was able to elicit threat-related stereotypes.

A different situation able to modulate MEPs amplitude, related to the concept of *affordance* (Gibson, 1977, 1979; Grafton et al., 1997) is object's location in the space. According to previous evidence (i.e. Cardellicchio et al., 2011) MEPs are higher when objects are placed in the near or reachable space as compared to the far or not reachable environment.

We played on this intrinsic property of the motor system to investigate whether a non-motor and complex phenomenon, such as the experience of power, is able to modulate participants' body schema and external space perception.

2. The use of MEPs in neuroeconomics

2.1 Introduction

"Human behaviour, in general, and presumably, therefore, also in the market place, is not under the constant and detailed guidance of careful and accurate hedonic calculations, but is the product of an unstable and irrational complex of reflex actions, impulses, instincts, habits, customs, fashions and hysteria."

The way in which we make or should make choices is an intriguing argument which occupied intellectuals from many different perspectives for many centuries.

As Jacob Viner (1925) suggested men are not rational creatures but instead our choices are deeply influenced by many psychological and contextual variables.

Neuroeconomics, which is a recent but thriving branch of neuroscience, is especially interested in studying economic behaviours by applying methods which are commonly used in the field of neuroscience with the main aim to develop a more accurate and brain-based model of choice and decision in the economic field.

The present line of research has the purpose to link motivational aspects of social economic interactions to corticospinal excitability by using a well-investigated property of HMs, that is motor facilitation elicited by grasping movements observation (e.g. Fadiga et al., 1995).

In the first study we assessed whether corticospinal excitability can be influenced by actions representing economic gain and loss inserted in different game-frames. Participants were involved in a Dictator Game and Theft Game in which a confederate could decide to endorse or steal a certain amount of money to them, who played instead as passive receiver. The dictator’s decisions were conveyed by a grasping action towards some tokens, previously associated to gain/fair or loss/unfair outcome.

In the second study we investigated whether other contextual features, such as the participants intended goal framed in either a promotion or prevention context, might modulate corticospinal excitability, more than the fairness of the Dictator's decisions or the outcome value per se. The promotion and prevention contexts were created by manipulating the type of money exchange involved in the task, namely consisting in sharing a gain in the promotion context and a loss in the prevention one

2.2 Study 1: Fairness in the brain

2.2.1 Background

One of the main interests of neuroeconomics is studying social interactions among participants by using economic games.

A classical paradigm used by behavioural economics is the Ultimatum Game (Güth et al., 1982) in which two players (a proposer =Player 1 and a receiver =Player 2) have to bargain how to share a sum of money. Player 1 has to do a proposal while Player 2 could accept it, in which case both participants receive the money following Player 1 decision, or reject it, in which case both players are not receiving any money. Despite for Player 2 the more convenient choice is always to accept (something is better than nothing), lots of studies showed that participants refuse to take offers that give them the 20% or less of the sum (Camerer & Thaler, 1995; Hoffman et al., 1996; Henrich et al., 2006).

Neuroimaging studies tried to investigate which brain regions are activated during these interactions, showing that unfair vs fair choices increased insula activity, which is typically involved in negative stimuli perception and disgust, and dorsolateral prefrontal cortex, which is instead active during emotional cognitive top-down control and during selfish behaviour inhibition (Sanfey et al., 2003; Güroĝlu et al., 2010; Hollman et al., 2011; Kirk et al., 2011).

At a physiological level, skin conductance response shows an increased arousal when participants receive unfair proposals and especially when they refuse them (van't Wout et al., 2006).

Moreover, behavioural data suggested that participants prefer fair vs unfair decisions, and that they are keen to make choices which are disadvantageous for them with the aim to punish unfair Dictator's choices (De Quervain et al., 2004; Brüne et al., 2012; Seymour et al., 2007). Some studies also tried to investigate whether economic decisions are influenced by the context in which they are settled, for example manipulating loss vs gain sharing frames (Zhou & Wu, 2011), suggesting that in loss contexts participants are more likely to refuse unfair proposals. Neuroimaging studies (Wu et al., 2014) showed an increase in DLPFC activation in a loss sharing context when the decision in highly unfair. As author suggested, this activation could be due to the inhibition of selfish feelings when refusing an offer at the cost of a consistent loss.

In the present study we investigated whether the meaning an action assumes when performed in an interpersonal economic exchange could affect MF.

Indeed, it is a well-known evidence that HMs is involved in action understanding and agent's intentions and goals recognition (Newman-Norlund et al.,a, 2010; Fecteau et al., 2010; Iacoboni et al., 2005; Hesse et al., 2009). It has also been suggested that HMs is particularly sensible to actions taking place in social and interpersonal situations (Becchio et al., 2012; Sartori et al., 2012).

Based on this evidence, here we aim at providing a direct neurophysiological measure of HMs modulation by changing the reward value of an action and recording MEPs during the observation of grasping actions embedded in two economic game-frameworks which imply fair and unfair interactions between two persons.

Here we used two modified version of the Dictator Game (Kahneman et al., 1986; Camerer, 2003): a Mini-Dictator Game (DG) and a Mini-Theft Game (TG).

In the DG, in each trial the Dictator (or Player 1) is endorsed with a certain sum of money and may share half or none of it with the receiver (or Player 2), who can only passively accept the proposal. In the TG, in every trial, the two players are endorsed with the same amount of money and Player 1, who in this game is named as “Theft”, has the possibility to steal or not Players 2’s endowment. The passive role of the payer B is what makes DG and TG different from the Ultimatum Game, where instead he/she can refuse Player A’s proposal.

In our experiment, participants always played as Player 2-receivers, whereas the Dictator and the Theft choices were controlled by a preset pc program.

Dictator/thief ’s choices were conveyed through a video in which Player 1’s right hand grasped one out of two tokens, which were previously associated with opposite reward values, specifically to fair or unfair decisions. Crucially in the DG, fair choices were associated with a sharing of the money, and determined an active modification of the initial economic equilibrium between the two players. The dictator indeed received an initial endowment at the beginning of each trial while Player 2 has no money. Conversely, dictator’s unfair choices maintained the starting status quo. In the TG, the pattern was reversed: fair choices (that is not stealing Player 2’s money) maintained the initial status quo and the unfair choices changed it (Cox et al., 2013).

For each game we pre-established four possible type of interactions, by manipulating trials’ percentage of fair and unfair dictator’s choices; in this way we generated a Gain block (80% of Fair and 20% of Unfair choices), a Loss block (20% of Fair and 80% of unfair choices) and two Mixed blocks (Mixed Block 1= 40% of Fair and 60% of Unfair choices; Mixed block 2 = 60% of Fair and 40% of Unfair choices).

We hypothesized that if HMs is modulated by both action meaning and social context, corticospinal excitability should be modified according to the different experimental frames.

2.2.2 Experiment 1

Material and methods

Participants

22 healthy students (11 male, Mage =25.6, SD = ±3.7) participated at the experiment. Only right-handed participants, i.e. with laterality coefficient higher than 0.5 according to the Edinburgh Handedness Inventory (Oldfield, 1971) and with normal or corrected to normal vision were recruited in the study.

Participants completed the Adult Safety Screening Questionnaire (Keel et al., 2001) and gave informed written consent before to start with the experiment. We excluded participants with any contraindication for TMS (Rossi et al., 2009).

The study was approved by the local Ethics Committee and was in accordance with the ethical standards of the revised Helsinki Declaration.

TMS and EMG recordings

TMS pulses were delivered using Magstim Rapid Transcranial Stimulator (Magstim, Whitland, Dyfed, UK) and a 70-mm figure-of-eight coil. The coil was positioned tangentially to the scalp with the handle pointing backward and at a 45° angle from the mid-sagittal axis of the subject's head. This is a standard placement to induce an electric current flowing in the brain in a posterior–anterior direction, perpendicularly to the central sulcus, which has been suggested to be optimal position to elicit trans-synaptic activation of the corticospinal volleys (Brasil-Neto et al., 1992; Mills et al., 1992).

The coil was moved over left M1 and the hotspot, that is the point where TMS pulses evoked the largest MEP from FDI muscle, was marked on a Lycra swimming cap that participants wore during the experiment.

We adjusted TMS intensity to establish the individual motor threshold, defined as the lowest intensity of the stimulator output that elicits MEPs with an amplitude of at least 50 μV in the contralateral FDI relaxed muscle with a 50% probability (Rossini et al., 1994).

TMS pulses were then delivered at 110% of individual motor threshold (Loporto et al., 2013). MEPs were recorded from the FDI muscle of the right hand using 9-mm diameter Ag–AgCl surface cup electrodes, with the active electrode placed on FDI muscle belly and the reference electrode over the metacarpo-phalangeal joint of the index finger. Responses were amplified with a Digitimer D360 amplifier (Digitimer Ltd, Welwyn Garden City, Hertfordshire, UK) through filters set at 20 Hz and 2 kHz, with a sampling rate of 5 kHz, digitized using an analog-digital converter (Power 1401, Cambridge Electronic Design (CED), Cambridge, UK).

MEPs were recorded and stored on a pc using the software SIGNAL version 3.9 (Cambridge Electronic Devices, Cambridge, UK).

Visual stimuli

During the experiment Player's 1 choices were shown through video clips which were presented on a 19-in. LCD screen at a distance of approximately 80 cm from participants' head. In each video participants saw two metal tokens which differed for the symbol placed on their upper side (a triangle or a square) and each one had a diameter of 2 cm and a height of 1.5 cm. Tokens were placed in front of actors' right and left hands. During the video four different actors (two males and two females) performed a grasping movement. Each grasp was a precision grip and was executed with the thumb and the index fingers of the right hand. Each video was shown with an egocentric perspective and action timings were strictly synchronized across videos: each video had a duration of 18.5 s and the grasping movements happened after 6 s from the video onset.

TMS pulses were delivered at the same time with the maximum index finger–thumb aperture, which has been shown to be the moment in which FDI motor cortex has the maximum excitability for MEPs recording (Gangitano et al., 2001, 2004).

Dictator and Theft Game structures

Participants sat in front of the computer screen and were made believe they were playing online with other people. They were told they had to play in the role of Player 2, i.e. passive receivers in four mini-games and that in each game they were playing with a different participant in the role of Player 1, alias the dictator. This cover story was created to induce participants to believe they were actually playing with other people, a belief that affects participants' reactions to the dictator choices (Hertwig and Ortmann, 2001).

Each mini-game was composed of 25 trials. Each trial started with Player 1 endorsed with 100 tokens which he/she could decide whether to share (Fair choice: 50 tokens for each player) or not (Unfair choice: 100 tokens for Player 1 and 0 for Player 2) with the participant.

Participants saw Player's 1 choices through a video in which the Player 1 right hand grasped one of the two tokens, each one with a symbol impressed on its top (a triangle and a square) to be easily recognized. Each symbol was associated at the beginning of the experimental session with the two possible offer conditions (Fair vs Unfair) and remained the same until the end of the experiment. The association between the economic meaning and the token's position and symbol was counterbalanced across participants: for half of them left token was coupled with the fair choice and the right one represents the unfair one and vice versa for the other half (see Fig.1 for the timeline of an experimental trial).

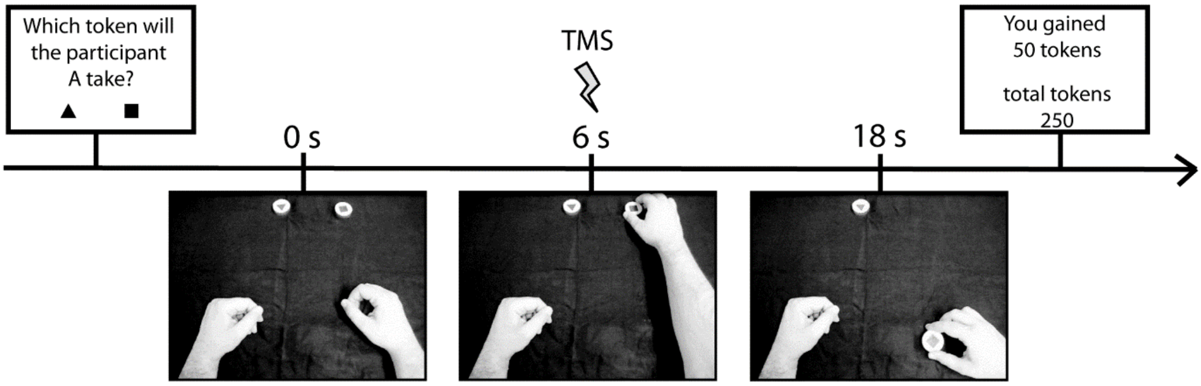

Fig. 1. Timeline of an experimental trial in the DG (from Pisoni et al., 2014).

In each trial participants were asked to predict Player 1's choice by pressing one of two mouse keys with their left hand. Participants were told that their previsions would not affect Player 1's choices.

Previsions could be congruent or incongruent with Player 1's choices (Congruency factor), leading to four possible combinations: fair/congruent, fair/incongruent, unfair/congruent, unfair/incongruent. After participants made their prediction, the video with Player 1 choice started and TMS pulse was delivered such to record the MEP. At the end of each video the screen displayed how much the participant had won (50 tokens corresponded to a monetary payment of 0.20€). As explained before (par.2.2.1), we created four different experimental blocks by manipulating gain and loss percentage, each one composed of 25 trials: a Gain block (80% of Fair and 20% of Unfair choices); a Loss block (20% of Fair and 80% of unfair choices); two Mixed blocks (Mixed Block 1= 40% of Fair and 60% of Unfair choices; Mixed block 2 = 60% of Fair and

40% of Unfair choices). The two mixed combinations were added in order to create a more plausible interaction style. At the end of the experimental session participants gained 2500 tokens, which corresponded to a payment of 10€. The order of blocks, the association between actors and blocks and cylinder's economic meaning were balanced across participants.

Experimental procedure

At the beginning of the procedure the experimenter placed the electrodes on the participant right hand and assessed TMS hotspot and motor threshold.

Participants were then informed about experimental procedures and they were instructed about the association between the cylinder and its economic meaning (fair vs unfair). At the beginning and at the end of the experiment two baseline sessions, each one composed of 25 MEPs, were recorded. In this condition participants had to watch a fixation cross at the center of the screen and TMS pulses were randomly delivered with an interval between 3800-4000 ms.

The first baseline was followed by the four blocks of the game, each one corresponding to a different experimental condition (Gain, Loss, Mixed block 1 and Mixed block 2). At the end of the experiment participants were debriefed and received their payment.

Preliminary analysis

EMG signal was processed offline. MEPs smaller than 50 μV, trials with EMG activity greater than 100 μV in the 100 ms before TMS pulse and outliers (trials with ±2 SD from the subject's mean value) were excluded from subsequent analysis.

Mean value missing MEPs (2.6% of cases) were replaced by using linear trend at point method in SPSS version 20 (Rinaldi et al., 2006; Vercoulen et al., 1994).

MEPs baseline was calculated by averaging the first and second baseline sessions and a single Mixed block value was derived averaging Mix 1 and Mix 2 blocks. We were able to collapse baseline and Mixed conditions because differences between baseline 1 and 2 and between Mix block 1 and 2 did not significantly differ at Wilcoxon test (Z= -.58; p=.57; Z= -.89; p=.37, respectively).

In each block (3 levels: Gain, Loss, Mix) an individual mean value for each condition (Fair/Congruent, Fair/Incongruent, Unfair/Congruent, Unfair/Incongruent) was derived by averaging the peak-to-peak amplitude of MEPs and a ratio between individual mean values and the individual baseline was calculated and transformed in z-scores.

Results

First, baseline MEPs were compared with MEPs in the other experimental conditions, in this way we were able to assess the presence of a motor facilitation effect due to grasping observation (Wilcoxon test Z = 2.68; p = .007).

A repeated measures ANOVA was then run on MEP z-scores, with three within subjects independent variables Block (3 levels: Gain, Loss and Mixed), Fairness (2 levels: Fair vs Unfair) and Congruency (2 levels: Congruent vs Incongruent).

The main effect of Block was significant [F(2,42) = 4.39; p = .019], MEPs were higher in the Loss compared to the Gain block (MEP z-scores .11 vs −.19 respectively).

The main effects of both Fairness [F(1,21) = .013; p = .91] and Congruency [F(1,21) = 2.88; p = .104] were not significant.

The interaction between Block and Fairness was significant [F(2,42) = 3.73; p = .032]. Post-hoc analyses highlight that MEPs amplitude was higher for Fair choices in the Loss compared to Gain (z-scores .22 vs −.27 respectively; p<.001) and Mixed (z-score −.10; p = .039) blocks. No other interaction reached significance (see Fig.2 for DG results).

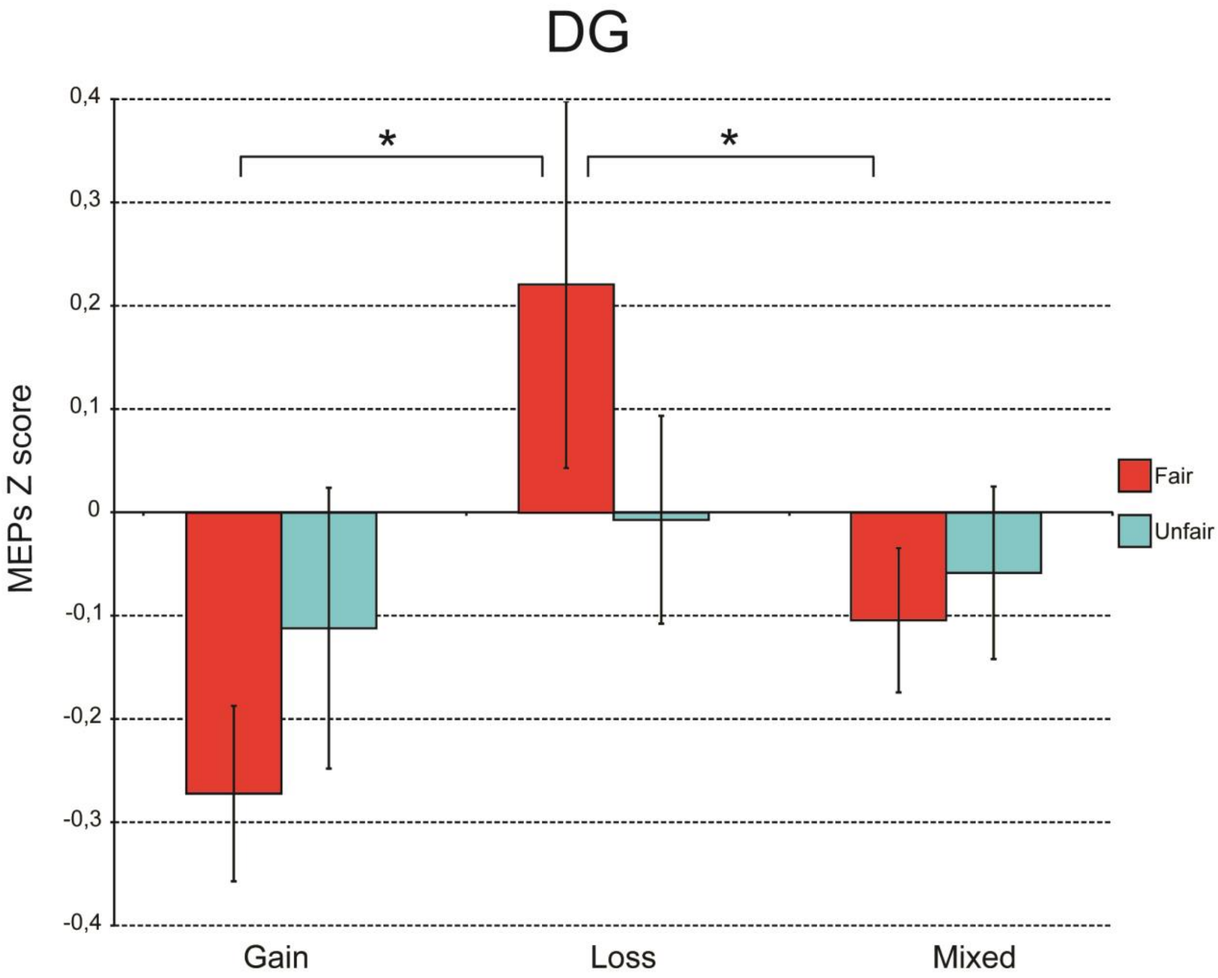

Fig. 2. MEP Z-scores for fair and unfair trials in the Gain, Loss and Mixed DGs. Error bars represent +/-1 MSE. Asterisks indicate significant differences at p b .05.Non z-transformed MEPs values are provided in the supplementary material section.

In order to rule out the presence of a similar pattern in FDI pre-contraction we ran the same analysis on the 100 ms pre-TMS EMG activity. These analyses did not show main effects or significant interactions (the crucial interaction between Block and Fairness was not significant [F(1.38, 28.95) = .67; p = .52).

We were further interested in testing whether participants were able to learn Dictator style, by correctly predicting his moves in each context-frame of the game (Gain, Loss, Mixed). In order to do so we divided each block it in three parts: T1 (trials 1–8), T2 (trials 9–17), T3 (trials 18–25). We than computed a Fair percentage, that is how many times participants predicted a fair choice, in each part of the block.

A repeated measure ANOVA with two independent within subject variables Block (3 levels: Gain, Loss, Mixed) and Time (3 levels: T1, T2, T3) was run on the arc sine square root transformation of the mean number of Fair predictions; Greenhouse Geisser correction was applied when sphericity assumption was violated.

The main effects of Block and Time were not significant (F(1.33, 27.94) = .997; p = .35 and F(2, 42) = .50; p = .61, respectively). However the interaction between the two variables was significant [F(4,84) = 10.85; p<.001, n^2 = .34].

Post-hoc showed that in the Gain block Fair predictions linearly increased at T2 (58.08%, p = .009) and T3 (65.78%, p<.0001) compared to T1 (41.4%). In the Loss block the reverse pattern was observable, with Fair predictions decreasing from T1 (60.55%) to T3 (48.61%, p = .039).

Crucially in the Mixed condition no difference at the three time points was highlighted (all ps <.9).

Moreover, at T1 Fair prediction percentage was higher in the Loss compared to the Gain block (p<.001), while in part 3 Fair predictions were more in the Gain compared to Loss (p = .002) and Mixed (p = .017) conditions (see Fig.3 for results).

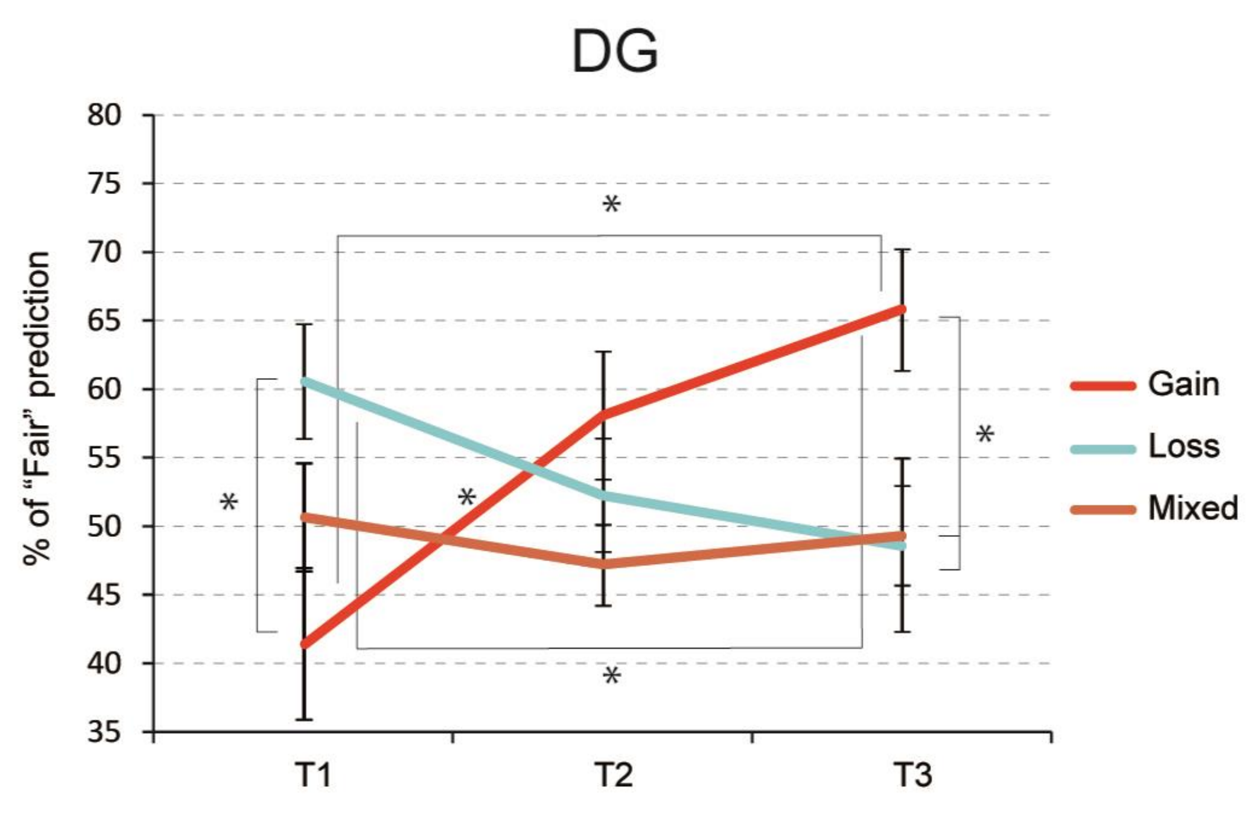

Fig. 3. Participants' percentage of "Fair" predictions over time for the three experimental conditions in the DG. Error bars represent ±/-1 MSE.

We then analyzed how MEPs amplitude changed over time by performing a repeated measure ANOVA with three within subjects independent variables: Block (3 levels: Gain, Loss and Mixed), Fairness (2 levels: Fair vs Unfair) and Time (3 levels: T1, trials 1–8; T2, trials 9–17; T3, trials 18–25). The main effect of Time [F(2,42) = 3.46; p = .041] was significant: MEPs amplitude was higher in T1 compared to T3 (p = .045) but the interaction of Time with the other variables was not significant (Block * Time [F(4,84) = .62; p = .65], the Block ∗ Fairness [F(4,84) = .63, p = .64]) and only the trend Time * Fairness approached significance [F(2,42) = 3.1, p = .059].

Experiment 1 discussion

In line with previous evidence our results confirmed that observing grasping movements induces corticospinal facilitation compared to a baseline condition (e.g. Tomeo et al., 2013; Sartori et al., 2011; Hogeveen & Obhi, 2012; Sartori & Castiello, 2013; Sartori et al., 2013a; Sartori et al., 2012; see Naish et al., 2014 for a review): indeed MEPs were higher in the four experimental blocks compared to the baseline in which participants had simply to fixate a cross condition.

The main effect of block and the significant interaction between block and fairness highlight the possibility that action meaning, namely fair vs unfair choices, modulated corticospinal excitability during economic interactions. MEPs were higher in the Loss condition compared to the other ones, however the interaction between block and fairness suggested that only fair proposals elicited higher MEPs in this block compared to Mixed and Gain ones. This result rules out a main effect of loss which could had been driven by the plausible negative emotional reactions, as foreseen by Loss Aversion Bias (Kahneman et al., 1991).

Crucially, unfair proposals did not affect corticospinal excitability in the Gain block compared to the other conditions, thus allowing us to exclude that stimuli rareness could explain MEPs amplitude.

We were also interested in investigating whether participants' expectations could influence corticospinal excitability. The main effect of congruency was not significant, however different studies suggest that during learning processes responses to surprising events engage more attentional resources to be processed compared to the expected ones, thus inducing participants to learn faster, as predicted by the Pearce-Hall unsigned prediction error (Courville et al., 2006; Hayden et al., 2011; Kaye & Pearce, 1984; Swan & Pearce, 1988).We can't entirely exclude that Pearce-Hall error affected our data: in the Loss condition MEPs were higher with unusual stimuli presentation. To test this possibility in a deeper way we first analyzed whether participants were able to learn the player style in each block and how fast.

Analyses showed that participants could easily learn block status: at T2 fair prediction increased in the Gain block and at T3 they decreased in the Loss one.

Secondly we tested whether block style learning could affect MEP amplitude: if that was true MEPs were expected to be higher while participants were learning and to be lower when the learning was completed/no learning was taking place. Our data actually followed this prevision, even though MEPs amplitude reduction could be also explained by a general arousal decrement in each block (De Gennaro et al., 2007; Sale et al., 2007). It has to be said, however, that not all our results were explainable by this Pearce Hall error: not all surprisingly events affected corticospinal excitability, for example unfair trials in the Gain block did not elicit higher MEPs.

Notably, in the game fair choices were the consequence of Player 1 active decision to modify the status quo, that is changing the situation at the moment of money endorsement at the beginning of each trial, when Player 1 owned 100 tokens and Player 2 owned 0, in a new condition in which both participants owned 50 tokens. At the contrary, unfair decisions did not to change this balance. A well-known phenomenon in decision making and economic theory suggests the existence of a status quo bias (Connolly & Zeelenberg, 2002; Kahneman et al.,1991; Samuelson & Zeckhauser, 1988), according to which decisions affecting the initial status quo are considered by participants less justifiable and less normal respect to decisions that maintain it. In the same vein, fair and unfair decisions altering the status quo are perceived as better or worse compared to actions that result from a lack of change in the initial situation (Baron & Ritov, 1994; Cox et al., 2013; Ritov & Baron, 1992, 1995).

In our experiment, higher MEPs were elicited by an active Dictator’s choice changing receiver’s status quo as defined at the beginning of the interaction, namely fair choices in the Loss block, which changed the initial endowment. Moreover, in our experiment the Loss block had the stronger status quo definition, since the status of “no endowment” was maintained in the 80% of the trials.

We then hypothesized that rather than a modulation induced by gain/loss or fairness/unfairness per se, MEPs modulation could be influenced by an active status quo change. To test this hypothesis we ran a second experiment, which mirrored the first one. In experiment 1 dicator choices changing the maximal satus quo settled in the loss block were fair ones. In order to disentangle the choice valence (fair and unfair) from status quo maintenance vs modification, we implemented a change in the game settings such to achieve also the opposite association (unfair choices which change the status quo).

2.2.3 Experiment 2

In the second experiment the Dictator was replaced by a Thief, whose moves were controlled by a pc program as in the first experiment; as in experiment 1 our participants always played as Player 2, alias passive receivers.

At the beginning of each trial both players were endorsed with 50 tokens and the Thief could decide to steal (active unfair – loss condition) or not (fair omission which maintain status quo – no loss) Player 2’s sum. Notably, respect to the previous experiment the combination of fair/unfair action/omission was reversed. This allowed us to investigate whether our hypothesis about status quo modification as main factor affecting MEPs amplitude was correct. If this was the case, we expected to find higher corticospinal excitability when the active/unfair choice, that is steal participant’s money, was taken in the Gain block, the one in which the status quo was stronger (Player’s 2 “endowment” maintained in the 80% of trials).

Materials and methods

Participants

22 healthy students (8 males, Mage =25.4, SD = ±2.5) participated at the experiment. None of these participants took part to Experiment 1. They were right-handed and the same exclusion criteria and recruitment procedures of Experiment 1 were applied.

Theft Game structure

As in Experiment 1 participants were told they were playing online as player 2 with four other participants, who received the role of player 1, alias, thieves. We used the same visual stimuli than Experiment 1.

Each trial started with an endorsement of 50 tokens for both players and the thief could decide to steal (unfair/active choice: 100 tokens for Player 1, 0 for Player 2) or not (fair omission which maintain status quo: 50 tokens for Player 1, 50 tokens for Player 2).

Thief's choices were expressed by showing participants the same video of Experiment 1 and also in this case choice meaning was explained at the beginning of the experiment.

We used the same TMS-EMG protocol and experimental Block design to Experiment 1.

As in Experiment 1 we created four different game contexts, a Gain block (80% of Fair and 20% of Unfair choices), a Loss block (20% of Fair and 80% of Unfair choices) and two Mixed blocks (Mixed block 1= 40% of Fair and 60% of Unfair choices; Mixed block 2= 60% of Fair and 40% of Unfair choices). We then balanced across participants actors, blocks and choice meaning-symbols coupling as for Experiment 1.

Participants were instructed that 50 tokens corresponded to 0.20€ and as for Experiment 1,;our procedure allowed a payment of 10€ for each subject.

Preliminary analyses

We performed the same analysis procedure than Experiment 1; missing mean MEP values in this case were the 3.4% of the total and were replaced with the same method of Exp 1.

Results

Wilcoxon test highlighted that the two baseline conditions were not different (Z = −.89; p = .37) and the same was true for Mixed block 1 and 2 (Z = −.54; p = .59), hence, as in Experiment 1, we then collapsed these variables in a baseline and a Mixed condition.

Also in this case Wilcoxon test performed on the experimental conditions vs baseline was significant (Z = 2.65; p = .008), thus confirming the motor facilitation induced by grasping movements sight (.67 vs .49 mV)

As in Experiment 1 we ran a repeated measure ANOVA with three independent within subject variables: Block (3 levels: Gain, Loss and Mixed), Fairness (2 levels: Fair vs Unfair) and Congruency (2 levels: Congruent vs Incongruent).

The main effects of Block [F(2,42) = 0.4; p = .67], Fairness [F(1,21) = .1.31; p = .26] and Congruency [F(1,21) = .014; p = .90] were not significant, while two significant interactions were found between Block and Fairness [F(2,42) = 7.17; p = .002] and between Block and Congruency [F(2,42) = 3.43; p = .04]. In the interaction between Block and Fairness post-hoc analyses revealed higher MEPs in the Gain block when Player 1 choices were Unfair compared to Fair (z-scores .18 vs −.19 respectively; p = .007) and for Unfair proposals in Gain block compared to Loss one block (z-scores .18 vs −.17; p = .013). Other interactions did not reach significance (see Fig.4 for results).

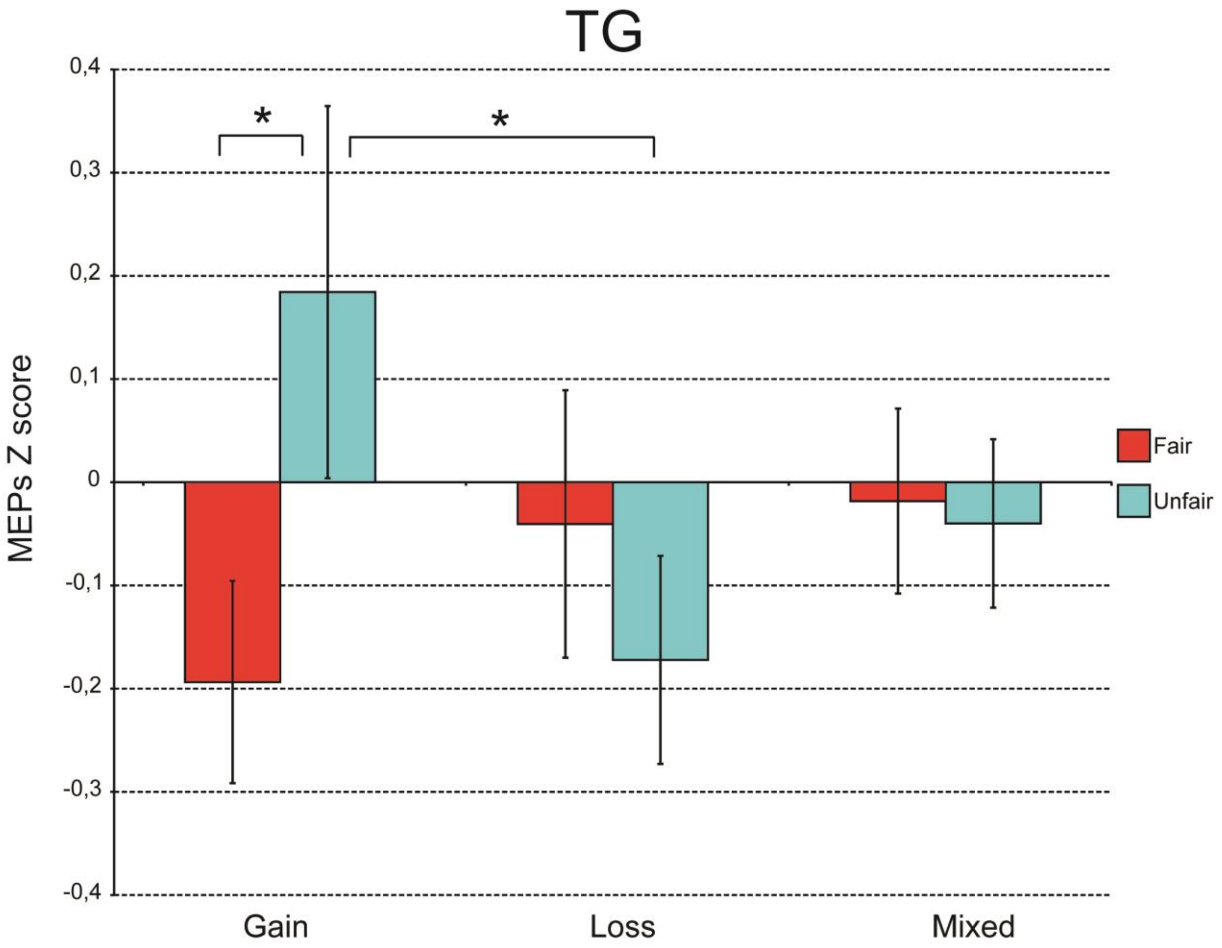

Fig. 4. MEP Z-scores for fair and unfair trials in the Gain, Loss and Mixed TGs. Error bars represent ±/-1 MSE. Asterisks indicate significant differences at p b .05. Non z-transformed MEPs values are provided in the supplementary material section.

The same ANOVA run on pre TMS-EMG muscle activity did not evidence significant main effects or interactions (all ps >.18). Crucially, the interaction between Block and Fairness was not significant [F(2,40) = .018; p = .98].

The analyses on participants' previsions revealed that the main effect of Time was not significant [F(2,40) = 2.7, p = .08; n2 = .12], whereas the main effect of Block [F(1.27,25.34) = 8.39, p = .005; n2 = .29] and the interaction between Block and Time [F(2.55, 51.11) = 6, p b .001; n2 = .23] were significant: participants expected a greater occurrence of Fair choices more often in the Gain (64%) vs Loss conditions (46.3%, p <.001) and post-hoc comparisons revealed that this effect increased with Time, being lower at T1 (52.27%) compared to T2 (65.61%; p = .043) and T3 (74.15%; p <.001).

In the Loss block, however, no differences were traceable at the three different Time: at T1 participants predicted Fair choices in the 50.74% of trials, while at T3 the percentage of Fair previsions were 43.01% (p=.8) and the same was true for Mixed condition, in this latter case replicating Experiment 1 findings (all ps >.9).

Moreover, at T1 the three blocks did not differ (all ps <.9), while at T2 participants predicted more Fair proposals in the Gain (65.6%) compared to the Loss block (45.18%, p < .001) and at T3 Fair predictions were more frequent in Gain (74.15%) compared to Loss (43.01%; p <.001) and Mixed (56.56%; p = .004) blocks (see Fig. 5 for results of the fair predictions).

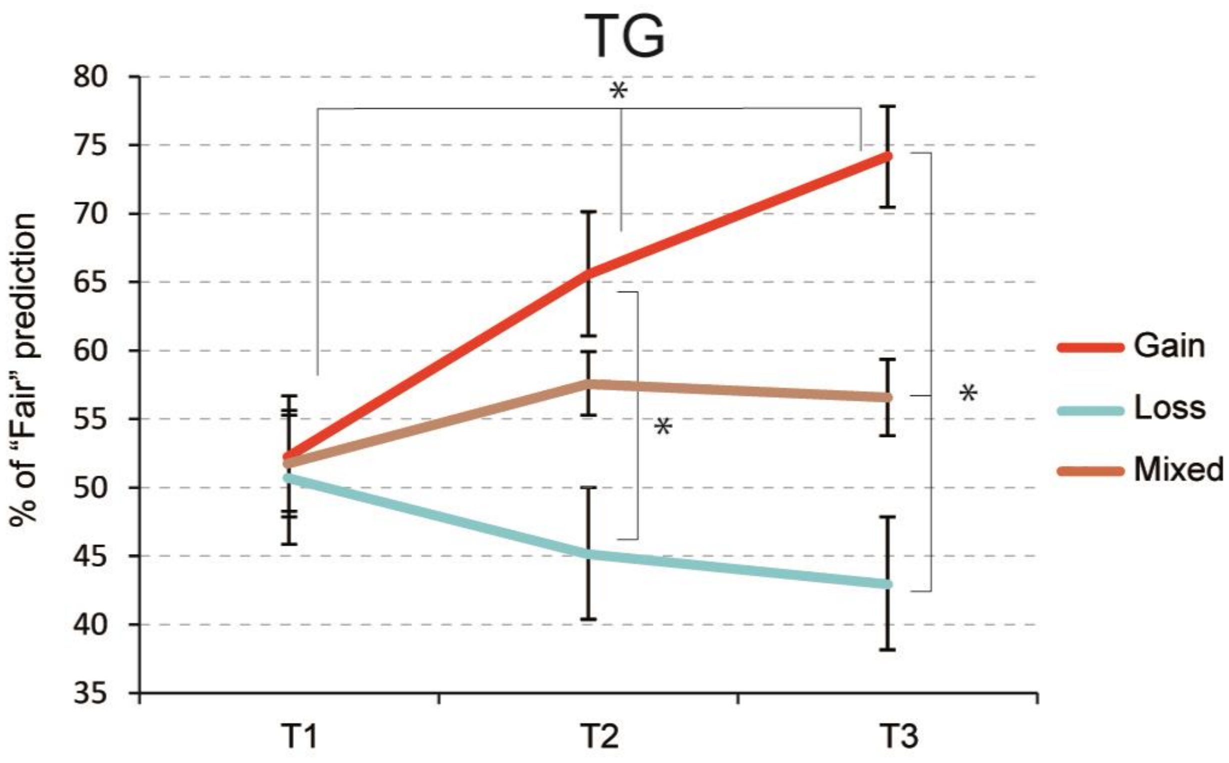

Fig. 5. Participants' percentage of Fair predictions over time for the three experimental conditions in the TG. Error bars represent +/-1 MSE.

As in Experiment 1 we analyzed MEPs amplitude changing over time. The main effect of Time was significant [F(2,40) = 7.67; p = .002]: MEPs recorded during T1 were higher compared to the one recorded during T2 (p = .023) T3 (p= .001). Also the three way interaction Block by Time by Fairness was significant [F(4,80) = 2.84; p = .031]: post-hoc analysis showed that at T1 MEPs were higher for Unfair trials in the Gain block compared to Fair ones in the same block (p <.001) and to Unfair choices in the Loss one; moreover in the Gain block MEPs were lower for Unfair choices at T3 compared to T1 (see Fig.6 for results).

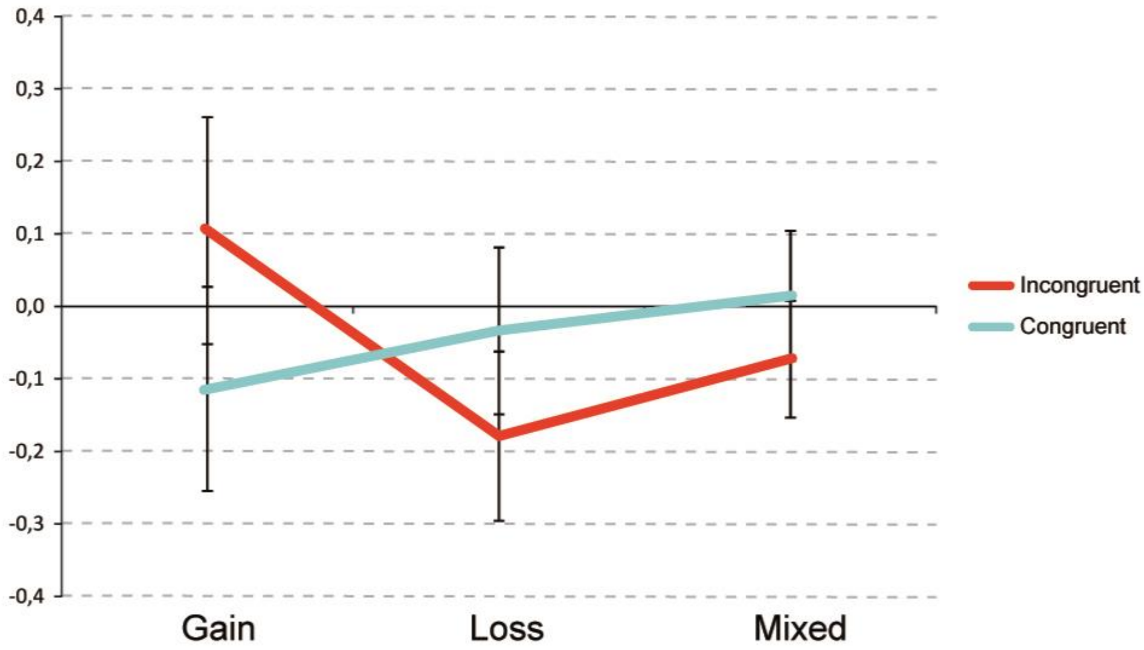

Fig.6. MEP modulation for congruent and incongruent trials over the Blocks in the TG. Error bars represent +/-1 MSE.

2.2.4 General discussion

We ran a set of two experiments with the aim to of testing whether fair and unfair social interactions taking place in economic games are able to influence motor corticospinal excitability.

In both experiments our findings confirm the presence of a motor facilitation effect induced by observing grasping movements (Clark et al., 2004; Fadiga et al., 1995; Gangitano et al., 2004; Maeda et al., 2002; see Fadiga et al., 2005 for reviewsee Naish et al., 2014 for a recent review):

indeed, MEPs were higher while participants were watching video compared to the baseline – rest condition.

In both experiments we manipulated the framework in which the interaction was taking place. The role of environment and social context in which an action takes place is essential to understand action meaning: indeed fMRI studies suggest that HMs can be modulated in a different way by a same action inserted in different contexts (Iacoboni et al., 2005; Kaplan and Iacoboni, 2006) and it seems to be particularly involved in actions with a certain social relevance (Oberman et al., 2007).

In both our experiments motor excitability was not influenced by action meaning (fair vs unfair) per se, indeed the main effect of fairness was not significant. Instead, we did find a significant interaction between Block and Fairness, suggesting that the framework in which an action took place (in our experiment Player's 1 interaction style) affected the specific valence assigned to the same action.

In the two games, namely the Dictator and Theft game, fair and unfair choices were oppositely coupled with a change/maintenance of the initial endowement of the trial, which can be considered as the status quo. Indeed, in the Dictator game, dictator's fair choices represented a gain, changing the status quo, whereas they were a no-loss, hence maintaining the status quo, in the Thief game; conversely, unfair choices were associated with a no-gain in the Dictator, maintaining the status quo, whereas conveyed a loss, changing the status quo, in the Thief game. These differences affected corticospinal excitability: in the Dictator game, during Loss blocks in which fair trials were the 20% of the total, fair choices elicited higher MEPs than the same action taking place in the Gain block, in which they represented the 80% of the total, and in Mixed blocks, in which fair and unfair choices were balanced.

At the opposite, in the Thief game, MEPs were significantly higher for Unfair choices compared to the fair ones in the Gain block and compared to Unfair trials in the Loss block. In Mixed blocks no differences were traceable in corticospinal excitability.

Thereby, the game frame manipulation changed participants' point of view and reactions to fair and unfair proposals even if the purely economic outcome of the two choices was absolutely identical in the two games (+50 tokens for fair trials and −50 tokens for unfair ones). This is a well-known effect in behavioural economics studies, which suggested that the evaluation of loss and gain during a choice is not based on absolute values but rather depends on subjective point of view and contexts in which the action takes place (Tversky & Kahneman, 1985).

Two alternative possible explanations could be that MEPs amplitude in our experiment was due to the frequency of the events or to participants' prediction errors, however both these hypotheses can't account for all our results.

In both games participants were able to learn Player's 1 style as assessed by analyzing their predictions over time and their MEPs amplitude was higher at the beginning of each block, suggesting that unexpected events could increase MEPs size. This explanation however is not able to describe the interaction between Block and Fairness on this variable. In both games Loss and Gain blocks had the same percentage of infrequent events, but only trials which actually changed the status quo showed higher MEPs.

Taken together, our findings could be explained by a difference in individual's status quo perception, specific for each game.

Crucially, corticospinal modulation was higher in the two blocks in which status quo changes were more salient, namely the Loss block in the Dictator game and the Gain block in the Thief game (Cox et al., 2013; Ritov & Baron, 1995; Samuelson & Zeckhauser, 1988).

Different research in experimental and ecological settings suggest the existence of a “status quo bias” defined as a decision-making tendency of having stronger preference for options which doesn’t change the initial condition (Connolly & Zeelenberg, 2002; Kahneman & Miller, 1986). Actions that imply the maintenance of the status quo are selected more frequently (Samuelson & Zeckhauser, 1988) and when an unfair choice, such as not helping someone, is the product of an active action vs an omission (this latter not changing the status quo) it is considered more negatively (Baron & Ritov, 1994; Ritov & Baron, 1992, 1995).

This bias is evident also in economic games, as previously shown by Cox and colleagues (2013). In their experiments participants were more keen to reward the Dictator when he executed Fair active choices compared to when fair choices were the product of an omission (these two scenarios are similar to our experiment 1 and 2, respectively). In a similar vein, when unfair choices came from active choices participants were more keen to punish the Dictator compared to when they were the end of an omission.

In our experiment we found a neurophysiological marker of the status quo bias: specifically, motor excitability was higher when fair behaviours were the product of an active choice contrary to the most frequent condition (Loss block/Experiment 1) and in the specular condition, i.e. when unfair choices came from active actions that interrupted the initial and most frequent pattern (Gain block/Experiment 2).

The modulation in corticospinal excitability can also depend on the emotional effect that Dictator choices elicit in our participants. Borgomaneri et al. (2013) showed for example that an increasing in MEPs amplitude followed the presentation of pictures with an emotional valence (positive and negative) vs neutral ones, thus suggesting a link between emotion perception and the motor system.

Neuroimaging studies suggested a strict link between emotional state and the status quo bias, highlighting stronger activity in left and right insula and medial prefrontal cortex after modification in the status quo (Nicolle et al., 2011) and for right inferior frontal gyrus and bilateral sub-thalamic nucleus (Fleming et al., 2010).

Consistent with these findings, our results showed that cortical excitability is linked to the emotions elicited by social interactions and in changes of the baseline relational balance in a specific context-way. A possible speculation about this effect is that an increase in excitability after status quo modification might indicate a change in the normal equilibrium between partners which may be potentially dangerous or vice versa convenient for the participant, thus preparing the motor system to respond in the most suitable way.

A possible limit of the present experiment is that we did not investigate participant's belief of being involved in an interaction with a real person. However, interaction with computer usually led to similar but attenuated responses both at the behavioural that at the neurophysiological levels as compared to human interactions (Rilling et al., 2004).

To conclude, in the present study we investigated whether action meaning, defined as economically fair or unfair choices, and context, defined from different dictator interaction styles, may modulate corticospinal excitability. Economic interactions can elicit positive or negative emotions depending on the context in which they occur and imply different moral evaluation and reactions influenced by the fact that an action could be the result of an active choice or a passive omission.

Taken together our findings suggest that economic choices differently modulate corticospinal excitability depending on the social context in which an action take place (Loss vs Gain frame) and the action meaning (fair vs unfair). Since motor facilitation is considered to be mediated by the HMs, the present result suggested that this system could be influenced by action meaning and could be a potential neurophysiological marker of the status quo bias.

In the present study in each game the amount of tokens (and money) that participants could gain or lose was fixed and did not change during the experiment. Indeed, Player 1 could choose to share (Experiment 1) or steal (Experiment 2) always 50 tokens.

We then wondered if the amount of the gain or the loss could influence motor excitability. To deeper investigate this hypothesis we created a second study, in which gain and loss frame were randomly presented to our experimental subjects during the same interaction. In this second study Player 1 could share a gain or a loss with our participants in three different sharing options: an equal one, one convenient to him and one favorable for our experimental subjects.

Many influent models in the field of behavioural economics (Tversky &Kahneman, 1991; Kahneman et al., 1986; Kahneman & Tversky, 1979; Thaler & Johnson, 1990; Higgins, 1997) indeed suggest that people react to gain and losses differently, according to several factors, among which their goal attainment perspective. Since corticospinal modulation, signaling HMs system activity in action understanding, was proved to be congruent with the predictions of status quo bias, we wondered whether it could follow also the previsions made by another influent model accounting for people reaction to gain and losses, such as Regulatory Focus Theory.

2.3 Second study: Regulatory focus theory

In the present study we investigated whether corticospinal excitability can be modulated by the goal attainment perspective of who is observing the action. People's economic goals have been defined in a different way by different theories.

Prospect Theory, for example, suggests that people perceive and treat losses and gains differently (Tversky &Kahneman, 1991; Kahneman et al., 1986; Kahneman & Tversky, 1979; Thaler & Johnson, 1990). Also known as "loss-aversion" theory, it highlights that people usually act in order to avoid potential losses rather than equivalent gains (Tversky & Kahneman, 1991).

Regulatory Focus Theory (Higgins, 1997; RFT), instead, posits that individuals actively follow a goal-attainment perspective, aiming to achieve the maximum advantage in the gain domains (promotion) and avoiding the maximum cost in the loss domain (prevention) (see e.g. Higgins, 1997; Idson et al., 2000; Higgins, 1998).

If the Regulatory Focus Theory is more appropriate to describe people behaviour, people should react differently to losses and gain between promotion and prevention context. Building on the results of study 1, suggesting the availability of a neurophysiological signature, such as corticospinal modulations indexed by MEPs, to tap people's way to perceive action conveying gain and losses, we decided to use a similar apparatus (observation of grasping action and MEP recordings) to investigate the appropriateness of Regulatory Focus Theory predictions, by measuring whether different conditions whithin this framework are able to influence MEP amplitude.

Specifically, we predicted deviations from goal attainment to influence motor excitability: that is failing to achieve the maximum gain in a promotion context or obtain the maximum loss in a prevention context.

To test this hypothesis, we used a modified version of the Dictator Game (Kahneman et al., 1986), which we called the Share Game, and manipulated the motivational context in which a same action (that is taking a token as in study 1) was inserted. Previous studies suggested that the regulatory focus system can be triggered by specific tasks and stimuli (e.g. Higgins et al., 1994). Specifically, a Loss frame usually activates a prevention focus whereas a Gain frame activates a promotion one (Shah et al, 1998). Accordingly, in our paradigm prevention and promotion contexts were induced by Dictator's proposals to share a gain or a loss of 50 tokens (equivalent to 1,25€): promotion contexts were elicited when the dictator was sharing a gain, whereas prevention contexts were induced by dictator sharing a loss.

Each trial the pc program randomly assigned a gain or a loss condition of a sum (50 tokens), shared with our participants. There were three different options for sharing either the gain or the loss of 50 tokens. Specifically, in case of a gain condition, the dictator could decide to share the won 50 tokens giving to the other participant: 10 (Dictator's gain: 40), 25 (equal sharing of gain the) or 40 tokens (Dictator gains only 10). Similarly, in the case of sharing a loss, the dictator could make the participant to lose either 10, 25, or 40 tokens corresponding for the dictator to a loss of 40, 25 or 10 tokens, respectively. During the experiment our participants passively observed dictator's choices. On the basis of RTF theory, our prediction was that MEPs would be modulated depending on participants' goals settled by the contextual frame, namely achieving the maximum gain in the promotion context (preferred option: 40 tokens in gain sharing) and avoiding the greatest loss in the prevention context (preferred option 10 tokens in the loss sharing). On the contrary we did not expect that equal sharing would produce any modulation in MEPs amplitude.

2.3.1 Material and methods

Participants

24 healthy students (11 males, Mage = 23.3, SD ± 1.9) participated at the experiment. Only right-handed participants according to the Edinburgh Handedness Inventory, i.e. with a laterality coefficient higher that 0.5 (Oldfield, 1971) and with normal or corrected to normal vision were accepted in the study.

Participants completed the Adult Safety Screening Questionnaire (Keel et al., 2001) and gave informed written consent before to start with the experiment. We excluded participants with any contraindication for TMS (Rossi et al., 2009).

The study was approved by the local Ethics Committee and was in accordance with the ethical standards of the revised Helsinki Declaration.

TMS and EMG Recordings

We used the same Study 1 procedure for TMS and EMG recordings. In the present study however we used an Eximia TMS stimulator (Nexstim™, Helsinki, Finland) and responses were amplified and recorded using eXimia EMG (Nexstim™, Helsinki, Finland) amplifier, filtered with a band pass of 10 – 500 HZ and digitized at a sampling rate of 3 KHz.

The NSB Nextim neuronavigation system was used to monitor the coil-position during the experiment thus preventing any change in stimulation site due to small movements of participant's head during data collection (Sartori et al., 2013).

TMS pulses were delivered using Eximia TMS stimulator (Nexstim™, Helsinki, Finland) using a focal bi-pulse figure-of-eight 70-mm coil. The coil was placed in the standard optima position to optimize MEPs induction, exactly as in Study 1 and 2.

We assessed the participant rMT, set the TMS intensity, and placed the recording electrodes to target FDI following exactly the same procedure described in in study 1 and 2.

Share Game Structure

In our experiment we modified the Dictator Game and called our experimental paradigm Share game.

At the beginning of each trial the pc program could randomly assign a gain or a loss of 50 tokens and the decision was showed to the participant through the sign on the screen “+50” or “-50”, respectively. Noteworthy, this sign anticipated to participants if they were going to share a gain or a loss, thus eliciting two different game-frames: the loss frame elicited a prevention context, whereas the gain frame elicited a promotion context.

Also Share game entailed two different players: Player A, that is the dictator or the active player, and Player B, that is the passive player.

When pc choice was +50 tokens, which elicited a promotion context, Player A could decide how to share this sum among three different options (+40/+10, +25/+25 and +10/+40, where the first number indicated Player A part of the sum and the second number indicated Player B part of the sharing).

When pc choice was -50 tokens, which elicited a prevention context, Player A could decide how to share the loss among three different options (-40/-10, -25/-25 and -10/-40, and also in this case the first number indicated Player A tokens to be taken and the second number indicated Player B loss).

In the gain sharing condition, corresponding to the promotion context, Player B could then face three levels of goal attainment according to the corresponding sharing option chosen by Player A: no (+40/+10), medium (+25/+25) and maximum (+10/+40) goal attainment, since participant’s aim was to reach the maximum gain. In the loss condition, which elicited a prevention context, the three conditions of goal attainment were oppositely distributed: no (-10/-40), medium (-25/-25) and maximum (-40/-10) goal attainment, since in this frame participants meant to avoid the maximal loss.

Experimental Design and Procedure

Our experimental procedure was composed of three different parts.

Phase 1: Social Value Orientation measurement

In the first phase participants played a brief attentional dummy task on a computer screen. The task served to give participants an economical reward which corresponded to their initial monetary endowment in the Share game. In this task they were asked to discriminate the orientation of a T letter in a circular array of L and all participants at the end received a fixed amount of 500 tokens for their performance.

Secondly, in this phase we asked participants to complete a Social Value Orientation (SVO) Slider Measure (Murphy et al., 2011), a questionnaire useful to measure prosociality in our participants. Recent studies have shown that people reactions to other player's choices are affected by the concern people have for others, that is prosociality (Bieleke et al., 2016; on prosocial behaviour in economic games, see also Camerer, 2003).

SVO was calculated from a series of choices made during several dictator games in which our participants acted the part of the Player 1-Dictator and had to share a certain amount of tokens with another player.

Participants' decisions led to different possible scores at SVO: perfect altruism, that is maximizing the other participant payoff; individualism, that is maximizing his/her payoff; competitiveness, that is minimizing the differences between the two payoffs or maximizing both gains.

Phase 2: Share Game as Player A

The second phase had the aim to assess the economic goal of participants within the context of the Share game, thus we asked participants to perform the Share game in the role of Player A with other five dummy participants playing as Player B.

Participants were told they were playing via internet with other participants located in another experimental room.

The Share game was composed of 20 trials (10 in a loss frame and 10 in a gain frame, presented in a random order); in this way participants were playing four times with each of the five players B, without knowing which player B s/he was playing with. All participants started phase 2 with the 500 tokens earned in Phase 1.

Phase 3: Share Game as player B

In the third phase our participants performed the Share game as Player B, namely they could only passively accept Player A decisions. In this phase subjects were playing with other 5 dummy Players A for 150 trials, 30 trials with each one. Participants started this phase of the interaction with the amount of token won at the end of Phase 2.

As in the previous studies, participants expectations on the incoming condition of gain or share loss were collected.

Player A’s decisions were showed through a video in which an actor’s right hand reached and grasped the token that represented the option chose by Player A. TMS was synchronized with the grasping action and a pulse was delivered to participant's left M1 at the moment of the maximum amplitude of grasping movement, eliciting a MEP in FDI muscle.

At the end of each trial a screen reported how many tokens were won or lost by Player B and the total sum owned by player B was updated and showed at the end of each trial. In order to maintain participants focused on the task, in 30% of the trials we asked participants to report Player A's decisions and participants' verbal answers were recorded by the experimenter.

Each share option (+10/+40, +25/+25, +40/+10, -10/-40, -25/-25, -40/-10) was randomly presented 25 times, so that participants ended the game with the same endowment they had at the beginning. Specifically, at the end of the experiment participants received 0.025 € for each token they earned during the experimental phase and the average payoff was 19.6 €.

Visual Stimuli

We recorded a set of video clips which were presented on a 19-in. LCD screen that was placed approximately 80 cm from participants' head. In each video an actor's right hand grasped one of six metal tokens (diameter 2 cm; height 1.5 cm) which were horizontally placed on a table at 57 cm from his hand's position at the beginning of the video. The grasping movement was showed in an egocentric view, that has been suggested as the best perspective to elicit motor facilitation (Maeda et al., 2002).

Each token had impressed on its top one of the possible share options with three tokens representing the three gain conditions (40/10; 25/25; 10/40) and three representing the three loss conditions (-40/-10; -25/-25; -10/-40). The first number impressed on the token represented the amount won or loss by Player A and the second number the of Player B.

The 6 tokens were aligned in a row, centered to the midline of the table. In this way three tokens representing a loss were on a side of the table respect to the midline and the three representing a gain were on the other side (see Figure 7 for the timeline of an experimental trial).

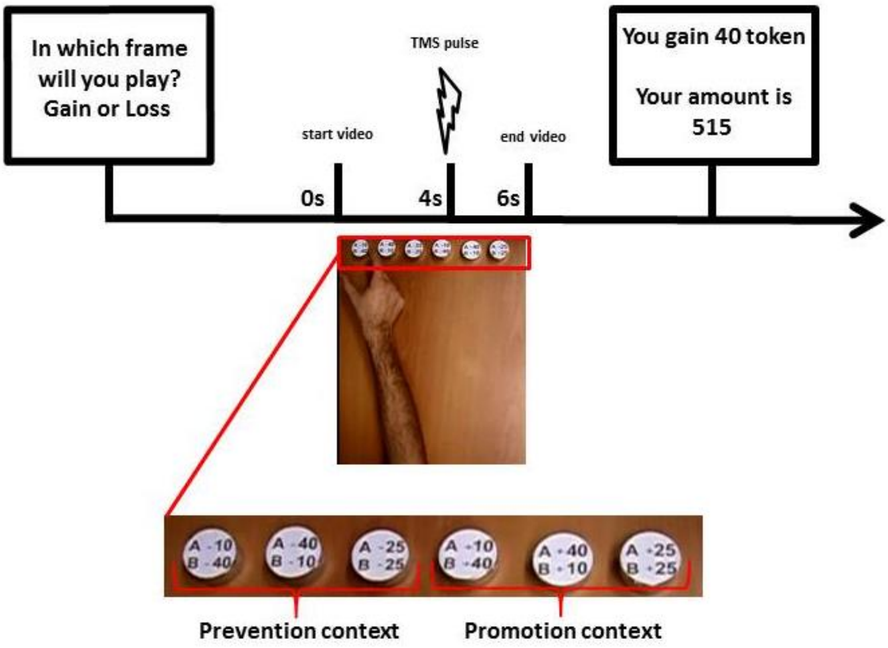

Fig 7: Timeline of an experimental trial in the Share Game (Phase 3).

The side of gains and losses was counterbalanced across participants. This procedure was made to create a clear association between promotion/prevention contexts and the side of the table: as the video started, the direction of the grasping movement to left or right side immediately indicated the choice's context. The order of the three options within loss and gain conditions was balanced across participants.

Control Experiment

Data from 10 additional participants (6 males, mean age = 23.9 years, SD = 1.6 years) were collected following exactly the same procedure of the main study. Our control experiment had the double aims to verify whether i) our results were muscle-specific and ii) to check whether MEP modulation registered during the economic interaction represented an inhibition or a facilitation respect to the simple view of the same action but without any economic association.

We addressed to the first question recording MEPs from both FDI and from the right ADM, which is not involved in the precision grasping movements showed in the video. MEPs from FDI and ADM were simultaneously recorded with the coil positioned over the FDI hotspot.

To investigate the second question we collected two baseline measurements, each one made of 30 trials, before the beginning of the experimental phase. During baseline recordings, participants watched the same video showed in the experimental phase, in which the hand grasped one out of six metal cylinders, but without the sharing options impressed on them.

In this session, the coil was positioned over the FDI hotspot following the previously described procedure. For ADM recording, the active electrode was placed over the muscle belly and the reference electrode over the metacarpo-phalangeal joint of the right pinky finger.

MEPs preprocessing

MEPs collected in Phase 3 were recorded and off-line processed. Trials with electromyographic activity prior to TMS pulses were removed from subsequent analyses (Avenanti et al., 2006; Catmur et al., 2011). We measured MEPs amplitude peak-to-peak and for each participant and each condition trials in which the amplitude exceeded ±2 SD were removed from subsequent analyses. At the end of this procedure the 12% of main experiment trials and the 6.5% of control experiment trials were removed). Remaining MEPs were logarithmically normalized.

Conditions did not differ in the number of discarded trials (p=0.947).

Statistical analyses

Statistical analyses were performed in the statistical programming environment R (R Development Core Team, 2014).

First we wanted to analyze participants' choices in Phase 2, in which our participant acted as Player A or dictator. A Poisson regression was run with Number of choices per condition as dependent variable and Sharing option (6 levels: gain +10, +25 or +40 and loss -10, -25 or -40 tokens) as independent variable.

Secondly, we applied linear mixed effects models (Baayen et al., 2008) over logarithmic transformed MEPs recorded in Phase 3, with participants acting as Player B. This procedure allowed us to account for inter-subject variability by adding a by-subject random slope (see Baayen et al., 2008). As MEPs are a continuous dependent variable, the "lme4" R package (version 1.1-5, Bates et al., 2014) was used to run a series of mixed effect regressions.

Fixed effects inclusion in the final model has been tested with a series of likelihood ratio tests by progressively including each effect which significantly increased the overall model's goodness of fit (Gelman and Hill, 2006).

We included as fixed effect the Share amount (factorial, 3 levels: 10, 25 and 40 tokens), the motivational Regulatory Focus context (factorial, 2 levels: promotion vs. prevention) and their interaction; as covariates we included Expectation (factorial, 2 levels: gain vs. loss), the responses given at the SG in phase 2 and the scoring at the SVO questionnaire. Concerning the random structure, a by-subjects and a by-items random intercept were included into the model. We also tested a by-subjects and by-trial random slope for Share amount and motivational Regulatory Focus context and their interaction (Matuscheck et al., 2015; Bates et al., 2015; for likelihood ratio tests outcomes for the model selection see Table 1,2).

Fixed Effects			
Effect	**DF**	χ^2	**p**
Dictator	1	0.43	0.51
Expectation	1	1.61	0.2
SVO	1	0.72	0.4
RF Context	1	0.29	0.59
Share amount	2	0.029	0.98
RF Context*Share amount	2	14.76	0.0006 *
Random Effects			
Trial			
Share amount*RF Context	11	1.81	0.99
RF Context	4	0.72	0.95
Share amount	7	7	0.42
ID			
Share amount*RF Context	NA	NA	NA
RF Context	2	5.72	0.057 *
Share amount	5	3.6	0.6

Table 1: Model selection: Likelihood ratio tests results

Random Effects						
	sd		**corr**	**n**		
trial	0.12			180		
ID	0.498			24		
RF Context|ID	0.01		-0.41			
	est	**SE**		**DF**	**t**	**p**
intercept	6.5	0.1		25.7	62.9	<.001
Share amount 10:25	-0.015	0.4		3028.7	-0.37	0.71
Share amount 10:40	0.08	0.4		3042.9	1.11	0.03 *
Share amount 25:40	0.1	0.04		3030	2.47	0.013 *
RF Context Promotion:Prevention	0.04	0.45		96.8	0.92	0.36
Share amount 10:25* RF Context Promotion:Prevention	0.023	0.057		3038.7	0.4	0.69
Share amount 10:40* RF Context Promotion:Prevention	-0.18	0.0057		3036.3	-3.15	0.002 *
Share amount 10:40* RF Context Promotion:Prevention	-0.2	0.0057		3020.3	-3.54	<0.001 *

Table 2: Final model parameters

LN ~ Share amount * RF ContextV_P + (1 + RF ContextV_P | ID) + (1 | Trial)

We explored significant interactions using the R package “phia” (Martinez, 2015) and applying FDR correction for multiple comparisons.

Results

Phase 1

80% of our participants showed a preference for prosociality at the SVO Slider Measure.

Phase 2

Poisson regression showed a significant effect of Sharing option ($\chi2(5)=221$; $p<.001$). Specifically, in the loss frame participants chose more often the possibility to lose 10 tokens (6.33 times) compared to 25 (3.5 times; p<.001) and 40 (0.12 times; p<.001), and to lose 25 compared to 40 (p<.001). In the gain frame participants chose more often to gain 40 tokens (5.58 times) compared to 25 (3.66 times; p=.033) and 10 (0.75 times; p<.001), and to gain 25 compared to 10 (p<.001). In a direct comparison between gain and loss, participants chose more frequently to gain 40 than lose the same amount (p<.001), and to lose 10 compared to gain 10 (p<.001). A trend was found between gain 10 and lose 40 (p=.06), showing that participants were more likely to choose the gain option. No other differences were found (all ps >.1). See Fig. 8 for Poisson regression results.

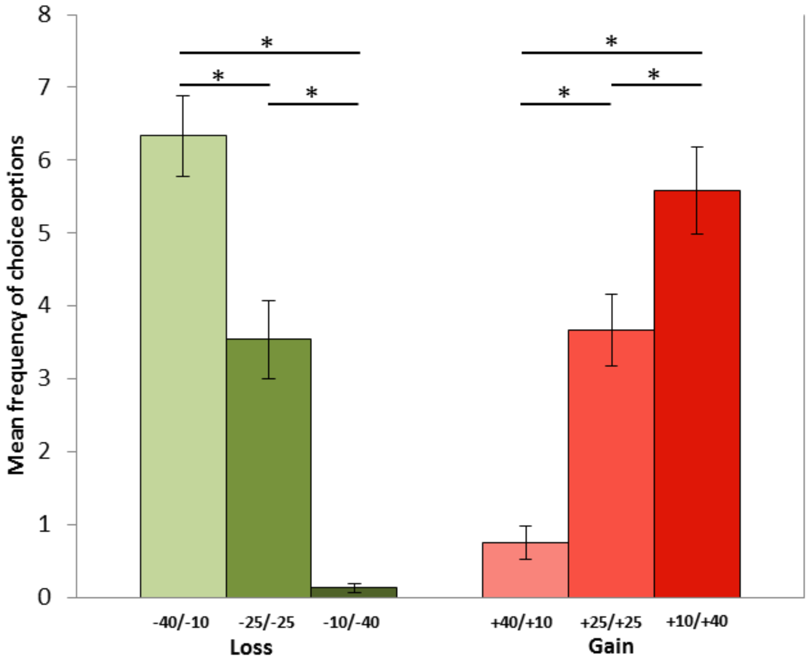

Fig 8. Mean frequencies for each choice option during phase 1. Options represent -40/-10, -25/-25 and -10/-40 in the loss, and +40/+10, +25/+25 and +10/+40 in the gain context. The first and the second number indicate player A and player B part of the sum, respectively).

Phase 3. Main Experiment

The final model of the main experiment included the main effects of Share amount, motivational RF contexts and their interaction as fixed effects, while the random effects structure included the random intercept for Trial and Subject, as well as a by Subject random slope for motivational RF context.

The main effect of share amount was significant, with higher MEPs when the token amount was 40 (1.73mV) compared to both the 10 (b=0.08, t(3042.9)=2.11; p=.03) and 25 (b=0.1, t(3030)=2.47; p=.013) tokens (1.61 mV and 1.51mV respectively).

Crucially, the interaction between the share amount and the motivational RF context was also significant: in both the prevention and promotion contexts, the 40 tokens choice was significantly different from both the 25 (b=-0.2, t(3020.3)=-3.54; p=<.001) and 10 (b=-0.18, t(3036.3)=-3.15; p=.002) tokens choice.

Within the loss/prevention motivational context, the 40 tokens choice (sharing option -10 Player A /-40 Player B), which symbolized the goal attainment failure for this context, elicited greater MEPs compared to both the 25 (sharing option -25 Player A /-25 Player B; p=.038) and 10 (sharing option -40 Player A /-10 Player B; p=.05) choices. In the same vein, in the gain/promotion frame the 25 (sharing option +25 Player A /+25 Player B; p=.038) and 10 (sharing option +40 Player A /+10 Player B; p=.038) tokens choices, which represented the two deviated outcomes in this context, elicited greater MEPs compared to the 40 tokens choice (sharing option +10 Player A /+40 Player B), which denoted instead the maximal goal attainment.

Comparing the two motivational frame for each amount, the -40 token choice in the loss/prevention context elicited greater MEPs (1.15mV) compared to the promotion one (0.99mV; p=.007), the two equal sharing ±25 were not significantly different in the two frames (1.03mV vs. 1.07mV; p=.23) as well as the 10 tokens shares (1.06mV and 1.065mV; p=.36). See Fig. 9 for the interaction results.

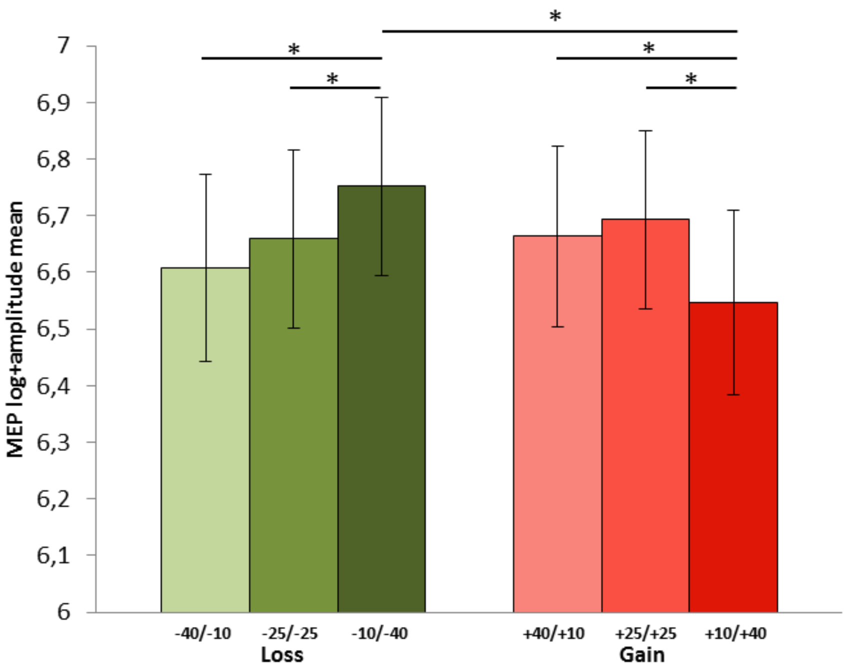

Fig 9. MEP log-amplitude mean for each choice options of in the two contexts during phase 2 (-40/-10, -25/-25 and -10/-40 in the loss and +40/+10, +25/+25 and +10/+40 in the gain context. The first and the second number indicate player A and player B part of the sum, respectively)). Error bars represent +/- MSE. Asterisks indicate significant differences at $p < .05$

Control Experiment

In the control experiment we checked MEPs amplitude recorded on ADM muscle performing the same analysis described above for FDI muscle. In this case both the main effects of Share amount ($\chi^2(2) = 0.072$ p=0.96), Regulatory Focus context ($\chi^2(1) = 0.146$ p=0.7) and their interaction ($\chi^2(2) = 0.588$ p=0.74) did not reach significance.

Secondly, we performed a model with MEPs recorded on ADM and FDI muscles as dependent variable and condition (factorial, 2 levels: baseline vs experimental procedure) as fixed factor; random intercepts of Trial and Subject were entered as random factor. Analyses showed higher MEPs during the experimental vs baseline condition for both ADM ($\chi^2(1) = 207.73$ $p<0.001$; baseline mean = 0.476 mV, experimental mean = 0.853 mV) and FDI ($\chi^2(1) = 30.106$ $p<0.001$; baseline mean =1.234 mV; experimental mean = 1.713).

2.3.2 Discussion

In the present study we manipulated the motivational context of economic interactions by creating a promotion and a prevention frames in which a Dictator or Player A decided how to share a gain or a loss of 50 tokens with Player B, who could only passively accept Player's A decision.

Our aim was to investigate whether corticospinal excitability can be modulated by the economic goal of an observed action, using with theoretical frame the Regulatory Focus Theory (RFT; Higgins, 1997).

Promotion context was created by settling the sharing options in a gain frame, i.e. Player A could choose among three tokens' divisions (+10/+40; +25/+25; +40/+10, the first number indicating Player's A and the second one Player's B amount) to be sum up to the quantity already owned by Player B.

Conversely, prevention context was generated by settling the three sharing options in a loss frame, with three different possible divisions (-10/-40; -25/-25; -40/-10 tokens) to be subtracted to the amount already owned by Player B.

At the beginning of the experiment (Phase 2) we asked participants to play as dictator to assess their behaviour in sharing an economic gain or loss with other players and evaluate which goal they were pursuing in promotion and prevention frames.

Consistently with RFT previsions, in loss/prevention frames participants sought the minimum loss (-10) whereas in gain/promotion frames they pursued choices which gave them the maximum gain (+40). Crucially, we did not find differences in the frequency for the other economic choices.

Accordingly, when our participants were playing as Player B/passive receivers (Phase 3), MEPs were higher when Player A chose the sharing options less desired by them in the second phase. Specifically, in prevention/loss frames, which elicited participants' behaviour to contain losses, MEPs were higher when Dictator chose to subtract 40 tokens from our subject (Dictator's option +40/+10), a choice which was clearly against participants goal of minimizing their loss.

In the same vein, in the promotion/gain frame, higher MEPs were recorded when participants did not reach their goal, that is to reach the maximum gain (40 tokens, Dictator's option +10/+40).

At the opposite, when participants were able to achieve their goal in both preventions and promotion contexts (i.e. when participants gained 40 or lost 10 tokens) MEPs were smaller.

To the best of our knowledge, this is the first proof suggesting that corticospinal excitability can be influenced by reaching individual goal attainment during economic interactions. More specifically, our data offer a neurophysiological measure to RTF behavioural previsions and highlight the possibility that the human neuron mirror system (HMs) is involved in understanding actions' goals in economic interactions.

Previous neuroimaging studies investigated the neural underpinnings of RFT, suggesting that in promotion frames maximizing gains increased activation in the medial prefrontal cortex and in the anterior cingulate cortex (ACC) and achieving prevention goal minimizing losses increased activations in the bilateral posterior cingulated cortex and the precuneus (Johnson et al., 2006; Sharon et al., 2007). Cunningham and colleagues (2005) indicated that performing verbal judgements in promotion and prevention frames increased activation of amygdala, ACC and extrastriate cortices. Some of these regions show connections with the premotor cortex, which is a core hub for the HMs (Leung et al., 2015). This complex network supports the idea that RFT, being a motivational model, includes both cognitive evaluations and emotions in reactions and expectations linked to the different outcomes in economic interactions. Specifically, gain/promotion success elicits positive emotions, such as cheerfulness related emotions, while promotion failure evokes low-intensity sadness. Prevention success induces quiescence-related emotions, and failure in prevention focus generates agitation-related emotions (Idson et al., 2004).

In line with this idea, previous studies suggested that motivations and emotions associated with the observation of monetary actions may influence corticospinal excitability. For example, short intra-cortical inhibition (Thabit et al., 2011) and MEPs amplitude (Suzuki et al., 2014; Kapogiannis et al., 2008) can be modulated by the presence of a monetary reward. Recently, Vicario et al. (2015) found that economic losses are associated with higher MEPs and negative emotions elicited by the economic outcome increased with corticospinal excitability.

A point of discussion is that our data could be explained by the fact that corticospinal excitability is influenced by the mere negative emotions elicited by maximum losses and non-maximum gains. However, previous studies evaluated how emotional stimuli affect corticospinal excitability, without reaching a univocal interpretation. Indeed, while some authors highlighted MEPs increasing with unpleasant stimuli (Coelho et al., 2010; Coombes et al., 2009; Oliveri et. al., 2003; Nogueira-Campos et al., 2016) other showed increase of MEPs amplitude for emotional vs neutral stimuli (Borgomaneri et al., 2012; Hajcak et al., 2007). The majority of these studies, however, triggered emotions with external stimuli such as images or sounds, while only few studies investigated the role of internally generated emotional states (Vicario et al., 2015).

In the present study, only the negative emotions associated to failure in the specific goals of each contextual frame increased corticospinal excitability, suggesting a complex relationship between economic interaction, motivation and emotions which is traceable and measurable also at cortico-motor level.

Moreover, our findings contribute to the debate about the role of the HMs in understanding action goals in social interactions. Previous studies investigate how action's goals are able to influence motor facilitation, however the meaning of "goal" is not shared or consistent across studies. To elicit motor facilitation participants watched grasping movements toward objects, in which goals were defined by the object's context and properties (if it was visible or hidden, reachable or not) (Iacoboni, 2005; Gazzola et al., 2007; Umiltà et al., 2008; Urgesi et al., 2010; Cavallo et al., 2013). In other works, instead, action's goal implicates a social purpose, for example reaching a ball to throw it to someone else (Bucchioni et al., 2013).

In our study, we considered not only the real goal of the observed actions, that is sharing money in an economic interaction, but also its implicit goal, or better the deviation between the desired frame-specific outcome and the real action result.

Taken together our findings fit nicely with RFT predictions, while they are only partially in line with Prospect Theory previsions and loss-aversion behaviours (Tversky and Kahneman, 1981). The main idea of Prospect Theory is that the subjective experience of pain due to loss is greater that the pleasure experience from a gain of the same entity. In our data the difference between MEPs amplitude in the higher loss (-10/-40 tokens) and the higher gain (+10/+40 tokens) was significant, but for the intermediate levels (-25/-25 vs 25/25 and -40/-10 vs 40/10) MEPs did not differ between gains and losses. Our results are not directly connected with the amount of token in each trial: MEPs were not different in loss frames when participants were losing 10 vs 25 or gaining 10 and 25.

In conclusion, our findings suggest that the HMs is sensitive to individual's present goal pursuits (Huang & Bargh, 2013), shaping the meaning and valence of an observed action according to the motivational contextual frame.

Our results provide a neurophysiological support to RFT suggestion that economic decision-making processes crucially depend on frame-specific and contingent goals and in this specific case trying to achieve the maximum gain vs avoiding the undesired one (Florack et al., 2013).

Merging the results of the two studies, it could be argued that corticospinal excitability is modulated while observing exactly the same grasping movements, by the action outcomes, not in term of fairness/ unfairness or gain/loss as it could be expected, but as consequence of more sophisticated and complex phenomena, such as status quo modification and motivational context. Our findings highlight that motor facilitation, which is thought to reflect HMs activity is not only shaped by intrinsic action features, but also from the value which is determined by action meanings and interaction consequences.

To conclude, our results suggest that MEPs are a reliable measure to investigate the neurophysiological underpinnings of previsions based on economics models accounting for complex human behaviour in social interaction context.

3. The use of MEPs in social interaction

3.1 Introduction

Recent studies showed that corticospinal excitability is influenced by the social value assumed by actions in interpersonal interactions and contexts, which is one of the most ecological setting in which the HNMs is supposed to play a relevant role (Hogeveen & Obhi, 2012).

In a series of studies, for example, Sartori and colleagues (2011, 2012) showed that complementary actions induced higher MEPs as compared to action in isolation and Bucchioni and colleagues (2013) suggested that this effect was not due to the onlooker's implicit or explicit involvement.

Among social variables, stereotypes are able to affect information processing and interaction thus strongly influencing our behaviour (e.g. Snyder et al., 1977).

In our everyday life we categorize people and apply stereotypes to simplify our knowledge about the world (Tajfel et al., 1971).

One of the most salient features to categorize people is ethnicity, it is early and automatically coded and influences behaviour (Snyder et al., 1977) and decision making (Kinzler et al., 2010).

Behavioural (Capellini et al., 2016; Pavan et al., 2011), neuroimaging (Xu et al., 2009; Azevedo et al., 2013), electrophysiological (Gutsell & Inzlicht, 2010, 2013) and neurophysiological (Désy & Théoret, 2007; Avenanti et al., 2010) studies consistently suggested the pervasiveness of this categorization.

In a famous study from Avenanti and colleagues (2005), for example, the sight of a needle penetrating in a seen arm induced a freezing effect in corticospinal excitability, suggesting an instinctive ability to empathize with others. Crucially, when the same painful stimuli were delivered to an outgroup member, however, the corticospinal modulation disappeared (Avenanti et al., 2010).

Not only top-down influences such as stereotypical knowledge, however, could be able to influence our social perception of outgroup members: this effect can interact, and maybe be empowered, by bottom-up information such as contextual features (Trawalter et al., 2008).

In the present line of research, we aimed at providing a further contribute to this field of investigation, exploring whether corticospinal excitability can be modulated by agents' membership (ingroup vs outgroup) and contextual cues (threatening vs relaxing sound) during the sight of a same action, i.e. grasping a neutral object (a glass).

3.2 Study: manipulating context to elicit social threat

3.2.1 Background

Through the evolutionary process, the human brain developed the ability to adapt to complex social group living (Dunbar, 2011). One of the way to understand and simplify our knowledge about it is to create simpler categories usually relying upon trivial criteria (Tajfel et al., 1971).

One of the most common categorization is based on the differentiation between *ingroup vs outgroup* (Amodio, 2008; Tajfel, 1981) and it's usually based on people characteristics such as gender, age, profession, education and so on (Molenberghs, 2013).

Being part of a group is extremely important from an adaptive point of view: it provides security against common enemies and easier access to supplies; indeed membership offered survival and strengthened collective group adaptability (Caporael, 1997). Many authors investigated the neural underpinnings of this evolutionary legacy, which influenced our perceptual, affective and cognitive skills to develop and maintain a group society (Brewer & Caporael, 1990).

Our brains, indeed, responds differently to ingroup and outgroup members (see Molenberghs 2013 for a review), even when membership is based on circumstantial and trivial criteria, such be divided in yellow and blue teams, on the basis of task performance, immediately before the experiment (minimal group paradigm, Tajfel et al., 1971; Billig & Tajfel, 1973, Tajfel & Billic, 1974; see Volz et al., 2009 for a fMRI example).

Among the possible categories in which we separate our ingroup from our outgroup, race represents a powerful cue (Sacheli et al., 2015).

Ethnic categorization has been showed to influence a broader range of processes and functions, such as intention comprehension and imitation (Liew et al., 2011; Earls et al., 2013; Losin et al., 2012), joint action processes (Sacheli et al., 2015), social attention through gaze-orienteering (Pavan et al., 2011), bodily illusion (Maister et al., 2013; Peck et al., 2013) and empathy (Avenanti et al., 2010; Azevedo et al., 2013; Berlingeri et al., 2016).

As suggested by some authors, however, categories are not fixed concepts but instead they are fluid and context dependent (Turner et al., 1994).

Context is able to influence social categorization (Freeman et al., 2013) for example by modifying face’s emotion perception (Barrett & Kensinger, 2010; Masuda et al., 2008; Righart & De Gelder, 2008).

Threatening contextual features, for instance, can weaken or strengthen race-based stereotypes of aggressiveness and menace (Trawalter et al., 2008): a threatening context is likely to activate negative stereotypes associated with specific social categories, thus activating the perception of a menace.

A large body of evidence suggests that attentional resources are easily captured by threatening stimuli, such as biologically dangerous animals (see Öhman et al., 2001 for a review) and social menacing stimuli (Fox et al., 2002), thus interfering with goal-directed behaviour (Williams et al., 1988, 1996).

Moreover, people are highly sensitive to dangerous objects since their childhood (Anelli et al., 2012a,b, 2013) and the dangerousness of objects placed in our environment influences, for example, the boundaries of our peripersonal space (Coello et al., 2012).

Among social groups, Blacks, Latinos and more recently Arabians, are stereotypically linked to aggression and threat (e.g., Payne, 2001; Mange et al., 2012), thus eliciting aggressive responses in social perceivers.

In their recent study, for example, Mange and colleagues (2012) observed that participants were faster to decide to shoot against an armed target when they were primed with words associated to the category Arab or Muslim as compared to a no-priming condition, thus suggesting that the simple accessibility to subjectively threatening social categories facilitates aggressive responses (Mange et al., 2012)

In a previous study by Capellini et al. (2016) social menace was induced by manipulating contextual cues (i.e. neutral vs threatening objects) and agent's group membership (ingroup vs outgroup) . Reaction times were recorded through a MouseTracker. Results showed faster reaction times both in starting a response and in producing it, when participants observed an action performed by the ingroup members rather than by the outgroup only when threatening objects were presented. These findings were interpreted by authors as a measure of higher motor resonance with members of the ingroup compared to the outgroup, especially when contextual cues appeared on the scene and activated threat perception and thus outgroup's related stereotypes.

Previous work on threatening stimuli effect on corticospinal excitability suggested a freezing like effect, i.e. an inhibitory modulation of corticospinal excitability. This pattern has been induced by potentially dangerous stimuli such as loud acoustic (Furubayashi et al., 2000), unexpected visual flashes (Cantello et al., 2000) and approaching virtual objects (Makin et al., 2009) or visual painful stimuli (e.g. Avenanti et al., 2005).

Building on this body of work, the present study aimed to explore whether and how corticospinal excitability triggered by observing others' grasping movements toward a neutral object (a glass) can be modulated by social variables such as ethnic group membership and whether contextual cues, such as sounds, were able to modulate this effect.

Our specific hypothesis was that threatening context caused an inhibitory effect on corticospinal excitability and that this pattern should be amplified when the agent of the action was a member of the outgroup.

In order to test this hypothesis we manipulated agent's membership (ingroup, i.e. Caucasian, vs. outgroup, i.e. Arabic) and the contextual cues by asking participants to listen to threatening vs neutral external sounds.

3.2.2 Methods

Participants

19 right-handed healthy students (12 male, *Mage* = 23.2, SD = ±1.7) took part in the study. Only right-handed participants, i.e. with an laterality index higher than 0.5 according to the Edinburgh Handedness Inventory (Oldfield, 1971), were accepted in the study. Participants completed the Adult Safety Screening Questionnaire (Keel et al., 2001) and gave informed written

consent before to start with the experiment. We excluded participants with any contraindication for TMS (Rossi et al., 2009).

The study was approved by the local Ethics Committee and was in accordance with the ethical standards of the revised Helsinki Declaration.

TMS and EMG recordings

We used the same procedure described in the second Neuroeconomic study (paragraph *2.2.2 TMS and EMG recordings, page 19*). MEPs were recorded from FDI and ADM muscles.

Visual stimuli and context manipulation

During the experiment actions were shown through video clips which were presented on a 19-in. LCD screen at a distance of approximately 80 cm from participants' head.

In each video participants saw two different agents (a Caucasian guy - ingroup condition vs an Arabian - outgroup condition) grasping a neutral object (a glass).

Each grasp was a precision grip and was executed with the thumb and the index fingers of the right hand. In each video actors were shown from behind with an egocentric perspective (see Figure 1) and action timings were strictly synchronized across videos: each video had a duration of 3000 ms and the grasping movements happened after 2500 ms from the video onset.

TMS pulses were delivered at the same time with the maximum index finger–thumb aperture, which has been shown to be the moment in which FDI motor cortex has the maximum excitability for MEPs recording (Gangitano et al., 2001, 2004).

We manipulated context valence by asking participants to listen to two different background sounds: a neutral one, i.e. nature sounds and a threatening one, i.e. war noises. The neutral sound (original duration 45 seconds) consisted in the murmur of seawaves, while the war sound (original duration 39 seconds) was composed of noises of bombing, air-raid siren and shooting. Both original durations were transformed and run in a loop to cover the duration of the whole block.The volume was checked to be balanced for each participant in the two conditions.

Procedure

Participants were comfortably seated in a chair positioned 70 cm from the computer screen and electrodes were placed on the right hand.

Then for each participant we found TMS hotspot and after motor threshold was assessed, participants received instructions about the procedure .

We recorded two baseline sessions, each one composed of 20 MEPs, at the beginning and at the end of the experiment. In this condition participants had to watch a fixation cross at the center of the screen and TMS pulses were randomly delivered with an interval between 3800-4000 ms.

Participants were then presented with photos and a brief description of the actors they were going to watch during the experiment (name, age and nationality). Actor’s pictures and descriptions (Gabriele, 26 years old, Italian vs Haashim, 27, Iraqi) were printed on a paper which was placed on the desk in a visible position for the whole experiment.

After actors’ introduction, we started with the experiment.

A fixation cross was shown at the center of the screen and after 2000 ms the video started and MEPs were recorded (see Fig. 1 for a timeline).

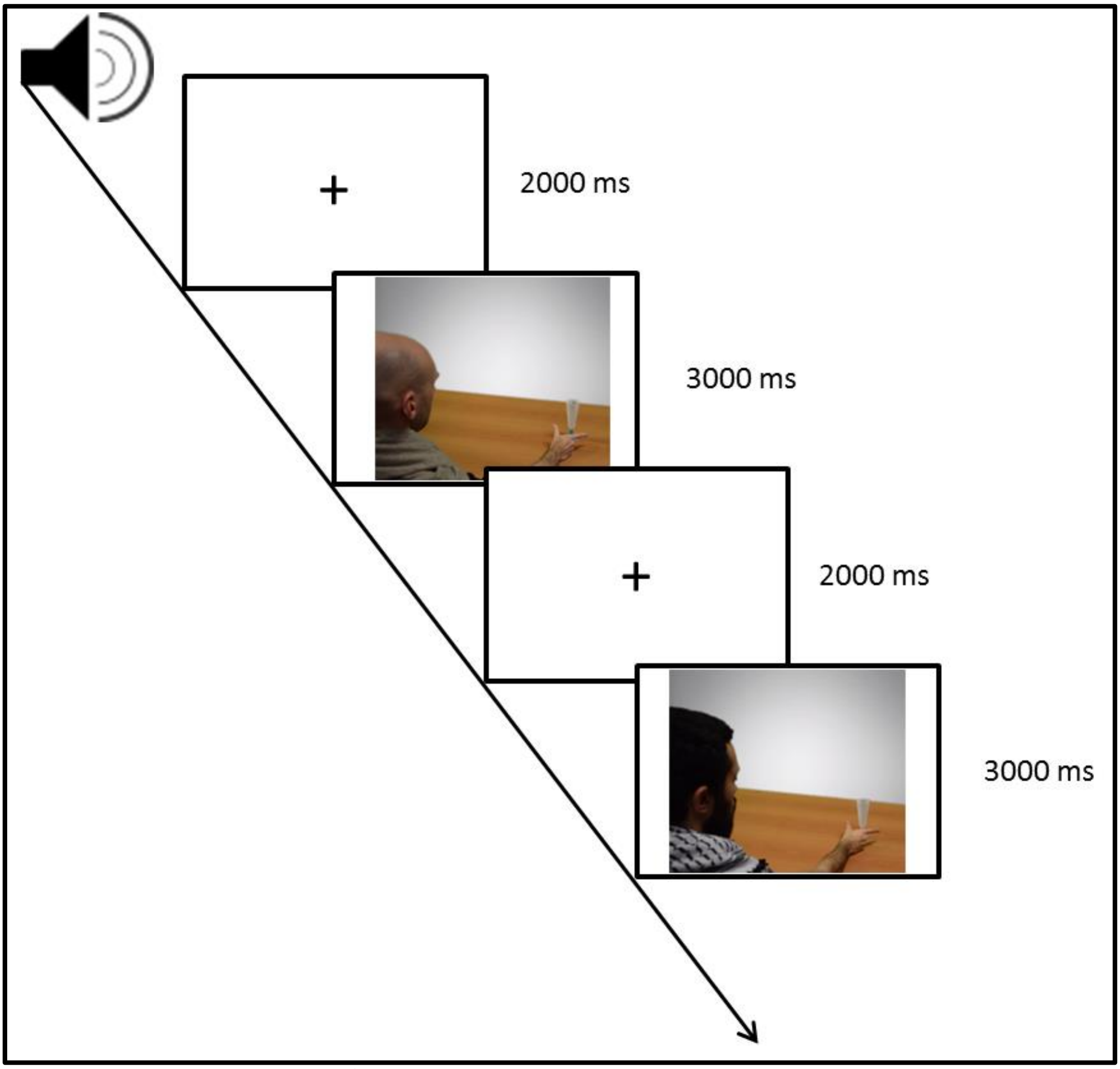

Fig. 1: Experimental timeline for the two actors

The experiment was divided in two blocks: one block elicited menace through the background sound of war, whereas the other one create a neutral setting with nature noises. We chose a block design, i.e. in one block videos picturing the two actors were randomly presented in a menace context and in the other they were presented in the neutral setting. This procedure was based on the evidence that participants implicitly connected threatening contextual cues to the negative stereotype of the outgroup and once this link is active it’s difficult to eliminate it. However, our dependent variable was constituted by MEPs which are shown to be affected by cumulative effects (Pellicciari et al., 2016), so we tried to found a compromise between this two conditions and counterbalanced the order of threat and neutral context across participants separating the two blocks by asking participants to play a dummy task, in order to switch the attention from the experiment to another job.

Each block was composed of 80 trials each, with a 2 minutes break after the first 40 trials.

To check that participants were paying attention to videos, 10% of trials were randomly followed by a slide asking participants to indicate the agent of the previous action.

Video presentation and TMS single pulse delivering were controlled by E-Prime 2 Software.

EMG Results

We excluded from analysis trials with EMG activity greater than 100 μV in the 100 ms before TMS thus avoiding MEPs contamination by background activity and MEPs smaller than 100 μV or with a latency inferior to 5 ms (Sartori et al., 2013). We chose to use a cut off of 100 μV to be more conservative compared to the cut off of 50 μV suggested by Sartori et al. (2013). Indeed in our previous experiments the intensity used usually gives an average amplitude around 1 mV (e.g. Pisoni et al., 2014).We measured off-line the peak-to-peak MEPs amplitude and for each block outlier trials (±2 SD from the individual mean value) were removed from subsequent analysis. With this procedure we discharged the 3.8% of MEPs. Remaining MEPs were normalized using the natural logarithm.

First a linear mixed model analysis was run to analyze MEPs differences in the three experimental conditions. *Condition* (3 levels: baseline, neutral context, threatening context) and *muscle* (2 levels: FDI, ADM) were entered as fixed factors, while subject intercepts was entered as random factor.

The main effect of condition was significant F(2,7178)= 33.3, p<.001, post-hoc comparisons with Bonferroni correction highlighted lower MEPs in the baseline as compared to both the threatening and the neutral context (p<.001 and p=.017, respectively) and in the neutral as compared to the threatening one (p<.001). See Fig. 2 for results.

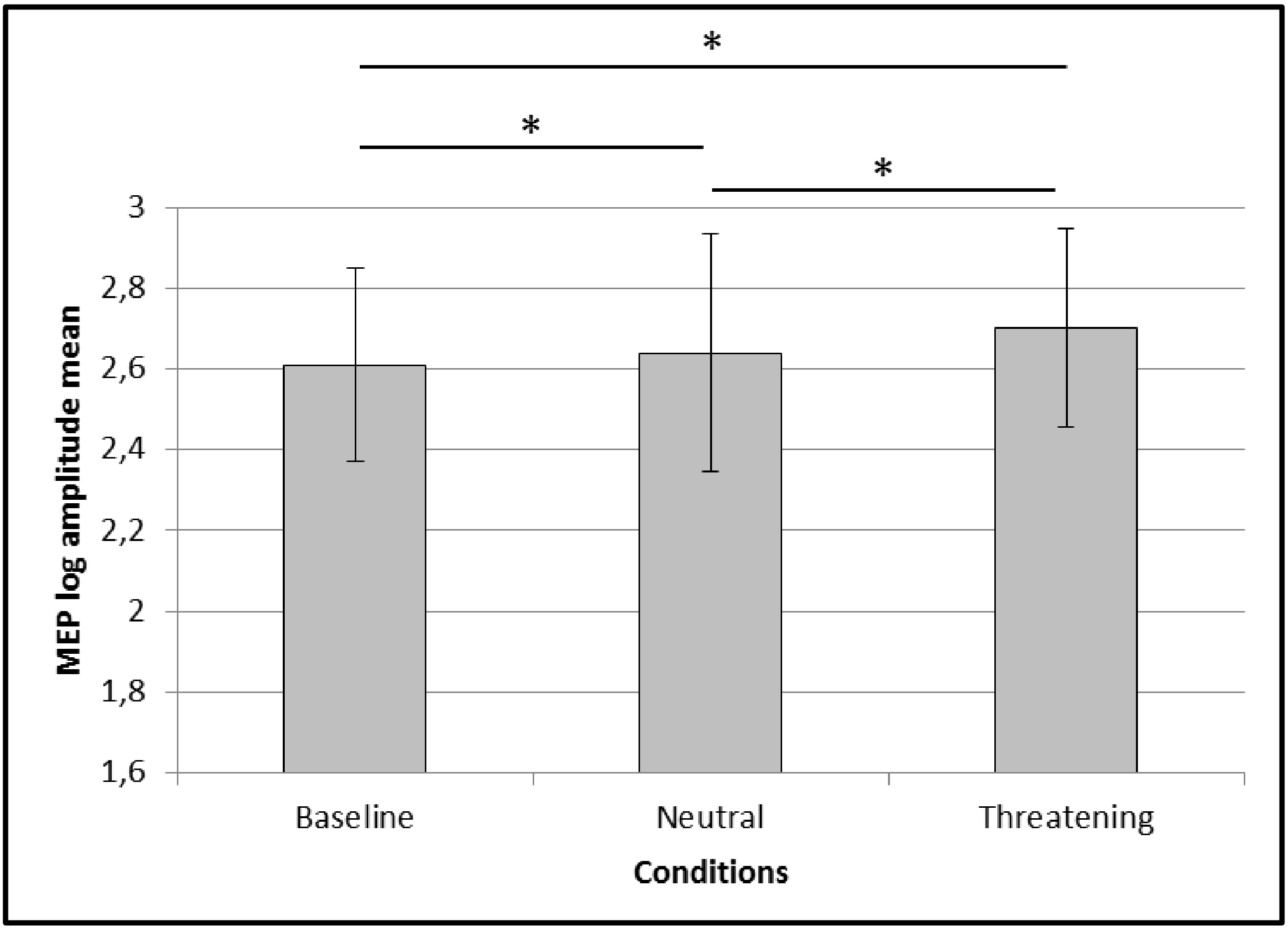

Fig 2. MEP log-amplitude mean for condition (Baseline, Neutral, Threatening). Error bars represent +/- MSE. Asterisks indicate significant differences at p < .05.

The main effect of muscle was significant F(1,7178)= 3207.7, p<.001: MEPs amplitude was higher for FDI as compared to ADM muscle.

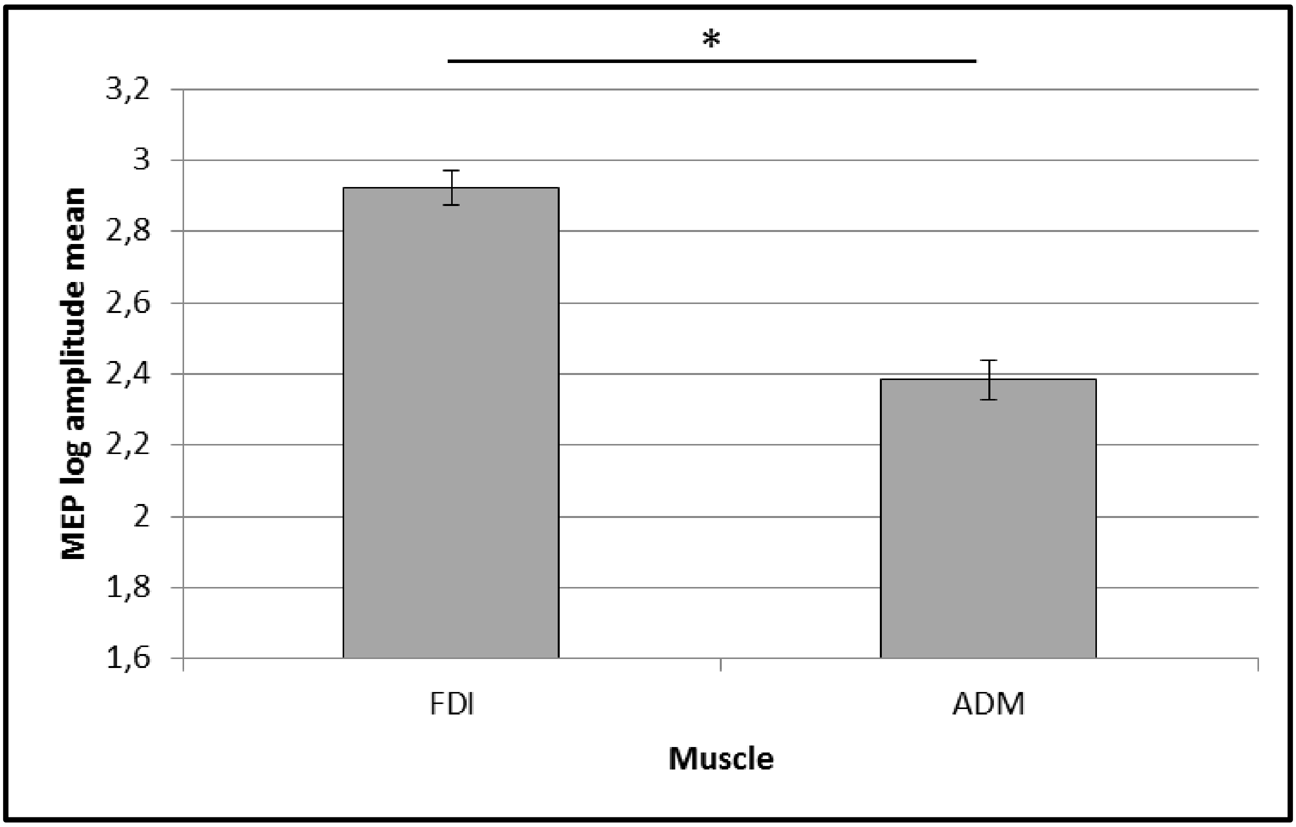

Fig 3. MEP log-amplitude mean for each muscle (FDI, ADM). Error bars represent +/- MSE. Asterisks indicate significant differences at p < .05.

The interaction between condition and muscle was significant (2,7178)=42.8, p<.001: for FDI muscle MEPs were higher in the two experimental conditions as compared to the baseline (p<.001), but they did not differ between them (p=.218). For ADM muscle MEPs were smaller in the neutral context as compared to the baseline and to the threatening context (p=.011 and p<.001 respectively) and showed a facilitatory effect in the threatening condition as compared to the baseline and to the neutral context (p<.001). See Fig. 4 for results.

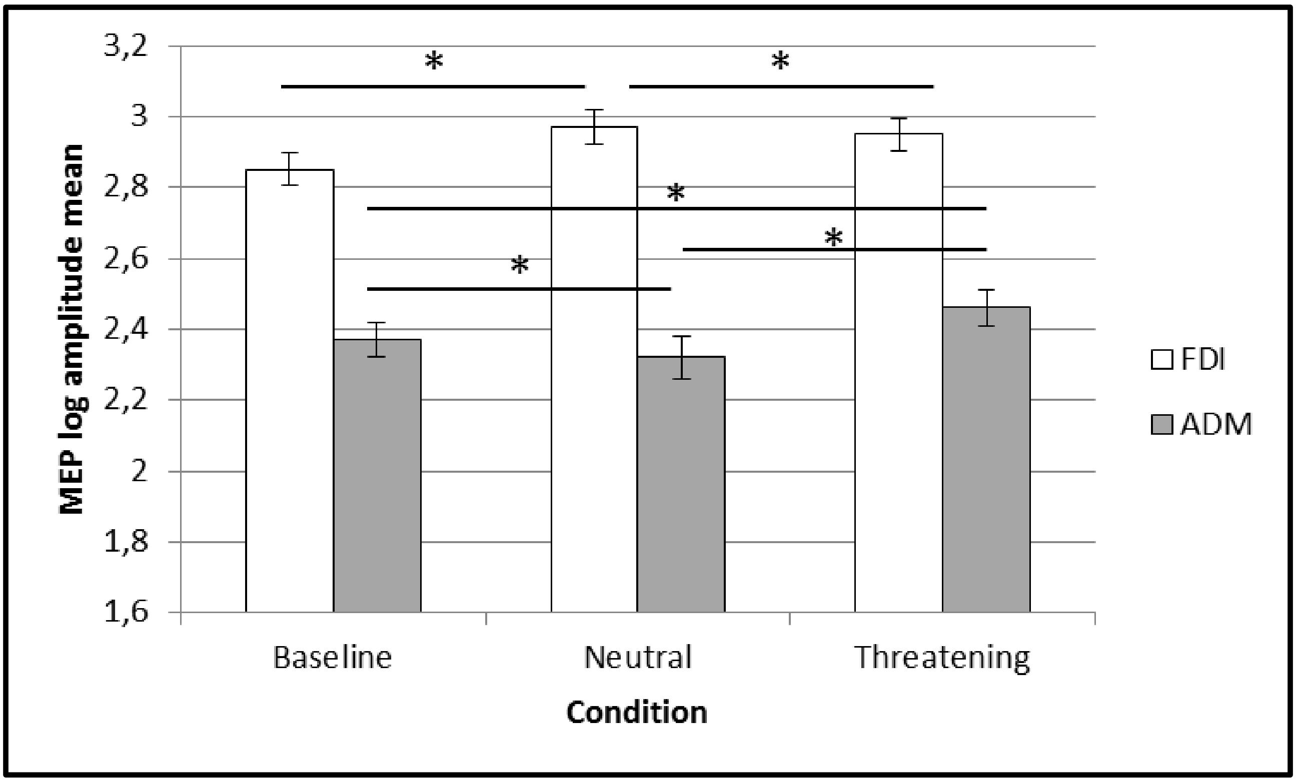

Fig 4. MEP log-amplitude mean for each condition (Baseline, Neutral, Threatening) and each muscle (FDI, ADM). Error bars represent +/- MSE. Asterisks indicate significant differences at p < .05.

We then run a linear mixed model to analyze the effect on MEPs amplitude of the within subjects factors Membership (2 levels: Ingroup vs Outgroup), Context (2 levels: Threat vs Neutral) and Muscle (2 levels: FDI vs ADM) with subject intercept as random factor.

The main effect of Context was significant F(1,5774) = 35.4, p<.001, with higher MEPs in the threatening condition (see Fig. 5 for results).

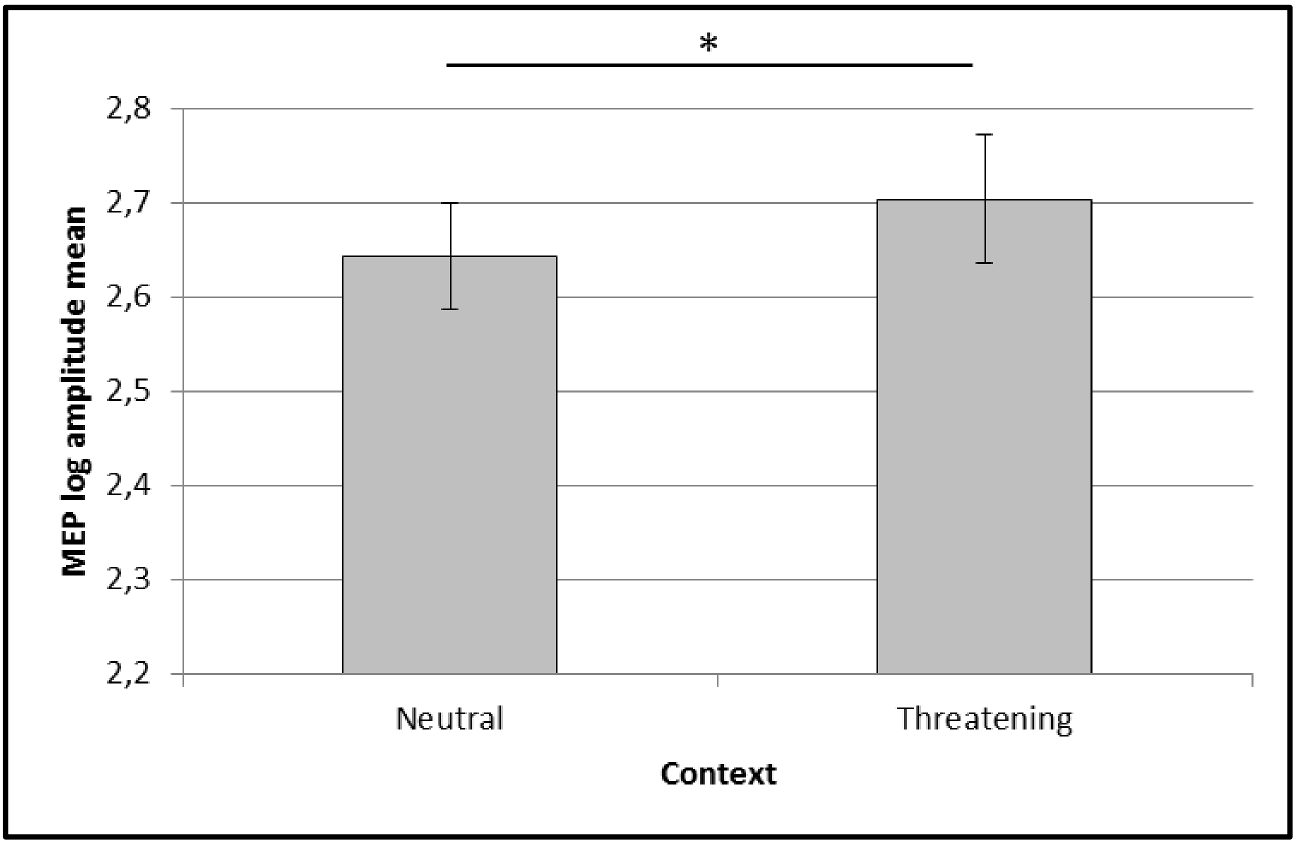

Fig 5. MEP log-amplitude mean for each Context (Neutral, Threatening). Error bars represent +/- MSE. Asterisks indicate significant differences at $p < .05$.

The main effect of Muscle was significant F(1,5774) = 3238.1, p<.001, MEPs were higher for FDI as compared to ADM muscle.

The main effect of Membership was not significant F(1,5774) = 2.5, p=.115.

The interaction between Context and Muscle was significant F(1,5774) = 72.1, p<.001: for FDI muscle there was a trend for higher MEPs in the neutral as compared to the threatening context (p=.072), while for ADM MEPs were significantly higher in the threatening as compared to the neutral condition (p<.001). See Fig. 6 for results.

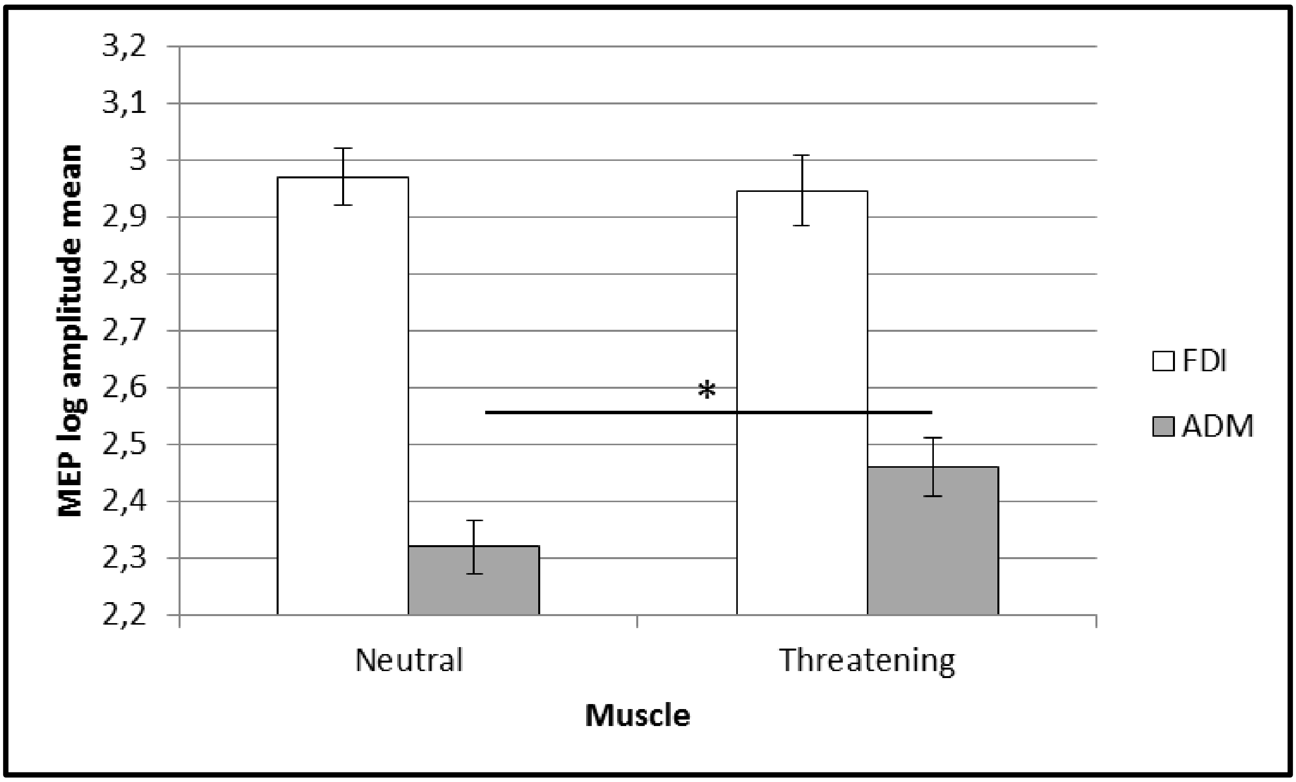

Fig 6. MEP log-amplitude mean for each Context (Neutral, Threatening) and each muscle (FDI, ADM). Error bars represent +/- MSE. Asterisks indicate significant differences at $p < .05$.

The interaction between Context and Membership showed a trend toward significance F(1,5774) = 3.5, p=.062; exploratory post-hoc analysis with Bonferroni correction highlighted that in the threatening condition, namely when MEPs were higher, no differences between ingroup and outgroup were present (p=.837) while for the neutral condition MEPs were higher for the outgroup as compared to the ingroup (p=.015). See Fig. 7 for results.

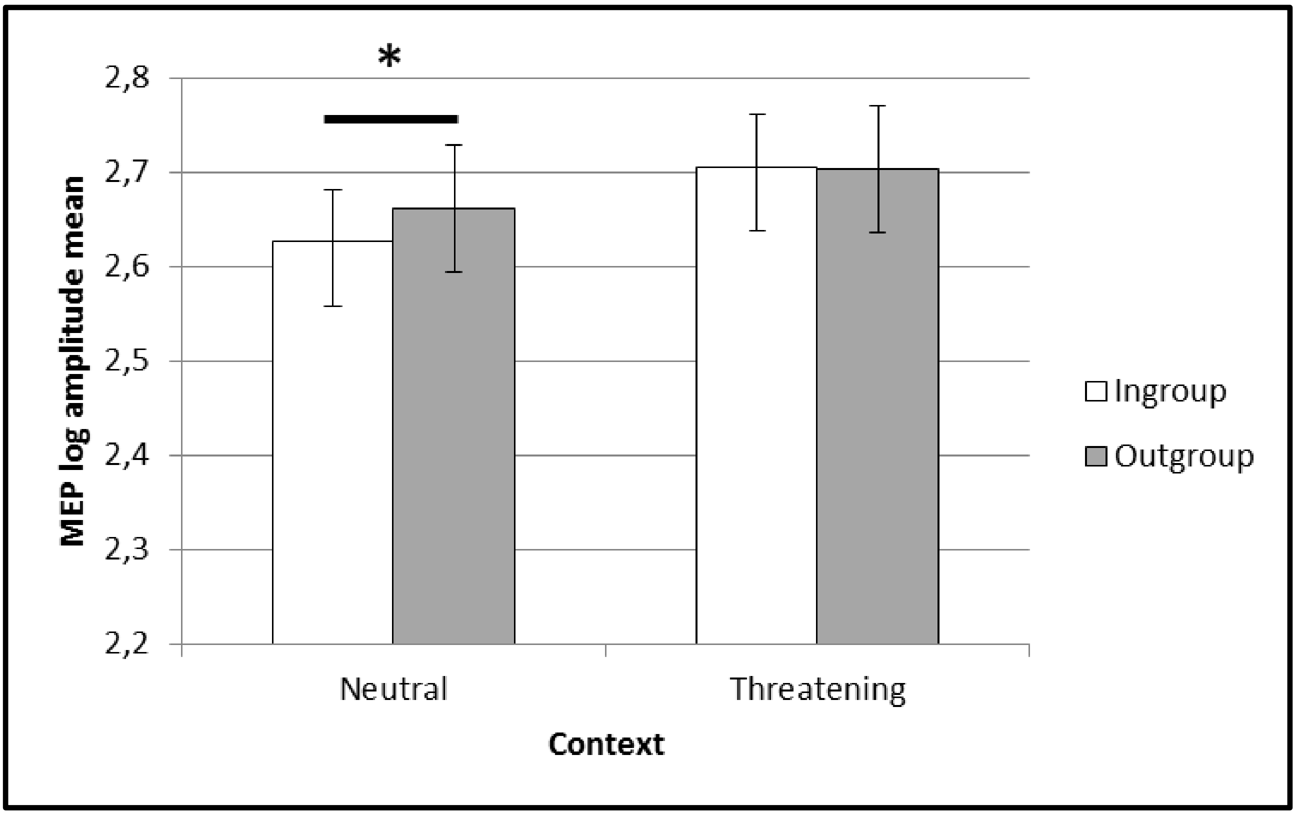

Fig 7. MEP log-amplitude mean for each Context (Neutral, Threatening) and each groups (FDI, ADM). Error bars represent +/- MSE. Asterisks indicate significant differences at p < .05.

The interaction between Membership and Muscle and the three-way interaction among Context, Membership and Muscle were not significant (*ps>.222*).

3.2.3 Discussion

In the present study we aimed at investigating whether contextual cues, such as surrounding sounds, are able to trigger social menace in the perception of an outgroup member, thus in turn modulating corticospinal excitability.

Our specific hypothesis was that threatening context caused an inhibitory effect on corticospinal excitability and that this pattern resulted amplified when action's agent was a member of the outgroup.

In order to investigate this hypothesis 19 neurologically unimpaired students of Milano-Bicocca University were enrolled in the study, in which video depicting a member of the ingroup (Caucasic actor) or of outgroup (Arabian actor) in the act of grasping a neutral object were showed in a threatening vs neutral setting. In order to activate and maintain threat perception the experiment was divided in two blocks, one with war sounds and the other one with neutral sounds, while videos picturing the two actors were randomly presented in each block.

TMS pulses were delivered over left M1 and MEPs were recorded from the right FDI and ADM muscles.

Preliminary analysis aimed at comparing corticospinal excitability during the baseline condition, in which participants were asked to watch a fixation cross in the center of the screen, to the two experimental conditions, in which actors were grasping the object.

In line with previous studies (e.g. Pisoni et al., 2014; see Naish et al., 2014 for a review) we found smaller MEPs during the baseline as compared to the two experimental conditions. Surprisingly, however, this first analysis highlighted higher MEPs during the threatening as compared to the neutral condition.

In the comparison between the two muscles, MEPs were higher for FDI as compared to ADM, thus reflecting a muscle-specific effect induced by the precision movement observed (e.g. Fadiga et al., 1995)

Moreover, the interaction between condition and muscle was significant: for FDI MEPs were higher in the two experimental conditions as compared to the baseline with no difference between the threatening vs neutral context; at the opposite for ADM MEPs were higher in the threatening as compared to the baseline and the neutral context, and in the baseline as compared to the neutral context.

These pattern of results allowed us to think that two different processes were involved: on one hand FDI seemed to reflect the motor resonance effect due to the observation of a grasping movement, indeed a motor facilitation was found on both contexts involving an action observation, regardless of emotional valence (i.e. the facilitation was found also in the neutral condition); on the other one, ADM activity suggested a more general arousal effect due to context manipulation, since the only condition showing an increased excitability was the threatening one. Moreover, for ADM, MEPs were even smaller in the neutral condition compared to the baseline, further confirming the non-involvement of this muscle in the observed grasping action.

Then we run the main analysis of the experiment, thus eliminating the baseline condition and comparing the two experimental contexts (threatening vs neutral) to the actor's membership (ingroup vs outgroup) and the two muscles (FDI vs ADM).

As expected, the main effect of muscle was significant, with higher MEPs for FDI as compared to ADM.

The main effect of context was also significant, with higher MEPs in the threatening as compared to the neutral condition. As highlighted by the significant interaction between context and muscle, however, the effect of context was different on FDI and ADM: for FDI a trend was found in the expected direction, that is lower MEPs in the threatening as compared to the neutral context, while for ADM muscle the effect was in the opposite direction, that is higher MEPs in the threatening condition compared to the neutral one, thus corroborating our idea that the results were reflecting two different processes.

On the one hand, FDI showed a trend toward our predicted pattern, more similar to the one described in literature, i.e. smaller MEPs during the presentation of threatening/painful stimuli (Furubayashi et al., 2000; Cantello et al., 2000; Makin et al., 2009; Avenanti et al., 2005).

At the opposite ADM seems to reflect a more general arousal-driven excitability increment, due the threatening context, which might initiate a *"fight or flight"* reaction.

Crucially the interaction between context and membership was significant: in the threatening context MEPs were not different when the agent was a member of the ingroup or of the outgroup. Therefore in the case of threatening condition sounds elicited menace regardless of the agent's membership. Conversely, in the neutral context when the agent was a member of the outgroup MEPs were higher as compared to ingroup condition. Previous studies on the effect of emotional stimuli on corticospinal excitability showed contrasting results, sometimes showing a reduction of excitability for happy and fearful emotional bodies (Borgomaneri et al., 2015), in some case recording higher MEPs during emotional (positive or negative) vs neutral stimuli (Hajcak et al., 2007), while in other studies higher MEPs were found only during negative stimuli presentation, such as fearful vs happy or neutral facial expression (Shutter et al., 2008). In this latter case and consistently with our present data, the increased corticospinal excitability in the threatening condition could be interpreted as an increased arousal induced by stimuli negatively connotated (Öhman, 1986; Davis & Whalen, 2001). Following this explanation, higher MEPs in the neutral-outgroup condition highlight that also in the neutral context participants perceived the member of the outgroup as potentially more threatening.

4. Human neuron mirror system: our contribute to the debate

In our everyday life actions are not something abstract and isolated, but they are always embedded in a context which help us extracting their meaning in a proper way.

Traditionally motor resonance has been considered as an automatic response triggered by an observed action that elicited in the onlooker's motor system the activation of the same motor regions (Fadiga et al., 2005). Indeed, motor resonance was thought to be influenced only from low-level intrinsic observed action's features, such as the muscle involved (Alaerts et al., 2009; Gangitano et al., 2001, 2004; Valchev et al., 2015), time-locking sequence (Alaerts et al., 2012) and kinematics (Borroni et al., 2011).

If this was the case, however, motor resonance should not be affected by non-motor connected features, such as intentions, goals and contexts. Recent studies, and ours among them, suggest instead that motor resonance is strongly influenced by other variables and modulated in a top-down way.

In a series of studies, Sartori and colleagues (2011; 2012) suggested for example that observing a same action increases MEPs size when it suggested the complementary movement in the onlooker. Bucchioni and colleagues (2013) showed that the mere presence of a social context is able to facilitate corticospinal excitability, even when two kinematically identical actions are observed.

Recently Amoruso and Urgesi (2016) showed that context is crucial not only for predicting intentions and goals, but it also plays a role in affecting lower-level information, thus influencing corticospinal excitability also during kinematics and muscular activity coding. In their study, authors showed participants actions which could be embedded in different scenarios, namely congruent, incongruent and ambiguous. During the experiment videos were stopped before ending and participant should give their prediction. Corticospinal excitability decreased during the incongruent condition compared to congruent and ambiguous ones and this reduction correlated with an impairment in the ability to correctly predict action outcomes.

As different authors pointed out (Fadiga et al., 2005; Naish et al., 2014; Bestmann & Krakauer, 2015), MEPs are usually considered an output measure of corticospinal activity, however the modulation of this index could be influenced also in other ways.

In their review Fadiga et al., (2005) discussed about the possibility that action observation induces MEPs modulation by-passing M1 and activating descending volleys and thus motoneurouns through a parallel route, for example from the premotor cortex passing through the brainstem. This hypothesis, however, was rejected in the same review citing a work of Strafella & Paus (2000) in which action observation reduced intracortical processes (in terms of facilitation and inhibition).

Another compelling hypothesis suggests that MEP size is influenced by processes occurring outside M1 through excitatory or inhibitory cortico-cortical connections directly or indirectly linked to M1.

Some evidence supporting this idea comes from paired-pulse TMS studies (e.g. Koch et al., 2006, 2008), in which typically a first conditioning stimulus is delivered over a distal cortical region and its influence on MEPs amplitude is assessed by a second pulse, delivered some milliseconds later over M1. This procedure showed, for example, that delivering a conditioning pulse over the prefrontal motor cortex (ventral or dorsal) is able to elicit higher MEPs during action observation (Catmur et al., 2011).

Following this reasoning, during action observation different brain areas involved in the HMs could influence in a top-down way corticospinal excitability. In this direction recent studies drove attention on the role of the inferior frontal cortex in predicting actions (Avenanti et al., 2017): anodal tDCS over this region increased performance in an action prediction task, while cathodal showed an impairment in the same task.

In their recent review, Naish and colleagues (2014) suggested the existence of a two-stage model of corticospinal excitability during action observation, characterized by an early activation of the motor system based on low-level processing of the stimulus. This earlier phase is automatic and is not muscle-specific and could be activated as soon as the visual motion associated with an action is perceived (around 80-100 ms). The later phase of modulation, from 200 ms onwards is instead muscle-specific and sensible to the higher-level cognitive variables.

In our studies we controlled for action's low-level parameters: in the experimental conditions the precision grip was always the same, the object grasped was kept constant, as well as kinematics and timing. However, corticospinal excitability was influenced by other variables, such as action meaning (Neuroeconomics, Study 1), motivational context of onlooker's (Neuroeconomics, Study 2), contextual manipulation (Social threat).

Although we interpreted our results in the light of HMs theory, we want to highlight that it is not the only possible explanation about our findings. Indeed whenconsidering MEPs measurement, an important issue is that changes in corticospinal excitability does not give us information about which brain regions are involved in this modulation. M1 is connected with a large number of non-motor areas, hence a change in its excitability could be generate in each of these regions. We cannot be sure that changes in motor-spinal excitability are induced by the activation of different regions as compared to the ones involved in HMs which influence M1 through cortico-cortical connections.

Studies aiming at investigating brain connectivity with other techniques, such as TMS-EEG could further address this issue.

Studies aiming at investigating brain connectivity with other techniques, such as TMS-EEG could further address this issue.

The integrated system of TMS-EEG allows indeed a direct measurement of the excitability of any cortical area (beyond primary motor or visual area) by directly perturbing the cortical activity, by means of TMS, and recording with the EEG the cortical response to this perturbation with a high temporal resolution (Taylor et al., 2008), computed as TMS-Evoked Potentials (TEPs). Moreover, continuous high definition EEG recording permits to track how activation spreads from the stimulated area to interconnected ones, thus allowing a direct measure of effective connectivity. TEPs are considered a reliable measure of brain activation state (Miniussi and Thut, 2010); beside, as long as the same parameters across sessions are maintained, the reliability of the technique has been probed (Casarotto et al., 2010) allowing to link any observed changes in TEPs to the experimental condition. Therefore, applying TMS over M1 and using EEG on top of EMG, during action observation including contextual manipulation, would allow to answer to the previous question and this is the line of research the lab will pursue as future development of the present studies. Compared to MEPs, TEPs will directly tap M1 cortical excitability; moreover, comparing TEPs across conditions on target brain areas (e.g. inferior frontal cortex) will allow to explore which cortico-cortical connections plays a role in the observed results.

5 The use of MEPs in embodied cognition

5.1 Introduction

Forty years ago, in his ecological approach to vision, Gibson (1977, 1979) first introduced the concept of affordance, referring to the idea that the visual perception of an object automatically generates a set of possible actions we can perform on and with it. Affordances are automatically triggered by object's sight even if there is not an explicit intention to interact with it and are limited by the observer's action abilities and possibilities.

Animals (Murata et al., 1997), behavioural (Tucker & Ellis, 2001, 2004) and neuroimaging (Grafton et al., 1997; Grèzes et al., 2003; Chao & Martin, 2000) studies consistently suggested that the dorsal stream might constitute the neural underpinning for Gibson's affordance concept, transforming visual object's information, such as size and orientation, into the appropriate hand shape necessary to grasp it (Jeannerod et al., 1995).

Neurophysiological studies on corticospinal excitability gave their contribution to the debate highlighting that object presentation elicited higher MEPs as compared to a non-object condition (Franca et al., 2012) and that object's features such as ease-of-grasp (Cardellicchio et al., 2011; Buccino et al., 2009) and structural properties such as intact handles (Buccino et al., 2009) are able to influence MEPs amplitude.

Another important variable able to affect motor excitability is the object's location in the space: Cardellicchio and colleagues (2011), for example, showed that when a virtual object is presented in the near – reachable space MEPs are higher as compared when the same object is in the far – unreachable space.

A concept involved in the refinement of what belongs to peripersonal space is body schema, defined as a multimodal brain representation that constantly integrates multisensory (proprioception, somatosensory, visual, auditory) information about the body (Berlucchi & Aglioti, 1997; Head & Holmes, 1911; Holmes & Spence, 2004; Maravita & Iriki, 2004).

Body schema is a plastic concept and can be updated after permanent changes due to surgery (e.g. Di Russo et al., 2006) or by manipulating artificial tools (Maravita & Iriki, 2004; Pazzaglia et al., 2013).

Recent studies in social psychology (e.g. Duguid & Goncalo, 2012) suggested that the psychological experience of power also affects individuals' subjective sense of height: when people felt powerful they perceived themselves as taller.

However, no work tested whether change of self-perception due to the experience of power are induced by traceable modification of own body schema.

We reasoned that the corticospinal modulation induced by object's position could be used to trace whether power experience affects own body schema. More specifically, if in a powerful condition people expand their body schema boundaries by overestimating own height, this in turn would affect the surrounding space perception along the vertical axis, such to encode objects presented in the closest portion of extrapersonal space as being nearer, thus falling within the peripersonal space. MEPs could be used then to investigate the presence of an unconscious remapping of the external space after power manipulation by using motor facilitation properties. Building on this, in the present study we manipulated participants' power experience and measured the MEPs induced by the vision of a graspable object, such as a pencil sharpener, presented at different positions along the vertical axis, both in the peripersonal and extrapersonal space.

More specifically, participants' experienced power was manipulated by random assigning them to three conditions and asking them to recall a specific event in which they experienced i) high power; ii) low power; iii) positive feelings without any connection to power (control condition).

The object’s distance was manipulated by placing the pencil sharpener at 5 different positions in the vertical space: two in the peripersonal space, two in the extrapersonal space, plus a midline condition. We expected that in powerful condition participants’ MEP induced positioning the pencil sharpener in the extrapersonal space would be comparable to those induced in the peripersonal space.

Traditionally, studies manipulating object’s location in the space considered only the horizontal axis (Rossetti et al., 2015), while only few recent studies that tested object presentation along the vertical axis (De Paepe et al., 2017; Azañón et al., 2016; Rossetti et al., 2015).

Therefore, in order to have a baseline of corticospinal modulation in the vertical space we ran a control study in which we tested the same object positions on both the horizontal and vertical axis, without any power manipulation.

5.2 Study 1: Power in the brain

5.2.1. Background: Peripersonal and extrapersonal space

In everyday life, we perceive the external world as a unified and indivisible whole.

Despite our own experience, evidence from studies on both animals and humans unveiled the existence of different space representations. One of the most studied space representation regards the distinction the brain makes between the so called peripersonal and extrapersonal spaces. From an evolutionary point of view, this distinction is crucial to discriminate which stimuli are potentially threatening for own survival (Hediger, 1955; Dosey & Meisels, 1969) and body integrity (Graziano and Cooke, 2006).

Most of researches focused on peripersonal space, defined as the space immediately surrounding our body, within which we can reach and manipulate objects; it is a multisensory-motor interface between our body and the external world, where external stimuli coded by our senses are integrated with online proprioceptive and kinesthetic information about our body parts (Graziano et al., 1994; Makin et al., 2007; Serino et al., 2011).

Recently, it has been suggested a dual-model to account for peripersonal space abilities and properties: De Vignemont & Iannetti (2015) suggested a functional distinction between bodily protection and goal-directed action, which require different sensory and motor processes.

Extrapersonal space is not such a well-defined and studied concept, it starts where peripersonal space finishes and is conceived as the space in which objects are unreachable unless moving towards them (Rizzolatti et al., 1983; Coello et al., 2008).

First evidence of a double dissociation between peri and extrapersonal space in humans comes from neuropsychological studies with patients affected by neglect: some participants showed behavioural patterns indicating that neglect was restricted to the near - peripersonal space vs cases with a specific deficit to code for the far – extrapersonal space (see Lavadas, 2002 for a review).

This double dissociation was further confirmed by neuroimaging (Weiss et al., 2000, 2003), neurostimulation (Bjoertomt et al., 2002; Lane et al., 2013), and electrophysiological (Valdés-Conroy et al., 2014) studies on healthy participants, suggesting that whereas performing tasks in the near space involves the dorsal visual system, when tasks were completed in the far space the ventral system is involved instead.

A growing body of evidence suggest that peripersonal space can be considered as a dynamic and flexible concept (e.g. Clery et al., 2015) with boundaries that can be influenced by manipulating sensory-motor functions and abilities, such as experiencing tool use (Berti & Frassinetti, 2000; Farné & Làvadas, 2000; Holmes, 2012; Maravita & Iriki, 2004; Longo & Lourenco, 2006) or precluding/altering participants possibility to act, for example asking participants to carry wrist weights (Lourenco & Longo, 2009) or a heavy backpack (Proffitt et al., 2003). Similar results were obtained comparing peripersonal space perception with amputees wearing or not their prosthetic limb (Canzoneri et al., 2013) and with blind individuals handling or not their cane (Serino et al., 2007). Also body illusions and not only the direct manipulation of objects are able to influence space perception (Maister et al., 2015) even when the other body belongs to a non-human but to a virtual avatar (Noel et al., 2015).

Peripersonal space perception is also influenced by higher cognitive functions as object's ease of grasp (Linkenauger et al., 2009), object's affective valence (Coello et al., 2012; Valdés-Conroy et al., 2012), social context and interactions (Teneggi et al., 2013), individual goals (Brozzoli et al., 2010). Also participants features and traits such as age (Bloesch et al., 2013), pathology (Park et al., 2009) and claustrophobic fear (Hunley et al., 2017) are able to affect participants space representation.

Behavioural studies suggested that participants are faster in performing motor actions (such as grip movements) when objects are located in the peripersonal space (Costantini et al., 2010). Participants are also faster to discriminate if they can reach an object or not when it is presented in the peripersonal compared to the extrapersonal space (Valdés-Conroy et al., 2012).

Only few studies focused on the effects of object presentation in peripersonal and extrapersonal space on corticospinal excitability, as measured by MEPs. Franca et al. (2012) suggested that corticospinal excitability is modulated by the presentation of familiar and graspable objects (Franca et al., 2012), but only when TMS pulses were delivered 120 ms from object's presentation.

Cardellicchio and colleagues (2011) recorded MEPs during the virtual presentation of a graspable (mug) vs a non-graspable (cube) objects which could appear in peripersonal (30 cm) and extrapersonal (150 cm) horizontal space. MEPs were higher when the graspable object appeared in participants' peripersonal space, compared to the presentation of either a non-graspable object or of a graspable object in the extrapersonal space.

Traditionally, studies regarding space perception were conducted considering only the horizontal axis (Rossetti et al., 2015). For instance, effects of tool use in peripersonal space representation were investigated only on the horizontal plan.

Only few recent studies manipulated object presentation also along the vertical axis, but with different aims and specific hypothesis.

In Rossetti et al. (2015), for instance, Skin Conductance Response (SCR) was recorded in order to investigate the autonomic response to painful stimuli in the peripersonal space and test the possibility to trace its plastic changes (i.e. after tool use) by using this physiologic and automatic measure. Authors showed that pain anticipatory responses were significantly lower when threatening stimuli were presented far from the hand: SCR was higher when the needle actually touched the hand, but it was also higher for the positions immediately near to the hand compared to the far distance. Of interest for the purposes of tour study was that an overall greater response was found when stimuli were delivered along the vertical axis. Regarding this latter effect, the author argued that stimuli delivered along vertical axis were perceived as closer to the rest of the body and suggested that space representation might be different between horizontal and vertical space.

5.2.2 Power concept and manipulation

Power, that is the ability to act in an effective way in the environment and to influence people through resources control, has a strong transformative effect on relationships and cognitive functions (Fiske, 1993; French et al., 1959; Keltner et al., 2003; Magee & Galinsky, 2008). Indeed, power can affect our thoughts, feelings and behaviours by leading to higher perceived control over social events (Fast & Cheng., 2009) and enhancing executive functioning (Smith et al., 2008). Behavioural studies also suggested that experiencing power promotes action, risk taking, and competitive interpersonal exchange (Anderson & Galinsky, 2006; Galinsky et al., 2003; Magee et al., 2007).

Our everyday language is full of words referring to size and height for describing power relationships (e.g., “at the top of the ladder”; "Royal Highness") and such metaphors influence both physical experience and the visual perceptual system (Duguid & Goncalo, 2012; Schubert, 2005; Yap et al., 2013). Research on embodied cognition also suggested that linguistic metaphors are not simply communication devices, but instead represent abstract concepts grounded in sensorimotor experience, or with other words, thinking about abstract concepts implies the activation and the simulation of the sensations and perceptions relevant to metaphor (Barsalou, 2008; Semin & Smith, 2002; Williams & Bargh, 2008; see also Jostmann et al., 2009).

In line with this evidence, recent research focused on the symbolic link between power and space representation (Chiao et al., 2009; Chiao et al., 2010) and specifically to the idea that verticality is used when encoding concepts associated to power. For example, Schubert (2005) suggested that we are quicker to identify powerful groups when they are described as higher, rather than lower, than other groups. In the same way, Giessner & Schubert (2007) showed that leaders are judged to be more powerful with a longer vertical line compared to a shorter one. Power experience causes a misperception of the social targets physical size (Yap et al., 2013): indeed, powerful individuals are likely to underestimate other’s height, while powerless overestimate it. Duguid & Goncalo (2012) showed that the psychological experience of power also affects individuals’ subjective sense of height: when people felt powerful they perceived themselves as taller.

Although these studies revealed that at the behavioural level the psychological experience of power influence individuals’ subjective sense of height, the neurophysiological counterpart of this phenomenon has not been addressed so far and no prior studies have tested whether changes of self-perception due to experiencing power might be the consequences of traceable modifications of own body schema.

The present research aimed to extend prior behavioural studies on the psychological experience of power into the domain of perceptual experience, exploring whether feeling powerful lead people to modify own body schema and thus the surrounding space perception. If feeling powerful leads to a modification of own body schema by overestimating own height, this change should in turn influence the representation of the surrounding space, by slightly modifying the boundaries of peripersonal space along the vertical axis. We then reasoned that corticospinal excitability modulation induced by an object presentation at different positions along the vertical axis could be a valuable way to trace and prove such change in body schema induced by power experience. In particular, we hypothesized that in condition of power experience, corticospinal modulation as measured by MEPs will show a remapping of the peripersonal space such to include also the nearer portion of the extrapersonal space. In other words, whereas in no power condition a difference in MEPs is expected between object presentation in the peripersonal and extrapersonal space (Cardellicchio et al. 2011), in high power condition this difference should be abolished or reduced.

5.2.3Methods

Participants

55 right-handed healthy students (18 male, Mage = 23.1, SD = ±2.5, mean laterality coefficient .81 ± 0.16). Participants completed the Adult Safety Screening Questionnaire (Keel et al., 2001) and gave informed written consent before to start with the experiment. We excluded participants with any contraindication for TMS (Rossi et al., 2009).

The study was approved by the local Ethics Committee (protocol number: 208) and was in accordance with the ethical standards of the revised Helsinki Declaration.

Power Manipulation

Emotional state was manipulated by randomly assigning participants to three experimental conditions and asking them to remember an event of their life (Galinsky et al., 2003; Lammers et al., 2017) varying for the specific content: high-power, low-power and control conditions.

To elicit high power experience we gave participants the following instruction:

"Please recall an episode of your life in which you felt powerful. Specifically, we ask you to think to an occasion in which you felt competent, to be able to influence others or events, or an episode in which you excelled or had taken a position of high status. Please describe the situation, the dynamic, as well as the emotions and the feelings you experienced on that occasion".

To elicit low power experience we gave participants the following instruction:

"Please recall an episode of your life in which you felt powerless. Specifically, we ask you to think to an occasion in which you felt incompetent, to be influenced by others or events, or an episode in which you felt weak and had taken a position of submission. Please describe the situation, the dynamic, as well as the emotions and feelings you experienced on that occasion".

In the control condition we tried to induce positive feelings without explicitly referring to power: indeed powerful feelings always elicit positive mood, so we aimed at disentangling the effect of power per se from that of positive mood in general.

To elicit positive feelings we gave participants the following instruction:

"Please recall an episode of your life in which you felt relaxed. Specifically, we ask you to think to an occasion in which you felt happiness, serenity, or an episode in which you felt at ease and peaceful. Please describe the situation, the dynamic, as well as the emotions and feelings you experienced on that occasion".

Manipulation of distance

Distance was manipulated by changing the position of a real pencil sharpener in the space. The pencil sharpener was chosen because it is a graspable and familiar tool and it was already used in Franca's et al. (2012) paradigm.

The pencil sharpener was hung over participants' head with a hook on the ceiling, using a transparent nylon wire.

The different heights at which the pencil sharpener could be suspended were obtained by fixing the other wire end to five different nails which were vertically distributed on the wall and were not visible to participants.

We established five different positions: two in the peripersonal space, where the pencil sharpener was easily graspable by participants by simply stretching their arms, two in the extrapersonal space, where the pencil sharpener was not reachable anymore.

By fastening the wire to one of the five nails, from the lower to the upper one, the pencil sharpener could be set at all the five different positions during the experimental session and each position has 5 cm of distance to the other one.

Before starting the experimental session, participants sat on a height-adjustable chair and the midline position of the pencil sharpener was established for each subject. the pencil sharpener was fixed at the nail in the mid position on the wall, and the chair's height was adjusted for each participants such to be the maximal distance at which they could grasp the pencil sharpener, by stretching completely their own arm, but holding the shoulder leaning against the back of the chair. With this procedure the midline distance was individually established in relation to the length of the subjects' arm and it delimited the area of the reachable space. It's worthy to note that this was the only pencil sharpener's position that the participants actually experimented as graspable (see Fig 1 for a graphical representation of our experimental setting).

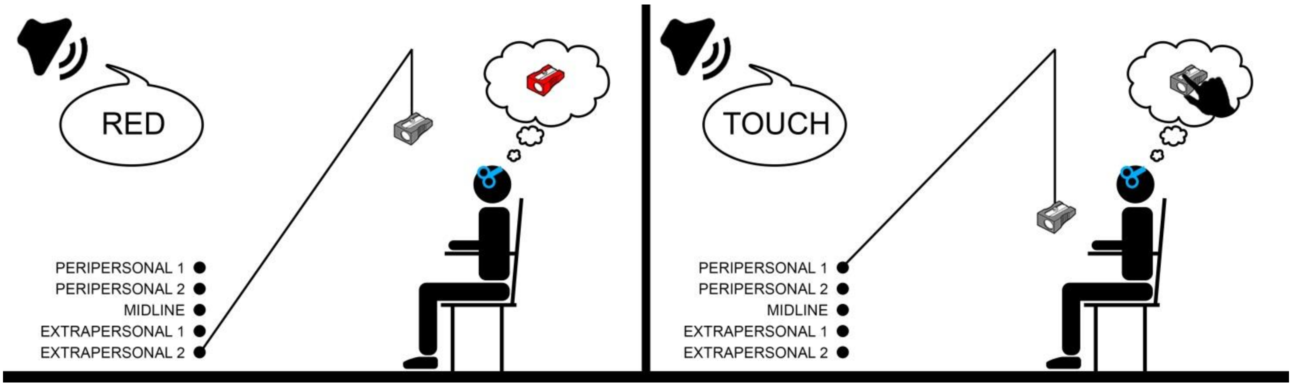

Fig 1 shows our experimental setting: in the example on the left participants heard the word "red" and had to imagine the hung pencil sharpener as red. In the picture on the right participants heard the word "touch" and had to imagine to touch it. Two different height are represented in the picture: on the left the object was placed in the furthest position (extrapersonal 2) on the right it was placed in the nearest one (peripersonal 1).

Experimental procedure

After the assessment of the midline position of the pencil sharpener, we placed the electrodes on the right hand. Specifically, we placed the active electrode on FDI muscle belly and the reference electrode over the metacarpo-phalangeal joint of the index finger, then TMS hotspot and motor threshold were assessed.

The entire experiment was composed by five different blocks of 40 trials each, for a total of 200 TMS delivered pulses. Each block corresponded to a different position of the pencil sharpener. The order of the positions along the experiment was randomly changed across participants.

During each trial participants heard one of ten randomized acoustic stimuli: five were motor verbs (rotate, use, draw, take, touch) five were related to perceptual features (blue, red, green, cold, hot). We asked to participants to observe the pencil sharpener and imagine each word related to it: for instance, if they heard the word “take” they had to imagine to grasp the object, if they heard the word “red” they had to imagine a red pencil sharpener. TMS pulses were randomly delivered at an interval of 150–300 ms from the acoustic stimulus and MEPs were recorded. This procedure was useful to be certain that participants were paying attention to the object at the moment of the stimulation. Moreover, we were interested in investigating whether perceptual vs motor words and imagination triggered differences in corticospinal excitability.

Between one block and the following one participant’s eyes were briefly covered so that the experimenter could change the pencil sharpener position.

Before to start with the first block we asked participants to remember and speak about the life event corresponding to the condition they were assigned to.

During the experiment, at the beginning of each session participants were asked to remember for a minute the episode they recalled at the beginning of the experiment, thus allowing us to keep their recalling salient.

To check the efficiency of our manipulation, at the end of the experiment participants were asked to indicate the extent to which they feel power on eight items (i.e., "I feel...influential", "powerful", "important", α=.94). Participants provided their answers on 7-point likert scales ranging from 1 (not at all) to 7 (extremely).

At the end of the experiment we asked participants to evaluate for each position if they could or could not grasp the object.

The auditory stimuli and the TMS stimulation were controlled by E-Prime 2 Software.

TMS and EMG recordings

TMS pulses were delivered using Eximia TMS stimulator (Nexstim™, Helsinki, Finland) using a focal bi-pulse figure-of-eight 70-mm coil in the optimal position described for the previous studies (Brasil-Neto et al., 1992; Mills et al., 1992). The coil was moved over left M1 and hotspot and motor threshold were individually assessed.

TMS pulses were then delivered at 110 % of motor threshold (Loporto et al., 2013) and MEPs were recorded from the right FDI muscle with the same procedure previously described (see *2.2.2 TMS and EMG recordings, page 19*).

We used the NBS Nextim neuronavigation system to monitor the coil-position during the experiment thus preventing any change in stimulation site due to small movements of participant's head during data collection (Sartori et al., 2013).

Results

Power Manipulation Check

We created a dependent variable labeled *power index* by averaging the eight items included in the manipulation check described at page XXand a one-way analysis of variance (ANOVA) was carried out using Condition (high power, low power, and control) as between subject factor. Condition's effect was significant F(2, 54)=12.9, p<.001, d=2.1; post-hoc analysis with Bonferroni correction indicated that participants in the high power condition reported significantly higher power feelings compared to both control (p=.04) and low power conditions (p<.001); in addition, participants assigned to the control condition experienced higher powerful sensations than subjects assigned to the low power one (p=.04).

Preliminary analyses

We excluded from analysis trials with EMG activity greater than 100 μV in the 100 ms before TMS thus avoiding MEPs contamination by background activity and MEPs smaller than 100 μV or with a latency inferior to 5 ms (Sartori et al., 2013). We measured off-line the peak-to-peak MEPs amplitude and for each block outlier trials (±2 SD from the individual mean value) were removed from subsequent analysis. With this procedure we discharged the 6.8% of MEPs. The remaining MEPs were normalized using natural logarithm.

Then for each participant we coded if the five pencil sharpener positions were perceived as subjective reachable or not reachable (in the following sections this variable will be labeled Perceived Distance).

EMG Results

A linear mixed model was run to analyze the effects on MEPs amplitude of the within subjects factors Distance (2 levels: reachable vs unreachable), Perceived Distance (2 levels: subjective reachable vs subjective not reachable) and Word (2 levels: motor vs. perceptual) and of the between subjects factor Condition (3 levels: high power, low power, control) with subject intercept as random factor and controlling for the experienced power.

Statistical analyses were performed by using SPSS 24 and post-hoc interactions were tested with Bonferroni correction.

The main effect of Word (p = .97) and its interaction with the other three factors (ps > .59) were not significant, so we collapsed data across this factor.

The main effect of Condition, F(2,50) = 1.97, p =.150, Distance, F(1, 9348) = 4.13, p =.305 and Perceived Distance, F(1,9230) = .010, p = .922 were not significant. Interestingly, results showed a significant interaction between Condition and Distance, F(2, 9349) = 3.89, p = .021: in the control (p=.021) and low power conditions (p=.025) MEPs amplitude was significantly higher when the object was located in the extrapersonal compared to the peripersonal space , whereas in the high power condition there was no difference between peri and extrapersonal object's position (p=.137). See Fig. 2 for the interaction results.

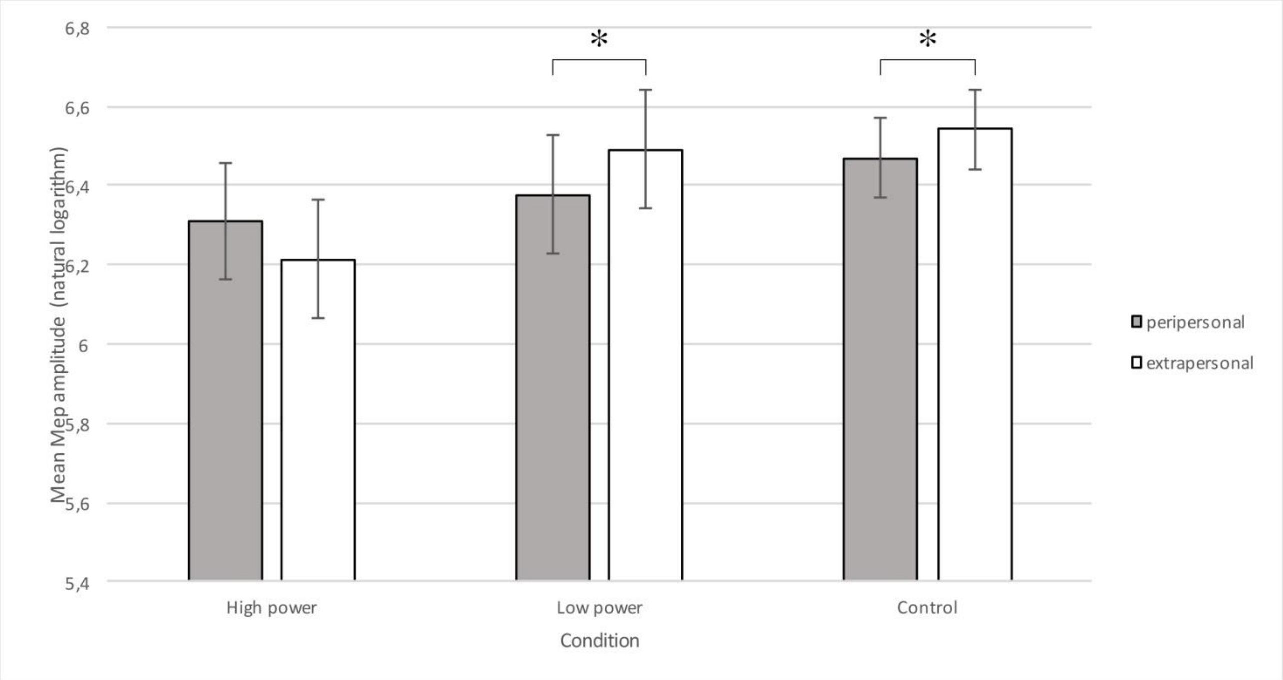

Fig. 2 shows MEP log-amplitude mean for peripersonal and extrapersonal space for the three experimental conditions (high power, low power, control). Error bars represent +/- SE. Asterisks indicate significant differences.

The interaction between Distance and Perceived Distance was significant, F(1,9349) = 14.9, p<.001: when the object was in the extrapersonal space MEPs were smaller if participants perceived it as reachable than when they perceived it as not reachable (p=.024). At the same time, when participants thought the object was unreachable, MEPs were higher if the object was actually in the extrapersonal space compared to the peripersonal one (p=.003). See Fig.3 for the interaction results.

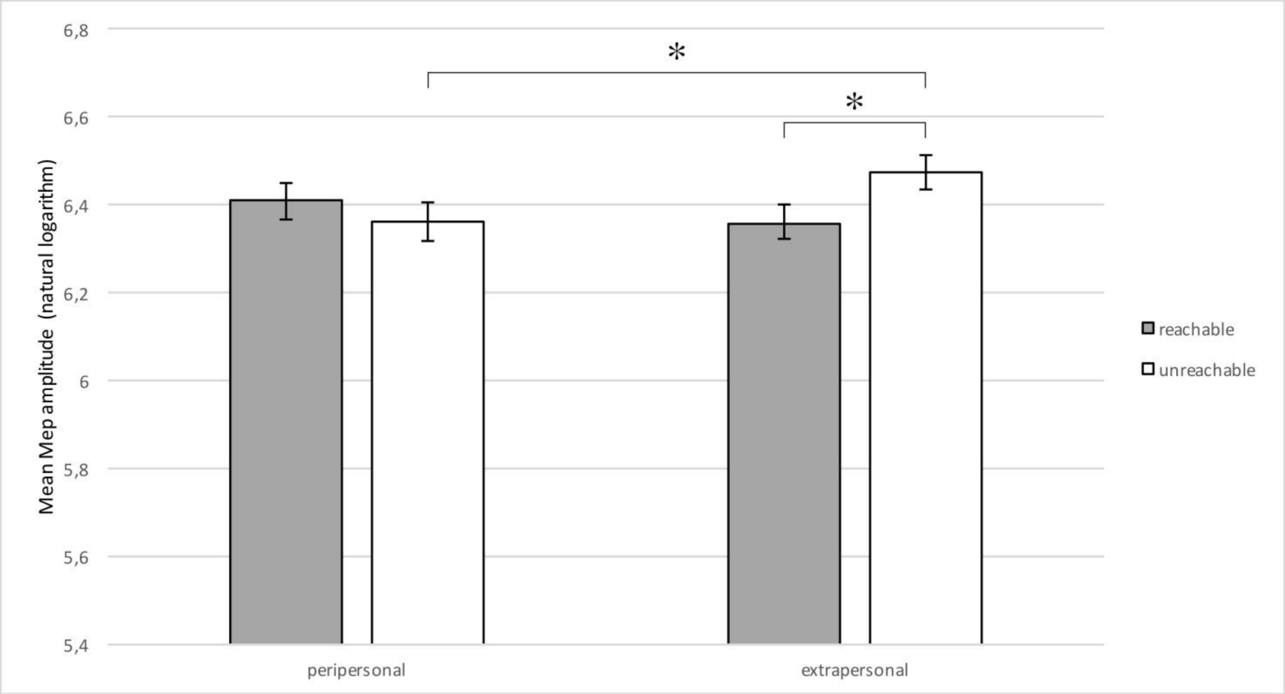

Figure 3 shows MEP log-amplitude mean for peripersonal and extrapersonal space for subjective reachable vs subjective unreachable heights. Error bars represent +/- SE. Asterisks indicate significant differences.

Results showed also a significant three-way interaction between Condition, Distance and Perceived Distance F(2, 9348) = 3.76, p=.023.

Only in the high power condition, when the pencil sharpener was in the extrapersonal space, MEPs were smaller when participants thought they were able to reach it compared to the condition in which they thought they were not able to do it (p=.006). In the control condition with the positive event, when the object was in the peripersonal space MEPs were smaller when participants thought they could not reach it compared to when they thought they were able to reach it (p=.031). See Fig. 4 for the three-way interaction results

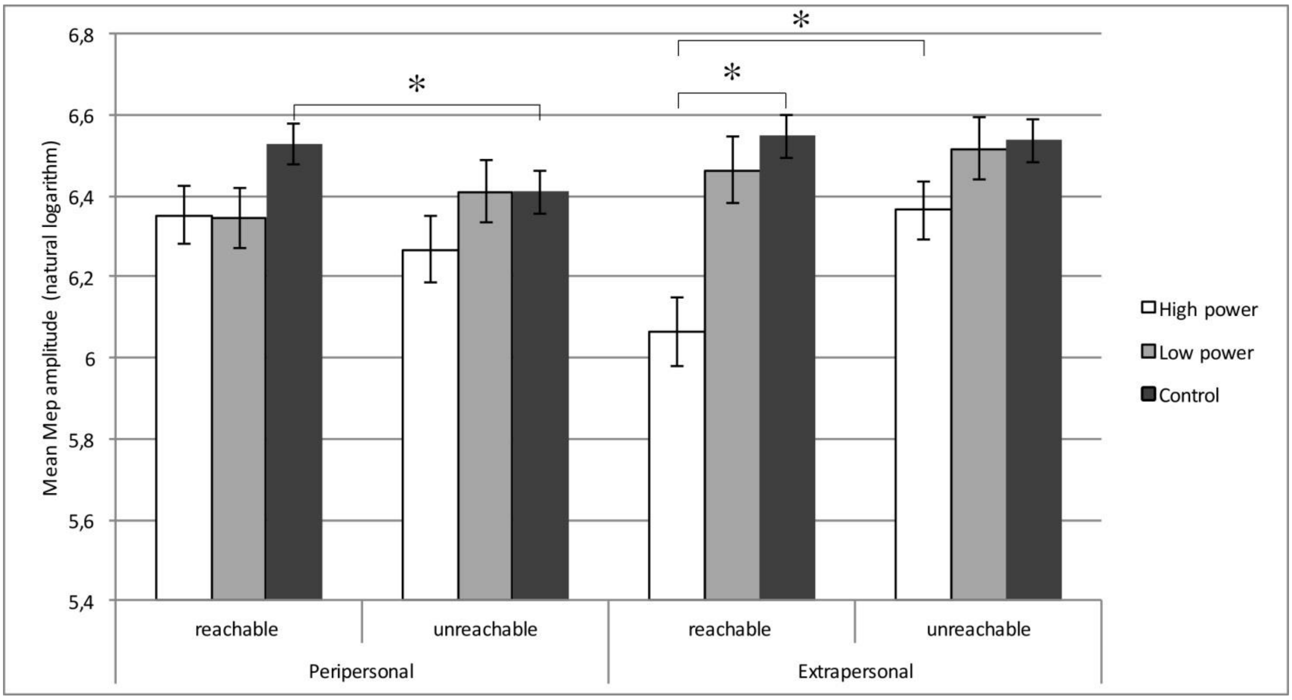

Fig. 4 shows differences between the three experimental conditions in MEP log-amplitude mean for peripersonal and extrapersonal space and subjective reachable vs subjective unreachable heights. Error bars represent +/- SE. Asterisks indicate significant differences.

5.2.4 Discussion

Our present study aimed at identifying a neurophysiological signature and an implicit measure of the phenomenon of overestimating own height when experiencing power. We used the affordance effect and the modulation of corticospinal excitability induced by an object position in the space to assessed whether the experience of power was able to modify own body schema and consequently affect participants' surrounding space representation. In our initial hypothesis we predicted that power experience would affect individual's sense of height and thus body schema, modifying the boundaries between peri-and extrapersonal space in the vertical plane. To test this hypothesis, we manipulated participants' sense of power randomly assigning participants to a high power, a low power and a control – positive conditions, and employed a TMS-EMG co-registration approach to assess corticospinal excitability during the view of an object positioned in the vertical peripersonal and extrapersonal space.

Our findings showed an interaction between distance and condition: in the control and in the low power conditions MEPs were higher in the extrapersonal compared to the peripersonal positions, while in the high power condition MEPs did not differ between peripersonal and extrapersonal positions.

We interpreted this pattern suggesting that recalling a powerful event can induce a change in body schema and consequently to the surrounding space representation that is observable also at the corticospinal level and might arise from a remapping of peripersonal space boundaries. In our opinion, in the high power condition, the pencil sharpener placed in the extrapersonal positions was implicitly perceived as reachable, whereas when we explicitely asked to participants whether they were able or not to reach the object (*perceived distance*) the logistic regression did not show differences among the three groups (p=.929).

The perception of own height falls into the proprioceptive knowledge belonging to the domain of body schema. Body schema and surrounding space representation in turn are tightly interconnected, i.e. modification of former might affect the latter, as it has been shown for instance by incorporating a tool (e.g. Maravita & Iriki, 2004; Pazzaglia et al., 2013) or after a surgery (e.g. Di Russo et al., 2006).

Noteworthy, body schema and peripersonal space are often overlapping concepts (Holmes & Spence, 2004; see Cardinali et al., 2009 for a critical discussion). The experimental procedure in the present study does not allow us to disentangle whether the modulation of corticospinal excitability was due to a change in the body schema and/or in the peripersonal space processing. Although clear evidence is not yet available and future studies might aim at disentangling between the two, we speculated that a modification in space representation might be ascribed to a change in own body schema, since behavioural studies suggested a symbolic association between power and verticality (Schubert, 2005; Yap et al., 2013), showing that the psychological experience of power influences individuals' subjective sense of height, thus inducing people who experience power to actually overestimate their own height (Duguid & Goncalo, 2012).

Looking to literature studies, a possible point of discussion is that more than power per se what modulated corticospinal excitability was the positive valence induced by positive emotions.

To rule put this hypothesis we included a control condition in which we asked participants to recall a positive but not power related event, that allowed us to disentangle the power effect from that of a positive valence event: MEPs pattern in the control condition did not differ from the low power condition. To the best of our knowledge, this is the first study in which a powerful condition is directly compared to a positive valence one.

Results showed an interaction between distance and perceived distance that, although being outside the direct aim of the present study, rise a certain interest and allow some speculations. In our experimental paradigm, the peripersonal space (including the midline position) and extrapersonal space were objectively established by assessing the midline position as the fairest point at which the participants could reach the object by stretching their arm. Therefore, our distinction between peripersonal and extrapersonal was *objective*. By asking our participant to state for each of the 5 positions whether they perceived the object as reachable or not, we assessed instead a *subjective* and aware perception of peripersonal and extrapersonale space, with boundaries that did not entirely coincide with those of the objective peripersonal and extrapersonal space. Noteworthy, in our experiment design all the positions were within 10 cm up or low the midline position. Therefore, participants could not clearly perceive each distance as reachable or not and accordingly made incorrect judgements about the possibility to reach the object. We chose this distance manipulation because we thought that if a person remaps the external space on his power feelings basis, this remapping would take place in a twilight zone rather than for distances clearly attainable or unattainable. Interestingly, within the objective peripersonal space, MEPs were reduced, regardless of being perceived as reachable or not. The reduction of corticospinal excitability for object in the closest portion of space could be explained as an automatic effect of freezing-like reaction toward stimuli potentially dangerous (Avenanti et al., 2012; Makin et al. 2009; Serino et al., 2009) because approximating to the body. The automaticity is suggested by the fact that subjective perception does not influence such mechanism, indeed MEPs are reduced when objectively in the peripersonal space, even though the object is erroneously perceived as not reachable i.e. belonging to the subjective extrapersonal space. On the contrary, when objects are in the objective extrapersonal space, the subjective evaluation seems to play a role, since the MEPs are reduced if an object is misleadingly considered as reachable, suggesting a top-down influence on the mechanism from aware and subjective perception of peripersonal space. Future research is needed to further corroborate these suggested explanations.

We also found an interaction among condition, distance and perceived distance: indeed, only in the high power condition the pencil sharpener placed in the extrapersonal space induced smaller MEPs if participants believed they could reach it. Again, this result confirms the above mentioned mechanism, adding that in power condition is more likely that subjective and objective extrapersonal space representations diverge, further corroborating our main result.

Taken together our results extend previous behavioural works on how psychological experience of power influences individuals' self-perception and subjective sense of height, providing an implicit measure of power feelings affect our surrounding space representation, likely arising from a body schema modification.

An unexpected result of our data is the fact that MEPs were higher in the extrapersonal vs peripersonal space. As discussed before, this corticospinal excitability reduction in peripersonal space could be due to a defensive reaction because object nearly suspended over the head can be perceived as unsafe. However, it is worth to note that this result is in a opposite direction of what has been reported in literature (Cardellicchio et al., 2011), even if only the horizontal axis has been assessed.

To further address the existence of a possible dissociation between near and far space and to corroborate our results, we run a control experiment by recruiting 40 new participants and randomly assigning them to a horizontal and vertical distance manipulation.

5.3 Control experiment: corticospinal excitability on vertical and horizontal plan

5.3.1 Methods

Participants

We recruited for the study 40 healthy students (13 male, Mage =22.6, SD = ±1.6). Participants were right-handed according to the Edinburgh Handedness Inventory (Oldfield, 1971, mean laterality coefficient .81 SD = ± .14).

Participants completed the Adult Safety Screening Questionnaire (Keel et al., 2001) and gave informed written consent before to start with the experiment. We excluded participants with any contraindication for TMS (Rossi et al., 2009).

The study was approved by the local Ethics Committee (protocol number: 208) and was in accordance with the ethical standards of the revised Helsinki Declaration.

Manipulation of distance

Participants were randomly assigned to the vertical or the horizontal conditions. The only difference with the first study was that we decided to use the midline position only to set the right distance with the object and we did not record MEPs in this position.

For the vertical condition the pencil sharpener was hung over participants' head with a hook on the ceiling, using a transparent nylon wire. The different heights at which the pencil sharpener could be suspended were the same of the main experiment, still obtained by fixing the other wire end to five different nails which were vertically distributed on the wall and were not visible for the participants.

For the horizontal condition, instead, the pencil sharpener was hung in front of the participants trunk midline by means of a cane positioned on the ceiling, hang to a transparent nylon wire, as for the previous condition. We marked the with five nicks at steps of 5 cm. By moving the wire along the cane, the pencil sharpener could be allocated at the five different positions for the horizontal plane during the experimental session.

In both cases we had five different positions: two in the peripersonal space, with the pencil sharpener easily graspable by participants by simply stretching their arms, two in the extrapersonal space, with the pencil sharpener not reachable anymore and the midline condition, used at the beginning of the experiment to set the correct distance between participants and objects.

Procedure and TMS-EMG recordings

We followed the same procedure than Study 1 except that in this case participants were not asked to recall any life event.

TMS-EMG recording were performed in the same way than experiment 1.

Results

Preliminary analysis

MEPs preprocessing followed the same procedure of the previous study, leading to a 13% discharged MEPs. The remaining MEPs were normalized using natural logarithm.

A linear mixed model was run to analyze the effects on MEPs amplitude of the within subjects factors Distance (4 levels: peripersonal 1 & 2, extrapersonal 1 & 2), Word (2 levels: motor vs. perceptual) and of the between subjects factor Axis (2 levels: horizontal vs vertical) with subject intercept as random factor.

Statistical analyses were performed by using SPSS 24 and post-hoc interactions were tested with Bonferroni correction.

The main effects of Axis F(1,37) = .61, p =.44 and Word (1,6644) = .26, p=.608 were not significant.

The main effect of Distance (3,6644) = 4.15, p=.002 was significant: the trend with smaller MEPs in peripersonal 1 as compared to extrapersonal 1 (p=.066) positions reached significance in the comparisons among peripersonal 2 and extrapersonal 1 (p=.022); extrapersonal 2 elicited smaller MEPs as compared to extrapersonal 1 (p=.001).

Crucially the interaction between Distance and Axis was significant F(3,6644)=4.99, p=.001: post-hoc analysis highlighted that for vertical manipulation MEPs were smaller in the comparison among peripersonal 1 as compared to extrapersonal 1 (p=.01) and 2 (p=.044) positions and among peripersonal 2 as compared to extrapersonal 1 (p=.044). On the horizontal manipulation, instead, only MEPs in the extrapersonal 2 position (the one farer from participant’s trunk) were smaller as compared to all the other conditions (p<.01). Fig. 5 shows MEPs differences among the four positions on the vertical plan and Fig. 6 differences on the horizontal one.

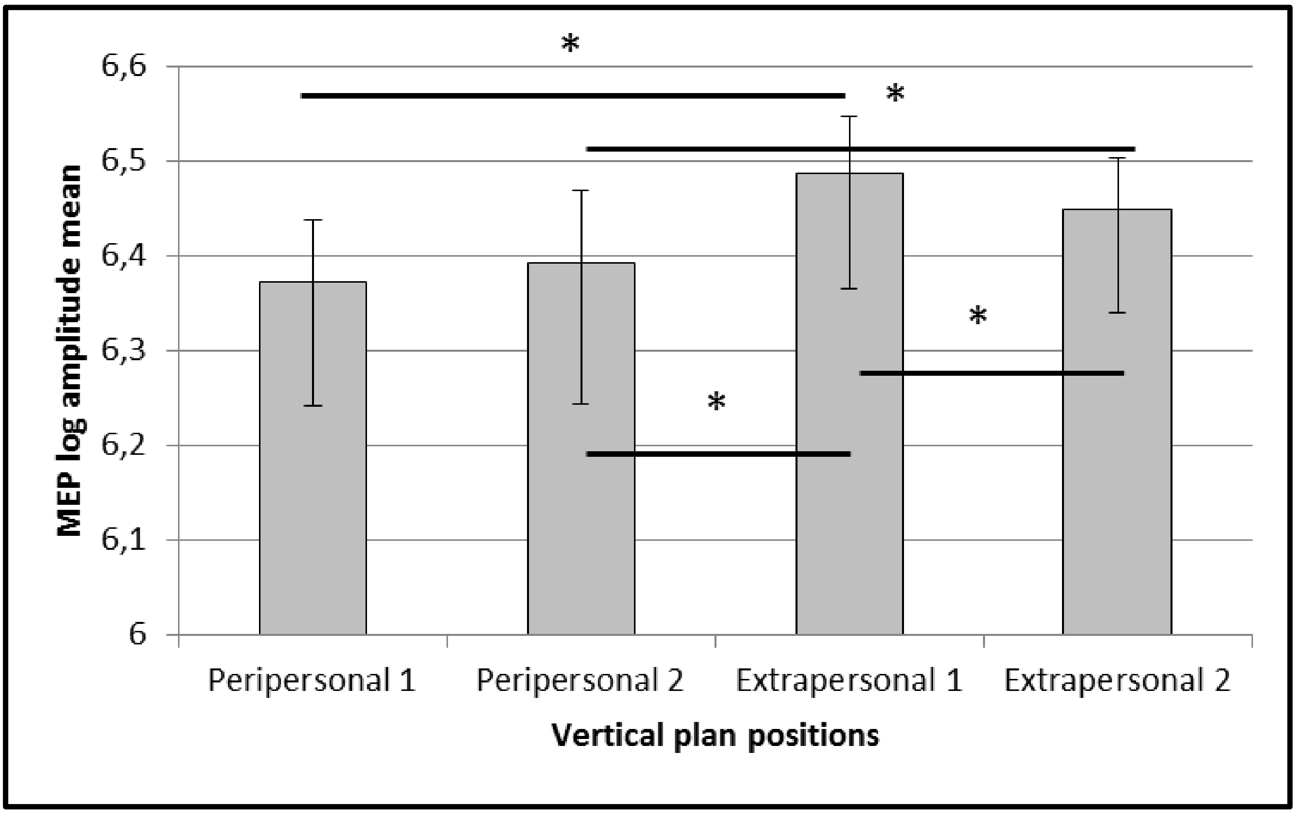

Fig. 5 shows MEP log-amplitude mean for the four positions on the vertical plan. Error bars represent +/- SE. Asterisks indicate significant differences.

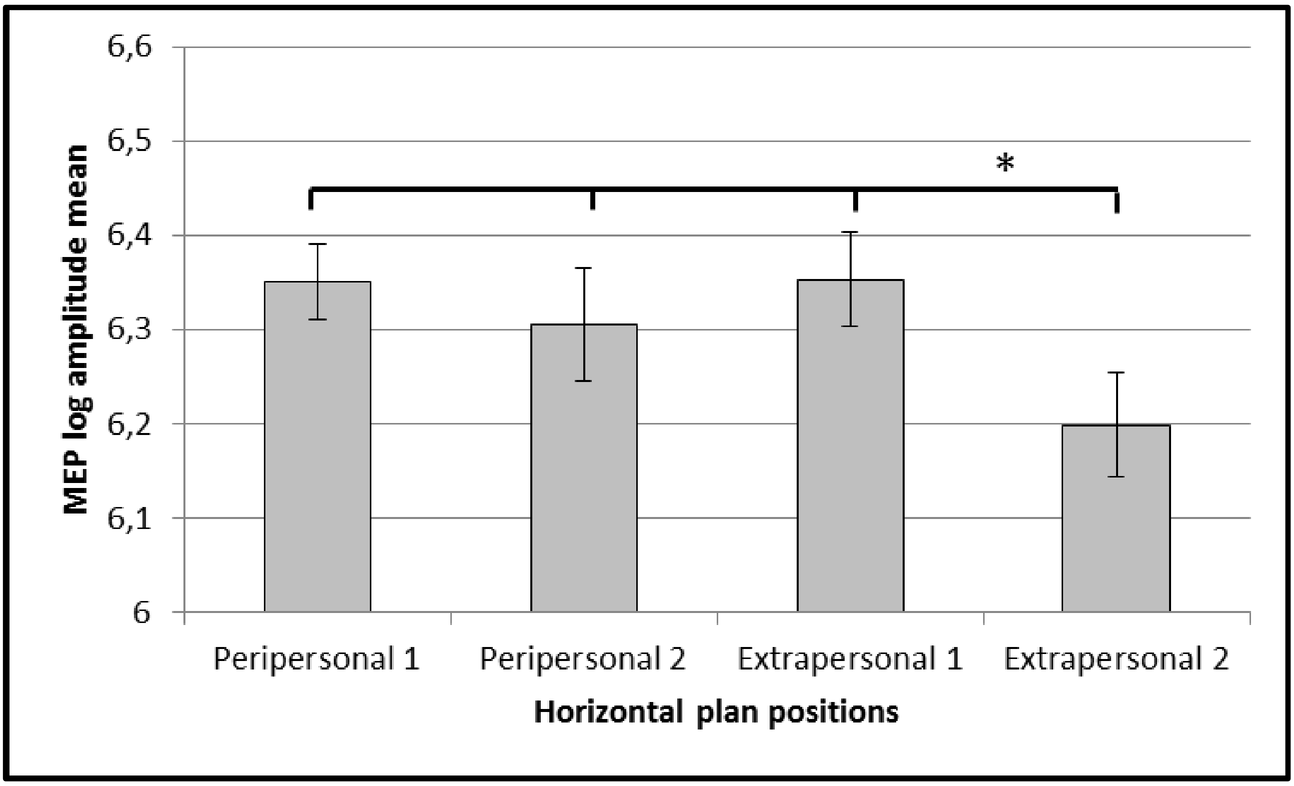

Fig. 6 shows MEP log-amplitude mean for the four positions on the horizontal plan. Error bars represent +/- SE. Asterisks indicate significant differences.

Interestingly, also the interaction between Axis and Word was significant F(1, 6644) = 5, p =.025: MEPs amplitude was influenced by the type of word only in the horizontal condition, with higher MEPs when the word was related to an action compared to a perceptual one (p=.055). See Fig. 7 for interaction results.

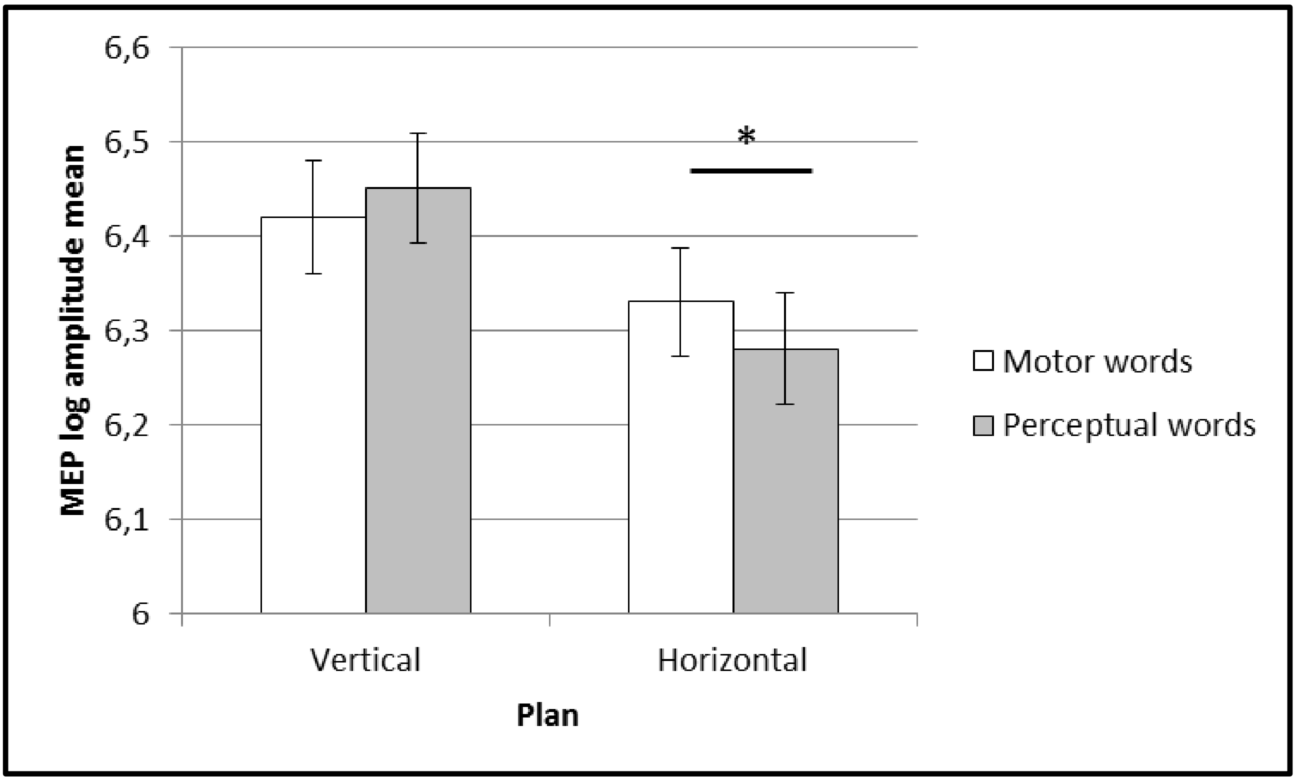

Fig. 7 shows MEP log-amplitude mean for motor and perceptual words in the vertical vs horizontal space manipulation. Error bars represent +/- SE. Asterisks indicate significant differences.

To conclude, the interaction between Distance and Word F(4,6644)=1.06, p=.375 and the three way interaction among Distance Axis and Word were not significant F(4,6644)=.03, p=.889.

In this experiment we ran a logistic regression with Axis and Distance as fixed factors and the accuracy on perceived distances as dependent. The main effect of Distance was significant, F(3,185)=5.95, p<.001, post-hoc analysis showed that accuracy was worst in the extrapersonal 1 condition compared to all other condition (all p<.05). See Fig. 8 for the logistic regression results.

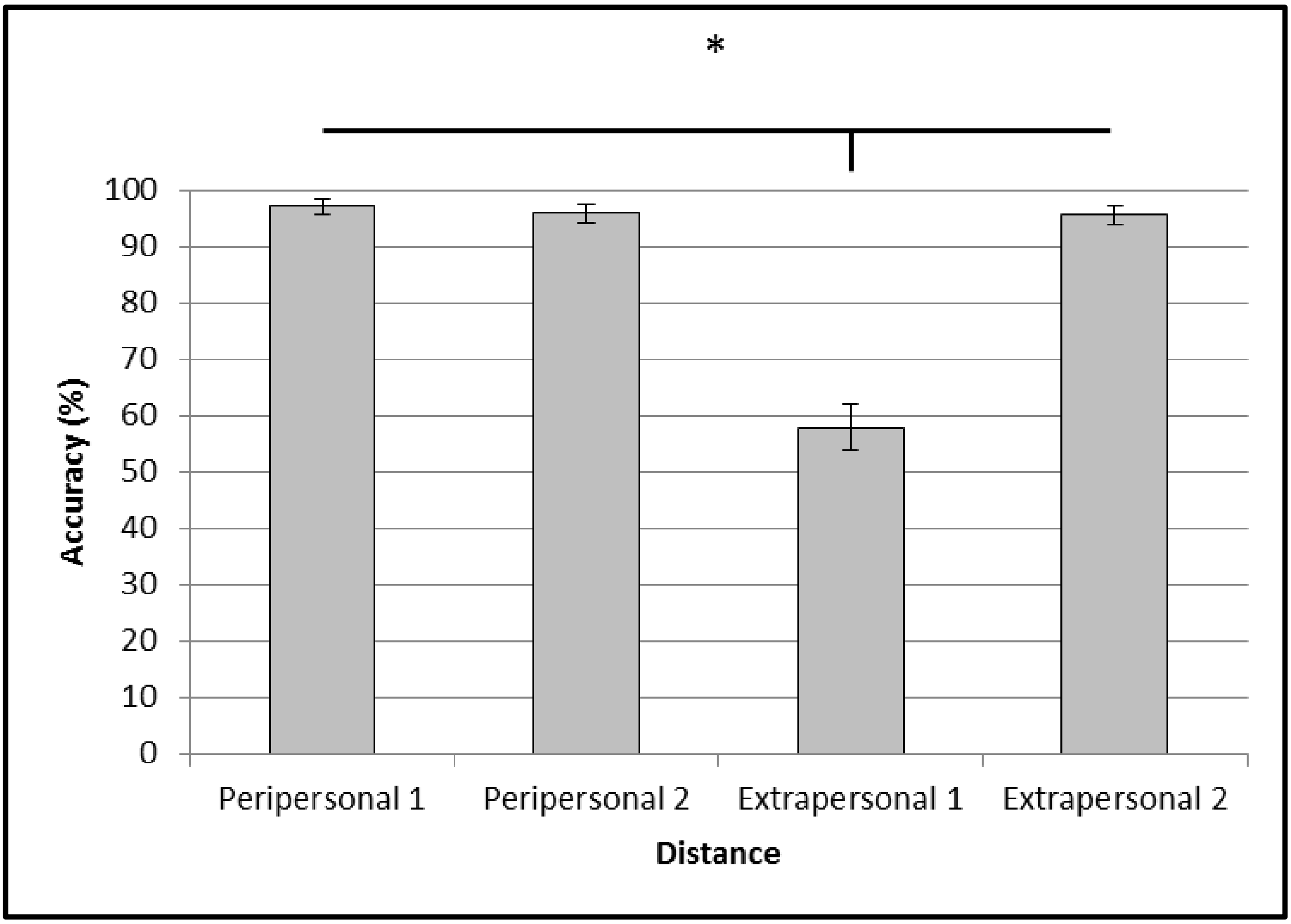

Fig. 8 shows Accuracy responses on perceived distance. Error bars represent +/- SE. Asterisks indicate significant differences.

5.3.2 Discussion

The aim of the control experiment was to deeper investigate whether corticospinal excitability was differently modulated by manipulating the pencil sharpener distance along the vertical vs horizontal plan.

40 right-handed neurologically unimpaired subjects participated in the study and received single-pulse TMS over left M1 while MEPs were recording from the right FDI.

Participants were asked to look at a hung pencil sharpener which distances were systematically manipulated across the experiment. For 20 participants the pencil sharpener was moved along the vertical axis, while for the other half the position was changed along the horizontal one.

Interestingly we found an interaction between Axis and Distance: while for vertical axis our findings were consistent with the first experiment, i.e. MEPs were smaller in the two peripersonal conditions as compared to the furthest ones, at the contrary on the horizontal axis MEPs were smaller only in the furthermost position as compared to the other four distances. As shown in Fig 9, on the basis of MEPs amplitude and assuming that similarities and difference on MEPs outline space representation borders – object positions within the same space representation (peri- vs extra-personale space) induce similar MEPs and, viceversa, difference in MEPs' amplitude should indicate that positions belongs to different space representations- it could be argued that the peripersonal space is larger in the horizontal vs vertical axis. Since what makes the distinction between the two space representation is object reachability, this result suggests that a larger space of action and reachability is conceived for the horizontal than the vertical plane, likely due to the familiarity with actions executed in front of us rather than over our head.

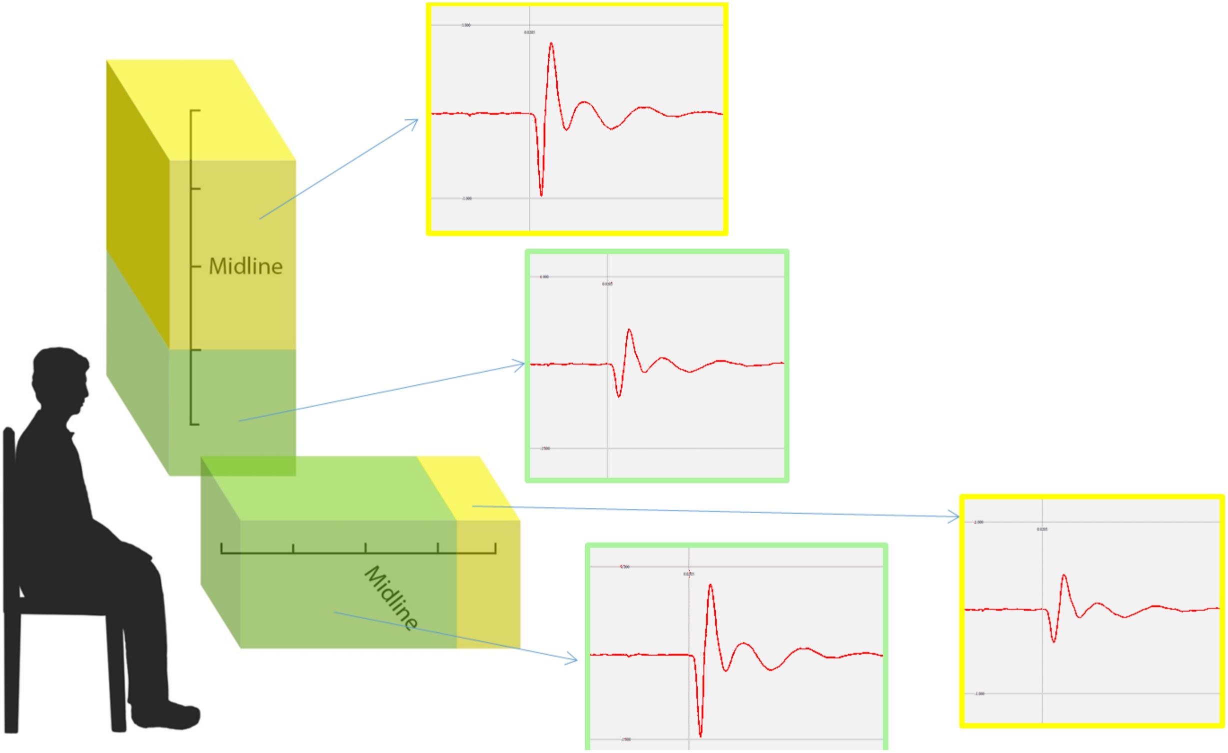

Figure 9 shows results of the interaction between Axis and Distance

Previous behavioural and neurophysiological studies in which the distance between participants and stimuli has been manipulated are consistent in suggesting a higher corticospinal excitability when the stimulus was presented in participants’ peripersonal space (Cardellicchio et al., 2011; Buccino et al., 2009).

To the best of our knowledge, all studies in which a manipulation of distance similar to our procedure has been applied, used a manipulation along the horizontal plan. Accordingly, to these evidences, we can suppose that our data on the horizontal plan are consistent with previous work, thus suggesting a facilitation when objects are presented in the reachable space vs not reachable space. It is possible that participants recognized only the furthermost position as really not reachable, thus influencing motor facilitation, as suggested by the analysis of the explicit perceived distance and in line with what discussed in the previous paragraph.

When the manipulation of distance was along the vertical axis, the pattern was reversed: MEPs were higher when pencil sharpener distance increased (i.e. in extrapersonal 1 and extrapersonal 2 conditions) compared to the two peripersonal distances. These results are not consistent with both literature on distance manipulation on the horizontal plan and studies about motor facilitation induced by object's sight.

To the best of our knowledge, however, no previous studies investigated how changing distances on the vertical axis affected motor facilitation. We here propose some possible explanations about this phenomenon, which we are now deeper investigating in our lab.

Our first hypothesis is that we perceive and code differently objects presented along the vertical vs horizontal plans. This hypothesis is partially supported by some neuropsychological findings in which some patients with unilateral spatial neglect also showed on patients with altitudinal spatial neglect (Pitzalis et al., 1997, 2001; Shelton et al., 1990; Mennemeier et al., 1992; Adair et al., 1995; Lavadas et al., 1994). Usually patients with unilateral visuo-spatial neglect ignore information from the controlesional hemisphere, usually the left side as a result of a lesion of the right hemisphere (Bisiach & Vallar, 1988). Adair and colleagues (1995), for example, described a patient who showed selective bias for stimuli presented in the upper visual hemifield. At the opposite, Lavadas and colleagues (1994) and Pitzalis et al. (1997) described patients with stronger attentional deficit for stimuli in the lower hemifield. The presence of different deficits along the longitudinal plan suggest the possibility that horizontal and longitudinal axis are coded and represented at least partially in different ways.

Another compelling hypothesis, suggested discussing the results of the main study, is that MEPs amplitude decrease in the two peripersonal vertical positions was due to a freezing-like effect.

Freezing effect is an inhibitory modulation of corticospinal excitability traceable across different conditions, such as presentation of salient stimuli (Tamburin et al., 2001; Farina et al., 2001; Urban et al., 2004), loud acoustic stimuli (Furubayashi et al., 2000), unexpected visual flashes (Cantello et al., 2000) and visual stimuli depicting pain in others (Minio-Paluello et al., 2006; Fecteau et al., 2008; Avenanti et al., 2009) .

Crucially freezing effects have been described for visual approaching (Makin et al., 2009) and auditory (Serino et al., 2009; Avenanti et al., 2012) stimuli presented near or far from the hand

In an interesting work Serino and colleagues (2009) presented an auditory stimulus either near the hand, with a loudspeaker placed~5 cm from the right hand which corresponded to~60 cm from participant’s head, or far, with a second loudspeaker placed~100 cm away to the first one which corresponded to~165 cm to participant’s head. TMS pulses were randomly delivered at 50 ms or 300 ms after sound presentation. MEPs recorded 50 ms in the near-sound condition were higher as compared to far sounds, but at 300 ms this pattern was reversed showing higher MEPs in the far-sound condition. Authors interpreted these results suggesting that the early facilitation induced by near-sound presentation could reflect an urgent motor reaction, while at 300 ms the far stimulus could require a motor response thus influencing corticospinal excitability.

Avenanti and colleagues (2012) used the same paradigm by delivering TMS pulses 50, 175 and 300 ms after sound presentation. Corticospinal excitability resulted inhibited when sounds were presented near the hand as compared to their farer presentation.

Makin et al. (2009), instead, recorded MEPs during a simple visuo-motor task in which a virtual task-irrelevant distracting ball could approach the hand (above the middle finger), be directed far from it (30 cm) or appear in a static position. Results showed that MEP amplitude was reduced when the ball approached the hand compared to when the distractor was moving far from it. No modulation was found for the presentation of static distractors as compared to the baseline condition. Authors proposed that the freezing effect could be the result of a defensive response to threatening and potentially harmful approaching objects.

These studies are not overlapping with our paradigm: first our object was static and was not moving, secondly our participants were not involved in a primary task, but instead the pencil sharpener was the focus of the experiment, indeed participants had to imagine to perform actions or features of it, third the object was always visible. However, the pencil sharpener was hung over participants' head, who could perceive it as instable and they could feel as it could at every moment fall on them, thus inducing a freezing-like effect. We did not explicitly ask our participants whether they perceived the pencil sharpener as a threat, instead we asked them whether they perceived to be able to reach the object or not for each of the five distances.

Interestingly, the first extrapersonal position, i.e. the one in the no-reachable space nearer to participants, was wrongly classified by half of participants as reachable (mean accuracy = 57.9%). Distance explicit esteems were more accurate for the extrapersonal 2, which was accurately discriminate as not reachable by the 82.1% of participants, peripersonal 1 and 2, which were accurately discriminated as reachable by the 97.1% and 95.9% of participants, respectively. These results are in line with our previsions and distance manipulation: the extrapersonal1 position was just 5 cm above the midline position, which was the extreme position in which participants were able to grasp the object, so with only a small movement participants would have been able to reach it.

Another possible explanation of our data, however, concerns the concept of motor planning and of the required effort necessary to perform an action. Motor execution, motor imagery and action observation have been shown to rely on a similar cortical network (Jeannerod, 2001). Both neuroimaging (e.g. Decety & Jannerod, 1996; Guillot et al., 2007) and neurophysiological studies (Alaerts et al., 2010; Mizuguchi et al., 2013) suggested that effort and force are represented at the cortical level (You & Cole, 1992; Carroll et al., 2006; Lee & Carroll, 2007). Specifically TMS studies measuring corticospinal excitability during imagined actions (e.g. Helm et al., 2015) showed an increase in MEPs amplitude for effortful movements, suggesting that imagining a movement which requires higher effort also recruits more interneurons in M1, thus influencing MEPs size measured in the target muscle (Reis et al., 2008).

This hypothesis, however, is able to explain only our results for the vertical axis, along which MEPs were higher for extrapersonal as compared to peripersonal positions, while along the horizontal axis the pattern was reversed.

An interesting result is MEPs difference for auditory stimuli presentation: for the vertical axis motor vs perceptual words did not elicit differences in MEP amplitude, at the contrary for horizontal axis MEPs were higher after motor stimuli, that is when participants imagined to perform action on the pencil sharpener.

Neuroimaging studies provided converging evidence on motor areas activation induced by action word presentation (e.g. Hauk et al., 2004; Rüschemeyer et al., 2007), while neurophysiological works showed mixed results, suggesting sometimes a reduction of MEPs size for sentences expressing hand and foot actions compared to abstract content sentences (Buccino et al., 2005) and sometimes higher corticospinal excitability (Oliveri et al., 2004; Fadiga et al., 2005).

We can speculate that this facilitation limited to the horizontal plan could be due to a predominant way of interaction with the external word: indeed, we are more used to interact with objects placed in front of us compared to objects above us. With this perspective in our experimental paradigm the horizontal axis could be considered as the more ecological.

However, a main limit of the present study is that we did not recorded a baseline condition, thus we can’t be sure about the direction, in terms of facilitation or inhibition, but we can only make a comparison between our experimental conditions. Moreover, we did not check for muscle-specificity, but recorded only FDI muscle.

As a further development of the present study, in our lab we are now testing the same paradigm, recording two baseline conditions (at the beginning and at the end of the experiment) and checking ADM activity, which should not be involved in precision grasping movements, as a control muscle.

6. General discussion: MEPs as a measure of human behaviour

Among the type of measures is possible to collect applying TMS over cerebral cortex, MEPs represent one of the most valuable, since are a direct output of TMS induced activity, are quantifiable and can be easily recorded during task performance. Being a direct measure of corticospinal excitability, MEPs have been largely use for clinical purposes to assess the integrity of motor pathway (Rossini & Rossi, 2007; Groppa et al., 2012; Rossini et al., 2015; Menon et al., 2015). In neuroscientific research, MEPs have been primarily used to explore the excitability and connectivity as well as the functional properties of the motor system (Barker et al., 1986; Rossini et al., 1998; Kobayashi & Pascual-Leone, 2003; Koch et al., 2006). However, MEPs usefulness can go beyond the study of motor function.

In the present thesis several example of how MEPs can be used to make inferences about human behaviour and cognition were illustrated. First MEPs were used as a measure of motor resonance, which is thought to directly reflect the activity of the HNMs. More specifically, corticospinal excitability modulations, measured by MEPs, during economic games allowed us to find a neurophysiological marker for known phenomena ruling human economic interactions and to test the validity of a famous model, such as Regulatory Focus theory, about the way people react to gain and losses. Secondly, still based on motor resonance properties, we tested the presence and automaticity of a prejudice toward outgroup members. As a third case, building on the properties of corticospinal facilitation induced by affordance, we used MEPs to tap changes in body schema and surrounding space perception following the experimental manipulation of participant’s power experience.

On top of being handy and useful, MEPs could also be a misleading measure. The nature of MEPs is indeed complex, with several components and generators, and increase in MEPs amplitude reflects both cortical and spinal excitability (Reis et al., 2008).

As pointed out in the fourth chapter, a main pitfall is a misunderstanding in MEPs results interpretation: MEPs amplitude does not allow to derive conclusions about which brain regions are involved in the ongoing cognitive processes. Indeed MEPs modulation can be influenced by processes occurring not only in the primary motor cortex but also in regions directly or indirectly connected to it, through excitatory or inhibitory cortico-cortical pathways.

Moreover, many variables influence MEPs measurement and not all of them can be controlled. Therefore, caution is warranted when interpreting results, and a rigorous study design is needed. Hence, in discussing our results our approach is twofold, enthusiastic on one side for the potentialities of this measure but also concerned of their limits.

From a methodological perspective, on top of the specific results of each study, which have already been discussed in the corresponding discussion sessions, a hidden "result" to be argued here is the enhancement in the procedural knowledge obtained.

One of the main issue on MEPs use regards comparability across studies. A potential limit in comparing studies on MEPs is the baseline choice. As pointed out in a recent review from Naish et al. (2014, Supplementary Table) the majority of works on corticospinal excitability during action observation highlighted an increasing in MEPs amplitude as compared to a baseline condition. However, it is not clear what does the concept of baseline mean: indeed, previous studies applied a wide range of possibilities from this point of view, from participants' eyes being closed (e.g. Jola et al., 2012), to a low-level baseline such as the observation of a fixation cross (e.g. Bucchioni et al., 2013) or a blank screen (Ohno et al., 2011), or a static image depicting a hand or an actor (e.g. Aglioti et al., 2008); only a study used a baseline in which a video depicted the beginning of a movement (Borroni et al., 2011).

Connected to the previous point, another crucial issue concerns the way in which data are normalized: this measure changes across studies, with MEPs being normalized directly to a baseline condition, for example using a ratio index between the experimental condition and the baseline (Hogeveen & Obhi, 2012) and others normalizing MEPs on the average of muscle, block, condition, participants (see Naish et al., 2014 for a recent review).

Stimulation intensity is a variable which strongly impact MEPs generation and amplitude, however this issue did not receive a lot of consideration by literature. In the domain of action observation studies applied intensities from low (110% of resting motor threshold, e.g. Gangitano et al., 2001, 2004; Montagna et al., 2005) to high (130% of resting motor threshold, e.g. Avenanti et al., 2005; Aglioti et al., 2008). In a recent study Loporto and colleagues (2013) suggested a motor facilitation only with low TMS intensities (110% of motor threshold).

In the first neuroeconomic study, the baselines consisted of a fixation cross at the center of the screen before and after experimental conditions. Aware of the limits of this approach, in our second neuroeconomic experiment we employed as a baseline the same videos used in the experimental condition, eliminating the crucial experimental manipulated variable (i.e. tokens meaning, i.e. in the baseline the upper side was white). From our point of view this is the cleaner way to have a baseline condition, allowing to attribute every MEPs modulation to the manipulated variables. Similarly, in the study in which we manipulated contextual cues (threatening vs neutral sound and ingroup vs outgroup agents) on top of the baseline with a fixation cross, we added the neutral condition as a cleaner way to compare corticospinal modulations induced by threat.

From a statistical point of view, we opted to normalize MEPs by transforming their values using logarithm, which is a typical procedure when data are not normally distributed (e.g. Barbaranelli et al., 2006).

Increasing our knowledge about MEPs and their prominent variability at intra but especially at inter-individual level, only in the first neuroeconomics study we used a ratio between the mean value in the manipulated conditions and the baseline. In the following studies, instead, we applied mixed models to our analysis which, by means of random factors, are able to account for such variability, are not constrained by the assumption of independence of measurement and have more statistical power allowing the use of all data points instead of a unique mean value (Baayen et al., 2008).

To set the appropriate TMS intensity we chose to follow Loporto (2013) guide-lines and in all experiments we used the 110% of individual motor threshold to induced MEPs. Moreover, in all our experiment we monitored the coil-position during the experiment thus preventing any change in stimulation site due to small movements of participant's head during data collection (Sartori et al., 2013).

To conclude, MEPs can be a powerful tool to investigate human behaviour but the correctness and the generalizability of their results depends from a deep knowledge about the limitations and pitfalls of this measure.

References

Adair, J. C., Williamson, D. J., Jacobs, D. H., Na, D. L., & Heilman, K. M. (1995). Neglect of radial and vertical space: importance of the retinotopic reference frame. *Journal of Neurology, Neurosurgery & Psychiatry*, 58(6), 724-728.

Adrian, E. D., & Moruzzi, G. (1939). Impulses in the pyramidal tract. *The Journal of physiology*, 97(2), 153-199.

Aglioti, S. M., Cesari, P., Romani, M., & Urgesi, C. (2008). Action anticipation and motor resonance in elite basketball players. *Nature neuroscience*, 11(9), 1109-1116.

Alaerts, K., de Beukelaar, T. T., Swinnen, S. P., & Wenderoth, N. (2012). Observing how others lift light or heavy objects: time-dependent encoding of grip force in the primary motor cortex. *Psychological research*, 76(4), 503-513.

Alaerts, K., Heremans, E., Swinnen, S. P., & Wenderoth, N. (2009). How are observed actions mapped to the observer's motor system? Influence of posture and perspective. *Neuropsychologia*, 47(2), 415-422.

Amassian, V. E., Stewart M., Quirk G. J., Rosenthal J. L. (1987). Physiological basis of motor effects of a transient stimulus to cerebral cortex. *Neurosurgery* 20, 74-93.

Amodio, D. M. (2008). The social neuroscience of intergroup relations. *European review of social psychology*, 19(1), 1-54.

Amoruso, L., & Urgesi, C. (2016). Contextual modulation of motor resonance during the observation of everyday actions. *NeuroImage*, 134, 74-84.

Anderson, C., & Galinsky, A. D. (2006). Power, optimism, and risk-taking. *European journal of social psychology*, 36(4), 511-536.

Anelli, F., Borghi, A. M., & Nicoletti, R. (2012a). Grasping the pain: motor resonance with dangerous affordances. *Consciousness and cognition*, 21(4), 1627-1639.

Avenanti, A., Annela, L., & Serino, A. (2012). Suppression of premotor cortex disrupts motor coding of peripersonal space. *Neuroimage*, 63(1), 281-288.

Avenanti, A., Bueti, D., Galati, G., & Aglioti, S. M. (2005). Transcranial magnetic stimulation highlights the sensorimotor side of empathy for pain. *Nature neuroscience*, 8(7), 955-960.

Avenanti, A., Minio-Paluello, I., Sforza, A., & Aglioti, S. M. (2009). Freezing or escaping? Opposite modulations of empathic reactivity to the pain of others. *Cortex*, 45(9), 1072-1077.

Avenanti, A., Paluello, I. M., Bufalari, I., & Aglioti, S. M. (2006). Stimulus-driven modulation of motor-evoked potentials during observation of others' pain. *NeuroImage*, 32(1), 316-324.

Avenanti, A., Paracampo, R., Annella, L., Tidoni, E., & Aglioti, S. M. (2017). Boosting and decreasing action prediction abilities through excitatory and inhibitory tDCS of inferior frontal cortex. *Cerebral Cortex*, 1-15.

Avenanti, A., Sirigu, A., & Aglioti, S. M. (2010). Racial bias reduces empathic sensorimotor resonance with other-race pain. *Current Biology*, 20(11), 1018-1022.

Azañón, E., Radulova, S., Haggard, P., & Longo, M. R. (2016). Does the crossed-limb deficit affect the uncrossed portions of limbs?. *serino*, 42(9), 1320.

Azevedo, R. T., Macaluso, E., Avenanti, A., Santangelo, V., Cazzato, V., & Aglioti, S. M. (2013). Their pain is not our pain: brain and autonomic correlates of empathic resonance with the pain of same and different race individuals. *Human brain mapping*, 34(12), 3168-3181.

Baayen, R. H., Davidson, D. J., & Bates, D. M. (2008). Mixed-effects modeling with crossed random effects for subjects and items. *Journal of Memory and Language*, 59(4), 390-412.

Bagce, H. F., Saleh, S., Adamovich, S. V., Krakauer, J. W., & Tunik, E. (2013). Corticospinal excitability is enhanced after visuomotor adaptation and depends on learning rather than performance or error. *Journal of neurophysiology*, 109(4), 1097-1106.

Barbaranelli, C., & D'Olimpio, F. (2006). Analisi dei dati con SPSS (Vol. 2). Milano: Led.

Barker, A. T., Freeston, I. L., Jalinous, R., & Jarratt, J. A. (1986). Clinical evaluation of conduction time measurements in central motor pathways using magnetic stimulation of human brain. *The Lancet*, 327(8493), 1325-1326.

Barker, A. T., Jalinous, R., & Freeston, I. L. (1985). Non-invasive magnetic stimulation of human motor cortex. *The Lancet*, 325(8437), 1106-1107.

Baron, J., & Ritov, I. (1994). Reference points and omission bias. *Organizational Behavior and Human Decision Processes*, 59(3), 475-498.

Barrett, L. F., & Kensinger, E. A. (2010). Context is routinely encoded during emotion perception. *Psychological Science*, 21(4), 595-599.

Barsalou, L. W. (2008). Grounded cognition. *Annual Review of Psychology*., 59, 617-645.

Bates, D., Kliegl, R., Vasishth, S., & Baayen, H. (2015). Parsimonious mixed models. arXiv preprint arXiv:1506.04967.

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2014). lme4: Linear mixed-effects models using Eigen and S4. R package version, 1(7).

Becchio, C., Cavallo, A., Begliomini, C., Sartori, L., Feltrin, G., & Castiello, U. (2012). Social grasping: From mirroring to mentalizing. *NeuroImage*, 61(1), 240-248.

Berardelli, A., Inghilleri, M., Cruccu, G., & Manfredi, M. (1990). Descending volley after electrical and magnetic transcranial stimulation in man. *Neuroscience letters*, 112(1), 54-58.

Berlingeri, M., Gallucci, M., Danelli, L., Forgiarini, M., Sberna, M., & Paulesu, E. (2016). Guess who's coming to dinner: Brain signatures of racially biased and politically correct behaviors. *Neuroscience*, 332, 231-241.

Berlucchi, G., & Aglioti, S. (1997). The body in the brain: neural bases of corporeal awareness. *Trends in neurosciences*, 20(12), 560-564.

Berti, A., & Frassinetti, F. (2000). When far becomes near: Remapping of space by tool use. *Journal of cognitive neuroscience*, 12(3), 415-420.

Bestmann, S., & Krakauer, J. W. (2015). The uses and interpretations of the motor-evoked potential for understanding behaviour. *Experimental brain research*, 233(3), 679-689.

Bieleke, M., Gollwitzer, P. M., Oettingen, G., & Fischbacher, U. (2016). Social value orientation moderates the effects of intuition versus reflection on responses to unfair ultimatum offers. *Journal of Behavioral Decision Making*, 30(2), 569-581.

Billig, M., & Tajfel, H. (1973). Social categorization and similarity in intergroup behaviour. *European Journal of Social Psychology*, 3(1), 27-52.

Bisiach, E., & Vallar, G. (1988). Hemineglect in humans. In F. Boller, J. Grafman, G. Rizzolatti, & H. Goodglass (Eds.), Handbook of neuropsychology, Vol. 1, pp. 195-222. New York: Elsevier Science.

Bjoertomt, O., Cowey, A., & Walsh, V. (2002). Spatial neglect in near and far space investigated by repetitive transcranial magnetic stimulation. *Brain*, 125(9), 2012-2022.

Bloesch, E. K., Davoli, C. C., & Abrams, R. A. (2013). Age-related changes in attentional reference frames for peripersonal space. *Psychological scie*nce, 24(4), 557-561.

Borgomaneri, S., Gazzola, V., & Avenanti, A. (2012). Motor mapping of implied actions during perception of emotional body language. *Brain Stimulation*, 5(2), 70-76.

Borgomaneri, S., Gazzola, V., & Avenanti, A. (2013). Temporal dynamics of motor cortex excitability during perception of natural emotional scenes. *Social Cognitive and Affective Neuroscience*, 9(10), 1451-1457.

Borgomaneri, S., Gazzola, V., & Avenanti, A. (2015). Transcranial magnetic stimulation reveals two functionally distinct stages of motor cortex involvement during perception of emotional body language. *Brain Structure and Function*, 220(5), 2765-2781.

Borgomaneri, S., Vitale, F., & Avenanti, A. (2015). Early changes in corticospinal excitability when seeing fearful body expressions. *Scientific reports*, 5, 14122.

Borroni, P., Gorini, A., Riva, G., Bouchard, S., & Cerri, G. (2011). Mirroring avatars: dissociation of action and intention in human motor resonance. *European Journal of Neuroscience*, 34(4), 662-669.

Boyd, S. G., Rothwell, J. C., Cowan, J. M., Webb, P. J., Morley, T., Asselman, P., & Marsden, C. D. (1986). A method of monitoring function in corticospinal pathways during scoliosis surgery with a note on motor conduction velocities. *Journal of Neurology, Neurosurgery & Psychiatry*, 49(3), 251-257.

Brasil-Neto, J. P., Cohen, L. G., Panizza, M., Nilsson, J., Roth, B. J., & Hallett, M. (1992). Optimal focal transcranial magnetic activation of the human motor cortex: effects of coil orientation, shape of the induced current pulse, and stimulus intensity. *Journal of Clinical Neurophysiology*, 9(1), 132-136.

Brewer, M. B., & Caporael, L. R. (1990). Selfish genes vs. selfish people: Sociobiology as origin myth. *Motivation and emotion*, 14(4), 237-243.

Brozzoli, C., Cardinali, L., Pavani, F., & Farnè, A. (2010). Action-specific remapping of peripersonal space. *Neuropsychologia*, 48(3), 796-802.

Brüne, M., Scheele, D., Heinisch, C., Tas, C., Wischniewski, J., & Güntürkün, O. (2012). Empathy moderates the effect of repetitive transcranial magnetic stimulation of the right dorsolateral prefrontal cortex on costly punishment. *PloS one*, 7(9), e44747.

Buccino, G., Riggio, L., Melli, G., Binkofski, F., Gallese, V., & Rizzolatti, G. (2005). Listening to action-related sentences modulates the activity of the motor system: A combined TMS and behavioral study. *Cognitive Brain Research*, 24(3), 355-363.

Buccino, G., Sato, M., Cattaneo, L., Rodà, F., & Riggio, L. (2009). Broken affordances, broken objects: a TMS study. *Neuropsychologia*, 47(14), 3074-3078.

Bucchioni, G., Cavallo, A., Ippolito, D., Marton, G., & Castiello, U. (2013). Corticospinal excitability during the observation of social behavior. *Brain and cognition*, 81(2), 176-182.

Burke, D., Hicks, R., Gandevia, S. C., Stephen, J., Woodforth, I., & Crawford, M. (1993). Direct comparison of corticospinal volleys in human subjects to transcranial magnetic and electrical stimulation. *The Journal of Physiology*, 470(1), 383-393.

Camerer, C. (2003). Behavioral game theory: Experiments in strategic interaction. Princeton University Press.

Camerer, C., & Thaler, R. H. (1995). Anomalies: Ultimatums, dictators and manners. *The Journal of Economic Perspectives*, 9(2), 209-219.

Cantello, R., Civardi, C., Cavalli, A., Varrasi, C., & Vicentini, R. (2000). Effects of a photic input on the human cortico-motoneuron connection. *Clinical neurophysiology*, 111(11), 1981-1989.

Canzoneri, E., Marzolla, M., Amoresano, A., Verni, G., & Serino, A. (2013). Amputation and prosthesis implantation shape body and peripersonal space representations. *Scientific reports*, 3.

Capellini, R., Sacchi, S., Ricciardelli, P., & Actis-Grosso, R. (2016). Social Threat and Motor Resonance: When a Menacing Outgroup Delays Motor Response. *Frontiers in psychology*, 7.

Caporael, L. R. (1997). The evolution of truly social cognition: The core configurations model. *Personality and Social Psychology Review*, 1(4), 276-298.

Cardellicchio, P., Sinigaglia, C., & Costantini, M. (2011). The space of affordances: A TMS study. *Neuropsychologia*, 49(5), 1369-1372.

Cardinali, L., Brozzoli, C., & Farne, A. (2009). Peripersonal space and body schema: two labels for the same concept? *Brain topography*, 21(3-4), 252-260.

Casarotto, S., Lauro, L. J. R., Bellina, V., Casali, A. G., Rosanova, M., Pigorini, A., ... & Massimini, M. (2010). EEG responses to TMS are sensitive to changes in the perturbation parameters and repeatable over time. *PLoS One*, 5(4), e10281.

Caspers, S., Zilles, K., Laird, A. R., & Eickhoff, S. B. (2010). ALE meta-analysis of action observation and imitation in the human brain. *Neuroimage*, 50(3), 1148-1167.

Catmur, C., Mars, R. B., Rushworth, M. F., & Heyes, C. (2011). Making mirrors: premotor cortex stimulation enhances mirror and counter-mirror motor facilitation. *Journal of Cognitive Neuroscience*, 23(9), 2352-2362.

Cattaneo, L., & Rizzolatti, G. (2009). The mirror neuron system. *Archives of neurology*, 66(5), 557-560.

Cavallo, A., Becchio, C., Sartori, L., Bucchioni, G., & Castiello, U. (2012). Grasping with tools: corticospinal excitability reflects observed hand movements. *Cerebral Cortex*, 22(3), 710-716.

Cavallo, A., Bucchioni, G., Castiello, U., & Becchio, C. (2013). Goal or movement? Action representation within the primary motor cortex. *European Journal of Neuroscience*, 38(10), 3507-3512.

Chao, L. L., & Martin, A. (2000). Representation of manipulable man-made objects in the dorsal stream. *Neuroimage*, 12(4), 478-484.

Chiao, J. Y., Harada, T., Komeda, H., Li, Z., Mano, Y., Saito, D., ... & Iidaka, T. (2010). Dynamic cultural influences on neural representations of the self. *Journal of Cognitive Neuroscience*, 22(1), 1-11.

Chiao, J. Y., Harada, T., Oby, E. R., Li, Z., Parrish, T., & Bridge, D. J. (2009). Neural representations of social status hierarchy in human inferior parietal cortex. *Neuropsychologia*, 47(2), 354-363.

Clark, S., Tremblay, F., & Ste-Marie, D. (2004). Differential modulation of corticospinal excitability during observation, mental imagery and imitation of hand actions. *Neuropsychologia*, 42(1), 105-112.

Coelho, C. M., Lipp, O. V., Marinovic, W., Wallis, G., & Riek, S. (2010). Increased corticospinal excitability induced by unpleasant visual stimuli. *Neuroscience Letters*, 481(3), 135-138.

Coello, Y., Bartolo, A., Amiri, B., Devanne, H., Houdayer, E., & Derambure, P. (2008). Perceiving what is reachable depends on motor representations: evidence from a transcranial magnetic stimulation study. *PloS one*, 3(8), e2862.

Coello, Y., Bourgeois, J., & Iachini, T. (2012). Embodied perception of reachable space: how do we manage threatening objects?. *Cognitive processing*, 13(1), 131-135.

Connolly, T., & Zeelenberg, M. (2002). Regret in decision making. *Current directions in psychological science*, 11(6), 212-216.

Coombes, S. A., Tandonnet, C., Fujiyama, H., Janelle, C. M., Cauraugh, J. H., & Summers, J. J. (2009). Emotion and motor preparation: a transcranial magnetic stimulation study of corticospinal motor tract excitability. *Cognitive, Affective, & Behavioral Neuroscience*, 9(4), 380-388.

Costantini, M., Ambrosini, E., Tieri, G., Sinigaglia, C., & Committeri, G. (2010). Where does an object trigger an action? An investigation about affordances in space. *Experimental brain research*, 207(1-2), 95-103.

Courville, A. C., Daw, N. D., & Touretzky, D. S. (2006). Bayesian theories of conditioning in a changing world. *Trends in cognitive sciences*, 10(7), 294-300.

Cox, J. C., Ostrom, E., Sadiraj, V., & Walker, J. M. (2013). Provision versus appropriation in symmetric and asymmetric social dilemmas. *Southern economic journal*, 79(3), 496-512.

Craighero, L., Fadiga, L., Rizzolatti, G., & Umiltà, C. (1999). Action for perception: a motor-visual attentional effect. *Journal of experimental psychology: Human perception and performance*, 25(6), 1673.

Danner, N., Julkunen, P., Könönen, M., Säisänen, L., Nurkkala, J., & Karhu, J. (2008). Navigated transcranial magnetic stimulation and computed electric field strength reduce stimulator-dependent differences in the motor threshold. *Journal of neuroscience methods*, 174(1), 116-122.

Danner, N., Könönen, M., Säisänen, L., Laitinen, R., Mervaala, E., & Julkunen, P. (2012). Effect of individual anatomy on resting motor threshold–computed electric field as a measure of cortical excitability. *Journal of neuroscience methods*, 203(2), 298-304.

Darling, W. G., Wolf, S. L., & Butler, A. J. (2006). Variability of motor potentials evoked by transcranial magnetic stimulation depends on muscle activation. *Experimental brain research*, 174(2), 376-385.

Davis, M., & Whalen, P. J. (2001). The amygdala: vigilance and emotion. *Molecular psychiatry*, 6(1), 13.

Day, B. L., Rothwell, J. C., Thompson, P. D., Dick, J. P. R., Cowan, J. M. A., Berardelli, A., & Marsden, C. D. (1987). Motor cortex stimulation in intact man: 2. Multiple descending volleys. *Brain*, 110(5), 1191-1209.

De Gennaro, L., Marzano, C., Veniero, D., Moroni, F., Fratello, F., Curcio, G., ... & Bertini, M. (2007). Neurophysiological correlates of sleepiness: a combined TMS and EEG study. *Neuroimage*, 36(4), 1277-1287.

De Paepe, A. L., Crombez, G., & Legrain, V. (2017). Remapping nociceptive stimuli into a peripersonal reference frame is spatially locked to the stimulated limb. *Neuropsychologi*a, 101, 121-131.

De Quervain, D. J., Fischbacher, U., Treyer, V., & Schellhammer, M. (2004). The neural basis of altruistic punishment. *Science*, 305(5688), 1254.

De Vignemont, F., & Iannetti, G. D. (2015). How many peripersonal spaces?. *Neuropsychologia*, 70, 327-334.

Désy, M. C., & Théoret, H. (2007). Modulation of motor cortex excitability by physical similarity with an observed hand action. *PLoS One*, *2*(10), e971.

Di Lazzaro, V., Oliviero, A., Profice, P., Insola, A., Mazzone, P., Tonali, P., & Rothwell, J. C. (1999). Effects of voluntary contraction on descending volleys evoked by transcranial electrical stimulation over the motor cortex hand area in conscious humans. *Experimental brain research*, 124(4), 525-528.

Di Lazzaro, V., Oliviero, A., Pilato, F., Saturno, E., Dileone, M., Mazzone, P., ... & Rothwell, J. C. (2004). The physiological basis of transcranial motor cortex stimulation in conscious humans. *Clinical neurophysiology*, 115(2), 255-266.

Di Lazzaro, V., Ziemann, U., & Lemon, R. N. (2008). State of the art: physiology of transcranial motor cortex stimulation. *Brain Stimulation*, 1(4), 345-362.

Di Lazzaro, V., & Ziemann, U. (2013). The contribution of transcranial magnetic stimulation in the functional evaluation of microcircuits in human motor cortex. *Frontiers in neural circuits*, 7.

Di Lazzaro, V., Profice, P., Ranieri, F., Capone, F., Dileone, M., Oliviero, A., & Pilato, F. (2012). I-wave origin and modulation. *Brain stimulation*, 5(4), 512-525.

Di Lazzaro, V., Oliviero, A., Meglio, M., Cioni, B., Tamburrini, G., Tonali, P., & Rothwell, J. C. (2000). Direct demonstration of the effect of lorazepam on the excitability of the human motor cortex. *Clinical Neurophysiology*, 111(5), 794-799.

Di Pellegrino, G., Fadiga, L., Fogassi, L., Gallese, V., & Rizzolatti, G. (1992). Understanding motor events: a neurophysiological study. *Experimental brain research*, 91(1), 176-180.

Di Russo, F., Committeri, G., Pitzalis, S., Spitoni, G., Piccardi, L., Galati, G., ... & Pizzamiglio, L. (2006). Cortical plasticity following surgical extension of lower limbs. *NeuroImage*, 30(1), 172-183.

Dosey, M. A., & Meisels, M. (1969). Personal space and self-protection. *Journal of personality and social psychology*, 11(2), 93.

Duguid, M. M., & Goncalo, J. A. (2012). Living large: The powerful overestimate their own height. *Psychological Science*, 23(1), 36-40.

Dunbar, R. I. (2011). Evolutionary basis of the social brain. Oxford handbook of social neuroscience. Oxford University Press, Oxford, 28-38.

Dunnewold, R. J., van der Kamp, W., van den Brink, A. M., Stijl, M., & van Dijk, J. G. (1998). Influence of electrode site and size on variability of magnetic evoked potentials. *Muscle & nerve*, 21(12), 1779-1782.

Earls, H. A., Englander, Z. A., & Morris, J. P. (2013). Perception of race-related features modulates neural activity associated with action observation and imitation. *Neuroreport*, 24(8), 410-413.

Fadiga, L., Craighero, L., Buccino, G., & Rizzolatti, G. (2002). Speech listening specifically modulates the excitability of tongue muscles: a TMS study. European *Journal of Neuroscience*, 15(2), 399-402.

Fadiga, L., Craighero, L., & Olivier, E. (2005). Human motor cortex excitability during the perception of others' action. *Current opinion in neurobiology*, 15(2), 213-218.

Fadiga, L., Fogassi, L., Pavesi, G., & Rizzolatti, G. (1995). Motor facilitation during action observation: a magnetic stimulation study. *Journal of Neurophysiology*, 73(6), 2608-2611.

Farina, S., Valeriani, M., Rosso, T., Aglioti, S., Tamburin, S., Fiaschi, A., & Tinazzi, M.

(2001). Transient inhibition of the human motor cortex by capsaicin-induced pain. A study with transcranial magnetic stimulation. *Neuroscience letters*, 314(1), 97-101.

Fast, N. J., & Chen, S. (2009). When the boss feels inadequate: Power, incompetence, and aggression. *Psychological Science*, 20(11), 1406-1413.

Fecteau, S., Pascual-Leone, A., & Théoret, H. (2008). Psychopathy and the mirror neuron system: preliminary findings from a non-psychiatric sample. *Psychiatry research*, 160(2), 137-144.

Fecteau, S., Tormos, J. M., Gangitano, M., Théoret, H., & Pascual-Leone, A. (2010). Modulation of cortical motor outputs by the symbolic meaning of visual stimuli. *European journal of neuroscience*, 32(1), 172-177.

Fiske, S. T. (1993). Social cognition and social perception. *Annual review of psychology*, 44(1), 155-194.

Fleming, S. M., Thomas, C. L., & Dolan, R. J. (2010). Overcoming status quo bias in the human brain. *Proceedings of the national Academy of Sciences*, 107(13), 6005-6009.

Florack, A., Keller, J., & Palcu, J. (2013). Regulatory focus in economic contexts. *Journal of Economic Psychology*, 38, 127-137.

Fox, E., Russo, R., & Dutton, K. (2002). Attentional bias for threat: Evidence for delayed disengagement from emotional faces. *Cognition & emotion*, 16(3), 355-379.

Franca, M., Turella, L., Canto, R., Brunelli, N., Allione, L., Andreasi, N. G., ... & Fadiga, L. (2012). Corticospinal facilitation during observation of graspable objects: a transcranial magnetic stimulation study. *PLoS One*, 7(11), e49025.

Freeman, J. B., Ma, Y., Han, S., & Ambady, N. (2013). Influences of culture and visual context on real-time social categorization. *Journal of experimental social psychology*, 49(2), 206-210.

French, J. R., Raven, B., & Cartwright, D. (1959). The bases of social power. Classics of organization theory, 7.

Furubayashi, T., Ugawa, Y., Terao, Y., Hanajima, R., Sakai, K., Machii, K., ... & Kanazawa, I. (2000). The human hand motor area is transiently suppressed by an unexpected auditory stimulus. *Clinical neurophysiology*, 111(1), 178-183.

Galinsky, A. D., Gruenfeld, D. H., & Magee, J. C. (2003). From power to action. *Journal of personality and social psychology*, 85(3), 453.

Gallese, V., Fadiga, L., Fogassi, L., & Rizzolatti, G. (1996). Action recognition in the premotor cortex. *Brain*, 119(2), 593-609.

Gallese, V., Gernsbacher, M. A., Heyes, C., Hickok, G., & Iacoboni, M. (2011). Mirror neuron forum. *Perspectives on Psychological Science*, 6(4), 369-407.

Gallese, V., & Goldman, A. (1998). Mirror neurons and the simulation theory of mind-reading. *Trends in cognitive sciences*, 2(12), 493-501.

Gangitano, M., Mottaghy, F. M., & Pascual-Leone, A. (2001). Phase-specific modulation of cortical motor output during movement observation. *Neuroreport*, 12(7), 1489-1492

Gangitano, M., Mottaghy, F. M., & Pascual-Leone, A. (2004). Modulation of premotor mirror neuron activity during observation of unpredictable grasping movements. *European Journal of Neuroscience*, 20(8), 2193-2202.

Gazzola, V., Rizzolatti, G., Wicker, B., & Keysers, C. (2007). The anthropomorphic brain: the mirror neuron system responds to human and robotic actions. *NeuroImage*, 35(4), 1674-1684.

Gelli, F., Del Santo, F., Popa, T., Mazzocchio, R., & Rossi, A. (2007). Factors influencing the relation between corticospinal output and muscle force during voluntary contractions. *European Journal of Neuroscience*, 25(11), 3469-3475.

Gelman, A., & Hill, J. (2006). Data analysis using regression and multilevel/hierarchical models. Cambridge University Press.

Gibson, J. J. (1977). The Theory of Affordances. In: Shaw, R.E., Bransford, J. (Eds.), Perceiving, acting, and knowing: Toward an ecological psychology. Lawrence Erlbaum Associates, New York, 62-82.

Gibson, J. J. (1979). The ecological approach to visual perception. Houghton-Mifflin Co, Boston.

Giessner, S. R., & Schubert, T. W. (2007). High in the hierarchy: How vertical location and judgments of leaders' power are interrelated. *Organizational Behavior and Human Decision Processes*, 104(1), 30-44.

Grafton, S. T., Fadiga, L., Arbib, M. A., & Rizzolatti, G. (1997). Premotor cortex activation during observation and naming of familiar tools. *Neuroimage*, 6(4), 231-236.

Graziano, M. S., & Cooke, D. F. (2006). Parieto-frontal interactions, personal space, and defensive behavior. *Neuropsychologia*, 44(6), 845-859.

Graziano, M. S., Yap, G. S., & Gross, C. G. (1994). Coding of visual space by premotor neurons. SCIENCE-NEW YORK THEN WASHINGTON-, 1054-1054.

Grèzes, J., Tucker, M., Armony, J., Ellis, R., & Passingham, R. E. (2003). Objects automatically potentiate action: an fMRI study of implicit processing. *European Journal of Neuroscience*, 17(12), 2735-2740.

Groppa, S., Oliviero, A., Eisen, A., Quartarone, A., Cohen, L. G., Mall, V., ... & Rossini, P. M. (2012). A practical guide to diagnostic transcranial magnetic stimulation: report of an IFCN committee. *Clinical Neurophysiology*, 123(5), 858-882.

Groppa, S., Schlaak, B. H., Münchau, A., Werner-Petroll, N., Dünnweber, J., Bäumer, T., ... & Siebner, H. R. (2012). The human dorsal premotor cortex facilitates the excitability of ipsilateral primary motor cortex via a short latency cortico-cortical route. *Human brain mapping*, 33(2), 419-430.

Güth, W., Schmittberger, R., & Schwarze, B. (1982). An experimental analysis of ultimatum bargaining. *Journal of economic behavior & organization*, 3(4), 367-388.

Gutsell, J. N., & Inzlicht, M. (2010). Empathy constrained: Prejudice predicts reduced mental simulation of actions during observation of outgroups. *Journal of experimental social psychology*, 46(5), 841-845.

Gutsell, J. N., & Inzlicht, M. (2013). Using EEG mu-suppression to explore group biases in motor resonance. Neuroscience of Prejudice and Intergroup Relations, eds B. Derks, D. Scheepers, and N. Ellemers (Milton Park: Psychology Press), 279-297.

Hajcak, G., Molnar, C., George, M. S., Bolger, K., Koola, J., & Nahas, Z. (2007). Emotion facilitates action: a transcranial magnetic stimulation study of motor cortex excitability during picture viewing. *Psychophysiology*, 44(1), 91-97.

Hauk, O., Johnsrude, I., & Pulvermüller, F. (2004). Somatotopic representation of action words in human motor and premotor cortex. *Neuron*, 41(2), 301-307.

Hayden, B. Y., Heilbronner, S. R., Pearson, J. M., & Platt, M. L. (2011). Surprise signals in anterior cingulate cortex: neuronal encoding of unsigned reward prediction errors driving adjustment in behavior. *Journal of Neuroscience*, 31(11), 4178-4187.

Head, H., Holmes H.G. (1911–1912). Sensory disturbances from cerebral lesions. *Brain*. (34), 102–254.

Hediger, H. (1955). Studies of the psychology and behavior of captive animals in zoos and circuses.

Henrich, J., McElreath, R., Barr, A., Ensminger, J., Barrett, C., Bolyanatz, A., ... & Lesorogol, C. (2006). Costly punishment across human societies. *Science*, 312(5781), 1767-1770.

Hertwig, R., & Ortmann, A. (2001). Experimental practices in economics: A methodological challenge for psychologists?. *Behavioral and Brain Sciences*, 24(3), 383-403.

Hess, C. W., Mills, K. R., & Murray, N. M. (1987). Responses in small hand muscles from magnetic stimulation of the human brain. *The Journal of physiology*, 388(1), 397-419.

Hesse, M. D., Sparing, R., & Fink, G. R. (2009). End or means—the “what” and “how” of observed intentional actions. *Journal of cognitive neuroscience*, 21(4), 776-790.

Heyes, C. (2010). Where do mirror neurons come from?. *Neuroscience & Biobehavioral Reviews*, 34(4), 575-583.

Higgins, E. T. (1997). Beyond pleasure and pain. *American Psychologist*, 52(12), 1280.

Higgins, E. T. (1998). Promotion and prevention: Regulatory focus as a motivational principle. *Advances in Experimental Social Psychology*, 30, 1-46.

Higgins, E. T., Higgins, C. J., Crowe, E., & Hymes, C. (1994). Ideal versus ought predilections for approach and avoidance distinct self-regulatory systems. *Journal of Personality and Social Psychology*, 66(2), 276.

Hickok, G. (2009). Eight problems for the mirror neuron theory of action understanding in monkeys and humans. *Journal of cognitive neuroscience*, 21(7), 1229-1243.

Hickok, G., & Hauser, M. (2010). (Mis) understanding mirror neurons. *Current Biology*, 20(14), R593-R594.

Hoffman, E., McCabe, K., & Smith, V. L. (1996). Social distance and other-regarding behavior in dictator games. *The American Economic Review*, 86(3), 653-660.

Hogeveen, J., & Obhi, S. S. (2012). Social interaction enhances motor resonance for observed human actions. *Journal of Neuroscience*, 32(17), 5984-5989.

Hollmann, M., Rieger, J. W., Baecke, S., Lützkendorf, R., Müller, C., Adolf, D., & Bernarding, J. (2011). Predicting decisions in human social interactions using real-time fMRI and pattern classification. *PLoS One*, 6(10), e25304.

Holmes, N. P. (2012). Does tool use extend peripersonal space? A review and re-analysis. *Experimental brain research*, 218(2), 273-282.

Holmes, N. P., & Spence, C. (2004). The body schema and multisensory representation (s) of peripersonal space. *Cognitive processing*, 5(2), 94-105.

Huang, J. Y., Ackerman, J. M., & Bargh, J. A. (2013). Superman to the rescue: Simulating physical invulnerability attenuates exclusion-related interpersonal biases. *Journal of Experimental Social Psychology*, 49(3), 349-354.

Hunley, S. B., Marker, A. M., & Lourenco, S. F. (2017). Individual differences in the flexibility of peripersonal space. *Experimental psychology*, 64(1), 49-55.

Iacoboni, M. (2005). Neural mechanisms of imitation. *Current Opinion in Neurobiology*, 15(6), 632-637.

Iacoboni, M., Molnar-Szakacs, I., Gallese, V., Buccino, G., Mazziotta, J. C., & Rizzolatti, G. (2005). Grasping the intentions of others with one's own mirror neuron system. *PLoS biology*, 3(3), e79.

Idson, L. C., Liberman, N., & Higgins, E. T. (2000). Distinguishing gains from nonlosses and losses from nongains: A regulatory focus perspective on hedonic intensity. *Journal of Experimental Social Psychology*, 36(3), 252-274.

Idson, L. C., Liberman, N., & Higgins, E. T. (2004). Imagining how you’d feel: the role of motivational experiences from regulatory fit. *Personality and Social Psychology*, 30(7), 926-937.

Jeannerod, M. (2001). Neural simulation of action: a unifying mechanism for motor cognition. *Neuroimage*, 14(1), S103-S109.

Jeannerod, M., Arbib, M. A., Rizzolatti, G., & Sakata, H. (1995). Grasping objects: the cortical mechanisms of visuomotor transformation. *Trends in neurosciences*, 18(7), 314-320.

Johnson, M. K., Raye, C. L., Mitchell, K. J., Touryan, S. R., Greene, E. J., & Nolen-Hoeksema, S. (2006). Dissociating medial frontal and posterior cingulate activity during self-reflection. *Social Cognitive and Affective Neuroscience*, 1(1), 56-64.

Jola, C., Abedian-Amiri, A., Kuppuswamy, A., Pollick, F. E., & Grosbras, M. H. (2012). Motor simulation without motor expertise: enhanced corticospinal excitability in visually experienced dance spectators. *PloS one*, 7(3), e33343.

Jostmann, N. B., Lakens, D., & Schubert, T. W. (2009). Weight as an embodiment of importance. *Psychological science*, 20(9), 1169-1174.

Julkunen, P., Säisänen, L., Danner, N., Niskanen, E., Hukkanen, T., Mervaala, E., & Könönen, M. (2009). Comparison of navigated and non-navigated transcranial magnetic stimulation for motor cortex mapping, motor threshold and motor evoked potentials. *Neuroimage*, 44(3), 790-795.

Kahneman, D., & Miller, D. T. (1986). Norm theory: Comparing reality to its alternatives. *Psychological review*, 93(2), 136.

Kahneman, D., & Tversky, A. (1979). Prospect theory: An analysis of decision under risk. *Econometrica*, 263-291.

Kahneman, D., Knetsch, J. L., & Thaler, R. H. (1986). Fairness and the assumptions of economics. *Journal of Business*, S285-S300.

Kahneman, D., Knetsch, J. L., & Thaler, R. H. (1991). Anomalies: The endowment effect, loss aversion, and status quo bias. The journal of economic perspectives, 5(1), 193-206.

Kahneman, D., Knetsch, J. L., & Thaler, R. (1986). Fairness as a constraint on profit seeking: entitlements in the market. *American Economic Review*, 76(4), 728-741.

Kammer, T., Beck, S., Thielscher, A., Laubis-Herrmann, U., & Topka, H. (2001). Motor thresholds in humans: a transcranial magnetic stimulation study comparing different pulse waveforms, current directions and stimulator types. *Clinical neurophysiology*, 112(2), 250-258.

Kaneko, K., Kawai, S., Fuchigami, Y., Morita, H., & Ofuji, A. (1996). The effect of current direction induced by transcranial magnetic stimulation on the corticospinal excitability in human brain. *Electroencephalography and Clinical Neurophysiology/Electromyography and Motor Control*, 101(6), 478-482.

Kaplan, J. T., & Iacoboni, M. (2006). Getting a grip on other minds: Mirror neurons, intention understanding, and cognitive empathy. *Social neuroscience*, 1(3-4), 175-183.

Kapogiannis, D., Campion, P., Grafman, J., & Wassermann, E. M. (2008). Reward-related activity in the human motor cortex. *European Journal of Neuroscience*, 27(7), 1836-1842.

Kaye, H., & Pearce, J. M. (1984). The strength of the orienting response during Pavlovian conditioning. *Journal of Experimental Psychology: Animal Behavior Processes*, 10(1), 90.

Keel, J. C., Smith, M. J., & Wassermann, E. M. (2001). A safety screening questionnaire for transcranial magnetic stimulation. *Clinical neurophysiology*, 112(4), 720.

Keltner, D., Gruenfeld, D. H., & Anderson, C. (2003). Power, approach, and inhibition. *Psychological review*, 110(2), 265.

Kernell, D., & Chien-Ping, W. U. (1967). Responses of the pyramidal tract to stimulation of the baboon's motor cortex. *The Journal of physiology*, 191(3), 653-672.

Kiers, L., Cros, D., Chiappa, K. H., & Fang, J. (1993). Variability of motor potentials evoked by transcranial magnetic stimulation. *Electroencephalography and Clinical Neurophysiology/Evoked Potentials Section*, 89(6), 415-423.

Kinzler, K. D., Shutts, K., & Correll, J. (2010). Priorities in social categories. *European Journal of Social Psychology*, 40(4), 581-592.

Kirk, U., Harvey, A., & Montague, P. R. (2011). Domain expertise insulates against judgment bias by monetary favors through a modulation of ventromedial prefrontal cortex. *Proceedings of the National Academy of Sciences*, 108(25), 10332-10336.

Klein-Flügge, M. C., Nobbs, D., Pitcher, J. B., & Bestmann, S. (2013). Variability of human corticospinal excitability tracks the state of action preparation. *Journal of Neuroscience*, 33(13), 5564-5572.

Kobayashi, M., & Pascual-Leone, A. (2003). Transcranial magnetic stimulation in neurology. *The Lancet Neurology*, 2(3), 145-156.

Koch, G., Franca, M., Albrecht, U. V., Caltagirone, C., & Rothwell, J. C. (2006). Effects of paired pulse TMS of primary somatosensory cortex on perception of a peripheral electrical stimulus. *Experimental brain research*, 172(3), 416-424.

Koch, G., Oliveri, M., Cheeran, B., Ruge, D., Gerfo, E. L., Salerno, S., ... & Rothwell, J. C. (2008). Hyperexcitability of parietal-motor functional connections in the intact left-hemisphere of patients with neglect. *Brain*, 131(12), 3147-3155.

Kourtis, D., Sebanz, N., & Knoblich, G. (2010). Favouritism in the motor system: social interaction modulates action simulation. *Biology Letters*, rsbl20100478.

Kuhnen, C. M., & Knutson, B. (2005). The neural basis of financial risk taking. *Neuron*, 47(5), 763-770

Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2015). lmerTest: tests in linear mixed effects models. R package version 2.0-29.

Làdavas, E. (2002). Functional and dynamic properties of visual peripersonal space. *Trends in cognitive sciences*, 6(1), 17-22.

Làdavas, E., Carletti, M., & Gori, G. (1994). Automatic and voluntary orienting of attention in patients with visual neglect: Horizontal and vertical dimensions. *Neuropsychologia*, 32(10), 1195-1208.

Lammers, J., Dubois, D., Rucker, D. D., & Galinsky, A. D. (2017). Ease of Retrieval Moderates the Effects of Power: Implications for the Replicability of Power Recall Effects. *Social Cognition*, 35(1), 1-17.

Lane, A. R., Ball, K., Smith, D. T., Schenk, T., & Ellison, A. (2013). Near and far space: understanding the neural mechanisms of spatial attention. *Human brain mapping*, 34(2), 356-366.

Lang, P. J., Bradley, M. M., & Cuthbert, B. N. (1990). Emotion, attention, and the startle reflex. *Psychological Review*, 97(3), 377.

Lemon, R. N., Johansson, R. S., & Westling, G. (1995). Corticospinal control during reach, grasp, and precision lift in man. *Journal of Neuroscience*, 15(9), 6145-6156.

Leung, M. K., Chan, C. C., Yin, J., Lee, C. F., So, K. F., & Lee, T. M. (2015). Enhanced amygdala–cortical functional connectivity in meditators. *Neuroscience Letters*, 590, 106-110.

Liew, S. L., Han, S., & Aziz-Zadeh, L. (2011). Familiarity modulates mirror neuron and mentalizing regions during intention understanding. *Human brain mapping*, 32(11), 1986-1997.

Linkenauger, S. A., Witt, J. K., Stefanucci, J. K., Bakdash, J. Z., & Proffitt, D. R. (2009). The effects of handedness and reachability on perceived distance. *Journal of Experimental Psychology: Human Perception and Performance*, 35(6), 1649.

Liuzza, M. T., Candidi, M., Sforza, A. L., & Aglioti, S. M. (2014). Harm avoiders suppress motor resonance to observed immoral actions. *Social cognitive and affective neuroscience*, 10(1), 72-77.

Longo, M. R., & Lourenco, S. F. (2006). On the nature of near space: Effects of tool use and the transition to far space. *Neuropsychologia*, 44(6), 977-981.

Longo, M. R., & Lourenco, S. F. (2007). Space perception and body morphology: extent of near space scales with arm length. *Experimental brain research*, 177(2), 285-290.

Loporto, M., Holmes, P. S., Wright, D. J., & McAllister, C. J. (2013). Reflecting on mirror mechanisms: motor resonance effects during action observation only present with low-intensity transcranial magnetic stimulation. *PLoS One*, 8(5), e64911.

Losin, E. A. R., Iacoboni, M., Martin, A., Cross, K. A., & Dapretto, M. (2012). Race modulates neural activity during imitation. *Neuroimage*, 59(4), 3594-3603.

Lourenco, S. F., & Longo, M. R. (2009). The plasticity of near space: Evidence for contraction. *Cognition*, 112(3), 451-456.

Maeda, F., Keenan, J. P., Tormos, J. M., Topka, H., & Pascual-Leone, A. (2000). Modulation of corticospinal excitability by repetitive transcranial magnetic stimulation. *Clinical Neurophysiology*, 111(5), 800-805.

Maeda, F., Kleiner-Fisman, G., & Pascual-Leone, A. (2002). Motor facilitation while observing hand actions: specificity of the effect and role of observer's orientation. *Journal of Neurophysiology*, 87(3), 1329-1335.

Magee, J. C., & Galinsky, A. D. (2008). 8 Social Hierarchy: The Self-Reinforcing Nature of Power and Status. *Academy of Management annals*, 2(1), 351-398.

Magee, J. C., Galinsky, A. D., & Gruenfeld, D. H. (2007). Power, propensity to negotiate, and moving first in competitive interactions. *Personality and Social Psychology Bulletin*, 33(2), 200-212.

Magistris, M. R., Rösler, K. M., Truffert, A., & Myers, J. P. (1998). Transcranial stimulation excites virtually all motor neurons supplying the target muscle. A demonstration and a method improving the study of motor evoked potentials. *Brain: a journal of neurology*, 121(3), 437-450.

Maister, L., Cardini, F., Zamariola, G., Serino, A., & Tsakiris, M. (2015). Your place or mine: Shared sensory experiences elicit a remapping of peripersonal space. *Neuropsychologia*, 70, 455-461.

Maister, L., Sebanz, N., Knoblich, G., & Tsakiris, M. (2013). Experiencing ownership over a dark-skinned body reduces implicit racial bias. *Cognition*, 128(2), 170-178.

Makin, T. R., Holmes, N. P., & Zohary, E. (2007). Is that near my hand? Multisensory representation of peripersonal space in human intraparietal sulcus. *Journal of Neuroscience*, 27(4), 731-740.

Makin, T. R., Holmes, N. P., Brozzoli, C., Rossetti, Y., & Farnè, A. (2009). Coding of visual space during motor preparation: approaching objects rapidly modulate corticospinal excitability in hand-centered coordinates. *Journal of Neuroscience*, 29(38), 11841-11851.

Mange, J., Chun, W. Y., Sharvit, K., & Belanger, J. J. (2012). Thinking about Arabs and Muslims makes Americans shoot faster: Effects of category accessibility on aggressive responses in a shooter paradigm. *European Journal of Social Psychology*, 42(5), 552-556.

Maravita, A., & Iriki, A. (2004). Tools for the body (schema). *Trends in cognitive sciences*, 8(2), 79-86.

Marshall, P. J., & Meltzoff, A. N. (2014). Neural mirroring mechanisms and imitation in human infants. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 369(1644), 20130620.

Martinez, H. D. R. (2015). phia: Post-Hoc Interaction Analysis. R package version 0.2-0.

Masuda, T., Ellsworth, P. C., Mesquita, B., Leu, J., Tanida, S., & Van de Veerdonk, E. (2008). Placing the face in context: cultural differences in the perception of facial emotion. *Journal of personality and social psychology*, 94(3), 365.

Matuschek, H., Kliegl, R., Vasishth, S., Baayen, H., & Bates, D. (2015). Balancing type I error and power in linear mixed models. arXiv preprint arXiv:1511.01864.

Mc Cabe, S. I., Villalta, J. I., Saunier, G., Grafton, S. T., & Della-Maggiore, V. (2014). The relative influence of goal and kinematics on corticospinal excitability depends on the information provided to the observer. *Cerebral Cortex*, bhu029.

Mennemeier, M., Wertman, E., & Heilman, K. M. (1992). Neglect of near peripersonal space: Evidence for multidirectional attentional systems in humans. *Brain*, 115(1), 37-50.

Menon, P., Geevasinga, N., Yiannikas, C., Howells, J., Kiernan, M. C., & Vucic, S. (2015). Sensitivity and specificity of threshold tracking transcranial magnetic stimulation for diagnosis of amyotrophic lateral sclerosis: a prospective study. *The Lancet Neurology*, 14(5), 478-484.

Michael, J., Sandberg, K., Skewes, J., Wolf, T., Blicher, J., Overgaard, M., & Frith, C. D. (2014). Continuous theta-burst stimulation demonstrates a causal role of premotor homunculus in action understanding. *Psychological Science*, 25(4), 963-972.

Mills, K. R., Boniface, S. J., & Schubert, M. (1992). Magnetic brain stimulation with a double coil: the importance of coil orientation. *Electroencephalography and Clinical Neurophysiology/Evoked Potentials Section*, 85(1), 17-21.

Minio-Paluello, I., Avenanti, A., & Aglioti, S. M. (2006). Left hemisphere dominance in reading the sensory qualities of others' pain?. *Social Neuroscience*, 1(3-4), 320-333.

Miniussi, C., & Thut, G. (2010). Combining TMS and EEG offers new prospects in cognitive neuroscience. *Brain topography*, 22(4), 249.

Mogenson, G. J., Jones, D. L., & Yim, C. Y. (1980). From motivation to action: functional interface between the limbic system and the motor system. *Progress in Neurobiology*, 14(2), 69-97.

Molenberghs, P. (2013). The neuroscience of in-group bias. *Neuroscience & Biobehavioral Reviews*, 37(8), 1530-1536.

Molenberghs, P., Cunnington, R., & Mattingley, J. B. (2012). Brain regions with mirror properties: a meta-analysis of 125 human fMRI studies. *Neuroscience & Biobehavioral Reviews*, 36(1), 341-349.

Montagna, M., Cerri, G., Borroni, P., & Baldissera, F. (2005). Excitability changes in human corticospinal projections to muscles moving hand and fingers while viewing a reaching and grasping action. *European Journal of Neuroscience*, 22(6), 1513-1520.

Murata, A., Fadiga, L., Fogassi, L., Gallese, V., Raos, V., & Rizzolatti, G. (1997). Object representation in the ventral premotor cortex (area F5) of the monkey. *Journal of neurophysiology*, 78(4), 2226-2230.

Murata, A., Gallese, V., Luppino, G., Kaseda, M., & Sakata, H. (2000). Selectivity for the shape, size and orientation of objects in the hand-manipulation-related neurons in the anterior intraparietal (AIP) area of the macaque. *Journal of Neurophysiology*, 83, 2580-2601.

Murphy, R. O., Ackermann, K. A., & Handgraaf, M. (2011). Measuring social value orientation. *Judgment and Decision Making*, 6(8), 771-781.

Naish, K. R., Houston-Price, C., Bremner, A. J., & Holmes, N. P. (2014). Effects of action observation on corticospinal excitability: Muscle specificity, direction, and timing of the mirror response. *Neuropsychologia*, 64, 331-348.

Nakamura, H., Kitagawa, H., Kawaguchi, Y., & Tsuji, H. (1996). Direct and indirect activation of human corticospinal neurons by transcranial magnetic and electrical stimulation. *Neuroscience letters*, 210(1), 45-48.

Nakamura, H., Kitagawa, H., Kawaguchi, Y., & Tsuji, H. (1997). Intracortical facilitation and inhibition after transcranial magnetic stimulation in conscious humans. *The Journal of physiology*, 498(3), 817-823.

Newman-Norlund, R., van Schie, H. T., van Hoek, M. E., Cuijpers, R. H., & Bekkering, H. (2010). The role of inferior frontal and parietal areas in differentiating meaningful and meaningless object-directed actions. *Brain research*, 1315, 63-74.

Nicolle, A., Fleming, S. M., Bach, D. R., Driver, J., & Dolan, R. J. (2011). A regret-induced status quo bias. *Journal of Neuroscience*, 31(9), 3320-3327.

Nitsche, M. A., & Paulus, W. (2000). Excitability changes induced in the human motor cortex by weak transcranial direct current stimulation. *The Journal of physiology*, 527(3), 633-639.

Noel, J. P., Pfeiffer, C., Blanke, O., & Serino, A. (2015). Peripersonal space as the space of the bodily self. *Cognition*, 144, 49-57.

Nogueira-Campos, A. A., Saunier, G., Della-Maggiore, V., De Oliveira, L. A., Rodrigues, E. C., & Vargas, C. D. (2016). Observing grasping actions directed to emotion-laden objects: effects upon corticospinal excitability. *Frontiers in Human Neuroscience*, 10.

Oberman, L. M., Pineda, J. A., & Ramachandran, V. S. (2007). The human mirror neuron system: a link between action observation and social skills. *Social cognitive and affective neuroscience*, 2(1), 62-66.

Obhi, S. S., Swiderski, K. M., & Brubacher, S. P. (2012). Induced power changes the sense of agency. *Consciousness and cognition*, 21(3), 1547-1550.

Öhman, A. (1986). Face the beast and fear the face: Animal and social fears as prototypes for evolutionary analyses of emotion. Psychophysiology, 23(2), 123-145.

Öhman, A., Flykt, A., & Esteves, F. (2001). Emotion drives attention: detecting the snake in the grass. *Journal of experimental psychology: general*, 130(3), 466.

Ohno, K., Higashi, T., Sugawara, K., Ogahara, K., Funase, K., & Kasai, T. (2011). Excitability changes in the human primary motor cortex during observation with motor imagery of chopstick use. *Journal of Physical Therapy Science*, 23(5), 703-706.

Oldfield, R. C. (1971). The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia*, 9(1), 97-113.

Oliveri, M., Babiloni, C., Filippi, M. M., Caltagirone, C., Babiloni, F., Cicinelli, P., ... & Rossini, P. M. (2003). Influence of the supplementary motor area on primary motor cortex excitability during movements triggered by neutral or emotionally unpleasant visual cues. *Experimental Brain Research*, 149(2), 214-221.

Oliveri, M., Finocchiaro, C., Shapiro, K., Gangitano, M., Caramazza, A., & Pascual-Leone, A. (2004). All talk and no action: a transcranial magnetic stimulation study of motor cortex activation during action word production. *Journal of Cognitive Neuroscience*, 16(3), 374-381.

Palminteri, S., Justo, D., Jauffret, C., Pavlicek, B., Dauta, A., Delmaire, C., ... & Pessiglione, M. (2012). Critical roles for anterior insula and dorsal striatum in punishment-based avoidance learning. *Neuron*, 76(5), 998-1009.

Park, S. H., Ku, J., Kim, J. J., Jang, H. J., Kim, S. Y., Kim, S. H., ... & Kim, S. I. (2009). Increased personal space of patients with schizophrenia in a virtual social environment. *Psychiatry research*, 169(3), 197-202.

Patton, H. D., & Amassian, V. E. (1954). Single-and multiple-unit analysis of cortical stage of pyramidal tract activation. *Journal of Neurophysiology*, 17(4), 345-363.

Paulus, W., Classen, J., Cohen, L. G., Large, C. H., Di Lazzaro, V., Nitsche, M., ... & Ziemann, U. (2008). State of the art: pharmacologic effects on cortical excitability measures tested by transcranial magnetic stimulation. *Brain stimulation*, 1(3), 151-163.

Pavan, G., Dalmaso, M., Galfano, G., & Castelli, L. (2011). Racial group membership is associated to gaze-mediated orienting in Italy. *PLoS One*, 6(10), e25608.

Payne, B. K. (2001). Prejudice and perception: the role of automatic and controlled processes in misperceiving a weapon. *Journal of personality and social psychology*, 81(2), 181.

Pazzaglia, M., Galli, G., Scivoletto, G., & Molinari, M. (2013). A functionally relevant tool for the body following spinal cord injury. *PLoS One*, 8(3), e58312.

Peck, T. C., Seinfeld, S., Aglioti, S. M., & Slater, M. (2013). Putting yourself in the skin of a black avatar reduces implicit racial bias. *Consciousness and cognition*, 22(3), 779-787.

Pellicciari, M. C., Brignani, D., & Miniussi, C. (2013). Excitability modulation of the motor system induced by transcranial direct current stimulation: a multimodal approach. *Neuroimage*, 83, 569-580.

Pellicciari, M. C., Miniussi, C., Ferrari, C., Koch, G., & Bortoletto, M. (2016). Ongoing cumulative effects of single TMS pulses on corticospinal excitability: an intra-and inter-block investigation. *Clinical Neurophysiology*, 127(1), 621-628.

Perez, M. A., Lungholt, B. K., Nyborg, K., & Nielsen, J. B. (2004). Motor skill training induces changes in the excitability of the leg cortical area in healthy humans. *Experimental brain research*, 159(2), 197-205.

Pessiglione, M., Seymour, B., Flandin, G., Dolan, R. J., & Frith, C. D. (2006). Dopamine-dependent prediction errors underpin reward-seeking behaviour in humans. *Nature*, 442(7106), 1042-1045.

Phillips, J. C., & Ward, R. (2002). SR correspondence effects of irrelevant visual affordance: Time course and specificity of response activation. *Visual cognition*, 9(4-5), 540-558.

Pisoni, A., Gerfo, E.L., Ottone, S., Ponzano, F., Zarri, L., Vergallito, A., & Lauro, L.J.R. (2014). Fair play doesn’t matter: MEP modulation as a neurophysiological signature of status quo bias in economic interactions. *NeuroImage*, 101, 150-158.

Pitzalis, S., Di Russo, F., Spinelli, D., & Zoccolotti, P. (2001). Influence of the radial and vertical dimensions on lateral neglect. *Experimental Brain Research*, 136(3).

Pitzalis, S., Spinelli, D., & Zoccolotti, P. (1997). Vertical neglect: Behavioral and electrophysiological data. *Cortex*, 33(4), 679-688.

Proffitt, D. R., Stefanucci, J., Banton, T., & Epstein, W. (2003). The role of effort in perceiving distance. *Psychological Science*, 14(2), 106-112.

Raos, V., Umiltá, M. A., Gallese, V., & Fogassi, L. (2004). Functional properties of grasping-related neurons in the dorsal premotor area F2 of the macaque monkey. *Journal of neurophysiology*, 92(4), 1990-2002.

Raos, V., Umiltá, M. A., Murata, A., Fogassi, L., & Gallese, V. (2006). Functional properties of grasping-related neurons in the ventral premotor area F5 of the macaque monkey. *Journal of neurophysiology*, 95(2), 709-729.

Righart, R., & De Gelder, B. (2008). Rapid influence of emotional scenes on encoding of facial expressions: an ERP study. *Social cognitive and affective neuroscience*, 3(3), 270-278.

Rilling, J. K., Sanfey, A. G., Aronson, J. A., Nystrom, L. E., & Cohen, J. D. (2004). The neural correlates of theory of mind within interpersonal interactions. *Neuroimage*, 22(4), 1694-1703.

Rinaldi, L., Gallo, P., Calabrese, M., Ranzato, F., Luise, D., Colavito, D., ... & Ragazzi, E. (2006). Longitudinal analysis of immune cell phenotypes in early stage multiple sclerosis: distinctive patterns characterize MRI-active patients. *Brain*, 129(8), 1993-2007.

Ritov, I., & Baron, J. (1992). Status-quo and omission biases. *Journal of risk and uncertainty*, 5(1), 49-61.

Ritov, I., & Baron, J. (1995). Outcome knowledge, regret, and omission bias. *Organizational Behavior and Human Decision Processes*, 64(2), 119-127.

Rizzolatti, G., Camarda, R., Fogassi, L., Gentilucci, M., Luppino, G., & Matelli, M. (1988). Functional organization of inferior area 6 in the macaque monkey. *Experimental brain research*, 71(3), 491-507.

Rizzolatti, G., & Craighero, L. (2004). The mirror-neuron system. *Annual Review of Neuroscience*, 27, 169-192.

Rizzolatti, G., & Fadiga, L. (1998). Grasping objects and grasping action meanings: the dual role of monkey rostroventral premotor cortex (area F5). *Sensory guidance of movement*, 218, 81-103.

Rizzolatti, G., Fadiga, L., Gallese, V., & Fogassi, L. (1996). Premotor cortex and the recognition of motor actions. *Cognitive brain research*, 3(2), 131-141.

Rizzolatti, G., Fogassi, L., & Gallese, V. (2001). Neurophysiological mechanisms underlying the understanding and imitation of action. *Nature reviews neuroscience*, 2(9), 661-670.

Rizzolatti, G., & Luppino, G. (2001). The cortical motor system. *Neuron*, *31*(6), 889-901.

Rizzolatti, G., Matelli, M., & Pavesi, G. (1983). Deficits in attention and movement following the removal of postarcuate (area 6) and prearcuate (area 8) cortex in macaque monkeys. *Brain*, 106(3), 655-673.

Romani, M., Cesari, P., Urgesi, C., Facchini, S., & Aglioti, S. M. (2005). Motor facilitation of the human cortico-spinal system during observation of bio-mechanically impossible movements. *Neuroimage*, 26(3), 755-763.

Rossetti, A., Romano, D., Bolognini, N., & Maravita, A. (2015). Dynamic expansion of alert responses to incoming painful stimuli following tool use. *Neuropsychologia*, 70, 486-494.

Rossi, S., Hallett, M., Rossini, P. M., Pascual-Leone, A., & Safety of TMS Consensus Group. (2009). Safety, ethical considerations, and application guidelines for the use of transcranial magnetic stimulation in clinical practice and research. *Clinical neurophysiology*, 120(12), 2008-2039.

Rossini, P. M., Burke, D., Chen, R., Cohen, L. G., Daskalakis, Z., Di Iorio, R., ... & Hallett, M. (2015). Non-invasive electrical and magnetic stimulation of the brain, spinal cord, roots and peripheral nerves: basic principles and procedures for routine clinical and research application. An updated report from an IFCN Committee. *Clinical Neurophysiology*, 126(6), 1071-1107.

Rossini, P. M., & Rossi, S. (2007). Transcranial magnetic stimulation Diagnostic, therapeutic, and research potential. *Neurology*, 68(7), 484-488.

Rossini, P. M., & Rossi, S. (1998). Clinical applications of motor evoked potentials. *Electroencephalography and clinical neurophysiology*, 106(3), 180-194.

Rossini, P. M., Barker, A. T., Berardelli, A., Caramia, M. D., Caruso, G., Cracco, R. Q., ... & De Noordhout, A. M. (1994). Non-invasive electrical and magnetic stimulation of the brain, spinal cord and roots: basic principles and procedures for routine clinical application. Report of an IFCN committee. *Electroencephalography and clinical neurophysiology*, 91(2), 79-92.

Rothwell, J. C., Thompson, P. D., Day, B. L., Dick, J. P. R., Kachi, T., Cowan, J. M. A., & Marsden, C. D. (1987). Motor cortex stimulation in intact man: 1. General characteristics of EMG responses in different muscles. *Brain*, 110(5), 1173-1190.

Rozzi, S., Ferrari, P. F., Bonini, L., Rizzolatti, G., & Fogassi, L. (2008). Functional organization of inferior parietal lobule convexity in the macaque monkey: electrophysiological characterization of motor, sensory and *mirror responses and their correlation with cytoarchitectonic areas.* European Journal of Neuroscience, 28(8), 1569-1588.

Rüschemeyer, S. A., Brass, M., & Friederici, A. D. (2007). Comprehending prehending: neural correlates of processing verbs with motor stems. *Journal of cognitive neuroscience*, 19(5), 855-865.

Rusu, C. V., Murakami, M., Ziemann, U., & Triesch, J. (2014). A model of TMS-induced I-waves in motor cortex. *Brain stimulation*, 7(3), 401-414.

Sacheli, L. M., Christensen, A., Giese, M. A., Taubert, N., Pavone, E. F., Aglioti, S. M., & Candidi, M. (2015). Prejudiced interactions: implicit racial bias reduces predictive simulation during joint action with an out-group avatar. *Scientific reports*, 5.

Säisänen, L., Pirinen, E., Teitti, S., Könönen, M., Julkunen, P., Määttä, S., & Karhu, J. (2008). Factors influencing cortical silent period: optimized stimulus location, intensity and muscle contraction. *Journal of neuroscience methods*, 169(1), 231-238.

Sale, M. V., Ridding, M. C., & Nordstrom, M. A. (2007). Factors influencing the magnitude and reproducibility of corticomotor excitability changes induced by paired associative stimulation. *Experimental brain research*, 181(4), 615-626.

Samanez-Larkin, G. R., & Knutson, B. (2015). Decision making in the ageing brain: changes in affective and motivational circuits. *Nature Reviews Neuroscience*, 16(5), 278-289.

Samanez-Larkin, G. R., Gibbs, S. E., Khanna, K., Nielsen, L., Carstensen, L. L., & Knutson, B. (2007). Anticipation of monetary gain but not loss in healthy older adults. *Nature Neuroscience*, 10(6), 787-791.

Samuelson, W., & Zeckhauser, R. (1988). Status quo bias in decision making. *Journal of risk and uncertainty*, 1(1), 7-59.

Sanfey, A. G., Rilling, J. K., Aronson, J. A., Nystrom, L. E., & Cohen, J. D. (2003). The neural basis of economic decision-making in the ultimatum game. *Science*, 300(5626), 1755-1758.

Sartori, L., & Castiello, U. (2013). Shadows in the mirror. *Neuroreport*, 24(2), 63-67.

Sartori, L., Begliomini, C., & Castiello, U. (2013). Motor resonance in left-and right-handers: evidence for effector-independent motor representations. *Frontiers in human neuroscience*, 7.

Sartori, L., Betti, S., & Castiello, U. (2013). Corticospinal excitability modulation during action observation. *Journal of visualized experiments: JoVE*, (82).

Sartori, L., Bucchioni, G., & Castiello, U. (2012). When emulation becomes reciprocity. *Social cognitive and affective neuroscience*, 8(6), 662-669.

Sartori, L., Cavallo, A., Bucchioni, G., & Castiello, U. (2011a). Corticospinal excitability is specifically modulated by the social dimension of observed actions. *Experimental Brain Research*, 211(3-4), 557.

Schubert, T. W. (2005). Your highness: vertical positions as perceptual symbols of power. *Journal of personality and social psychology*, 89(1), 1.

Schutter, D. J., Hofman, D., & Van Honk, J. (2008). Fearful faces selectively increase corticospinal motor tract excitability: a transcranial magnetic stimulation study. *Psychophysiology*, 45(3), 345-348.

Semin, G. R., & Smith, E. R. (2002). Interfaces of social psychology with situated and embodied cognition. *Cognitive Systems Research*, 3(3), 385-396.

Serino, A., Annella, L., & Avenanti, A. (2009). Motor properties of peripersonal space in humans. *PloS one*, 4(8), e6582.

Serino, A., Bassolino, M., Farne, A., & Ladavas, E. (2007). Extended multisensory space in blind cane users. *Psychological science*, 18(7), 642-648.

Serino, A., Canzoneri, E., & Avenanti, A. (2011). Fronto-parietal areas necessary for a multisensory representation of peripersonal space in humans: an rTMS study. *Journal of cognitive neuroscience*, 23(10), 2956-2967.

Seymour, B., Daw, N., Dayan, P., Singer, T., & Dolan, R. (2007). Differential encoding of losses and gains in the human striatum. *Journal of Neuroscience*, 27(18), 4826-4831.

Shah, J., Higgins, T., & Friedman, R. S. (1998). Performance incentives and means: how regulatory focus influences goal attainment. *Journal of Personality and Social Psychology*, 74(2), 285.

Sharon, D., Jancke, D., Chavane, F., Na'aman, S., & Grinvald, A. (2007). Cortical response field dynamics in cat visual cortex. *Cerebral Cortex*, 17(12), 2866-2877.

Shelton, P.A., Bowers, D., & Heilman, K. M. (1990). Peripersonal and vertical neglect. *Brain*, 113(1), 191-205.

Smith, P. K., Jostmann, N. B., Galinsky, A. D., & Van Dijk, W. W. (2008). Lacking power impairs executive functions. *Psychological science*, 19(5), 441-447.

Snyder, M., Tanke, E. D., & Berscheid, E. (1977). Social perception and interpersonal behavior: On the self-fulfilling nature of social stereotypes. *Journal of Personality and social Psychology*, 35(9), 656.

Stadler, W., Ott, D. V., Springer, A., Schubotz, R. I., Schütz-Bosbach, S., & Prinz, W. (2012). Repetitive TMS suggests a role of the human dorsal premotor cortex in action prediction. *Frontiers in human neuroscience*, 6.

Strafella, A. P., & Paus, T. (2000). Modulation of cortical excitability during action observation: a transcranial magnetic stimulation study. *Neuroreport*, 11(10), 2289-2292.

Suzuki, M., Kirimoto, H., Sugawara, K., Oyama, M., Yamada, S., Yamamoto, J. I., ... & Onishi, H. (2014). Motor cortex-evoked activity in reciprocal muscles is modulated by reward probability. *PloS one*, 9(3), e90773.

Swan, J. A., & Pearce, J. M. (1988). The orienting response as an index of stimulus associability in rats. *Journal of Experimental Psychology: Animal Behavior Processes*, 14(3), 292.

Taylor, P. C., Walsh, V., & Eimer, M. (2008). Combining TMS and EEG to study cognitive function and cortico–cortico interactions. *Behavioural brain research*, 191(2), 141-147.

Tajfel, H. (1981). Human groups and social categories: Studies in social psychology. CUP Archive.

Tajfel, H., & Billic, M. (1974). Familiarity and categorization in intergroup behavior. Journal of Experimental Social Psychology, 10(2), 159-170.

Tajfel, H., Billig, M. G., Bundy, R. P., & Flament, C. (1971). Social categorization and intergroup behaviour. *European journal of social psychology*, 1(2), 149-178.

Tamburin, S., Manganotti, P., Zanette, G., & Fiaschi, A. (2001). Cutaneomotor integration in human hand motor areas: somatotopic effect and interaction of afferents. *Experimental brain research*, 141(2), 232-241.

Team, R. C. (2014). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. 2013.

Teneggi, C., Canzoneri, E., di Pellegrino, G., & Serino, A. (2013). Social modulation of peripersonal space boundaries. *Current biology*, 23(5), 406-411.

Thabit, M. N., Nakatsuka, M., Koganemaru, S., Fawi, G., Fukuyama, H., & Mima, T. (2011). Momentary reward induce changes in excitability of primary motor cortex. *Clinical Neurophysiology*, 122(9), 1764-1770

Thaler, R. H., & Johnson, E. J. (1990). Gambling with the house money and trying to break even: The effects of prior outcomes on risky choice. *Management Science*, 36(6), 643-660.

Thickbroom, G. W., Byrnes, M. L., & Mastaglia, F. L. (1999). A model of the effect of MEP amplitude variation on the accuracy of TMS mapping. *Clinical neurophysiology*, 110(5), 941-943.

Thompson, P. D., Day, B. L., Rothwell, J. C., Dressler, D., De Noordhout, A. M., & Marsden, C. D. (1991). Further observations on the facilitation of muscle responses to cortical stimulation by voluntary contraction. *Electroencephalography and Clinical Neurophysiology/Evoked Potentials Section*, 81(5), 397-402.

Todd, G., Rogasch, N. C., Flavel, S. C., & Ridding, M. C. (2009). Voluntary movement and repetitive transcranial magnetic stimulation over human motor cortex. *Journal of Applied Physiology*, 106(5), 1593-1603.

Tomeo, E., Cesari, P., Aglioti, S. M., & Urgesi, C. (2012). Fooling the kickers but not the goalkeepers: behavioral and neurophysiological correlates of fake action detection in soccer. *Cerebral Cortex*, 23(11), 2765-2778.

Trawalter, S., Todd, A. R., Baird, A. A., & Richeson, J. A. (2008). Attending to threat: Race-based patterns of selective attention. *Journal of Experimental Social Psychology*, 44(5), 1322-1327.

Tucker, M., & Ellis, R. (1998). On the relations between seen objects and components of potential actions. *Journal of Experimental Psychology: Human perception and performance*, 24(3), 830.

Tucker, M., & Ellis, R. (2001). The potentiation of grasp types during visual object categorization. *Visual cognition*, 8(6), 769-800.

Tucker, M., & Ellis, R. (2004). Action priming by briefly presented objects. *Acta psychologica*, 116(2), 185-203.

Turner, J. C., Oakes, P. J., Haslam, S. A., & McGarty, C. (1994). Self and collective: Cognition and social context. *Personality and social psychology bulletin*, 20(5), 454-463.

Tversky, A., & Kahneman, D. (1985). The framing of decisions and the psychology of choice. In Environmental Impact Assessment, Technology Assessment, and Risk Analysis (pp. 107-129). Springer Berlin Heidelberg.

Tversky, A., & Kahneman, D. (1991). Loss aversion in riskless choice: A reference-dependent model. *Quarterly Journal of Economics*, 1039-1061.

Umiltà, M. A., Intskirveli, I., Grammont, F., Rochat, M., Caruana, F., Jezzini, A., ... & Rizzolatti, G. (2008). When pliers become fingers in the monkey motor system. *Proceedings of the National Academy of Sciences*, 105(6), 2209-2213.

Umiltà, M. A., Kohler, E., Gallese, V., Fogassi, L., Fadiga, L., Keysers, C., & Rizzolatti, G. (2001). I know what you are doing: A neurophysiological study. *Neuron*, 31(1), 155-165.

Urban, P. P., Solinski, M., Best, C., Rolke, R., Hopf, H. C., & Dieterich, M. (2004). Different short-term modulation of cortical motor output to distal and proximal upper-limb muscles during painful sensory nerve stimulation. *Muscle & nerve*, 29(5), 663-669.

Urgesi, C., Candidi, M., Fabbro, F., Romani, M., & Aglioti, S. M. (2006). Motor facilitation during action observation: topographic mapping of the target muscle and influence of the onlooker's posture. *European Journal of Neuroscience*, 23(9), 2522-2530.

Urgesi, C., Maieron, M., Avenanti, A., Tidoni, E., Fabbro, F., & Aglioti, S. M. (2010). Simulating the future of actions in the human corticospinal system. *Cerebral Cortex*, 20(11), 2511-2521.

Valdés-Conroy, B., Román, F. J., Hinojosa, J. A., & Shorkey, S. P. (2012). So far so good: emotion in the peripersonal/extrapersonal space. *PloS one*, 7(11), e49162.

Valdés-Conroy, B., Sebastián, M., Hinojosa, J. A., Román, F. J., & Santaniello, G. (2014). A close look into the near/far space division: a real-distance ERP study. *Neuropsychologia*, 59, 27-34.

Valchev, N., Zijdewind, I., Keysers, C., Gazzola, V., Avenanti, A., & Maurits, N. M. (2015). Weight dependent modulation of motor resonance induced by weight estimation during observation of partially occluded lifting actions. *Neuropsychologia*, 66, 237-245.

Van't Wout, M., Kahn, R. S., Sanfey, A. G., & Aleman, A. (2005). Repetitive transcranial magnetic stimulation over the right dorsolateral prefrontal cortex affects strategic decision-making. *Neuroreport*, 16(16), 1849-1852.

Vercoulen, J. H., Swanink, C. M., Fennis, J. F., Galama, J. M., van der Meer, J. W., & Bleijenberg, G. (1994). Dimensional assessment of chronic fatigue syndrome. *Journal of psychosomatic research*, 38(5), 383-392.

Vicario, C. M., Rafal, R. D., & Avenanti, A. (2015). Counterfactual thinking affects the excitability of the motor cortex. *Cortex*, 65, 139-148.

Viner, J. (1925). The utility concept in value theory and its critics. *Journal of Political Economy*, 33(6), 638-659.

Vogt, S., & Thomaschke, R. (2007). From visuo-motor interactions to imitation learning: behavioural and brain imaging studies. *Journal of sports sciences*, 25(5), 497-517.

Volz, K. G., Kessler, T., & von Cramon, D. Y. (2009). In-group as part of the self: in-group favoritism is mediated by medial prefrontal cortex activation. *Social neuroscience*, 4(3), 244-260.

Wassermann, E. M. (1998). Risk and safety of repetitive transcranial magnetic stimulation: report and suggested guidelines from the International Workshop on the Safety of Repetitive Transcranial Magnetic Stimulation, June 5–7, 1996. *Electroencephalography and Clinical Neurophysiology/Evoked Potentials Section*, 108(1), 1-16.

Wassermann, E. M. (2002). Variation in the response to transcranial magnetic brain stimulation in the general population. *Clinical Neurophysiology*, 113(7), 1165-1171.

Weiss, P. H., Marshall, J. C., Zilles, K., & Fink, G. R. (2003). Are action and perception in near and far space additive or interactive factors? *Neuroimage*, 18(4), 837-846.

Weiss PH, Marshall JC, Wunderlich G, Tellmann L, Halligan PW, et al. (2000). Neural consequences of acting in near versus far space: a physiological basis for clinical dissociations. *Brain*, 123, 2531–2541.

Williams, J. M. G., Mathews, A., & MacLeod, C. (1996). The emotional Stroop task and psychopathology. *Psychological bulletin*, 120(1), 3.

Williams, J. M. G., Watts, F. N., MacLeod, C., & Mathews, A. (1988). Cognitive psychology and emotional disorders. John Wiley & Sons.

Williams, L. E., & Bargh, J. A. (2008). Experiencing physical warmth promotes interpersonal warmth. *Science,* 322(5901), 606-607.

World Medical Association Declaration of Helsinki. (2013). *Journal of the American Medical Association*, 310(20), 2191.

Wu, Y., & Zhou, X. (2009). The P300 and reward valence, magnitude, and expectancy in outcome evaluation. *Brain Research*, 1286, 114-122.

Wu, Y., Yu, H., Shen, B., Yu, R., Zhou, Z., Zhang, G., ... & Zhou, X. (2014). Neural basis of increased costly norm enforcement under adversity. *Social cognitive and affective neuroscience*, 9(12), 1862-1871.

Wurm, M. F., & Schubotz, R. I. (2012). Squeezing lemons in the bathroom: contextual information modulates action recognition. *Neuroimage*, 59(2), 1551-1559.

Xu, X., Zuo, X., Wang, X., & Han, S. (2009). Do you feel my pain? Racial group membership modulates empathic neural responses. *Journal of Neuroscience*, 29(26), 8525-8529.

Yap, A. J., Mason, M. F., & Ames, D. R. (2013). The powerful size others down: The link between power and estimates of others' size. *Journal of Experimental Social Psychology*, 49(3), 591-594.

Zhou, X., & Wu, Y. (2011). Sharing losses and sharing gains: increased demand for fairness under adversity. *Journal of Experimental Social Psychology*, 47(3), 582-588.