Department of Psychology

An investigation on the effects of social status on motor interactions and performance monitoring in social settings

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Preface

As social species, in our daily lives we continuously interact with our conspecifics to communicate, cooperate or compete for the same resources. Besides the role of cognitive and emotional factors in determining the quality and success of interpersonal interactions, social factors may also play a crucial role. In the present work, I will first describe the results from a research project that aimed at investigating how social status shapes implicit preference, the ability to coordinate with another person and the monitoring of owns' performance. In the second part of the thesis, I will present the results from a study that investigated the neural basis of performance monitoring during motor interactions. More in detail, the first two experiments, reported in chapters 2-3, investigated how the perceived (competence-based) social status of other people influences our implicit preference for them (Study 1) and our ability to coordinate with them while performing joint actions (Study 2). Shifting the perspective from other's to own's status, in the third experiment I have tested the hypothesis that the relative position a person occupies in a competence-based hierarchy influences their autonomic reactivity to positive and negative feedback after correct and error trials during a collective cognitive game (Study 3). In the last study (Study 4) I investigated the causal role of error-related EEG activity (i.e. frontal theta oscillations) in motor adjustment during a human-avatar motor interaction task by means of transcranial Alternating Current Stimulation (tACS).

1. Introduction

1.1 A social neuroscience perspective on social status.

From beehives to human societies, hierarchies are a ubiquitous feature of socially organised groups. A rise in complexity for social structures carries with it an increase in hierarchical differentiation between members. Our closest animal relatives, the great apes, are organised in highly complex social groups, where individuals seek, attain and try to defend their own status. Apes' (and other animal's) strive for a higher status is motivated by the fact that its possession leads to a preferential access to fundamental resources such as food and mating partners (Sapolsky, 2005). Human societies, which are characterised by possibly the highest level of social complexity known in nature, are for the most part intrinsically hierarchical. Among humans too, a low social stance (i.e. a low socioeconomic status) carries with it a reduced access to important resources (Chapais, 2015). However, when it comes to human beings, social status turns from a pure dominance imbalance to a multifaceted concept that encompasses different aspects such as dominance, power, prestige and socioeconomic level (Mattan et al., 2017).

For a long time, the study of human hierarchies has been a prerogative of sociology and social psychology (Ell, 1984; Oldmeadow and Fiske, 2010). In the past few years a growing interest has led neuroscientists to investigate how social status influences social cognition at the neural level. The greatest challenge encountered by scholars approaching this new field indeed was the lack of agreement on the definition of status. Indeed, the word "status" has been used interchangeably to define similar, although not overlapping concepts as prestige, power and dominance. In the attempt to operationalise social status as a subject of empirical research, Mattan and collaborators (Mattan et al., 2017) have proposed a taxonomy that distinguishes between status ("*The relative rank of an individual along one or more social dimensions within a given social hierarchy*"), power ("*One's degree of control over others' resources and/or outcomes*"), prestige ("*Freely conferred deference afforded to an individual on the basis of that individual's virtue or ability*") and dominance ("*Intimidation of others based on physical or social threats*"). Mattan and collaborator's model further distinguishes between antecedents ("*The perceptual cues or person knowledge allowing perceivers to differentiate an individual's hierarchical rank*"), dimensions ("*The domains in which an individual may be ranked such as dominance, prestige, or education/finances*") and consequences (i.e. how social status influences social cognition and behaviour).

Another important distinction needs to be drawn between the effects of the onlooker's status (i.e. the experimental subject) and those of the target's status (i.e. the model or interactor). Regarding the target, several studies have shown that the perceived status of a social target modulates attention (Cheng et al., 2013), memory for faces (Ratcliff et al., 2011), behavioural mimicry (Dalton et al., 2010) and action co-representation effect (Aquino et al., 2016). Similarly, neuroimaging studies have revealed that observing high or low status targets elicit differential neural responses associated with face perception (Santamaria-Garcia et al., 2015), and reward processing (Zink et al., 2008). This last finding is particularly relevant for the present work, as it seems to suggest that, similarly to other primates (Deaner et al., 2005), humans perceive high status individuals as more rewarding. However, whether high status individuals are actually evaluated more positively than, and preferred over, low status ones, it is still a matter of debate. On the other side, other studies have investigated social status from the subject's perspective with the aim of measuring the effects of possessing a high or low status on various neural and behavioural phenomena. Using this approach, it has been shown that subjective socioeconomic status (SES) has deep impact on brain development (Hackman and Farah, 2009) and on brain's functional network organization and anatomy during aging

(Chan et al., 2018). Moreover, participants' status was found to modulate their cortisol response to social threat (Gruenewald et al., 2006). Studies in which the participant's status was intentionally manipulated found that the experience of high or low status influences various aspects of social behaviour and cognition. Relevant for the studies reported in this thesis is that the social status of the observer modulates motor resonance to intransitive actions (Hogeveen et al., 2014) and feedback-related EEG activity in a social task (Boksem et al., 2011).

The present work focussed on prestige-based status (defined here as competence-based social status) and investigated its effects from both the onlooker's and the target's perspective. Competence-based social status is a form of status that individuals can acquire thanks to their outstanding ability in a specific field. Unlike dominance-based status, which is forcibly obtained through real or potential threats, competence-based status is freely conferred to those that are considered worthy of it. From an evolutionary perspective, deference toward highly competent individuals might have evolved as a mean to increase the probability of cultural transmission (Henrich and Gill-White, 2001). In modern society, where "*knowledge is power*", the cultural transmission of skills and information is more crucial than ever. Without denying the fact that also dominance can modulate different aspects of social cognition (not to mention social economic status), in the works presented here I chose to focus on competence-based status as a phenomenon that, in my opinion, more closely reflects everyday dynamics of real-life. Moreover, following the intriguing idea that this form of status might have evolved as a mean for cultural transmission through observation and imitation, I wanted to test the hypothesis that the ability to perform a joint action (which is indeed based on action observation and imitation) is influenced by it. Importantly, the paradigm used in the works here presented offers the opportunity to measure status attribution in a social context, where the contribution of each member, determined by his/her competence, can increase or reduce the group's profit. I feel this paradigm does a good job in recreating in the lab real-life situations, such as those encountered in workplaces or at school, where individuals' competence can make the difference at the group level. The same paradigm was used in Studies 1, 2 and 3. In Study 1 and 2 the status of two targets (i.e. high and low status) was manipulated to measure its contribution to implicit evaluation (Study 1) and to the ability to coordinate to perform a joint action (Study 2). Using the same paradigm, Study 3 manipulated the subject's status and measured how occupying the highest or the lowest position in a competence-based hierarchy modulates autonomic activity following positive and negative feedback.

1.2 The "who" in joint actions: how synchrony performance and hand movements kinematic can inform us on the social nature of the ongoing interaction.

The ability to represent and understand the actions of our conspecifics is of fundamental importance for our daily lives and mediates any form of face-to-face interpersonal interaction. Indeed, a quick and effective processing of other's actions can help us to avoid colliding with them in a busy road, to predict their intentions and to interact with them to achieve a shared goal. It is thus reasonable that perceived interactor's social status, as well as their position with respect to the agent's one, may modulate both other's action understanding (e.g. the meaning of a movement may convey different meaning according to who is performing it) as well as ones' one motor behaviour (e.g. we may move differently when interacting with partners of different social status).

Observed action representation in the human brain involves activity in visual as well as motor areas, including, but not limited to, the so-called mirror neurons system (Rizzolatti and Craghero, 2004; Van Overwalle and Baetens 2009) or Action Observation Network (AON; Avenanti et al., 2013; Gazzola and Keysers 2009; Grafton 2009; Caspers et al. 2010;). Simulation theories (Gallese and Goldman, 1998; Iacoboni et al., 2005) posit that intention understanding during action observation is made possible by the vicarious activation of the motor system. The idea that action simulation may help intention understanding is based on monkey evidence that activity in the motor (Umiltà et al., 2001) and parietal (Fogassi et al., 2005) nodes of the mirror-neurons system, or motor nodes in humans', is anticipatory with respect to the actual phase of an observed action AON (Urgesi et al., 2007; Urgesi et al., 2010; Avenanti et al., 2013), sensitive to observer's motor expertise in the domain of the observed action (Calvo-Merino 2005; 2006, Aglioti et al., 2008) and necessary to recognize deceptive intentions (Tidoni et al., 2013). Accordingly, motion kinematics and behavioural studies have demonstrated that intentions in goal-directed actions are reflected in the kinematics of performed hand movements (Ansuini et al., 2006; 2015) and can be quickly and easily inferred by an external observer (Cavallo et al., 2016; Koul et al., 2018). One interesting question is whether also *social* intentions (rather than object directed ones) are mapped in executed, and inferred from observed, body kinematics. Becchio and colleagues experimentally tested this hypothesis and found different motor patterns for the same action (i.e. grasping and moving an object) depending on whether it involved or not another human agent (Becchio et al., 2008). These results suggest that both social and non-social intentions can be read through the kinematics of observed hand movements.

In recent years, the social neuroscience field has witnessed a methodological shift from an "isolation paradigm" (Becchio et al., 2010), based on the passive observation of social stimuli to a "second person" approach (Schilibach et al., 2013), which emphasises the importance of studying on-line social interactions. In this vein, the investigation of joint actions (i.e. "*any form of social interaction whereby two or more individuals coordinate their actions in space and time to bring about a change in the environment*" (Sebanz et al., 2006a) offers the opportunity to shed light on how the human motor system supports the coordination of owns' and others' movements. Body kinematics during motor interactions can reveal a great deal of information about the mutual relationship between the two agents. On the one side, hand kinematics can reveal subtle and involuntary processes taking place during motor interactions, such as involuntary imitation (Sacheli et al., 2012; 2015). On the other side, hand posture, velocity and movement amplitude can be intentionally used by the co-agents as a mean of sensorimotor communication (Pezzulo et al., 2019) to make themselves more predictable, thus facilitating the interaction. Importantly, both intentional and involuntary variations on movement kinematics can be informative of the social relationship between the two co-agents.

Studies on action observation have revealed that action-simulation related activity in the motor system is sensitive to the social identity of the observed model (Molnar-Szakacs et al., 2007). Similarly, during motor interactions the social identity of the partner was found to shape various kinematic features of participants' hand movements, as well as their ability to synchronise his/her movements with those of the partner (see Introduction of Chapter 3 for an extensive literature review). In this sense, the "who" in joint actions (i.e. who is the person I am interacting with) influences the neural resources triggered by action observation, the kinematics of action performance as a function of the degree to which people integrate their own's and the partner's motor movements into a smooth dyadic motor plan (Sacheli et al., 2018), as well as the extent to which the other's movements are imitated. In Study 2 (Chapter 3) of the present thesis, I will present the results from an experiment that measured how hand kinematics and motor behaviour during an interpersonal motor interaction (i.e. a joint grasping task) are modulated by the interactor's social status.

Besides action understanding and motor communication, also performance monitoring is fundamental for efficient interpersonal interactions in social settings and recent studies have proposed the neural processes dedicated to ones' own action monitoring are also used to monitor the behaviour of an interaction partner.

1.3 Performance monitoring in social settings

As ancient Romans liked to say, *errare humanum est* (To err is human). Indeed, in our everyday life we often commit motor errors, from dialling the wrong phone number to missing a basketball shot. Errors can be useful for learning but, for this to happen, they need to be perceived and remembered. To this end, the human brain is equipped with a performance monitoring system that keeps track of ongoing goal-directed actions as well as of the external context and signals the occurrence of motor errors. FMRI and EEG studies suggest that the performance monitoring system involves the anterior cingulate cortex (ACC), a midline frontal region showing structural and functional connections with sensory and motor areas (see Ullsperger et al., 2014 for review). Error commission elicits specific neurophysiological signatures (error-related negativity, ERN, feedback-related negativity, FRN and positivity error, Pe) that are most likely generated by the ACC (Hermann et al., 2004). These error-related potentials share a common spectral signature in the Theta band (Cavanagh and Frank, 2014). Theta-band oscillations are thought to act as a long-distance signal which communicates the need for cognitive control to motor, sensory and associative areas through neural entrainment (Cavanagh and Frank, 2014). In this way, whenever an error is committed, the performance monitoring system allows the implementation of remedial actions. One interesting aspect is that errors and negative feedback also trigger autonomic responses (Hajcak et al., 2004; 2003; O’Connell et al., 2007; Critchley et al., 2005; Fiehler et al., 2004; van der Veen et al., 2004; Crone et al., 2003). Since activity in the insular cortex, a brain region involved in interoceptive awareness (Zaki et al., 2012), is modulated by error awareness (Klein et al., 2007; Ullsperger et al., 2010), it has been proposed that the autonomic component of error and feedback processing might serve the need of increasing the salience of the perceived error through the instantiation of visceral changes (Hajcak et al., 2003).

Considering that the most part of actions we perform take place in social contexts and that often our errors have consequences on other people, the study of “social errors” seems particularly promising. A recent research line has started to investigate whether the performance monitoring system is also activated by the perception of other people’s errors, showing that behavioural (Castiello et al., 2018) and neural (Miltner et al., 2004; van Schie et al., 2004) signatures of error commission were similarly elicited by committed and observed errors. When two or more people cooperate to achieve a common goal, individual errors have implications for the dyad or group and may require the implementation of remedial actions by the co-agents. In the present thesis, I will report the results from two experiments investigating performance monitoring in social settings from two different perspectives.

In Study 3 (Chapter 4), I have investigated how autonomic responses to performed errors (specifically, to negative feedback) are modulated by the degree to which a member of a group is helping the group with his/her performance (i.e. by his/her social status). The rationale behind Study 3 is that when errors occur in in a social context and affect other peoples’ outcomes, they might perceived as more salient than in a “solo” condition, akin to a football player failing at penalty kick, the effects of his error influencing the whole team. Moreover, the experience of a low social status (i.e. being the worst player in the group) has been found to modulate *neural* responses to negative feedback (Boksem et al., 2011). In Study 3 I have tried to answer the question of whether also *autonomic* responses are modulated by social status.

Study 4 (Chapter 5) investigated the neural basis of behavioural adaptation to “joint errors”, namely errors that occur in the context of joint actions. As in solo actions, joint actions can fail when one of the two co-agents (or both) commits an error or fails to comply with the interaction rules. The ability to interact with other people involves predictions about other’s actions and assumptions about a shared interaction goal. Violations of such predictions might be coded as errors, and often require one of the interaction partners to implement behavioural adaptation to compensate the other’s error. In Study 4 I have investigated the causal role of performance monitoring-related EEG activity (i.e. midfrontal Theta) on human-avatar motor interactions.

1.4 Overview of research methods

1.4.1 Human- human and human-avatar paradigms for motor interactions

Experimental investigations of social interactions in realistic settings can benefit from two different methodologies, each of one carrying its own pros and cons. One possibility for researchers is to use human-human paradigms where experimental subjects are asked to interact with a human partner, often a study confederate. In a classical confederate study, participants are led to believe that the experiment involves two or more subjects, the confederate being one of them. Motor interaction studies have made wide use of confederate subjects (e.g. Fantoni et al., 2016; Becchio et al., 2018). The main benefit of using confederates is the high ecological validity of such a set-up, as the experimental setting closely reproduces real-life encounters. This might be particularly important when the object of study is the effect of a social characteristic (e.g. attitude, perceived similarity, status) on the quality/unfolding of a social interaction. However, human-human paradigms offer a lower level of experimental rigor, since the confederate's behaviour is not under the full control of the experimenter and may be modulated automatically by the interaction itself (Kuhlen et al., 2013). Another possibility is to use virtual reality scenarios where participants interact with human-like virtual partners. Indeed, virtual reality offers the opportunity to create avatars varying in visual appearance (i.e. skin colour, attractiveness), thus allowing the investigation of motor interactions in semi-naturalistic social scenarios, while keeping all other features of their behaviour under experimental control. Studies from our research group have employed virtual reality to investigate motion kinematics and neural correlates of motor interactions in different contexts (Sacheli et al., 2015a; 2015b; Era et al., 2019). In these studies, the hand motion kinematics (i.e. velocity, trajectory, hand posture) of the virtual partner were previously recorded from a human agent while allowing at the same time a full control from the experimenter.

The experiments described in the present work took advantage of both methodologies. In Study 2, which was intended to measure the effects of social status on interactive hand motion kinematics, I chose to use confederates, as a human-human paradigm seemed more adequate for studying the effects of a social variable on motor interactions. Instead in Study 4, participants interacted with a human-like artificial agent in an immersive virtual reality environment. In this case, since no higher-level variable was attributed to the interaction partner, I preferred to opt for a methodology with a higher degree of experimental control.

1.4.2 Transcranial Alternating Current Stimulation (tACS)

Neural activity is essentially oscillatory. The synchronous firing of a population of neurons gives rise to macroscopic oscillations that can be recorded with the EEG. This oscillatory activity occurs at different frequency bands (i.e. number of cycles per second or Hertz), ranging from slow (i.e. Delta, 1-4 Hz, Theta, 4-8 Hz) to fast (Alpha, 8-12 Hz, Gamma, 30-150 Hz). After many decades of EEG research, there is a general consensus on the fact that brain oscillations at different frequency bands may support different neural computations and different cognitive, motor and perceptual processes (Wang, 2010; Fries, 2015). However, EEG results can only provide correlational information, namely that a particular oscillation and cognitive process tend to co-occur, without informing on the causal relationship between the two. One possible way to tackle the relation between a given brain oscillatory activity (in time and location in the brain) and a cognitive function is to modulate oscillatory activity and to measure a correspondent change in some behavioural index linked to the cognitive function under study. Transcranial Alternating Current Stimulation (tACS) is a non-invasive brain stimulation tool that takes advantage of Alternating Current (AC) to modulate endogenous brain oscillations in a frequency-specific manner (Zaehle et al., 2010; Hermann et al., 2016b;

Vossen et al., 2015; Krause et al., 2019). A weak current flow of sinusoidal AC (1-4 mA) is applied on the scalp through two conductive-rubber electrodes. Differently from transcranial Direct Current Stimulation (tDCS), in tACS the current flows back and forth from the two electrodes at the frequency that is set by the stimulator. The effects of tACS on endogenous brain oscillations have been observed in several EEG and MEG studies. It was found that externally applied AC can increase the amplitude of the endogenous targeted frequency (Herrmann et al., 2016b, Thut et al., 2017). Neural entrainment, namely the temporal synchronization of the endogenous oscillatory activity with an external force, has been proposed as a mechanism of action of tACS (Helfrich et al., 2014). One important aspect related to entrainment between systems is the Arnold Tongue phenomenon, which can be described as follows: "*The greater the difference between the internal and the external frequency the stronger the force needed to an external rhythm to entrain an internal oscillation*" (Vosskuhl et al., 2018). For that reason, while many studies have applied tACS at a standard frequency within the band of interest, there is a growing consensus regarding the fact that the stimulation should be delivered at the individual frequency. In Study 4 of the present work, tACS was applied at participant's individual theta and beta frequency, which was extracted from their resting-state EEG recording.

1.4.3 Event-related Heart Rate changes

The autonomic nervous system (ANS) is part of the peripheral nervous system and connects the brain to internal organs (i.e. heart, lungs, stomach) and glands (i.e. salivary) via sympathetic and parasympathetic fibres. While the sympathetic division of the ANS is responsible for fast responses to sudden environmental changes ("fight or flight"), the parasympathetic branch is associated to recuperative functions ("rest and digest"). The sympathetic and parasympathetic branches regulate the functioning of internal organ by increasing/reducing heart rate (i.e. the number of heart beats per minute), increasing/lowering blood pressure and accelerating/slowing gut mobility (Cannon, 1929). The heart is under the joint control of the sympathetic and parasympathetic nerves, which control the beat-to-beat variability in heart rate (Thayer and Lane, 2000; Bernston et al., 2007). Virtually every mental process is accompanied by autonomically-mediated bodily changes. While a plethora of studies exist on the relationship between autonomic reactivity and emotions (see Kreibig, 2010 or Levenson, 2014 for review), less studied are the autonomic correlates of cognitive process. The first report on the observation of cardiac slowing following erroneous responses dates back to 1971 (Danev and De Winter, 1971). From that time, autonomic responses to error and feedback processing have been observed not only in heart rate (Hajcack et al., 2003; 2005) but also in skin conductance response (O'Connell et al., 2007) and pupil diameter (Critchley et al., 2005). With respect to other indexes of autonomic activity, such as skin conductance response, the measurement of heart rate offers the opportunity to capture event-related changes occurring in a relatively short time. Indeed, feedback-related heart rate deceleration has been observed from the inter-beat interval (IBI, the distance between two consecutive heart peaks) following the feedback presentation (Crone et al., 2003; Hajcak et al., 2003, 2004). In Study 3 of the present thesis, heart rate changes following positive and negative feedback were recorded. The analyses focused on four IBIs following the feedback presentation and examined the effects of feedback valence on event-related deceleration and on the subsequent acceleratory return to baseline.

1.4.4 Linear Mixed Models

In recent years, new statistical methods beyond the classical inferential tests (e.g. ANOVA, ANCOVA) have been proposed for data analyses in social and biological sciences. Linear Mixed Models (LMM) involve a mix of fixed (e.g. covariates or factors) and random effects (i.e. random intercepts and slopes). Specifically, LMM include both the effect of the between-subject variance in the dependent variable (random intercept) and the between-subject variance for all main effects and interactions (random slopes) (Bates, 2015). Therefore, LMM allow researchers to estimate the effects of the experimentally manipulated variables while considering the effects of inter-individual variability. Another important feature of LMM is that analyses are carried out on the whole data set rather than on the mean, thus LMM take into account trial-by-trial variations in the dependent variable. In the present study, all datasets were analysed with LMM.

1.5 Overview of hypotheses tested

Study 1 tested the hypothesis that high status individuals are liked more than the low status ones not only at the explicit but also at the implicit level. It was expected that participants engaged in a cooperative game with two previously unacquainted individuals would implicitly evaluate them according to their position in a score-based hierarchy and that this would result in a change in the aesthetic evaluation of neutral visual stimuli paired with them (i.e. affective misattribution: neutral targets preceded by the picture of the high status partner would be rated as more pleasant than to those preceded by the low status one).

In Study 2, the same status-inducing procedure was used to test the hypothesis that participants would show different behavioural and kinematic patterns when coordinating with the high or the low status partner in a joint task. Specifically, it was expected that participants would achieve a better coordination performance with the high status and that they would show increased automatic imitation of his movements.

Study 3 used a slightly different version of the same procedure to test the hypothesis that individuals' autonomic reactivity to negative feedback would be modulated by participants' induced social status. Higher heart rate deceleration was expected to occur after negative feedback when feeling in the low status than in the high status condition.

Finally, Study 4 tested the hypothesis that error-related brain theta oscillations are causally involved in behavioural adaptation following unexpected motor changes in dyadic motor interactions. It was expected that Theta tACS would modulate participants' ability to coordinate their reach-to-press movements with those of a virtual partner, specifically when the virtual partner would operate an unexpected motor correction, thus forcing the participant to a quick behavioural adaptation.

In the following chapters I will describe the studies I have conducted during my PhD in the form of submitted or in preparation manuscripts.

2. Modulation of preference for abstract stimuli following competence-based social status primes (Study 1)

Abstract

In the present study, we measured whether competence-related social status attributed to two unknown individuals affects participants’ implicit reactivity to abstract stimuli primed with the identity of high and low status individuals. Participants were asked to play an interactive game with two (fake) players that gained high vs low status based on their game competence. Before and after the game, a modified version of the Affective Misattribution Procedure (AMP) was administered in which the players’ faces were used as primes of neutral images (i.e. chinese ideogram). There were two different presentation timings for the prime image: 75 ms and 17 ms. After the status-inducing procedure, the evaluation targets preceded by the High Status prime (i.e. best player’s face) were rated as more pleasant than those preceded by the Low Status prime (i.e. worst player’s face). This effect was only found, however, for the 75 ms lasting prime. Moreover, explicit ratings of the primes showed that the High Status player was rated as more intelligent, competent and dominant than the Low Status one. These results indicate that implicit preference and explicit evaluation of unacquainted individuals is rapidly modulated by competence-based social status attribution, thus hinting at the plastic nature of social categorization and, relatedly, the malleability of visual preference.

Introduction

Social status is defined as an individual’s relative position within a group. From military ranks to workplace roles, hierarchy is a fundamental characteristic of human groups and societies, and the ability to infer the status of our conspecifics, which is essential for successful social interactions, seems to be hard-wired in the human brain. Indeed, studies have shown that high-status individuals receive greater attention (Cheng et al., 2013; Dalmaso et al., 2012; Foulsham et al., 2010; Liuzza et al., 2011; Porciello et al., 2016) and are easier to recognize (Ratcliff et al., 2011). In addition, observing a high-status model facilitates perceptual decisions (Santamaria-Garcia et al., 2014), EEG correlates of face processing (N170 amplitude) (Santamaria-Garcia et al., 2015) and EEG correlates of social evaluation (P300 amplitude) (Gyurovski et al., 2018). Social status was found to modulate neural activity in brain regions involved in social evaluation, reward, salience and attention such as the ventromedial and dorsolateral prefrontal cortex (Cloutier et al., 2014; Zink et al., 2008; Marsh et al., 2009). Status has also been used to study the impact of social dimensions on implicit behavioral measures such as automatic imitation (Farmer et al., 2016), evaluative priming (Mattan, et al., 2019) and implicit associations (Shariff & Tracy, 2009).

Less studied are the affective reactions elicited by high or low status targets. Studies from social psychology suggest that high-status individuals are (explicitly) evaluated more positively than low-status individuals (Varnum, 2013; Jost and Burgess, 2000; Cheng et al., 2013) and that they are also more admired and respected (Fiske, Cuddy et al., 2002; Huo and Binning, 2008). Although it is generally accepted that high-status individuals are evaluated more positively than low-status ones, some important exceptions have been reported in the literature. For example, Cloutier and Gyurovsky (2014) found a preferential activation of ventral medial prefrontal cortex (a region associated with person evaluation) when observing high moral status targets compared to low ones. Beside this quite predictable result, they also found the same activation in response to low financial status targets compared to high ones, which suggests that similar neural responses may be associated to high- or low-status individuals evaluation depending on the (negative or positive) social dimension from which status is inferred (e.g. financial vs moral). Similar results were obtained in an EEG study, where the P300 component (the amplitude of which has been associated with the intensity of negative evaluation) was higher for targets high in financial status and low in moral status (Gyurovsky et al., 2018). Similarly, at a subjective level, Fragale and colleagues (2011) found that members of occupations associated with high-power and low-status (e.g. bill collectors or immigration officers) are evaluated negatively (i.e. more dominant and colder). Moreover, members of high-status competitive groups such as Asians and, again, rich people are evaluated as low in warmth (Fiske et al., 2002). This variety of results is extremely informative, as it seems to suggest that different dimensions of status may, indeed, lead to even opposite results in terms of personal evaluation while sharing similar neural responses.

We would like to propose that status-based evaluation of individuals is highly dependent on the degree to which the person's status is perceived as functional to the well-being of the group and on the strategies adopted to attain status. While status achievement in non-human primates is strictly related to dominance (Morgan et al., 2000), humans can use both dominance (i.e. use of force and intimidation) and competence (i.e. demonstration of superior skills and abilities) to gain a privileged position within a group (Cheng et al., 2013). Relevant for the present study is that people who attain status by displaying higher competence are more appreciated by group members than those who adopt a dominance strategy (Cheng et al., 2013). Previous studies that have investigated the impact of social status on implicit preference have mainly focused on groups rather than on individuals. Interestingly, many of these studies found a dissociation between implicit and explicit measures so that while members of high-status groups (e.g. white people, heterosexuals) are more likely to show in-group favoritism on implicit than explicit measures, the opposite pattern is observed for members of low-status groups (e.g. African-Americans, homosexuals) (Jost and Burgess, 2000; Jost and Banaji, 1994; Jost, Banaji and Nosek, 2004) which show implicit out-group favoritism. These results likely reflect a phenomenon known as system justification, namely the implicit, but not explicit, tendency for members of disadvantaged groups to legitimate the existing (hierarchical) social order (Jost et al., 2004). More importantly, these results highlight the value of implicit measures for the study of human attitudes and preferences. Indeed, they show that measuring preferences and attitudes with explicit or implicit methods might lead to even opposite results. As matter of fact, explicit measures can be biased by social desirability and adherence to social norms such as expressing support to own disadvantaged group (in the case of African-Americans) or avoiding been seen as discriminatory (in the case of white people), while implicit measures might reflect stronger, culture-based associations. In view of this, implicit measures are generally preferred over explicit ones since they can minimize the occurrence of strategic responding. It should also be noted that preferences measured with implicit methods can better predict subsequent behaviour than those measured with explicit methods (Green et al., 2007; Stanley et al., 2008; Greenwald et al., 2009).

With this in mind, we designed an experiment to investigate whether high- and low-competence-based hierarchical status acquired through an interactive cooperative game can modulate participants' implicit and explicit evaluation of two previously unacquainted individuals. We used a modified version of the Affect Misattribution Procedure (AMP Payne et al., 2005) in order to capture the implicit nature of this effect. The AMP has been widely used in social psychology research to test implicit preference or bias toward homosexual couples (Cooley et al., 2014), black people (Greenwald et al., 2009), Jews (Imhoff and Banse, 2009) and overweight people (Pryor et al., 2013). In a typical AMP trial, participants are presented with a prime picture which can have either a positive or negative valence, immediately followed by a neutral target stimulus, usually a Chinese ideogram. The participant is then asked to rate the neutral stimulus as pleasant or unpleasant. The task's rationale is based on the concept of affect misattribution, whereby affective reaction to the prime is misattributed and transferred to the (neutral) target (Murphy and Zajonc, 1993, Payne et al., 2005), leading to a valence-congruency effect (i.e. targets following positive primes are evaluated as more pleasant than targets following negative primes). We modified the AMP by using the photos of the two players' faces (high or low status) as primes. Our participants completed two AMP sessions, one before and one after the cooperative game. In each session, participants performed two blocks, one with the prime being presented for 17 ms and the other for 75 ms. The 17 ms timing was selected on the basis of previous studies (e.g. Murphy and Zajonc 1993) as sufficiently short to prevent the conscious processing of the image and effective in influencing the subsequent evaluation of neutral stimuli (when the primes consisted of emotionally charged images). The 75 ms timing was selected from Payne and colleagues (2005) where this timing is used as a standard timing for the AMP (although their Experiment 3 demonstrated that the misattribution effect also occurs at longer presentation timings). This timing has also been used to measure implicit social attitudes like implicit anti-black prejudice (Inzlicht et al., 2012). While the misattribution effect in the original version of the AMP (Murphy and Zajonc, 1993) was only found under short prime presentation time (where only implicit processing is likely to take place), subsequent studies have shown the effect to occur with long presentation times as well (Payne et al., 2005; Chiesa et al., 2015; Rohr et al., 2015). Moreover, Ponsi and colleagues (2017) found that subliminal and supraliminal presentation of emotional primes have opposite effects on autonomic reactivity during a social categorization task. Previous findings have shown that high status individuals are evaluated more positively than low status individuals (Anderson & Kilduff, 2009a; Varnum, 2013). Thus, we expected that the pleasantness ratings of the target stimuli associated with the High Status player would be higher than those associated with Low Status. In addition to the implicit task, however, we also measured explicit ratings of Competence, Intelligence, Dominance and (as a control measure) Attractiveness. Here, too, we expected the High Status player to be explicitly rated as more competent and intelligent than the Low Status one.

Methods

Participants

Thirty-five male students with no knowledge of the Chinese language were recruited from Sapienza University of Rome. Each gave their written informed consent for participation in the study. Five participants were excluded because they did not believe the cover story and four were excluded for technical problems during the experiment (i.e. data partially not recorded). Thus, our final sample was comprised of 26 participants (age = 24 ± 4.19 years). All had normal or corrected-to-normal vision and were naive to the real purpose of the experiment. The experimental protocol was approved by the ethics committee of the Fondazione Santa Lucia and was carried out in accordance with the ethical standards of the 1964 Declaration of Helsinki.

Procedure

Participants were told that the study had two unrelated aims, namely to investigate their time estimation ability and to test a new software for interactive games. Participants were told they were to play a virtual game with two partners in other rooms of the Psychology building. In reality, these partners were confederate actor models. A procedure was adopted so that participants would consider each game partner as High vs. Low Status (see below). Participants were assigned to one of two experimental actor-status combinations: Actor A as “High Status” and Actor B as “Low Status” (Combination 1), or vice versa (Combination 2). The experiment was structured as follows: participants began by completing the first AMP session (Session 1). They then participated in the status-inducing procedure, i.e. the interactive game before completing the second AMP session (Session 2). Worth noting is that there was no status associated to the game partner in Session 1, as this session was meant to index any possible automatic preference for one of the two players.

Affect misattribution procedure.

We used two different versions of the task, one with a short presentation (17 ms) of the prime and one with a long presentation (75 ms). While a 17 ms presentation timing is considered to be under the perceptual threshold, implying that the image is processed at an implicit level (see for example Killgore and Yurgelun-Todd 2001), a 75 ms presentation timing is considered to be sufficient for a fully conscious processing of the stimulus (Payne et al., 2005, Inzlicht et al., 2012). The AMP tasks were delivered using E Prime 2.0 (Psychology Software Tools, Pittsburgh, PA). Each AMP session (Session 1 and Session 2) included both AMP tasks, i.e. the 'short' (AMP_SP) and the 'long' presentation (AMP_LP). During the AMP_SP, 19 Chinese characters (on a grey background, 512 x 384 pixels) were used as target stimuli. Prime stimuli were two photos (292 x 400 pixels) of the two male confederates' faces (Actor A and Actor B), while the masks were two identically-sized, scrambled versions of the original pictures created with Matlab (Mathworks, Cherborn, MA, USA). Each trial started with a fixation cross for 1000 ms, after which a forward mask was presented for 100 ms, followed by the prime image (identity) for 17 ms, a backward mask (identical to the forward mask) for 100 ms and the target (ideogram) for 1000 ms (as in Era et al., 2015). Following each target, the sentence "How much do you like this image?" appeared on the screen. Below it was a vertical Visual Analogue Scale (VAS, height 10 cm) with the words "Extremely" and "Not at all" written at its top and bottom, respectively. This screen composition lasted until the question was answered (Fig 1, A). Participants were told that they would see one image and then a second one, a Chinese ideogram. They were asked to ignore the first image and rate the pleasantness of the ideogram by clicking with the mouse on the VAS point that corresponded to their judgment.

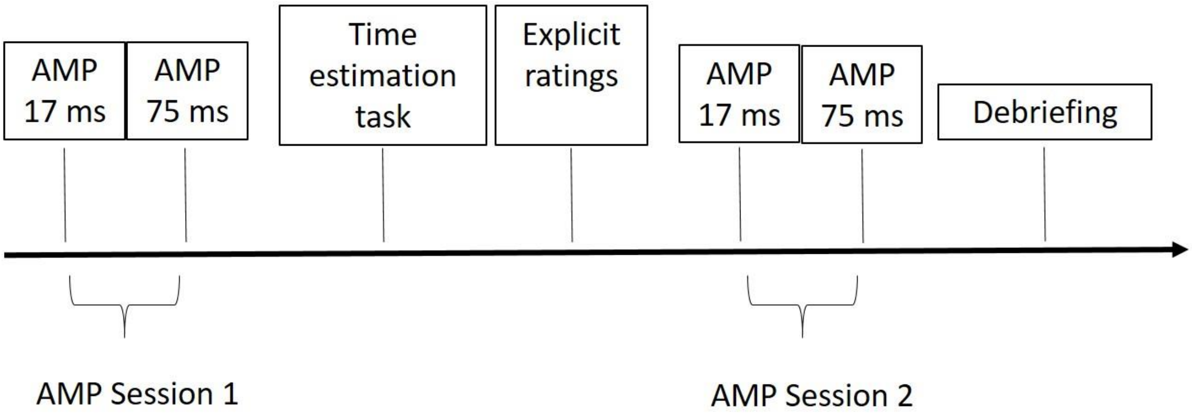


Fig. 1 – Timeline of the experimental procedure

Each target image appeared twice in each of the two 19-trial blocks, once preceded by the face prime of Actor A (unacquainted in Session 1 and either High or Low Status in Session 2) and once by the face prime of Actor B (unacquainted in Session 1 and either Low or High Status in Session 2, the opposite of Actor A). The AMP_LP procedure was the same as AMP_SP, apart from two differences: the prime image being presented for 75 ms and the mask being presented only after the prime, as in the classical version of the AMP (Payne et al., 2005) (Fig. 1, B). The order of short and long presentation AMP was kept constant during the task, with AMP_SP always preceding AMP_LP. Although we do acknowledge that randomizing the order would control for any sequence effect, we reasoned that having the 75 ms block before the 17 ms could make the participants more sensitive to the prime pictures perhaps to the extent that they could become able to perceive them even at 17 ms. To rule out the possibility that an order effect might contaminate the results, we ran a Status (High vs Low) x Block (Short vs Long presentation) x Session (before vs after the manipulation) ANOVA on the raw data (see Supplementary Materials).

Status-inducing procedure.

The status-inducing procedure was adapted from Boksem and colleagues (2012). Participants were informed that they were to play a cooperative time estimation game with two other players and that the score obtained by each individual player would be added to a shared score. They were also informed that, at the end of the game, the collective score would be split into three equal parts and distributed to each player in the form of candy. While participants could win actual money in some of the studies using a similar paradigm (e.g. Boksem et al., 2012; Zink et al., 2008), other studies indicate that the manipulation is effective with virtual rewards (e.g Santamaria-Garcia et al., 2013; 2015), suggesting that even low stake rewards can work with this kind of manipulation. Between the end of the first AMP session and the start of the status inducing procedure, the experimenter pretended to call a colleague on the phone in order to synchronize the start of the game. We did this to make the cover story more plausible. The time estimation task was administered with E-Prime 2.0 (Psychology Software Tools, Pittsburgh, PA). Each trial started with the presentation of a blue circle that turned green after a random time interval (ranging between 1500-3500 ms). Participants were required to press the space bar exactly 1 second after the circle had changed colour (Fig. 3). To avoid ceiling effects, we adopted a staircase-like procedure: at the start of the task, the ‘win’ threshold for the response time was set at 1 second +/- 550 ms. If the participant’s response fell within this threshold (i.e. if he pressed the space bar after 1 second +/- 550 ms), he scored 5 and the threshold was reduced of 50 ms. Again, on the following trial a response falling within 1 second +/- 500 ms would result in a score of 5 and in a further 50ms threshold reduction, and so on. Otherwise, if the response fell outside the threshold, the participant scored 0 and the threshold was increased by 50ms. This procedure ensured the task to be enough challenging while keeping participants’ score in the desired range, although participants always received a feedback that was coherent with their actual performance. In addition to the score, visual feedback was provided at the end of each trial: a smiley face for correct responses and a sad face for errors. In each trial, participants were only able to see their own result and their individual score. The staircase procedure was kept for the whole task. Therefore, participants always received a feedback that was coherent with their actual performance. In addition to the score, visual feedback was provided at the end of each trial: a smiley face for correct responses and a sad face for errors. In each trial, participants were only able to see their own result and their individual score.

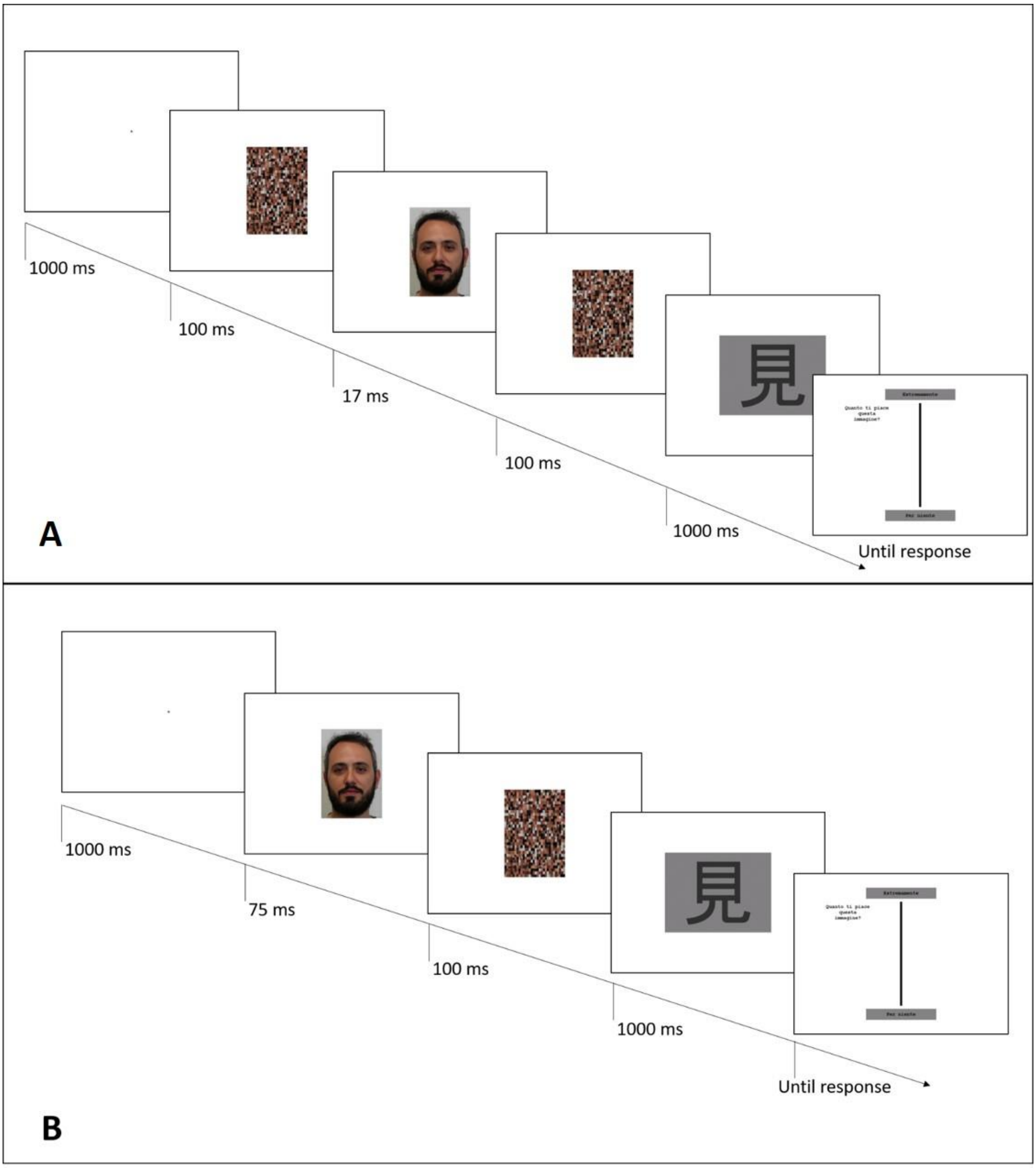


Fig. 2 AMP trial timeline. A) Short presentation task. A fixation cross was presented for 1000 ms, followed by a forward mask for 100 ms, the prime image (face of Player A or Player B) for 17 ms and a backward mask for 100 ms. The target image was then presented for 1000 ms, followed by a slide displaying the sentence “how much do you like this image?” and a vertical VAS ranging from “Extremely” (top end) to “Not at all” (bottom end). This slide remained until the participant responded to the question with a mouse click on the VAS. B)

Long presentation AMP. The trial structure was identical to the short presentation, with two exceptions: the prime lasted 75 ms and only the backward mask was presented.

Participants completed eight blocks of ten trials each. At the end of each block, a feedback slide (Fig. 4) was presented in which the photos of the three players (those of the two partners and that of the participant) were displayed, each one framed by a distinct color. The individual score was displayed below each picture, along with a number of stars that varied according to performance (3 stars for the best player, 2 for the middle and 1 for the worst). In the top right corner of the slide was a square containing three bars in different colors matching those of the participant's pictures frames. The width of each colored bar increased during the game according to the player's score in order to highlight the differences between their respective contributions. A progress bar was also displayed, indicating how far along the group was in the task.

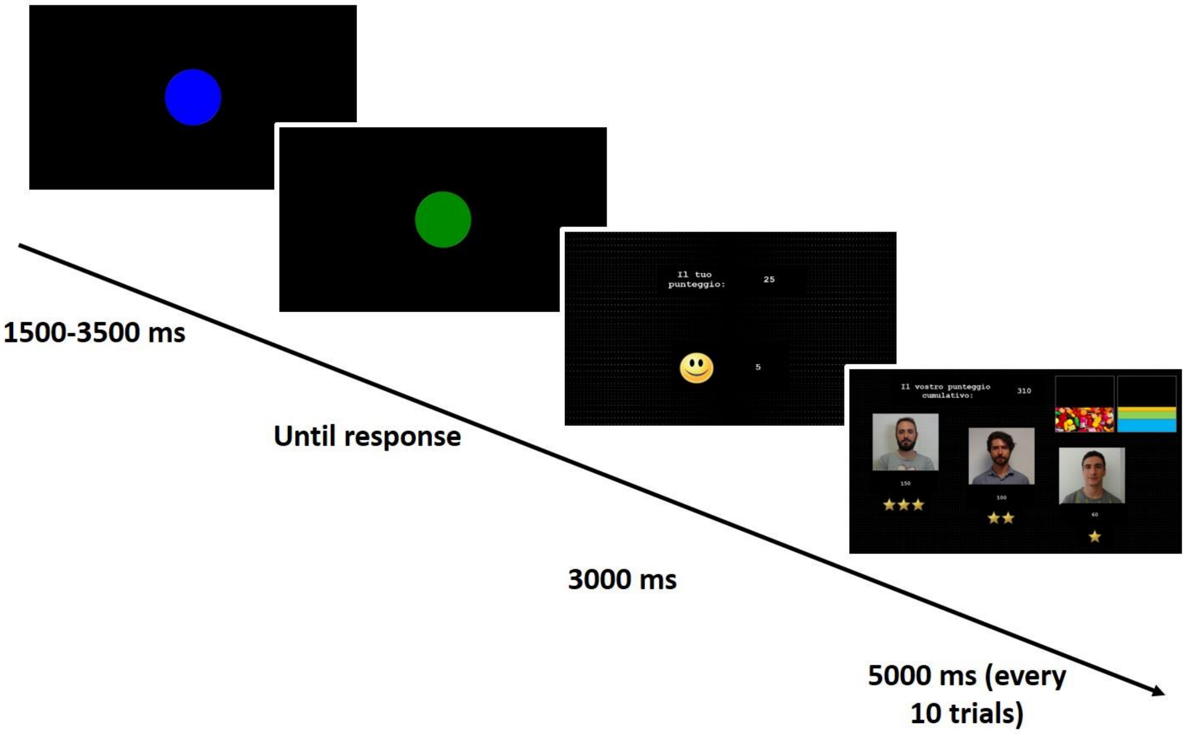


Fig. 3 - Time Estimation task trial timeline. A blue circle was presented for a time varying between 1500 and 3500 ms, when it turned green. Participants were asked to press the space bar exactly 1 second after the color change. After this response, a feedback slide was presented that featured a smile (correct response) or a frown (error), as well as the participant's score for the trial (5 for a correct response, 0 for errors). In the upper part of the slide, participants could also see their individual cumulative score. Every 10 trials a feedback slide featuring both the group score and player ranking was displayed (see Fig. 4).

Fig. 4 - Feedback slide presented every 10 trials during the Time Estimation task. Subjects were informed about their position within the hierarchy, which was made more explicit by stars below each picture. Displayed on the upper left side of the slide was the sentence "Your shared score." Next to this text was the corresponding number, which was updated with every feedback presentation.

Player ratings changed in each block for the first four blocks, with the participant moving through the first (block 1), second (block 2) and third (blocks 3 and 4) positions. From block 5 to 8, however, the ranking remained the same, with the experimental subject occupying the middle position. While the participant's displayed score reflected his real performance, we covertly manipulated the scores of the two fake players so that one always ranked first ("High Status") and the other last ("Low Status") in blocks 5 to 8. At the end of the task we presented a slide displaying the final ranking and the collective score. On each block of the Time Estimation task, the High and Low Status players' scores were determined in advance. To make sure that the participants' score would reflect their actual position in the hierarchy, we initially estimated on a separate sample the maximum and minimum scores that could be achieved in each block (the staircase procedure ensured that these boundaries could not be overcome) and we set two other players' scores accordingly. The distance between the High and Low Status players remained the same for all participants, as these two scores were set in advance. Similarly, the distance between the participant and the two other players varied very little from one participant to another. However, for all participants the distance between the participant and the High status was not equal to the distance between the participant and the Low status (HS-Participant mean difference = 118.46, sd = 6.89, LS-Participant mean difference = 46.53, sd = 6.89 – t value = 26.59, $p < 2.2e-16$). We therefore decided to investigate whether this might have influenced the results by running additional analyses and show that this difference does not invalid our results (see Supplementary Materials).

Explicit ratings concerning the game partners

Following the status inducing procedure, participants were requested to rate the two other players in terms of attractiveness, intelligence, competence and dominance by pressing a number from 1 to 9 on the keyboard. Immediately after, they completed the second AMP session (Session 2). They were then debriefed. Contrary to the implicit measure, the explicit evaluation of the two players was only collected after the status-inducing procedure. We adopted this method because we thought that asking participants to judge the competence and intelligence of the two players before the game might have revealed the real purpose of the experiment.

Funnel debriefing

At the end of the experiment, participants underwent a funnel debriefing procedure (Ferguson & Bargh, 2004; Bargh & Chartrand, 2000) to determine if they had any suspicion about the cover story. The experimenter started with a broad question (i.e. “Do you have any idea about what the purpose of this experiment may be?”) before getting more detailed: “Did you ever wonder whether the other players really existed”? Five participants reported suspicion about the procedure and were therefore excluded.

Statistical analyses

Affect misattribution procedure

As a first step, for each participant values from each trial in Session 2 were standardized by subtracting the corresponding average Session 1 value in the same condition. For example, each trial in the High Status – Long Presentation – Session 2 condition was standardized by subtracting the mean value of the same condition in Session 1.

Baseline-corrected AMP data were analysed with Multilevel Linear Mixed Models using the software R and the package *lme4* (version 1.1 -21, Bates et al., 2015). For each model, the random part was selected using the principal component analysis (PCA) method (Bates et al. 2015). We kept all random factors that explained at least 1% of variance. Statistical significance of fixed effects was determined using type III ANOVA test with the *mixed* function from *afex* package. P-values were calculated using the parametric bootstrap (PB) method. Post-hoc comparisons were performed with the ‘Estimated Marginal Means’ R package (version 1.3.3) via the *emmeans* and *emtrends* functions, respectively, and Tukey correction for multiple comparisons.

Our model included *Status* (High, Low), *Block* (LongPresentation, ShortPresentation), and their interactions as fixed factors. The random part included the random slope of *Block* over participants and the random intercept of Block over participants.

Explicit ratings

Using the dep.t.test R function we ran four separated one-way paired-sample t-tests (alternative = GREATER) to measure the explicit ratings of Attractiveness, Intelligence, Competence and Dominance given to the High Status player compared to those given to the Low Status player.

Results

Affect misattribution procedure

Model: VAS_difference ~ Block * Status + (Block|Subject)

Type III ANOVA revealed that the main effects of Block (Chisq = 0.64, p = 0.43) and Status (Chisq = 0.64, p = 0.42) were nonsignificant. However, there was a significant Block x Status interaction (Chisq = 5.67, p = 0.03), which we further analysed with Post Hoc tests. We found that, only in the Long Presentation (LP) block, VAS scores attributed to the High Status (HS) player were significantly higher than in those attributed to the Low Status (LS) player (estimate = 3.54 , SE = 1.57, t-ratio 2.25 = , p = 0.02), see Fig. 4. Conversely, in the Short Presentation (SP) block, there was no significant difference between the High and Low

Status condition (estimate = -1.76, SE = 1.57, t-ratio = -1.11, p = 0.26). Descriptive statistics are reported in Table 1.

Confederate Check analysis

In order to check whether the two prime stimuli (i.e. picture of Confederate A and picture of Confederate B) might have differently affected the evaluation of the target pictures independently of their attributed status, we ran an additional model where the factor Status was replaced with a new factor Model (Confederate A, Confederate B). The full model included Session (Session 1, Session 2), Block (SP, LP) and Model (Confederate A, Confederate B) as fixed factors. The random part included the random slope of *Block* over participants and the random intercept of Block over participants. Please note that here we used as a dependent variable the raw (uncorrected) VAS scores attributed to the target pictures.

Model: VAS ~ Block * Session * Model + (Block|Subject)

Type III ANOVA showed that the main effects of Block (F = 1.93, p = 0.17) and Model (F=1.96, p = 0.16) were nonsignificant. There was a significant effect of Session (F= 10.60, p = 0.001), indicating that the VAS scores in Session 2 were significantly lower than those in Session 1. None of the interactions reached significance: Block x Model (F=0.06, p = 0.81); Block x Session (F=0.46, p = 0.50); Model x Session (F=1.34, p = 0.25); Block x Model x Session (F= 0.02, p = 0.89). The fact that no significant interaction between Model and the other experimental factor was found suggests that the two stimuli did not evoke different affect ratings at baseline nor in Session 2.

	mean	sd
HS_SP	-3.86	6.04
LS_SP	-2.10	6.44
HS_LP	-0.18	4.28
LS_LP	-3.72	5.54

Table 1 Descriptive statistics (means and standard deviations) for baseline-corrected (Session 2 – Session 1) target evaluation VAS scores. HS = HighStatus prime; LS = LowStatus prime; SP = short presentation block; LP = long presentation block.

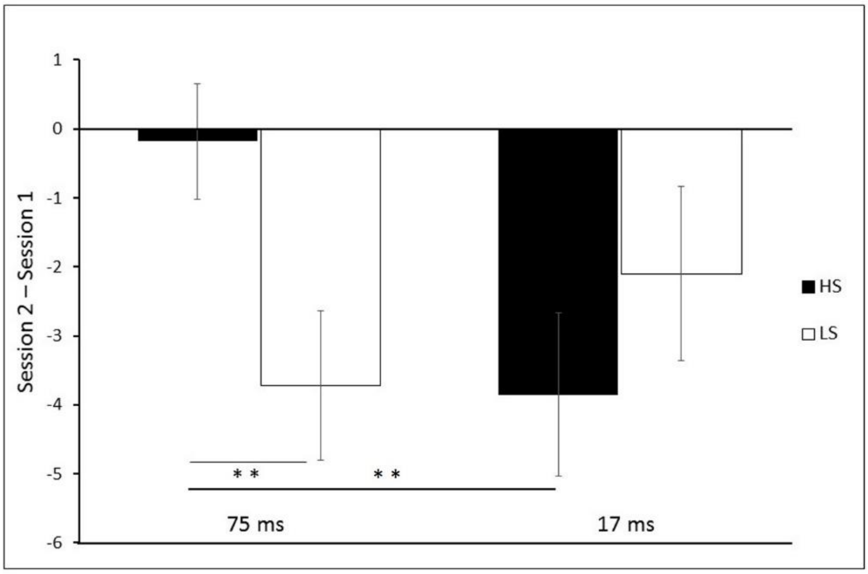
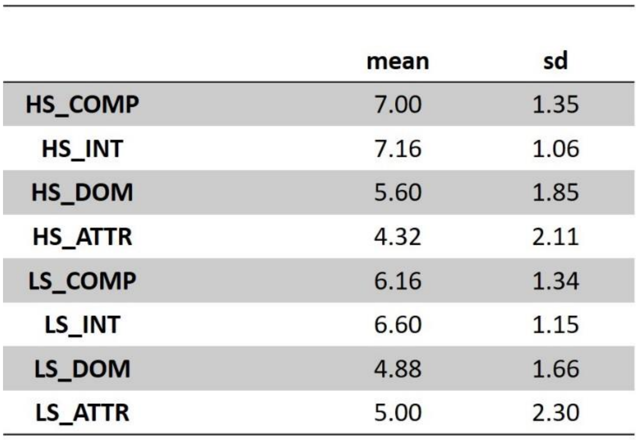


Fig. 4 - AMP results for long presentation (left side) and short presentation (right side) blocks. Values represent mean baseline-corrected (Session 2 – Session 1) VAS scores for target evaluation after the presentation of HighStatus (HS) and LowStatus (LS) primes. Marked differences are significant at p < 0.001.

Explicit ratings

We found a significant difference in the Competence ratings (t (24) = 2.37, p = 0.01, r = 0.43) between High Status (M = 7, SD = 1.35) and Low Status (M = 6.16, SD = 1.34). There was also a significant difference in the Intelligence ratings (t (24) = 2.16, p = 0.02, r = 0.40) between High Status (M = 7.16, SD = 1.07) and Low Status (M = 6.6, SD = 1.15). These results suggest that the participants rated the High Status player as more intelligent and competent than the Low Status player (Table 2). Moreover, the High Status player was rated as more dominant (M = 5.6, SD = 1.85) than the Low Status one (M = 4.88, SD = 1.67, t (24) = 2.12, p = 0.02, r = 0.39). There was no significant difference (t (25) = -1.60 p = 0.93) in Attractiveness rating scores between High (M = 4.32 SD = 2.12) and Low Status (M = 5, SD = 2.3), suggesting that the High Status and Low Status players were evaluated as equally attractive (Table 2, Fig 5).



	mean	sd
HS_COMP	7.00	1.35
HS_INT	7.16	1.06
HS_DOM	5.60	1.85
HS_ATTR	4.32	2.11
LS_COMP	6.16	1.34
LS_INT	6.60	1.15
LS_DOM	4.88	1.66
LS_ATTR	5.00	2.30

Table 2 Descriptive statistics (means and standard deviations) for explicit ratings after the status-inducing procedure. HS: HighStatus; LS: LowStatus; COMP: Competence; INT: Intelligence; DOM: Dominance; ATTR: Attractiveness.

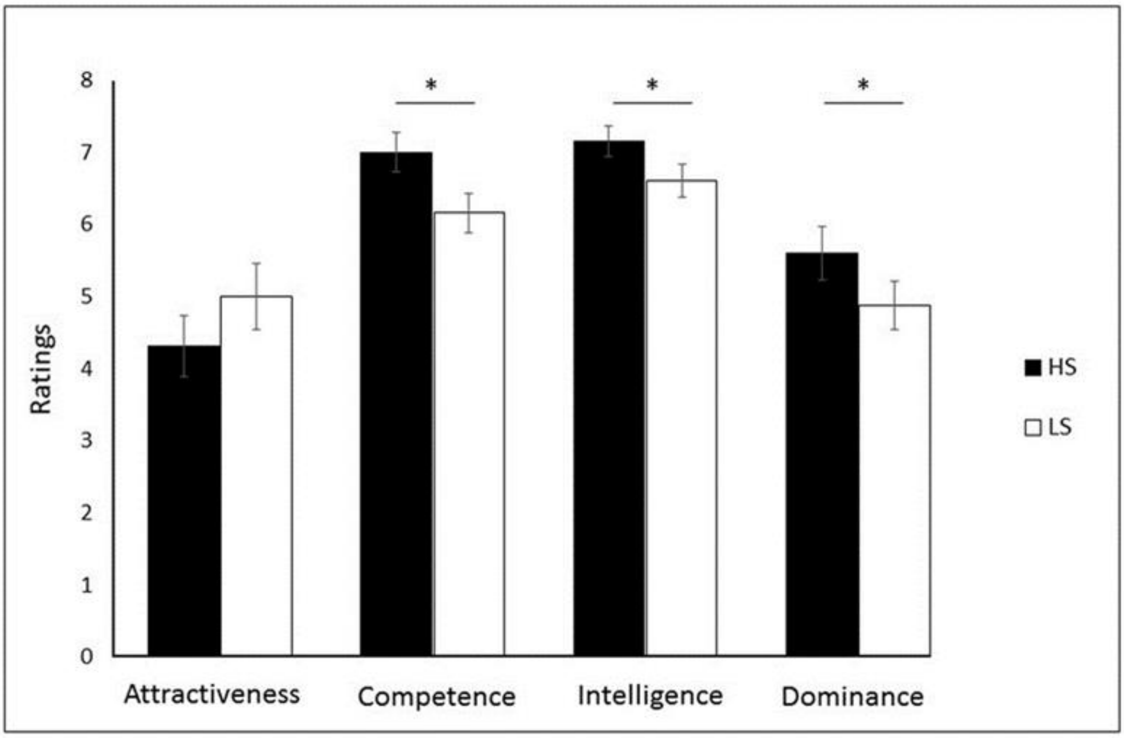


Fig. 5 Explicit ratings results. Marked differences are significant at $p < 0.05$.

Discussion

To explore how the dynamic induction of a given social status influences implicit and explicit person appreciation, and whether this impacts the preference for abstract visual stimuli associated to high- and low-status identity, we adapted a status-inducing procedure from Boksem (2012) in which participants were led to believe that they were playing a cooperative game with two other (unseen) players. A score-based hierarchy was displayed during the game that reflected the relative contribution of each player toward the common goal of increasing a collective score and thus a shared reward. Before and after the game, a modified version of the AMP task was used to investigate whether the evaluation of the two players had been influenced by their relative position in the hierarchy. Using two different prime durations we also explored whether the short vs long presentation time of the different social-status primes might impact the misattribution effect. To our knowledge, this is the first study to use an implicit method for investigating the effects of social status on person evaluation.

Instead, previous research has relied on explicit measures such as scales and questionnaires, limiting the possibility to shed light on implicit mechanisms characterizing social biases. Implicit tasks such as the AMP offer a controlled and rigorous way to measure attitudes and preferences without the participant being aware of what the experimenter is trying to measure, therefore reducing the chance of triggering compliance, adherence to social norms or individuals' dependency on social desirability.

Short presentation AMP

Baseline-corrected pleasantness ratings attributed to abstract stimuli in the High Status condition were not different from those in the Low Status condition, suggesting that the implicit evaluation of the two players in the short presentation task was not affected by their relative status, or that their evaluation was not strong enough to bias the evaluation of the abstract target stimuli. It should be noted that the two faces used as prime images in our study, rather than having an explicit, feature-based valence (e.g. images displaying negative or positive emotions, as in previous studies), were emotionally neutral, and coded as High Status or Low Status players with a competence-based induction procedure. One possible interpretation of this lack of difference in pleasantness ratings is that a presentation timing of 17 is not sufficient for the extraction of knowledge-based status antecedents (Mattan et al., 2017) from faces, and that a longer processing time is required. This would be in line with the EEG results reported by Breton and colleagues (2014), which suggest that hierarchy does not affect the structural encoding of neutral-expression faces.

It is worth noting that we observed a reduction in the pleasantness ratings of the target pictures from the first AMP session to the second that was independent of the status condition (see Fig 4). This result might suggest that repeating the AMP twice causes a lowering in pleasantness judgements of the target pictures due to habituation effects (see Tinio & Leder, 2009 for a discussion on boredom and mere exposure effect). Our finding that implicit preference for high-status individuals fails to occur when the status prime is presented for 17 ms raises some important issues for the study of implicit social evaluation. We suggest that, while the use of short presentation timings might be adequate when the object of study is a social dimension that is clearly visible (i.e. race, gender, attractiveness, body weight, dominant posture or facial expression), longer presentation timings might better suit the need to investigate the effects of knowledge-based characteristics on social evaluation.

Long presentation AMP

In the AMP_LP, we found that the neutral target's pleasantness ratings were significantly higher in the High Status than in the Low Status condition after the status-inducing procedure (i.e. Session 2 compared to Session 1). The presence of an affect misattribution effect (Payne et al., 2015) suggests that, with the long presentation timing, the pictures of the High Status and Low Status players acted as positive and negative primes, respectively. This result suggests that in the context of a cooperative game, where status is acquired by displaying superior competence and commitment to the common goal, high status individuals are preferred over low status ones. A preference for high-ranking individuals is common among non-human primates: for example, male rhesus macaques are willing to sacrifice a reward for viewing the picture of a high-status conspecific (Deaner et al., 2005). Moreover, when choosing partners for a collaborative task, chimpanzees tend to choose as partners those conspecifics that demonstrated better skills in the same task (Melis et al., 2006), suggesting that non-human primates may possess a rudimental form of competence-based status differentiation. This status bias has also been reported in 21 to 31 months-old toddlers, who showed a preference toward high-ranking puppets, but only if they did not make use of force to outrank the other puppet (Thomas et al., 2018).

From Session 1 to 2 of the AMP, we observed a drop in pleasantness ratings for target abstract stimuli only when paired with Low Status primes, while the difference between Session 1 and Session 2 for High Status primes was close to zero (see Fig. 4). One possible interpretation of such an effect is that, as the game went on, participants developed a negative attitude toward the Low Status player for contributing less to the collective goal (Willer, 2009), while their evaluation of the High Status player was not affected. However, considering the result in the short presentation task (i.e. an overall reduction in pleasantness ratings from Session 1 to Session 2 for targets paired with both High Status and Low Status primes), another possible interpretation could be that, after the status-inducing procedure, participants developed an implicit preference toward the High Status player that counteracted on the habituation effect of seeing the stimuli for a second time. In other words, we can hypothesize that in the long presentation task, the deteriorating judgement of targets paired with the Low Status primes would only reflect the effect of the repetition (as seen in the short presentation task), while the lack of change in the evaluation of targets paired with the High Status prime would reflect a positive bias toward the High Status player. Previous studies (see Baxter & Murray, 2002 for review) have linked the devaluation of rewarding stimuli due to satiation to amygdala habituation. In this vein, one possible neurobiological interpretation of our findings could be that in the long presentation task, the picture of the high-status player counteracted the effect of reward devaluation due to the repetition of the target stimuli. This interpretation would be in line with the finding that, at least in non-human primates, high status individuals elicit neural responses related to reward processing (Deaner et al., 2005).

While the neural bases of implicit attitudes have been extensively investigated in previous research (see Stanley et al., 2008 for a review), the neural mechanisms that support the process of affective misattribution in the AMP are far from being understood. Status perception involves a wide range of specific neural systems related to person evaluation, attention and salience (Cloutier et al., 2014; Zink et al., 2008; Marsh et al., 2009, Chiao et al., 2008, 2009; Koski et al., 2017; Santamaria-Garcia et al., 2015). One important finding is that high status individuals also elicit greater responses in areas involved in reward processing (Singer et al., 2004; Ly et al., 2011). A possible neural pathway supporting the implementation of the implicit preference toward the high status that we observed in our study would likely involve low-level perceptual areas (i.e. the fusiform face area – Kanwisher et al., 1997), frontal areas supporting face recognition (Haxby et al., 1996) and, finally, reward-related areas such as amygdala, striatum and orbitofrontal cortex (Singer et al., 2004). At a very speculative level, we would like to propose that the activation of reward-related brain areas might be the neural correlate of the misattribution effect, in the sense that, due to the very short interval between the prime and the target, reward processing triggered by the prime is “attached” to the neutral target. Coherent with such an interpretation is that a reduction of the misattribution effect has been reported when increasing the temporal distance between prime and target (Payne 2005, experiment 3). The investigation of the neural basis of affective misattribution with different presentation timings might constitute the object of future studies.

Explicit ratings

The implicit results in the long presentation AMP were paralleled at the explicit level by a significant difference in the ratings of the High Status and Low Status players in terms of Competence and Intelligence, confirming the effectiveness of our procedure in inducing a status-based differentiation of the two players (see Fig. 5). The High Status player was also rated as more dominant. This last finding seems at odds with the “two ways to the top” theory of status, which posits that dominance and competence are two separate (although equally effective) pathways for status acquisition (Heinrich and Gill-White, 2001; Cheng et al. 2013). However, this assumption has been questioned by other researchers, who suggested that dominance itself involves competence and the conferring of prestige, and that pure dominance status does not exist (Chapais, 2015). Our results seem to confirm this second stance.

Limits

This study is limited by the fact that, contrary to the implicit measure, the explicit evaluation of the two players was only collected after the status-inducing procedure. We adopted this method because we reasoned that asking participants to make a judgement about the competence and intelligence of the two players might have revealed the real purpose of the experiment. However, this method prevented us from measuring the change in the explicit evaluation before and after the manipulation. Since the High Status player was also contributing more to the common gain than the Low Status one, it is possible that the found effect might not be attributed to partners’ competence, but to the higher (or lower) economical contribution offered to the group and thus to the participant gain. Indeed, in the present study the dimensions of competence and the contribution to the common goal are linked to one-another in a way that makes it difficult to tease apart their possible independent role in the present results. Our intention was to study individuals’ implicit reactivity to others’ status in a cooperative scenario, because here the contribution to a common (cooperative) goal was manipulated as an important feature to induce social status. Our choice was specifically grounded on previous studies showing that an individual’s contribution to collective gain increases his or her perceived status (Hardy and Van Vugt, 2006; Willer, 2009). A wide variety of studies from social psychology has repeatedly shown that individuals seek social status in groups by displaying not only higher levels of competence but also stronger commitment to the common goal (see Anderson and Kilduff, 2009 for review). Moreover, our paradigm was adapted from a previous study (Boksem et al., 2012), in which it was shown that participant's stance within a competence- *and* contribution-based hierarchy influenced their neural response to a negative feedback, suggesting that this procedure is adequate to induce a status-based differentiation. Future studies are needed in order to try to dissociate, in a cooperative scenario, the impact of a partner's contribution from that of his/her perceived competence on individual's implicit affective response to his perceived status. We believe that our present work shows for the first time that, although contributing to a group gain might determine status attribution per se (Willer, 2009), competence-based (and eventually contribution-based) status attribution in a cooperative scenario modulates individual's implicit preferences.

We acknowledge that the choice of involving only male participants in the present study is somewhat arbitrary. The rationale behind this decision is that since the paradigm implemented in the study is entirely novel and studies indicate that gender may interact with susceptibility to status induction (Santamaria-Garcia et al., 2015; Breton et al., 2018), we wanted to reduce unduly sources of variance (including only images depicting males as stimuli and involving only male participants to include only same gender players). Future studies should explore whether any gender effect associated to status may modulate implicit preference.

Conclusion

Our results suggest that within a newly formed group of individuals who are trying to achieve a common goal, a status differentiation occurs based on the competence and goal commitment displayed by each member of the group. We show that this status-based differentiation leads to an implicit preference for the higher status identity and that this preference is misattributed to an abstract target when that target must be evaluated. Our results go beyond previous findings on status-based evaluation (Varnum, 2013; Jost and Burgess, 2000; Cheng & Tracy, 2013) by demonstrating that the more positive evaluation of high-status individuals occurs not only at the explicit but also at the implicit level. Previous studies using interactive games found neural and behavioral effects of competence-based social status (Santamaria-Garcia et al., 2013; 2015; Zink et al., 2008, Boksem et al., 2012). We further explored this issue by demonstrating that the target's relative status within a competence-based hierarchy also elicits congruent affective reactions which are projected over the preference evaluation of an abstract stimulus. Our results expand previous research on how social evaluation can be influenced by many visible characteristics of the model (e.g. race, gender, body weight) and demonstrate that social evaluation can also be influenced by non-visible, higher-order variables such as individuals' competence- and contribution to a common goal. In conclusion, the present findings support the view that high status individuals who attain status by demonstrating superior skills and by making higher contributions to the group are preferred over the low status individuals.

Supplementary materials

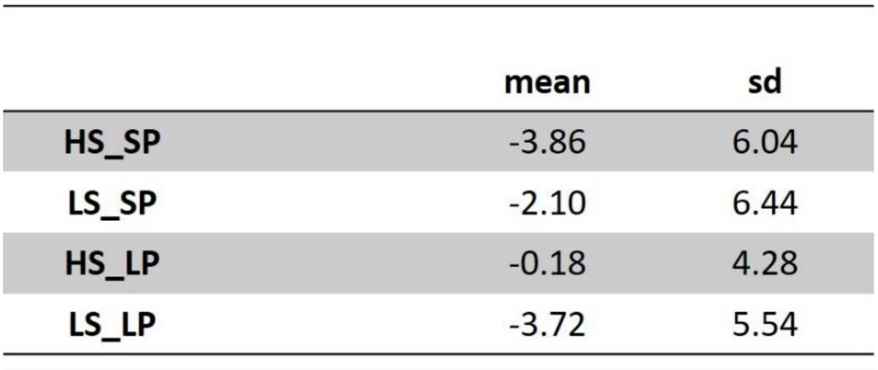
1- Statistical analyses on VAS scores using a frequentist (ANOVA) approach, as originally published in Experimental Brain Research (2019).

Statistical analyses were conducted using R (version 1.1.383) and STATISTICA (Statsoft). As a first step, we created baseline-corrected indexes for the High Status and Low Status conditions by subtracting the pleasantness ratings attributed to the Chinese characters in Session 1 from their pleasantness ratings in Session 2. Thus, we created two indexes for each task (AMP_SP and AMP_LP) and one for each condition (High Status and Low Status), resulting in four indexes: HS_SP, LS_SP, HS_LP, LS_LP. A 2x2 ANOVA on AMP effect indexes (HS_LP, HS_SP, LS_LP, LS_SP) was ran with Block (Long Presentation-Short Presentation) and Status (High-Low) as within-subject factors.

Results

While the main effects of Block and Status were not significant (Task: (F(1,25) = 0.62, p = 0.43; Status (F(1,25) = 1.36, p = 0.25), we found a significant Block x Status interaction (F(1,25) = 18.25, p < 0.001, partial eta-squared = 0.42). Bonferroni corrected post hoc tests revealed that in the Long presentation Block (75 ms) the AMP index associated to the High Status player were significantly higher than that associated to the Low Status player (p < 0.01), while this was not the case in the Short presentation Block (17 ms) (p = 0.23). Furthermore, the AMP index associated to the High Status player in the Long presentation block was significantly higher than the AMP index associated to the High Status player in the Short presentation block (p < 0.01) (see Fig. S1 and Table S1).

We conducted a post hoc power analysis with RStudio (version 1.2.1335) and the *pwr* package (version 1.2-2). The significance level was set at 0.01, and the effect size of the Status x Block interaction (partial eta squared = 0.42) was converted in the corresponding Cohen's f2. The analysis showed that, with a sample size of 26 subjects, the Status x Block interaction yielded a power of 0.96.



	mean	sd
HS_SP	-3.86	6.04
LS_SP	-2.10	6.44
HS_LP	-0.18	4.28
LS_LP	-3.72	5.54

Table S1 Descriptive statistics (means and standard deviations) for baseline-corrected (Session 2 – Session 1) target evaluation VAS scores. HS = HighStatus prime; LS = LowStatus prime; SP = short presentation block; LP = long presentation block.

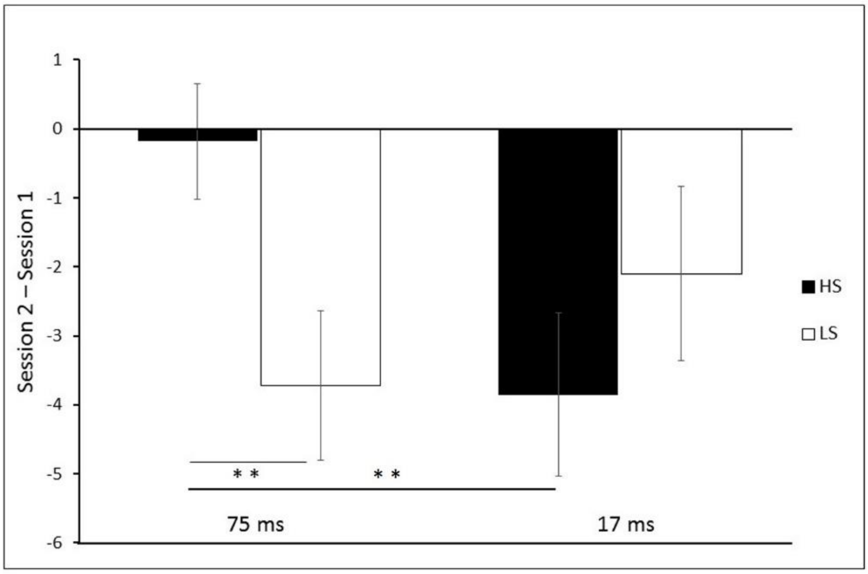


Fig. S1- AMP results for long presentation (left side) and short presentation (right side) blocks. Values represent mean baseline-corrected (Session 2 – Session 1) VAS scores for target evaluation after the presentation of HighStatus (HS) and LowStatus (LS) primes. Marked differences are significant at $p < 0.001$.

2- Supplementary Analyses on the effect of score distance on the main results

In order to investigate whether the difference between the HS-Participant and the LS-Participant score distances might have influenced our results, we decided to carry additional analyses. To this end, we created two indexes of distance: HS_Dist (HS final score – Participant final score) and LS_Dist (Participant final score – LS final score) and an index of distance difference (Dist_Diff = HS_Dist – LS_Dist). This last index was mean centered and added as a continuous predictor to a Block (long vs short) x Status (high vs low) ANCOVA. For exploratory purposes, we decided to further investigate the relationship between the score distance and the status effect on the two AMP blocks through correlational analyses. To this end, we created two new effect indexes (reflecting the difference in AMP indexes between High and Low status in the two blocks) by subtracting LS_LP to HS_LP (LP_Effect = HS_LP – LS_LP) and LS_SP to HS_SP (SP_Effect = HS_SP – LS_SP). We then ran correlation analyses between Dist_Diff and LP_Effect and SP_Effect. Furthermore, we ran correlation analyses between HS_Dist (distance between the HS and the participant) and LS_Dist, the AMP indexes (HS_LP, HS_SP, LS_LP, LS_SP) and the explicit ratings (Attractiveness, Competence, Intelligence and Dominance).

Supplementary Results

Block x Status x Dist_Diff ANCOVA

Main effects of Block (F(1,24) = 0.59, p = 0.44) and Status (F(1,24) = 1.30, p = 0.26) were not significant, nor were the Block x Dist_Diff (F(1,24) = 0.00, p = 0.98) or Status x Dist_Diff (F(1,24) = 0.00, p = 0.98) interactions. As before entering the covariate, there was a significant Block x Status interaction (F(1,24) = 22.77, p < 0.0001). However, we also found a significant Block x Status x Dist_Diff interaction (F(1,24) = 7.18, p = 0.01, partial eta squared = 0.23). We further explore this interaction with a correlational approach. Correlations between Dist_Diff and Status effect indexes. Results indicated that there was a nonsignificant correlation between LP_Effect and Dist_Diff (r = 0.30, p = 0.12) and also a nonsignificant correlation between SP_Effect and Dist_Diff (r = -0.29, p = 0.13).

Correlation between HS_Dist, LS_Dist and implicit/explicit evaluation of HS and LS

As shown in Tables S2, the Distance indexes were not correlated with any of the implicit or explicit status effect indexes after Holmes-Bonferroni correction for multiple correlations.

Discussion

We investigated whether our main results might have been influenced by the fact that participants' scores were closer to the Low status' than to those of the High status'. Our supplementary analysis showed that including the distance difference as a continuous predictor does not invalid the result, as the Block x Status interaction is still highly significant. However, although correlational analyses failed to show any significant results, the significant three-level interaction with the distance difference index seems to suggest that this distance might have played a role.

Table S2

	HS_Dist	HS_LP	HS_SP	HS_Attr	HS_Comp	HS_Int	HS_Dom
HS_Dist		0.40	0.03	-0.13	-0.15	-0.16	-0.22
HS_LP			0.18	-0.07	-0.31	-0.43	-0.31
HS_SP				-0.35	-0.18	-0.29	-0.11
HS_Attr					0.05	0.14	0.38
HS_Comp						**0.69****	0.31
HS_Int							0.37
HS_Dom							

Table of Pearson correlation coefficients. (HS_Dist = distance between participant's and HS player's score at the end of the game; HS_LP = AMP effect index for the HS player in the long presentation task; HS_SP = AMP effect index for the HS player in the short presentation task; HS_Attr = Attractiveness rating; HS_Comp = Competence rating; HS_Int = Intelligence rating, HS_Dom = Dominance rating). Marked correlations are significant at $p < 0.05$ (*) and $p < 0.01$ (**). Holmes correction for multiple correlations was applied.

	LS_Dist	LS_LP	LS_SP	LS_Attr	LS_Comp	LS_Int	LS_Dom
LS_Dist		-0.04	-0.27	0.41	0.19	0.02	0.26
LS_LP			0.13	0.25	0.21	0.19	0.39
LS_SP				-0.23	0.00	-0.15	-0.23
LS_Attr					0.30	0.35	0.47
LS_Comp						**0.60***	**0.67****
LS_Int							**0.62***
LS_Dom							

Table of Pearson correlation coefficients. (LS_Dist = distance between participant's and LS player's score at the end of the game; LS_LP = AMP effect index for the LS player in the long presentation task; LS_SP = AMP effect index for the LS player in the short presentation task; LS_Attr = Attractiveness rating; LS_Comp = Competence rating; LS_Int = Intelligence rating, LS_Dom = Dominance rating). Marked correlations are significant at $p < 0.05$ (*) and $p < 0.01$ (**). Holmes correction for multiple correlations was applied.

3- Supplementary analysis on the effects of AMP block order

In order to rule out the possibility that our results could be affected by the fact that the Short presentation block was always administered first, we ran a repeated measures Status (High vs Low) x Block (Short vs Long presentation) x Session (before vs after the manipulation) ANOVA on raw data

Supplementary results

The Status x Block x Session ANOVA on raw data showed that the main effects of Status (F(1,25) = 2.24, p = 0.14) and Block F(1,25) = 2.55, p = 0.12 were not significant, while the main effect of Session was significant (F(1,25) = 10.9, p = 0.002, partial eta-squared = 0.30). The Block x Session (F(1,25) = 0.63, p = 0.43) and Session x Status (F(1,25) = 1.36, p = 0.25) interactions were not significant. The Block x Session x Status interaction was significant (F(1,25) = 18.25, p = 0.0002, partial eta-squared = 0.42). Bonferroni-corrected post-hoc tests showed that in Session 1, VAS scores attributed to the HighStatus were not different from those attributed to the LowStatus neither in the Short Presentation (p = 0.15) nor in the Long Presentation (p = 1) block. Conversely, in Session 2 VAS scores were significantly higher for the HighStatus than for the LowStatus condition in the Long Presentation (p = 0.01) but not in the Short Presentation block (p = 1). This suggests that only after the Status manipulation, participants showed a preference for the HighStatus player. As for Session-related effects, we found that for the Short Presentation block there was a significant reduction in VAS scores from Session 1 to Session 2 both for the HighStatus (p < 0.0001) and the LowStatus (p < 0.0001). Conversely, in the Long Presentation block, VAS scores in Session 2 were significantly lower than in Session 1 only for the LowStatus (p < 0.0001) but not for the HighStatus (p = 1).

Discussion

Our results showed that both the main effect of Block (i.e. Short/Long presentation) and the Block x Session interaction were not significant. This suggests that our main results are not due to an order effect (i.e. to the fact that the Short Block was always administered first). Indeed, since the Short presentation block was always administered as first, the Block factor actually reflects the order factor. If there were an order effect, we should expect to see a main effect of Block. For that reason, VAS scores in the Short presentation block (the one administered as first) should be significantly different than the VAS scores in in Long presentation block (the one administered as last). Since this is not the case, we think that this possibility can be ruled out.

3. Hierarchical Interactions: competence-based social status and implicit preference shape hand kinematic and synchrony in joint actions (Study 2)

Abstract

The social status of observed individuals modulates not only the way we perceive them but also how we interact with them. In the present study, we investigated whether the (competence-based) social status of an interactor modulates the ability to coordinate with him to perform a joint action. In the first part of the experiment, two confederates were attributed high and low social status depending on their stance on a competence-based hierarchy in which the participant was always occupying the middle position. Participants were then asked to perform a joint grasping task with the high and low status confederates. Our results expand on previous research on the effect of social variables on action processing and social interactions by showing that participants' movements changed according to the social status of the interaction partner, both at behavioural (i.e. synchrony, movements' start) and motion kinematics (i.e. hand trajectory, posture) levels.

Introduction

The ability to coordinate our actions with those of other people is fundamental in everyday interactions. Joint actions have been defined as "any form of social interaction whereby two or more individuals coordinate their actions in space and time to bring about a change in the environment" (Sebanz et al., 2006a). Theoretical models of joint action suggest that this ability relies on a fronto-parietal brain network partially overlapping with the so-called mirror-neurons system (Rizzolatti et al., 1996; Gazzola and Keyser, 2009). Indeed, performing a joint action with a partner requires the prediction of the intentions and the consequences of the partner's actions (Kokal et al., 2009) as well as the integration of observed and executed actions, both processes likely occurring through visuo-motor transformation processes that take place in the human motor system (Keyser and Gazzola, 2014).

One important finding from recent research is that activity of the human sensorimotor system is not neutral to the social identity of the observed agent. Studies have shown that the sensorimotor mirroring of observed actions (Gutsell and Inzlicht 2010; Désy and Théoret 2007; Liew et al., 2011) as well as of observed pain (Avenanti et al., 2010; Azevedo et al. 2013) is modulated by group membership and skin colour of the model. Moving from passive observation to dynamic motor interactions, previous studies suggest that also the ability to coordinate with another agent to perform a joint grasping action is sensitive to high-level social influences such as race and interpersonal perception. Individuals' with higher racial bias show a reduction of visuo-motor interference while coordinating to perform a complementary grasping with out-group avatars compared to in-group ones (Sacheli et al., 2015). Visuo-motor interference in this study was indexed as a difference between imitative and complementary hand movements' kinematics, reflecting the automatic tendency to imitate the observed (complementary) movements in both cooperative and competitive interactions (Era et al., 2018). In another study, pairs of participants that received a negative interpersonal manipulation were less able to synchronise when the task required to coordinate their movements both in space and time rather than only in time (Sacheli et al., 2012). Moreover, manipulated (but not neutral) pairs showed visuo-motor interference in the second session of the task. Taken together, these results suggest that the ability to coordinate with another person to perform a joint action can be modulated by the interpersonal relationship between the two co-agents.

One important factor shaping interpersonal relationships is social status. As stated in the previous chapters, social status is defined as “the relative rank of an individual along one or more social dimensions within a given social hierarchy” (Mattan et al., 2017). Studies have shown that the gaze of high-status individuals induces a stronger cueing effect (Cheng et al., 2013; Dalmaso et al., 2012; Foulsham et al., 2010; Liuzza et al., 2011; Porciello et al., 2016) and that high status faces are easier to recognize (Ratcliff et al., 2011). In addition, observing a high-status model facilitates perceptual decisions (Santamaria-Garcia et al., 2014), EEG correlates of face processing (N170 amplitude) (Santamaria-Garcia et al., 2015) and EEG correlates of social evaluation (P300 amplitude) (Gyurovski et al., 2018). Social status was also found to modulate neural activity in brain regions involved in social evaluation, reward, salience and attention such as the ventromedial and dorsolateral prefrontal cortex (Cloutier et al., 2014; Zink et al., 2008; Marsh et al., 2009). Taken together, these results suggest that high-status individuals are a particularly attractive category of social stimuli.

The effects of social status on action simulation have mainly been tested from the point of view of the observer. Participants’ subjective power level (Hogeveen et al, 2014) and social status (Varnum et al., 2016) were found to modulate motor resonance to observed intransitive actions, as indexed by Motor Evoked Potentials (MEP) amplitude and mu-suppression, respectively. This decrease in motor resonance for high status and high power participants might reflect the fact that high status individuals do not rely on others for accessing important resources and, therefore, they need less to process their actions (Fiske and Depret, 1996). The social status of the partner influences action representation also in more interactive tasks. For example, action co-representation effect (indexed by stimulus–response compatibility) in a social version of the Simon task (where each participant has to press a different key in response to a target appearing either in congruent and incongruent spatial locations with respect to the laterality of the response key) is reduced or even absent in participants from a high-status group (Italians) playing with member of a low-status group (Albanians) but not in Albanians playing with Italians (Aquino et al. 2015). These findings suggest that the actions of low-status individuals are co-represented less than those of the high-status ones.

Thus, based on evidence that high status individuals receive more attention and that their actions are more co-represented, it would be expected that they are also imitated more. Congruent with this prediction is that, when imitation is measured in ecological settings in the form of behavioural mimicry (i.e. the tendency to involuntary imitate the gestures and postures of others, Chartrand and Bargh, 1999), mimicry of high-status models seems to be less cognitively demanding (Dalton et al., 2010) and enhanced with respect to low-status models, especially in individuals high in self-monitoring (Cheng et al., 2003) and narcissism (Ashton-James et al., 2013). Conversely, social status seems to have no effect on automatic imitation measured with a space compatibility response (SCR) task (Farmer et al., 2016). This apparent contradiction is explained by the fact that it is presently not known whether automatic imitation and mimicry rely on the same behavioural and neural mechanisms. One study that directly investigated their relationship, for example, found no evidence for a correlation between the automatic imitation and mimicry (Genschow et al., 2017). It should be noted that the two tasks differ between each other on many aspects. Indeed, while automatic imitation is measured on a difference in reaction times between congruent and incongruent trials during a task requiring a good level of awareness and control, behavioural mimicry is tested in naturalistic settings where participants are not aware of it occurring (Genschow et al., 2017).

The joint grasping task developed by Sacheli and colleagues (Sacheli et al., 2012; 2013; Candidi et al., 2015; Curioni et al., 2017; Era et al., 2018) offers the opportunity to measure different aspect of online motor interactions, from synchrony to the fine-grained kinematics of hand movements. Since social status seems to have a deep influence on the way we process other people, we hypothesised that the social status of the interactor might also modulate the ability to coordinate to perform a joint action. In the present study we tested this hypothesis, capitalising on the results of a previous study (Study 1, Chapter 2), where we have demonstrated that the perceived competence-based social status of individuals acquired in the context of an interactive game modulates implicit preference for them. Here, participants underwent the status-inducing procedure described in Study 1 and their implicit preference toward the high and low status players was measured with the Affect Misattribution Procedure. Participants were then asked to interact with the high and low status player and synchronise their reach-to-grasp movements with them. Our results showed that the social status of the interactor influences various parameters of participant's reach-to-grasp movements in the interaction task and that this effect is further modulated by participants' implicit preference toward the high and low status players.

Methods

Participants

Twenty-four male subjects (age = 24.3 ± 4.2 years) were recruited from the Sapienza University campus. All participants had normal or corrected-to-normal vision, were free from any psychiatric or neurological disorder and were naïve to the real purpose of the experiment. Five participants were excluded for having expressed suspicion about the cover story, so the final sample comprised 19 male subjects (age = 23.8 ± 4.1 years). The sample size was selected based on previous studies using a similar paradigm (Sacheli et al., 2012; 2013; 2015). Participants gave their written informed consent to participate in the study and received a reimbursement of 14 euros. The experimental protocol was approved by the ethics committee of the Fondazione Santa Lucia and was carried out in accordance with the ethical standards of the 1964 Declaration of Helsinki.

General procedure

Upon their arrival at the lab, differently from Study 1, in which participants didn't meet the confederates, subjects met the experimenter and the two confederates (which they believed to be other participants). The group was then told that they were about to play an interactive computer-based game from different rooms followed by a motor interaction task. The experiment started with a first AMP block that served as a baseline measure of implicit preference toward the two confederates. Immediately after, subjects underwent the status-inducing procedure (i.e. the interactive time estimation task), followed by the second AMP block (as in Study 1). This block was intended to measure whether the competence-based hierarchy established during the game changed the implicit preference toward the two confederates in terms of perceiving one of them as high-status (preferred) and the other low-status (not preferred). Subjects were then engaged in the joint action task with Confederate 1 (High Status or Low Status, order counterbalanced) and then with Confederate 2. Finally, the last AMP block was administered, to measure any possible change in implicit interpersonal preference due to the motor interaction itself, see Fig. 1. At the end of the experiment, participants underwent a funnel debriefing procedure (Ferguson & Bargh, 2004; Bargh &

Chartrand, 2000) to determine if they had any suspicion about the cover story and were then debriefed.

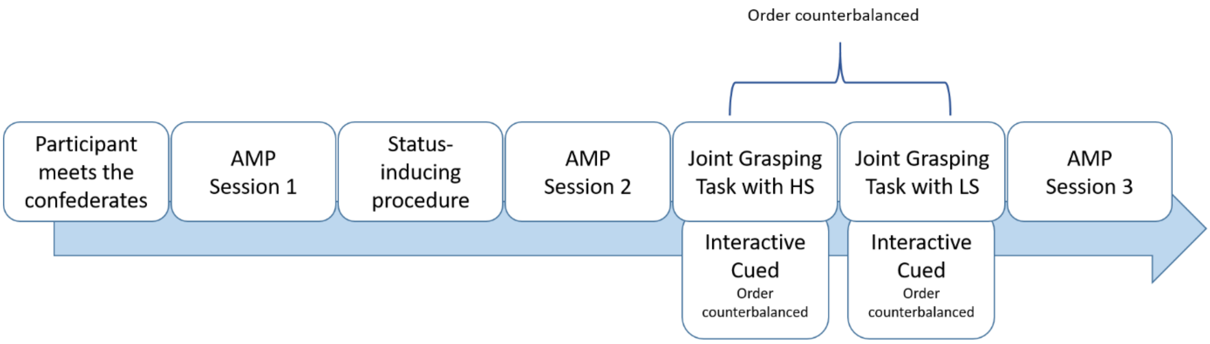


Fig. 1 – Experiment timeline

Implicit evaluation task (Affect Misattribution Procedure)

Nineteen Chinese characters (on a grey background, 512 x 384 pixels) were used as target stimuli. Prime stimuli were two pictures (292 x 400 pixels) of the two male confederates' face (Confederate 1 and Confederate 2) whereas the backward masks were two same-size scrambled versions of the original pictures, created with Matlab (Mathworks, Cherborn, MA, USA). The AMP task was delivered using E Prime 2.0 (Psychology Software Tools, Pittsburgh, PA). Each trial started with a fixation cross presented for 1000 ms at the center of the screen, followed the prime image (either identity of Confederate 1 or 2) for 75 ms, a backward mask for 100 ms and the target (ideogram) for 1000 ms (as in Era et al., 2015). Following each target (and backward mask), a vertical Visual Analogue Scale (VAS, height 10 cm) appeared on the screen under the sentence "How much do you like this image?", with the words "Not at all" and "Extremely" beside its bottom and top end, respectively, and lasted on the screen until a response was made. Participants were informed that they would see one image (no mention was given concerning the fact that these show the identity of the confederates) and then a Chinese pictograph, and that they should ignore the first and rate the pleasantness of the second stimulus by clicking with the mouse on the VAS point that corresponded to their judgment. Throughout two blocks of 19 trials, each target image was repeated twice, once preceded by the face prime of Confederate 1 and once by the face prime of Confederate 2.

Status-inducing procedure

As in Study 1, subjects were engaged in a cooperative time estimation task with the two confederates. Importantly, they were told that the individual score of each player would contribute to a collective score and that at the end of the experiment this score would be converted in real money to be split between the three players. The task was administered with E-Prime 2.0 (Psychology Software Tools, Pittsburgh, PA). At the start of each trial, a blue circle appeared on the computer screen for a random time interval (1500-3500 ms), then turned green. Subjects were asked to press the space bar exactly 1 second after the colour changed. To make the task more engaging and avoid ceiling effects, we used a staircase procedure. At the beginning of the task, the allowable response time was set at 1 second +/- 550 ms. If the participant response fell within the allowable response time, his performance was scored 5, and the threshold was set at 1 second +/- 500 ms. Otherwise, the threshold was incremented at 1 second +/- 600 ms and the player’s score was 0. Participants received a feedback (a smiley face for correct responses and a sad face for errors) after each trial and could see their individual cumulative score. Every 10 trials a collective feedback slide was presented, displaying the pictures of the three players, each one framed a distinct colour. Below each picture, the individual score and a different number of stars (3 stars for the best player, 2 for the middle and 1 for the worst) were displayed. To further highlight the differential contribution of each player in the game, a square containing horizontal bars in different colours (the same of the pictures frames) that had a different width according to respective player’s contribution was displayed in the top right of the feedback slide. The task consisted of 8 blocks. In the first four blocks we kept the hierarchy unstable, with the participant moving through the first (block 1), second (block 2) and third (blocks 3 and 4) positions. From block 5 to 8, however, the ranking remained stable, with the experimental subject in the middle position. Whilst the participant's displayed score reflected his real performance, we covertly manipulated the scores obtained by the two fake players so that the one who was to become the "High Status" ranked first from block 5 to 8, and the "Low Status" ranked last in the same 4 blocks. At the end of the task we presented a slide displaying the final hierarchy and the collective score.

Joint action task

Participants were asked to perform a Joint-Grasping Task (Sacheli et al., 2012; 2013; Candidi et al., 2015; Curioni et al., 2017; Era et al., 2018). Each subject-confederate pair was seated at the opposite sides of a table (120 x 100 cm) and were instructed to reach and grasp a bottle-shaped object placed in front of them (40 cm away from the participant and 5 cm from the midline) following auditory instructions delivered via headphones. Both the subject and the confederate had their own bottle-shaped object, which was constituted by two superimposed cylinders with different diameters (small, 2.5; large, 7.0 cm). Given their shape, the upper cylinder is to be grasped with a precision grip (index finger and thumb) while the lower cylinder is to be grasped with a power (whole hand) grip. Before the start of each trial, participants were asked to keep pressed with their right index finger and thumb a starting button placed 40 cm away from the bottle-shaped object and 10 cm right to the midline. Start movement time was recorded from button release, while touch-time on the bottle was recorded via two pairs of touch-sensitive copper plates that were placed on each cylinder at 15 cm and 23 cm of the total height of the object.

Each participant had three infrared reflective markers (5 mm diameter) each attached to: i) thumb, ulnar side of the nail, ii) index finger, radial side of the nail and iii) wrist, dorso-distal aspect of the radial styloid process. Movement kinematics were tracked and recorded with a SMART-D motion capture system (Bioengineering Technology & Systems [B|T|S]). Four infrared cameras with wide-angle lenses (sampling rate 100 Hz) placed about 100 cm away from each of the four corners of the table captured the movements of the markers in 3D space. Auditory instructions concerning the movement to be executed were delivered synchronously to both participants via headphones. The instructions consisted in four different sounds: i) ‘‘high-pitch’’, 1479 Hz, ii) ‘‘low-pitch’’, 115.5 Hz, iii) ‘‘opposite”, iv) “same”.

Participants were asked to synchronize their reach-to-grasp movements with those of the interaction partner in two different tasks. In the “Interactive” task, participants were instructed to perform an imitative (Same) or complementary (Opposite) movement (i.e. if the instruction is to perform a complementary movement, one participant grasps the lower part of the object while the other grasps the upper part). In the “Cued” task, participants were instructed to grasp the lower part of the object with a power grip after hearing a “low pitch” sound and the upper part with a precision grip after hearing a “high pitch” sound. Subjects completed one Interactive and one Cued block with each confederate (High Status and Low Status). In both tasks, participants performed four types of trials: Power_Same, Power_Opposite, Precision_Same, Precision_Opposite (see fig 2). The Interactive block comprised 60 trials (30 Imitative and 30 Complementary). The Cued Block comprised 60 trials (30 Precision and 30 Power for both the participant and the confederate, the combination resulting in 30 Imitative and 30 Complementary).

Power_Same **Power_Opposite**

Precision_Same **Precision_Opposite**

Fig 2 – Graphical representation of the Joint Grasping task. Power and Precision trials are considered from the point of view of the Participant (P, on the left side). Opposite and Same movements are considered from the point of view of both the Participant and the Confederate (C, on the right side).

Data analysis

As behavioural measures we collected:

1. Asynchrony (absolute of time delay between Subject's and Confederate's grasping time);
2. Start Delay (difference between Subject's and Confederate's start movement time).

As kinematic measures we collected (only for the experimental subject):

1. Max Aperture (MaxAp): index-thumb maximum grip aperture (maximum 3-D Euclidean distance);
2. Max Wrist Height (MaxH): maximum height reached by the wrist.

Affect misattribution procedure

VAS ratings were analysed with Multilevel Linear Mixed Models using the software R and the packages lme4 (version 1.1 -21, Bates et al., 2015). Statistical significance of fixed effects was determined using type III ANOVA test with the *mixed* function from *afex* package. Our model included *Status* (High, Low) and *Session* (1, 2, 3), and their interactions as fixed factors. The random part included the random intercept for each level of *Session* over subjects.

Explicit ratings

Ratings of Competence, Intelligence, Dominance and Attractiveness for the High and Low status confederates were compared using paired-sample t tests with the *t.test* function from the package Stats (version 3.6.0).

Joint Grasping task

As a first step, data were cleaned by removing 1) erroneous trials (i.e. trials in which the pairs failed to accomplish the instruction) and 2) trials with values higher than 2.5 standard deviations above the mean or smaller than 2.5 standard deviation below the mean. We ran Multilevel Linear Mixed Models using the software R and the packages lme4 (version 1.1 -21, Bates et al., 2015). For each model, the random part was selected using the principal component analysis (PCA) method (Bates et al. 2015). We kept all random factors that explained at least 1% of variance. Statistical significance of fixed effects was determined using type III ANOVA test with the *mixed* function from *afex* package. P-values were calculated using the parametric bootstrap (PB) method. Post-hoc comparisons were performed with the 'Estimated Marginal Means' R package (version 1.3.3) via the *emmeans* and *emtrends* functions, respectively, and Tukey correction for multiple comparisons.

Joint Grasping task Models

LMM for behavioural and kinematics data in the Joint Grasping task also included as a continuous predictor an index of the effect of the status-inducing procedure on implicit preference toward the two confederates. We reasoned that any status effect on the Joint Grasping task might have been mediated by the effect of the procedure on implicit liking (AMP). Namely, some participants could have been more susceptible to the AMP procedure than others. The continuous predictor (AMP) was extracted as follows: We first created two Session_effect indexes (HS_effect = HS Session 2 – HS Session 1 and LS_effect = LS Session 2 – LS Session 1), then we created a Status effect index (HS_effect – LS_effect) which we called AMP. The AMP status effect index was then entered as a continuous predictor in our models for the Joint Action task analyses.

The Asynchrony and Start Delay models included *Status* (High, Low), *Task* (Interactive, Cued), *Trial* (Opposite, Same), *AMP* and their interactions as fixed factors. The random part included the random slope of *Trial* for each level of the Participant x Task interaction and the random intercept for each level of the Participant x Task interaction.

The Max Aperture and Max Wrist Height models included *Status* (High, Low), *Task* (Interactive, Cued), *Trial* (Opposite, Same), *Movement* (Power, Precision), *AMP* (i.e. Status effect index of the AMP task) and their interactions as fixed factors. The random part included the random slope of *Trial* for each level of the Participant x Task interaction and the random intercept for each level of the Participant x Task interaction

Results

Affect Misattribution Procedure (AMP)

Model: VAS ~ Session * Status + (1+Session|Subject)

Type 3 ANOVA on VAS scores revealed that both the Status (F = 0.35, p =0.56) and the Session (F = 0.23, p = 0.80) factors were nonsignificant. The Status*Session interaction was also nonsignificant (F = 0.20, p = 0.82). This suggests that participants' implicit preference for the two confederates 1) did not change through the three sessions and 2) was not modulated by the confederates' status (see fig 3). We decided to further explore this result by carrying additional analyses only on the first two sessions (i.e. before and after the status-inducing procedure). Based on previous results (Study 1), we expected the pleasantness ratings of target pictures associated with the High status to be higher than those associated with the Low status in Session 2 (i.e. after the status-inducing procedure). We created a new model with only two levels for the Session factor (i.e. Session 1 and Session 2). Again, type 3 ANOVA failed to show any significant main effect or interaction (all Fs < 1, all ps > 0.1).

Confederate Check analysis

In order to check whether the two prime stimuli (i.e. picture of Confederate A and picture of Confederate B) might have differently affected the evaluation of the target pictures independently of their attributed status, we ran an additional model where the factor Status was replaced with a new factor Model (Confederate A, Confederate B). The full model included Session (Session 1, Session 2, Session 3) and Model (Confederate A, Confederate B) as fixed factors. The random part included the random intercept for participants.

Model: VAS ~ Session * Model + (1|Subject)

Type III ANOVA showed that the main effects of Session (F = 0.87, p = 0.42) and Model (F=0.27, p = 0.61) were nonsignificant. The Session x Model interaction was also nonsignificant (F=0.13, p = 0.88). Similarly to Study 2, the fact that no significant interaction between Model and the other experimental factor was found suggests that the two stimuli did not evoke different affect ratings at baseline nor in Session 2 or 3.

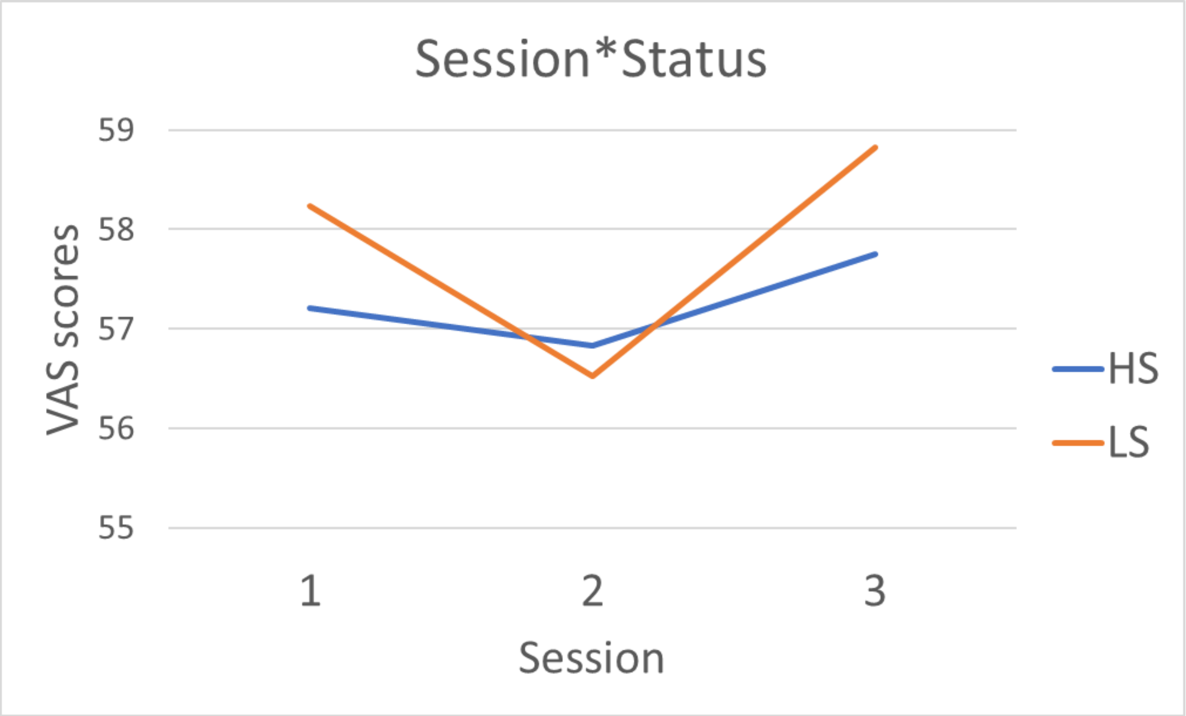


Fig. 3 – Vas scores attributed to the neutral primes preceded by the High status (HS) and the Low status (LS) confederates' picture in Session 1 (before the manipulation), Session 2 (after the manipulation) and Session 3 (after the Joint Grasping task).

Explicit ratings

Results showed that after the status-inducing procedure participants rated the High status confederate as more Dominant than the Low status (t (18) = 2.17, p = 0.04). We found no significant difference in the ratings of Competence (t(18) = 1.05, p = 0.30), Intelligence (t(18) = 0.56, p = 0.57) and Attractiveness (t(18) = 1.35, p = 0.19), see Fig. 4.

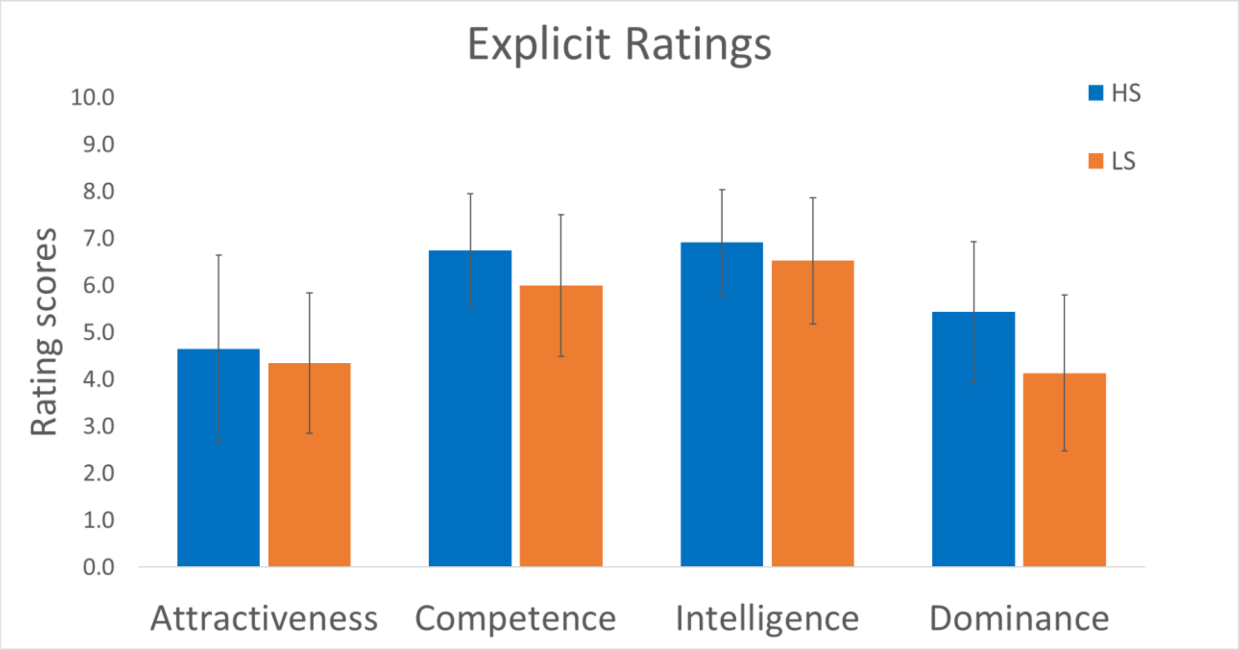


Fig 4 – Explicit ratings of the High and Low status confederate on Attractiveness, Competence, Intelligence and Dominance.

Joint Grasping task

Asynchrony (in touching the bottles)

Model: Asynchrony ~ Status * Task * Trial * (AMP) + (Trial|Subject:Task)

Type 3 ANOVA revealed a significant main effect of Task (F= 5.85, p = 0.02), indicating that Asynchrony was reduced in the Cued, compared to the Interactive Task (estimate = -13.41). Moreover, there was a Status*AMP (F= 3.86, p = 0.05) and a Status*Task*AMP interaction (F=20.71, p < 0.001). As a follow-up test on the interactions with the continuous predictor AMP, we used the R function *emtrends* to estimate the *slopes* of the covariate trend for each level of the factors. Simple slope analysis on the Status*Task*AMP interaction revealed that during the Interactive block with the Low Status confederate, Asynchrony yielded an increase of 3.41 ms for each 1-unit increase in AMP (SE = 1.56). The pairwise difference in the simple slope of AMP showed that at the averages, increasing AMP has the effect of increasing Asynchrony with the Low Status confederate while slightly decreasing it with the High Status (estimate = 4.08, SE = 0.88, z-ratio = 4.62, $p < 0.0001$). This result suggests that participants achieved a better performance (i.e. lower Asynchrony values) in the Interactive block when they had to coordinate their movements with those of the High, compared to the Low, status confederate. Interestingly, this result was mediated by their implicit preference. Specifically, the stronger was the implicit preference for the High over the Low status after the game (i.e. higher AMP values), the greater the difference in Asynchrony values in the two conditions (see Fig. 5 and 6 for the Task x Status x AMP interaction and Fig. 7 for the distribution of Asynchrony in the Task x Status factorial combination).

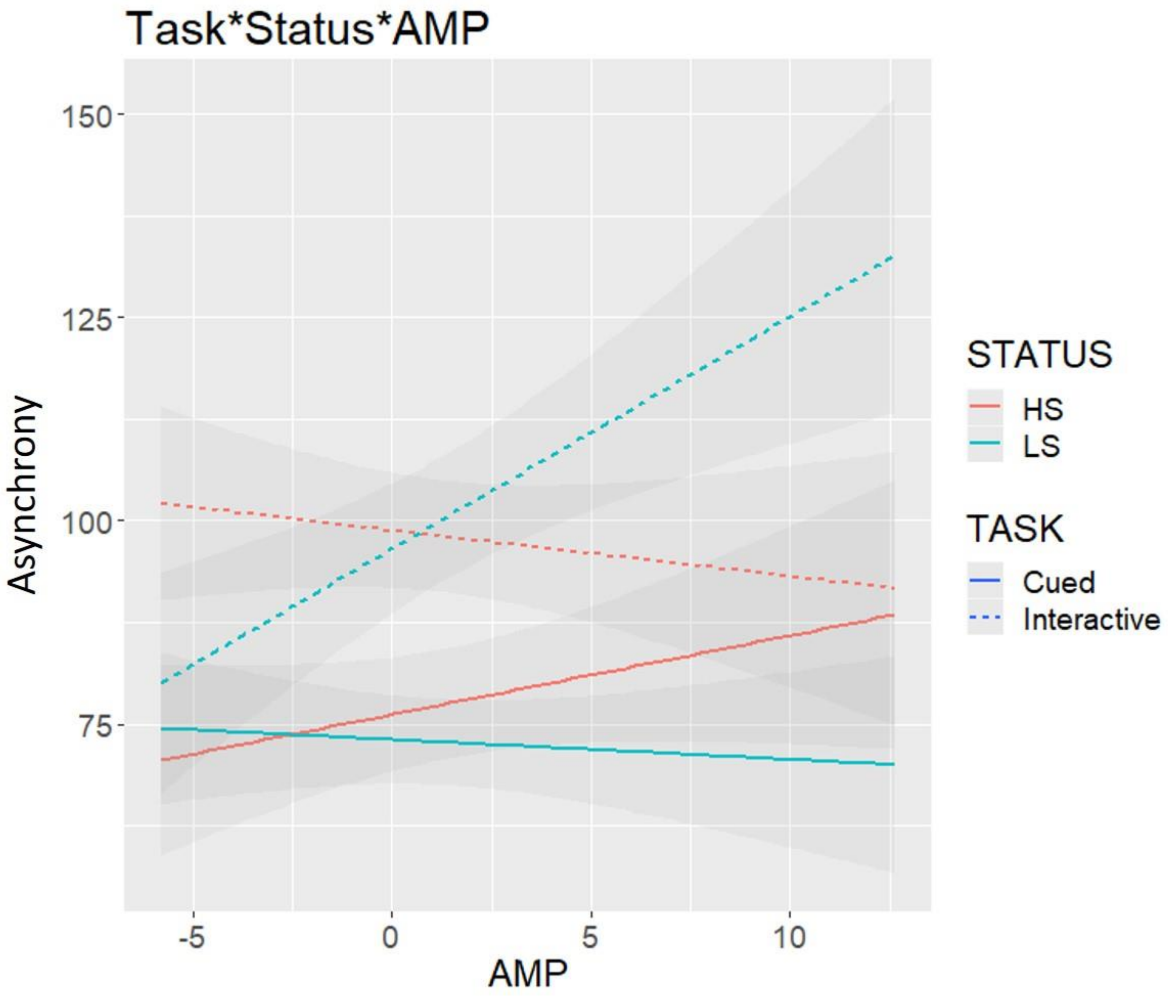


Fig. 5– Grasping Asynchrony with the high and low status confederates during the Interactive task was modulated by participants' implicit preference. Positive values of AMP indicate a preference for the high status, while negative values indicate a preference for the low status. Smaller values of Asynchrony indicate a better performance.

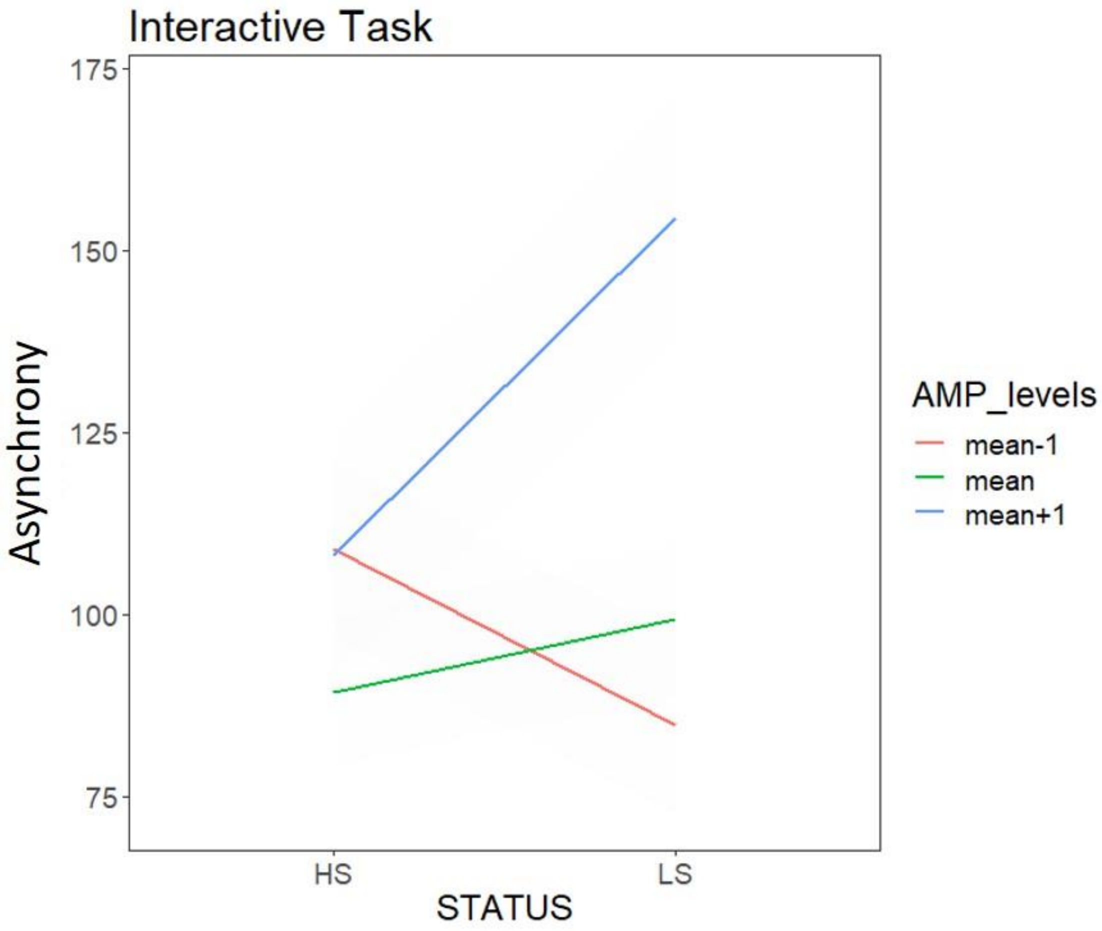


Fig 6 – Slopes of the high-low status difference in Grasping Asynchrony during the Interactive task. Participants with high levels of AMP (mean + 1, i.e. those displaying a strong preference for the high status) achieved better performance with the high status. Participants with low levels of AMP (mean – 1, i.e. those displaying a strong preference for the low status) achieved better performance with the low status.

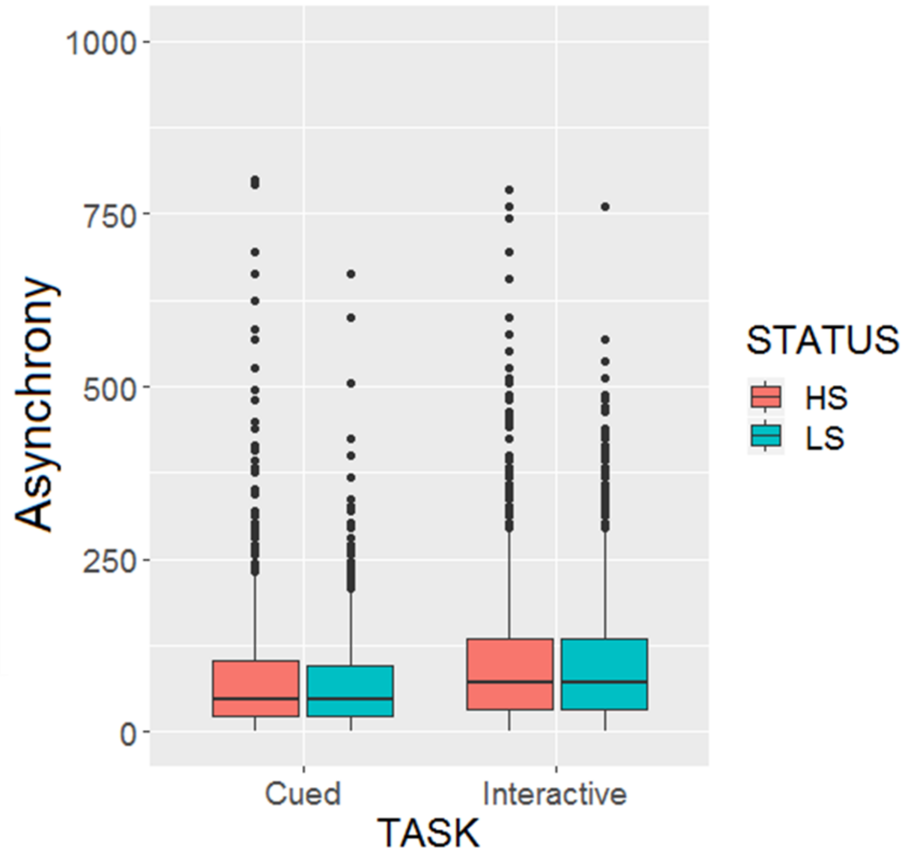


Fig. 7 – Distribution of the Asynchrony values in the Task x Status interaction (not significant).

Start Delay (RTs)

Model: StartDelay ~ Status * Task * Trial * (AMP) + (Trial|Subject:Task)

Type 3 ANOVA revealed a significant Status*Task interaction (F= 9.47, p = 0.005). Post hoc tests showed that Start Delay was higher when participants were interacting with the High, compared to Low, status confederate in the Interactive task (estimate = 18.87, SE = 4.15, z-ratio = 4.54, p < 0.0001) but not in the Cued one (estimate = 1.83, SE = 4.23, z-ratio = 0.43, p = 0.66), see Fig. 7. This means that during the Interactive task participants started their movements later when interacting the High than the Low status confederate (see figure 8). The fact that this effect was found only in the Interactive task, where pairs had to decide whether to grasp the bottle in the lower or upper part to perform an imitative or complementary action, seems to suggest that participants were more willing to let the High status than the Low status take the first decision, thus leading the interaction. In other words, they were “following” more the High than the Low status confederate. Our model also revealed a Status*AMP interaction (F = 79.19, p = 0.001), which we explored with simple slopes and post hoc tests. Results showed that Start Delay in the High status condition yielded an increase of 9.91 ms for each 1-unit increase in AMP (SE = 4.8). The pairwise difference in the simple slope of AMP showed that at the averages, increasing AMP has the effect of increasing Start Delay with the High Status confederate while slightly decreasing it with the Low Status one (estimate = 5.35, SE = 0.59, z-ratio = 8.93, p < 0.001), see Fig. 9. This effect was, however, independent from the type of task, as the Status*Task*AMP was nonsignificant (F = 1.35, p = 0.25).

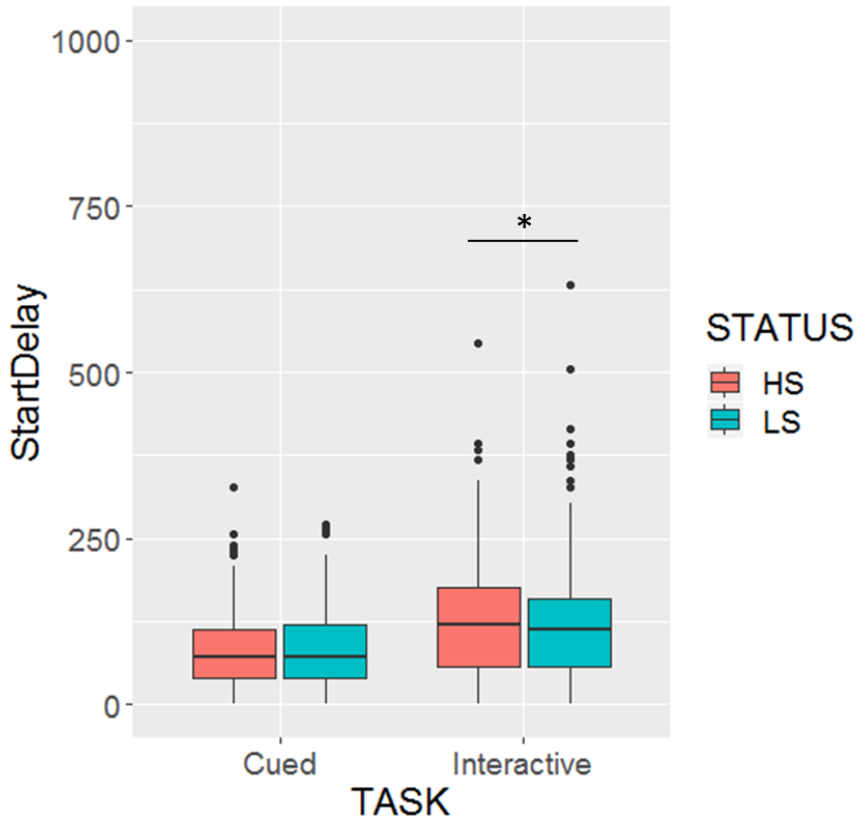


Fig 8 – Participants initiated their movements in the Interactive task with a higher delay with respect to the high status than to the low status confederate.

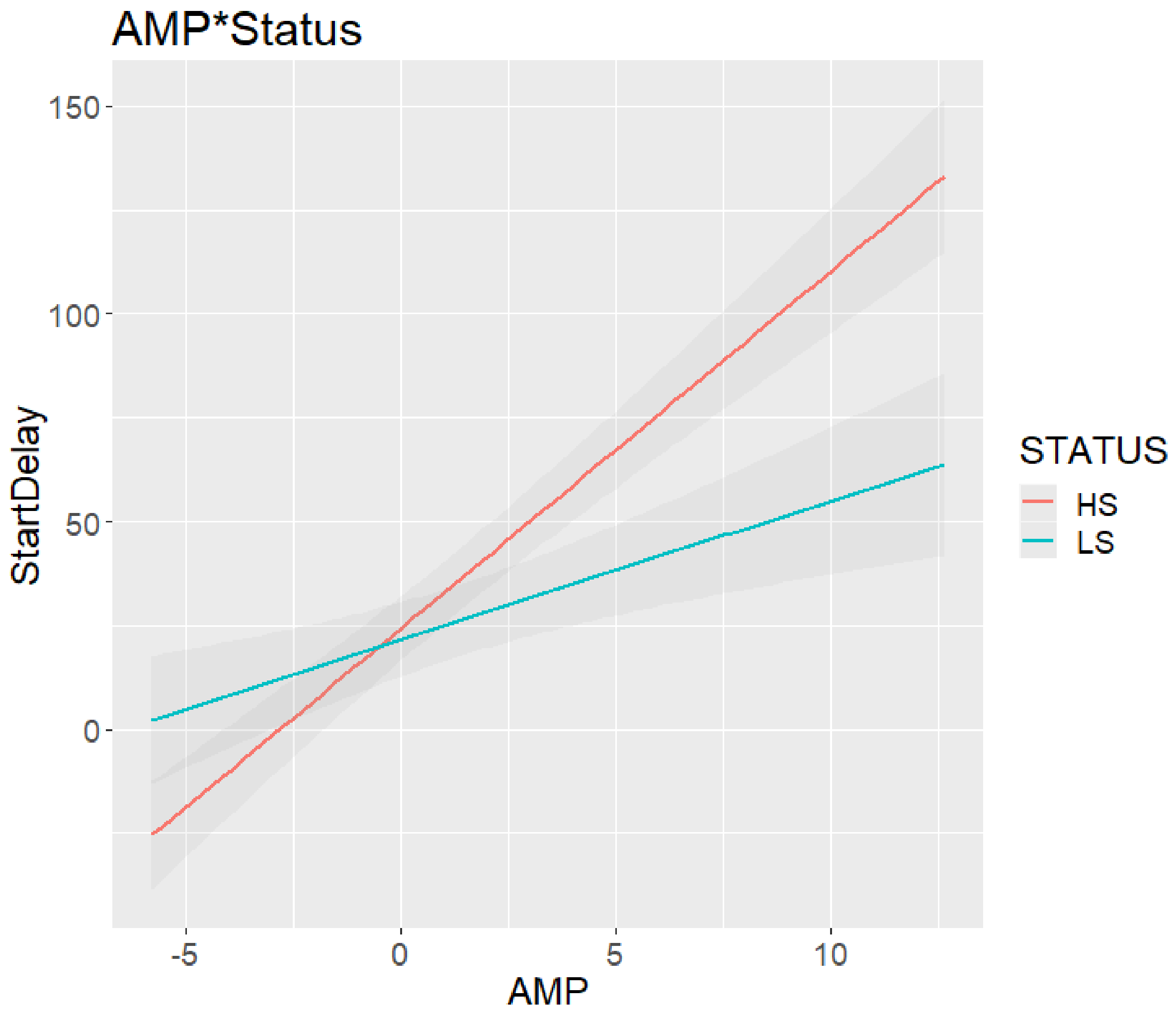


Fig 9– Participants' delay in movement initiation with respect to the high and low status confederates was modulated by their implicit preference for the two.

Max Aperture

Model: MaxAp ~ Status * Task * Trial * Movement (AMP) + (Trial |Subject:Task)

Type 3 ANOVA revealed main effects of Trial (F = 6.84, p = 0.007) and Movement (F = 4266, p = 0.001) and a Trial*Movement interaction (F= 8.33, p = 0.004). Post hoc tests showed that, for Precision grips, Max Aperture was significantly higher during Opposite, compared to Same, movements (estimate = 1.61, SE = 0.39, t-ratio = -4.89, p < 0.0001). This result indicates the emergence of visuo-motor interference, as participants were likely imitating the hand posture of the interaction partner. There was also a significant Task*Movement interaction (F= 83.36, p = 0.001). Post Hoc test, however, indicated that Max Aperture was higher for Power than for Precision grips both in both the Cued (estimate = 29.22, SE = 0.40, t-ratio = 71.45, p < 0.0001) and in the Interactive (estimate = 23.95, SE = 0.40, t-ratio = 58.70, p < 0.0001) tasks. A significant Status*Task interaction (F = 21.25, p = 0.001) showed that, while in the Interactive task Max Aperture was larger in the Low, compared to High status, condition (estimate = 1.94, SE = 0.39, t-ratio = 4.89, p < 0.0001), in the Cued task it was slightly larger for the High than in the Low status condition (estimate = -1.01, SE = 0.40, t-ratio = -2.52, p = 0.01, see Fig. 10). Furthermore, there was a Status*Movement*AMP interaction (F= 5.46, p = 0.02) which we explored with simple slopes and post hoc tests. Analysis of simple slopes failed to show any significant results (i.e. none of the slopes was significantly different from zero). However, the pairwise difference in the simple slopes of AMP showed that at the averages, increasing AMP has the effect of decreasing Max Aperture in Power grasping trials in the High status condition while slightly increasing it in the Low Status one (estimate = -4.33, SE = 0.85, t-ratio = - 0.50, p < 0.001). This indicates that the stronger was the implicit preference for the High over the Low status after the game (i.e. higher AMP values), the smaller Max Aperture for Power grasping was during the interaction with the High compared to the Low status confederate (see Fig. 11 and 12).

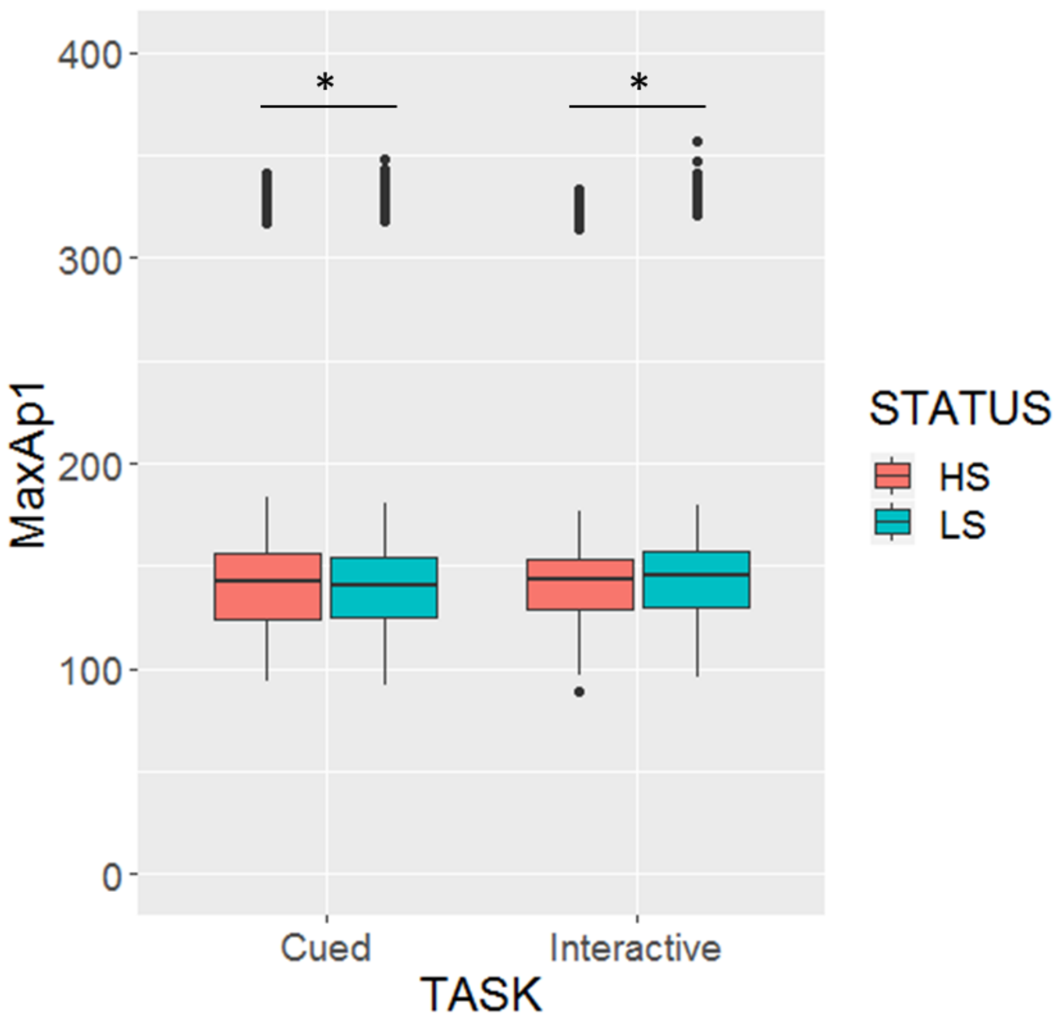


Fig 10 – Participants' hand aperture during the Interactive task was larger when interacting with the low status than with the high status. On the contrary, hand aperture was larger with the low status during the Cued task.

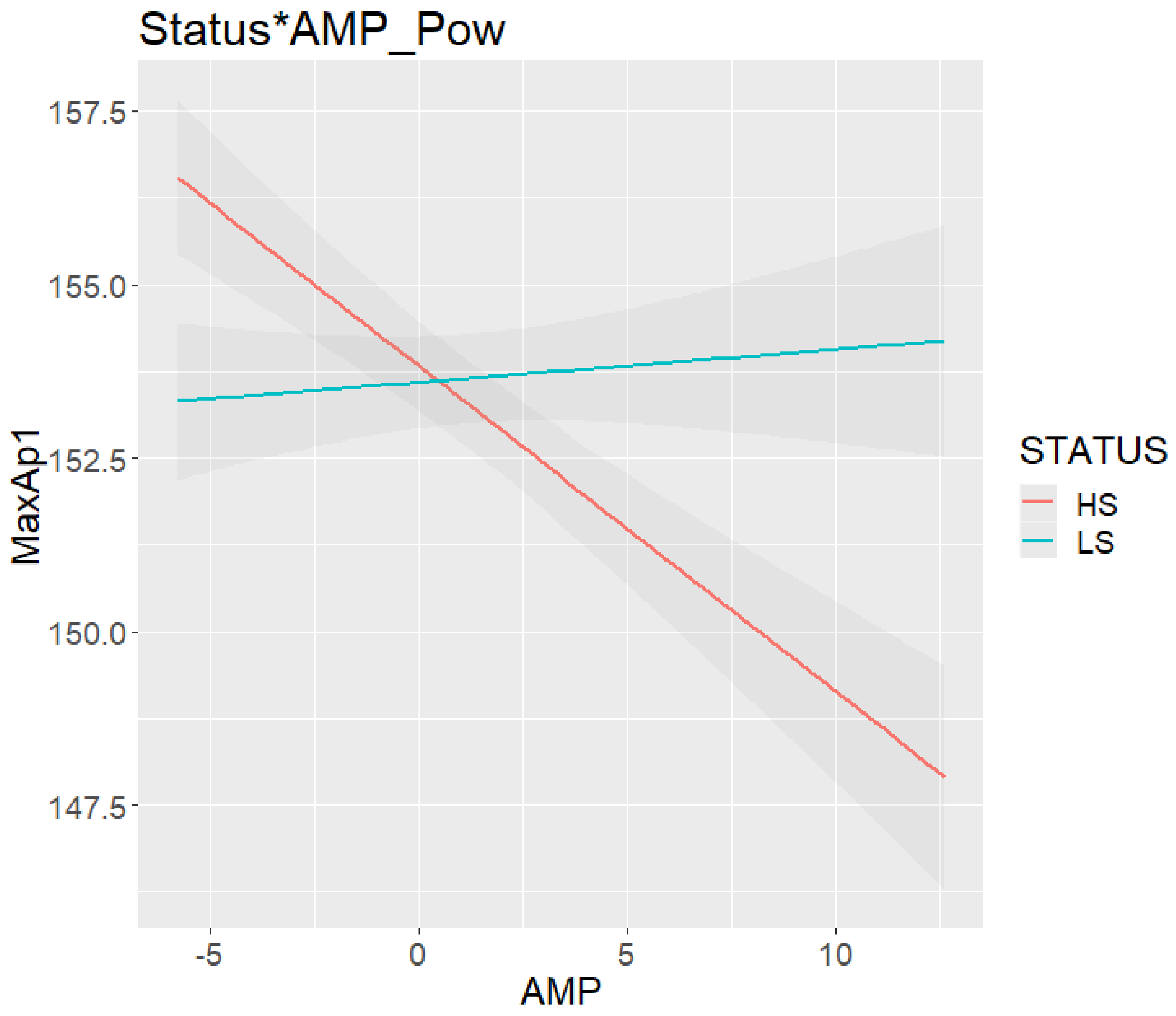


Fig 11 – Implicit preference for the high status confederate has the effect of decreasing hand aperture for Power grasping when interacting with him.

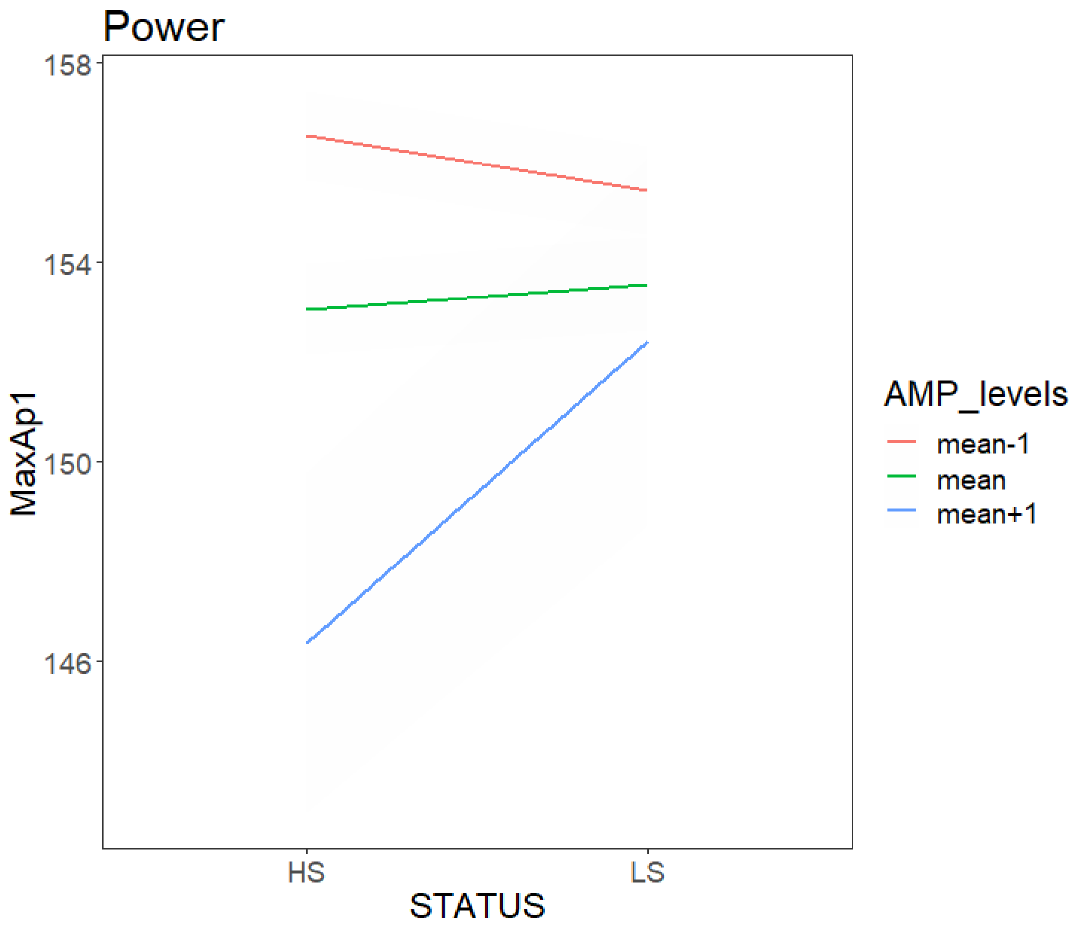


Fig 12 – Slopes of the high-low status difference in hand aperture for Power grasping. Participants with higher AMP levels (mean + 1, i.e. those displaying a strong preference for the high status) showed reduced hand aperture in Power grasping when interacting with the high, compared to the low, status confederate.

Max Wrist Height

Model: WristHeight ~ Status * Task * Trial * Movement (AMP) + (Trial |Subject:Task)

Type 3 ANOVA revealed significant main effects of Trial (F= 7.01, p = 0.02) and Movement (F= 5832, p = 0.001). Max Wrist Height was higher for Opposite compared to Same trials and, as expected, for Precision compared to Power grasping. We also found a significant Status*Task*Trial*Movement*AMP interaction (F= 8.16, p = 0.005). Simple slope analysis revealed that during the Interactive block with the High Status confederate, Max Wrist Height in Opposite_Power trials decreased of 2.37 mm for each 1-unit increase in AMP (SE = 1.14). The pairwise difference in the simple slope of AMP showed that at the averages, increasing AMP has the effect of decreasing Max Wrist Height during Power_Opposite trials while slightly increasing it in Power_Same Interactive trials (estimate = - 1.06, SE = 0.31, z-ratio = - 3.34, p = 0.01) during the interaction with the High status. Indeed, while during the interaction with the Low status Max Wrist Height in Opposite_Power was higher than in Same_Power for all levels of AMP (see fig 13) and therefore hinting to a general visuo-motor interference effect, when participants were interacting with the High status, visuo-motor interference was dependent on their AMP level (see Fig. 14). Surprisingly, the less participants preferred the High to the Low status, the higher was their visuo-motor interference with the High status (i.e. a larger difference between Opposite_Power and Same_Power,. Furthermore, simple slope analysis on Precision trials showed that during the Interactive block with the Low status confederate, Max Wrist Height in Opposite_Precision trials decreased of 2.58 mm for each 1-unit increase in AMP (SE = 1.13). The pairwise difference in the simple slope of AMP showed that at the averages, increasing AMP has the effect of decreasing Max Wrist Height during Precision_Opposite trials with the Low status while this effect was less pronounced with the High status (estimate = - 0.68, SE = 0.21, z-ratio = 3.12, p = 0.03) (see fig 15). This suggests that the more participants preferred the High over the Low status, the higher was their visuo-motor interference with the Low status.

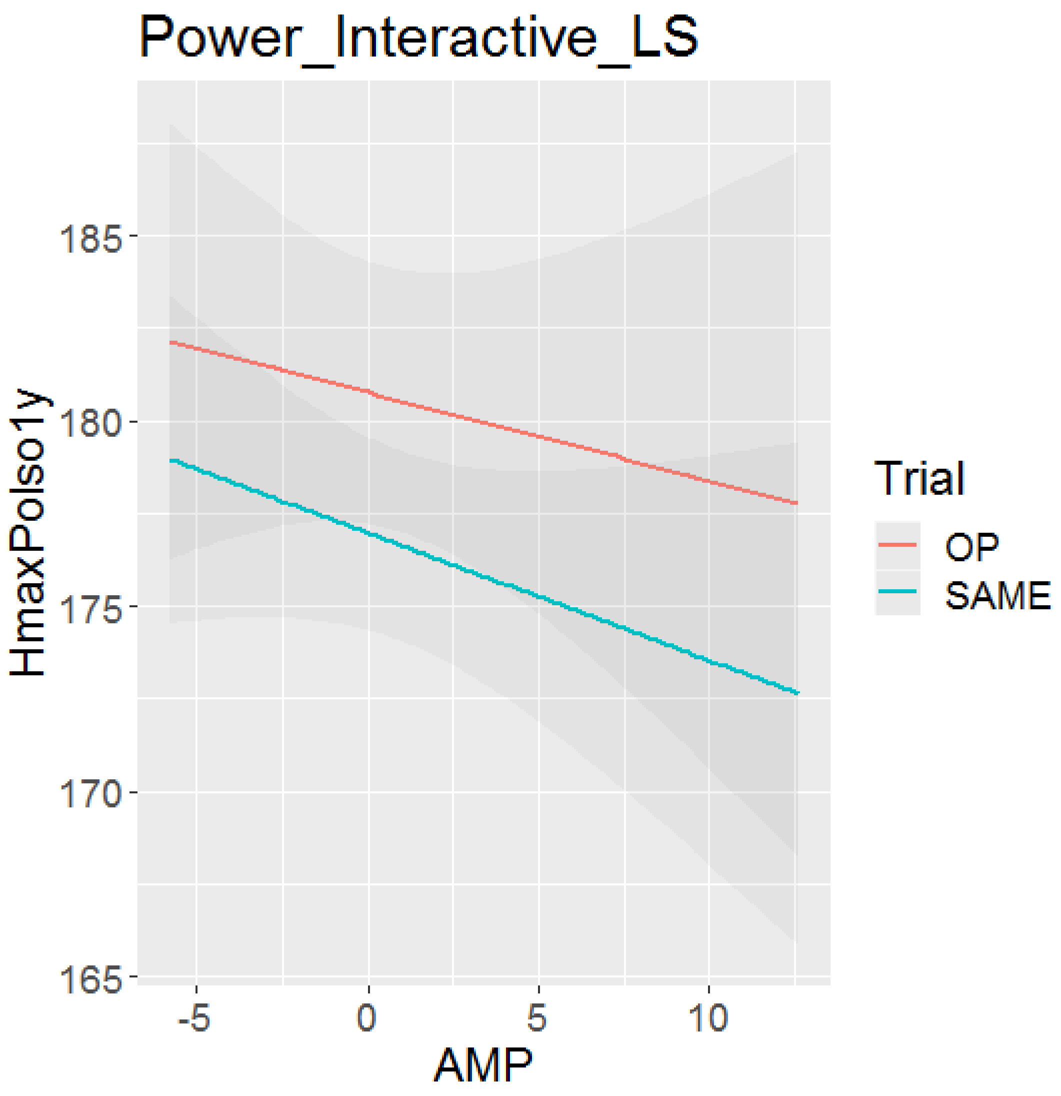


Fig 13 – When interacting with the low status confederate, participants' wrist height was higher for opposite than for same Power grasping. This suggests that they were imitating the low status confederate's movement (i.e. a Precision grasping).

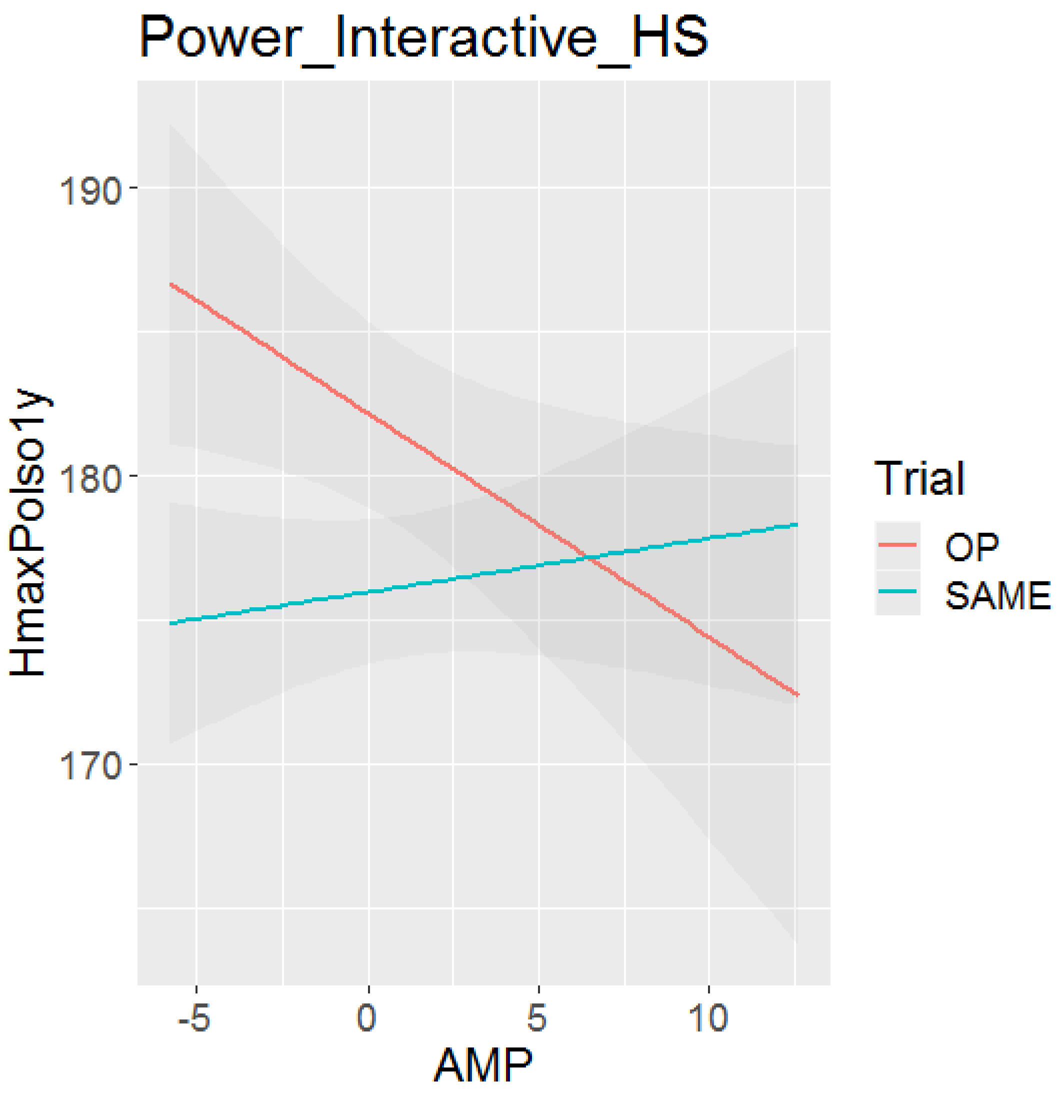


Fig 14 – When interacting with the high status confederate, participants' visuo-motor interference (i.e. higher wrist height for opposite than for same Power grasping) was dependent on their implicit evaluation.

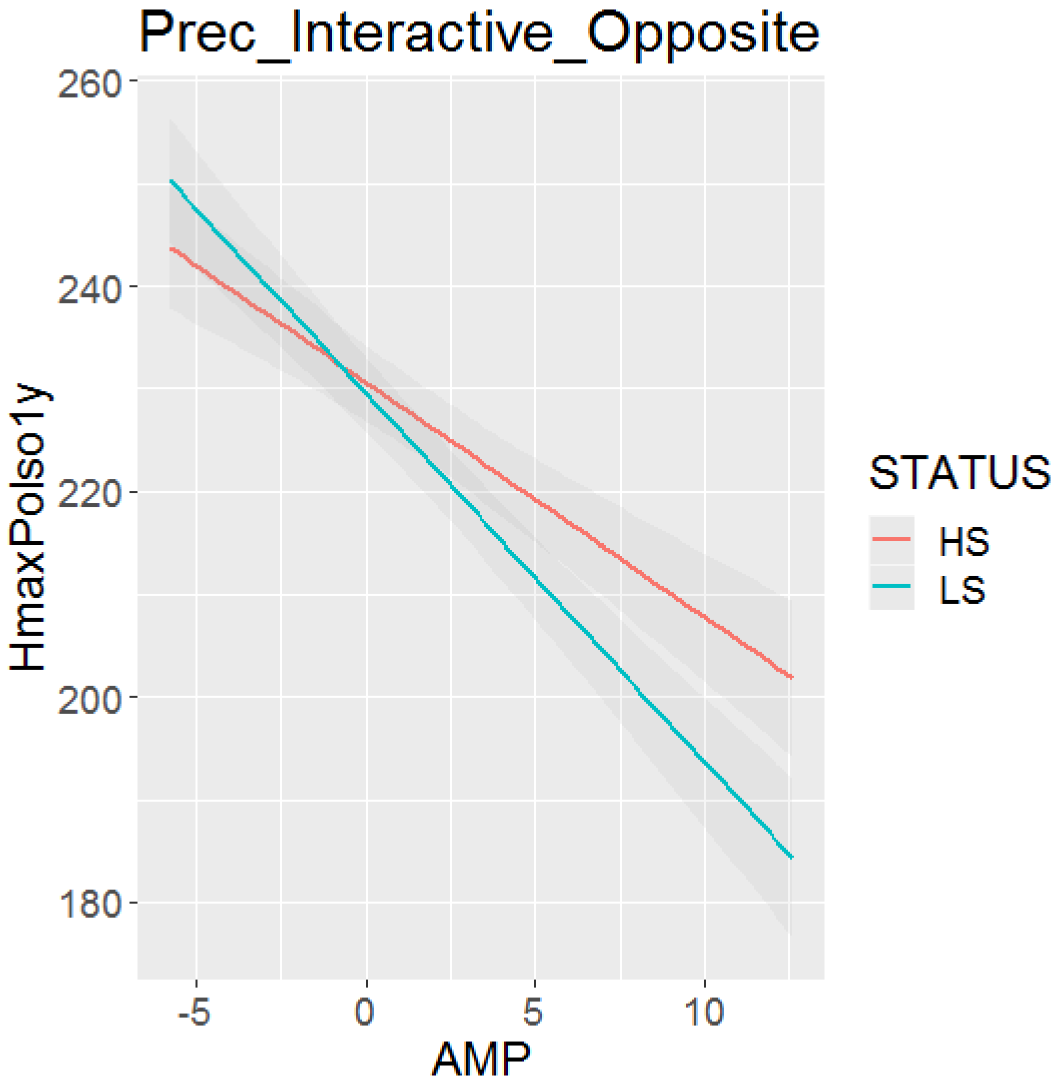


Fig 15 – Participants' wrist height during Precision grasping when performing a complementary movement with the low status confederate decreases as their implicit preference for him decreases. This seems to suggest that the less the participants liked the low status the more they were imitating him in complementary trials.

Discussion

In the present study, we investigated whether the competence-based social status of the interaction partner modulates the performance and hand motion kinematics of participants during a joint grasping task. To our knowledge, this is the first study to measure the effects of social status during a realistic joint action task. Previous studies investigating how status shapes motor interactions have relied on action observation-execution tasks (Farmer et al., 2016) or on the Joint Simon paradigm (Aquino et al., 2015) where two participants, rather than moving together, act on their own while observing or taking into account the partner's action. The Joint Grasping paradigm closely mimics a real-life joint action setting, where the partner's action, rather than being ignored or incidental, needs to be included in owns' motor plan (Sacheli et al., 2013). Our results suggest that both the performance and the hand kinematics of participants during a joint action task are heavily influenced by the social status of the interaction partner.

Competence-based social status did not modulate implicit preference.

Based on the findings reported in Study 1, we expected that after the time estimation game participants would give higher ratings of pleasantness to the neutral targets preceded by the high status prime than to those preceded by the low status prime. Contrary to our expectations, the implicit preference for the high status player was not significantly different from that of the low status after the status-inducing procedure (AMP session 2) nor after the joint action task (AMP session 3). One striking difference between Study 1 and Study 2 is, however, that in the latter participants actually met the two confederates before starting the status-inducing procedure. As a result, during their first encounter participants might have formed an impression of the two confederates and developed an implicit preference for one of the two. This preference based on a first impression might then have become impermeable to the status-inducing procedure. Indeed, research in social psychology seems to suggest that, while explicit impressions can be corrected on the light of new information, implicit first impressions are harder to change (Wyer, 2010), unless the new information is highly negatively diagnostic (Ferguson et al., 2019). It is therefore possible that our status-inducing procedure wasn’t strong enough to counteract the first-sight implicit impression that participants formed of the two confederates. It follows that the implicit preference toward the two confederates might have been influenced by both the first impression and the acquired status, therefore leading to higher levels of variability compared to Study 1.

The high status confederate was explicitly rated as more dominant.

Our results show that the only one dimension in which the explicit rating of the two confederates was influenced by their social status was Dominance. As discussed before (Study 1), although some scholars (Henrich and Gill-White, 2001; Cheng et al., 2013) have argued that competence and dominance are two distinct pathways for status acquisition, some others have raised the idea that dominance itself requires high levels of competence in specific domains, such as handling weapons, recruiting allies or being socially manipulative (Chapais, 2015). Surprisingly, we found that explicit ratings of Competence and Intelligence for the high status confederate were not significantly different from those given to the low status. As for the implicit ratings, meeting the two confederates before the game, and shaking their hands (Chaplin et al., 2000) might have influenced participants’ explicit evaluation.

Improved synchrony with the high status, modulated by implicit preference

Participants’ ability to synchronise their reach-to-grasp movements with those of the interaction partner was improved when interacting with the high, compared to the low, confederate. This effect was specific for the Interactive task, which required both the temporal and spatial coordination of the two partners' movements and the integration of predictions regarding owns' and others' motor plan with the information about the shared goal (Sacheli et al., 2015). Indeed, the presence of a shared goal (Sebanz et al., 2006), which can only be achieved through the integration of the individual's sub-goals into the same motor plan, is what distinguishes real joint actions from other forms of motor interactions. Different mechanisms can be called into action to explain how the social status of the interaction partner can interfere with this integrative process. Based on the fact that high status individuals attract attention more than the low status (Cheng et al., 2013; Dalmaso et al., 2012; Foulsham et al., 2010; Liuzza et al., 2011; Porciello et al., 2016), one could argue that the improvement in synchrony performance can be accounted for by an increase in attention. However, this is quite unlikely, since that in the Cued task participants achieved an equally good performance with the high and the low status confederate. Another possibility is that the social status of the interaction partner affected participants' ability to predict their movements. Although action simulation is not the only mechanism supporting motor interactions (Hamilton and Grafton, 2006; Kokal et al., 2009; Sacheli et al., 2015) its relevance is undisputed (Kourtis et al., 2010; Novembre et al., 2012; 2013). Indeed, results from previous studies support the idea that social status modulates motor resonance to observed actions (Hogeveen et al., 2014, Varnum et al. 2016). Lastly, our results could be explained by an effect of reward and/or motivation. There is a general consensus on the fact that high status individuals can be considered rewarding stimuli. Primate studies have demonstrated that monkeys are willing to sacrifice a reward to viewing the picture of a high status conspecific (Deaner et al., 2005). Neuroimaging studies have identified brain signatures related to reward processing during the presentation of high status individuals both in monkeys (Munuera et al., 2018) and in humans (Singer et al., 2004; Ly et al., 2011). The fact that our effect on synchrony performance was modulated by participants' implicit preference for the high and low status players seems to support the reward hypothesis. Indeed, it is possible that participants found the interaction with the high status confederate more rewarding and were therefore more committed to the common goal than when interacting with the low status one.

Emergence of follower-like behaviour when interacting with the high status.

In everyday life, it is quite uncommon that two partners initiate a joint action at the same time. Rather, a most common pattern is that one of the two (i.e. the leader) starts to move and the other follows (i.e. the follower). The emergence of leader-follower dynamics during joint actions (Konvalinka et al., 2014; Jiang et al., 2015) and the role that an asymmetric role has on behaviour and motion kinematics (Sacheli et al., 2013; Candidi et al., 2015; Fairhurst et al., 2014) have been repeatedly reported in literature. Here we show that in the Interactive task, where the pairs were asked to perform imitative or complementary movements according to the instruction received, participants started their movements later with respect to the high than the low status confederate. This seems to suggest that they were more likely to let the high status confederate decide where to grasp the bottle-shaped object. Social status and leadership are intrinsically linked to each other. Studies from social psychology have shown that both personality traits linked to high social status (Lord et al., 1986) and actual social status (Cheng et al., 2012) predict the degree to which individuals are perceived or chosen as group leader.

Reduction of signalling behaviour when interacting with the high status.

Participants’ hand aperture for Power grasping was reduced during the interaction with the high status confederate compared to the low status and this reduction was stronger as their preference for the high status increased. To enhance the hand aperture in Power grasping might be a form of signalling (i.e. the exaggeration of kinematic features to disambiguate the ongoing action from others) through which participants try to make their intentions as clear as possible. During nonverbal interactions, indeed, people use various forms of sensorimotor communication (Pezzulo et al., 2019; Era et al., 2019) to convey information about their intentions (i.e. whether they will grasp the upper or lower part of the object with a precision or power grip, respectively in the present task) through body signals. Sensorimotor communication helps the interaction by making agents' actions more predictable as partners are making their intentions visible in their motion kinematics. Indeed, when participants are assigned the role of 'leader' during the Joint Grasping task (Sacheli et al., 2013), they tended to enhance their wrist height and hand aperture to help the 'follower' in disambiguating between two possible grasps (i.e. precision/up and power/down). In our study, participants were reducing their 'signalling' behaviour when interacting with the high status confederate. Along with the fact that movement initiation times were also increased when interacting with the high status (i.e. they were more likely to let the high status decide where to grasp the bottle), our results suggest that participants were acting as 'followers' when required to coordinate their movements with those of the high status.

Implicit preference decreases visuo-motor interference.

Our results on wrist height showed an inverse relationship between visuo-motor interference and implicit preference for both the high and the low status confederates. Although previous research has shown increased involuntary imitation toward in-group models (Bourgeois and Hess, 2006; Sacheli et al., 2015), therefore suggesting that we might be more likely to imitate those that we like more (McIntosh et al., 2006; Miles et al., 2010), the results from a study that used our same task seem to suggest something different. Sacheli and colleagues (2012) tested pairs of participants that did or did not receive a negative interpersonal manipulation and found visuo-motor interference effects in the negatively manipulated but not in the neutral group. Furthermore, visuo-motor interference emerged in the manipulated group only in the second session of the task and was paralleled with an improvement in performance. The authors proposed that the presence of visuo-motor interference could be accounted for by the fact that the negative interpersonal relationship might have prevented a smooth integration of partners' motor plans. Our results show a different (although conceptually similar) pattern: similarly to the Sacheli and colleagues' neutral pairs, we observed a reduction in visuo-motor interference as the implicit preference for one of the two confederates increased, which was accompanied by an improvement in synchrony performance. A recent study from Sacheli and colleagues (Sacheli et al., 2018) found no evidence for interference effects (as indexed by a difference in performance between congruent and incongruent trials) in a joint action task. The authors have proposed that, during joint action participants, rather than passively simulating the movements of the inter-actor, recruit predictive processes to anticipate them and integrate them into a Dyadic Motor Plan (Sacheli et al., 2018). Our results suggest that the degree to which owns' and other's motor plans are integrated into a shared motor representation that serves the fulfilment of a shared goal could be dependent on motivational and social factors. In this vein, involuntary mimicry of complementary movements (and a reduction in synchrony performance) might be indicative of the fact that participants, when interacting with a disliked partner, rather than 'moving together' with him to achieve a shared goal were 'moving while observing another movement' and therefore displaying interference effects (Brass et al., 2001; Kilner et al., 2003; Sacheli et al., 2018).

Conclusion

Human societies are for the most part intrinsically hierarchical and the ability to categorise other individual according to their status and to modulate our behaviour is fundamental for social interactions. In the present study we investigated whether the ability to coordinate with another person to perform a joint action is influenced by the person's competence-based social status. Our results show that many aspects of motor behaviour are deeply influenced by this social variable. Interacting with the high status confederates led participants to better synchronise their grasping movements while reducing visuo-motor interference. Moreover, participants were more likely to let the high status participant decide where to grasp the bottle, thus hinting to a follower-like behaviour. Future research could examine whether also other status determinants (Mattan et al., 2017), such as occupational or economic status, can influence the dynamics of motor interactions.

5. Autonomic correlates of performance monitoring during a status-inducing procedure.

Introduction

Human societies and groups are characterized by unequal distribution of privileges. Attaining a low versus high-status position has several implications on health, well-being and longevity (Sapolsky, 2005; Marmot, 2006). A recent cohort study found that subjective social status (SSS, i.e. the self-perceived social position) is inversely associated with mortality (Demakakos et al., 2018). Furthermore, low status individuals display lower levels of heart rate variability (HRV), an index of sympathetic-parasympathetic balance that is also considered an indicator of an adaptive, well-regulated organism (Marmot et al., 1991; Thayer et al., 2009). According to the Status Syndrome theory (Marmot, 2006), health issues associated with having a low status, rather than just being a consequence of inequities in material resources, are direct effects of the stress arising from the lack of control on one’s life. It has been proposed that since low status individuals are more likely to experience social threat and receive negative evaluation, they tend to monitor their performance more than high status individuals (Boksem et al., 2011). Consistently with this notion, an EEG study showed that participants experimentally assigned to a low status position showed enhanced medial frontal negativity (MFN), an event-related potential reflecting performance monitoring, when presented with negative feedback during a cooperative task (Boksem et al., 2011).

Along with specific EEG signature such as the error-related negativity (ERN, Gehring et al., 1993), the positivity error (Pe, Hermann et al., 2004) and the feedback-related negativity (FRN, Hajcak et al., 2006), performance monitoring activity is reflected in an increased activation of the autonomic nervous system (ANS). Previous research has shown that error, feedback and conflict processing are accompanied by changes in the activity of the autonomic system as indexed by heart rate (HR), pupil diameter and skin conductance response (SCR) (Hajcak et al., 2004; 2003; O’Connell et al., 2007; Critchley et al., 2005; Fiehler et al., 2004; van der Veen et al., 2004; Crone et al., 2003). Neuroimaging studies have further shown that both error processing (Carter et al., 1998; Kiehl et al., 2000) and autonomic changes (Matthews et al., 2004; Critchley, 2005) activate the anterior cingulate cortex (ACC), a “hub-like” brain structure interconnected with several cortical and subcortical networks (Critchley et al., 2000b; 2001a; 2005; Matthews et al., 2004; Cavanagh & Frank, 2014). In addition, using a conjunction analysis Critchley and colleagues (Critchley et al., 2005) demonstrated that a subregion of the ACC was jointly activated by both error processing and error-related autonomic arousal. This finding suggests that the ACC might support the integration of the cognitive appraisal of error processing with the generation of autonomic response.

The amplitude of error-related responses seems to be modulated by contextual, emotional and personality variables. Meta-analytic evidence indicates that subjects with high levels of anxiety display higher EEG signatures in response to errors, conflict and negative feedback (Cavanagh & Shackman, 2015). Moreover, participants with higher levels of negative affect show increased autonomic activity following error commission (Hajcak et al., 2004) and a similar pattern can be observed in people with obsessive-compulsive disorder (Hajcak & Simons, 2002) and depression (Tucker et al., 2003). Building on the finding that low social status seems to hyper-activate the performance monitoring system (Boksem et al., 2011), in the present study we hypothesised that autonomic response to negative feedback might be modulated by individuals’ social status. To this end, we recorded heart rate (HR) whilst participants were engaged in a status-inducing procedure consisting in a social game with two other players. Previous research has shown that the presentation of negative feedback during cognitive tasks is followed by HR slowing (Somsen et al., 2000; Crone et al., 2003; van der

Veen et al., 2004, Gunter-Moor et al., 2010). Changes in phasic HR are associated with reactive attention (Sokolov, 1963; Porges, 1992) and HR deceleration is thought to reflect an orienting response of the organism to relevant stimuli (Sokolov, 1960; Wessel et al., 2011). Furthermore, Gunter-Moor and colleagues (Gunter-Moor et al., 2010) showed that the magnitude of HR deceleration was enhanced in a 'social' condition, when the negative feedback reflected peer rejection. In the present study, we hypothesised that the stressful experience of attaining a low status position (i.e. being at the bottom of a competence-based hierarchy) would modulate participants' autonomic responses to negative feedback and that HR deceleration would increase in the low (compared to high) status condition.

Methods

Participants

An a-priori simulation-based power analysis using the R package "pwr" and the "pwr.f2.test" function. Results indicate that a sample size of 52 is adequate to have 80% power for detecting a medium effect size of 0.15 (f2) in a 2x2x2 design. In this chapter, I will present preliminary results from a subsample of 24 participants (6 M, age = 20 ± 2.53 years) recruited among students from Brighton University and Sussex University.

General Procedure

Participants were informed that they were to play a cooperative time estimation game with two other players located in other rooms of the building while their computers were connected and that their physiological activity would be recorded during the game. Participants were informed regarding the cooperative nature of the game, namely that the score obtained by each individual player will be added to a shared account. They were also informed that, at the end of the game, the collective score would be split into three equal parts and distributed to each player in the form of a small monetary reward (which will be equal for all participants). After a 2-min physiological recording designed to assess baseline measures of HR, participants were provided with instructions concerning the time estimation task and were given the opportunity to perform a practice block. Participants then completed the Mac Arthur Subjective Social Status scale (SSS, Adler et al., 2000) and started the task, while their HR was recorded continuously. At the end of the experiment, participants received a funnel debriefing procedure to determine if they had any suspicion about the cover story. The experimenter started this debriefing with a broad question (i.e. "Do you have any idea about what the purpose of this experiment may be?") before getting more detailed: "Did you ever wonder whether the other players really existed"? The total time of the experiment was around 1 hour.

Time Estimation task

The task was adapted from Boksem et al. (2012). In that study, it was demonstrated that participant's status (according to their contribution to the collective game) influence their feedback-related EEG activity (Medial Frontal Negativity). Each trial started with the presentation of a blue circle that turns green after a random time interval (ranging between 1500-3500 ms). Participants were required to press the space bar exactly 1 second after the circle had changed colour. To avoid ceiling effects, we adopted a staircase-like procedure: at the start of the task, the 'win' threshold for the response time was set at 1 second +/- 550 ms. A response falling within this time was considered a 'win' trial and set the threshold for the following trial at 1 second +/- 500 ms. Otherwise, a response falling outside this time was considered a 'fail' trial and the threshold was changed to 1 second +/- 600 ms for the following trial. Visual feedback was provided at the end of each trial: a smiley face for wins and a sad face for fails. A digital trigger was sent to the physiological recording equipment at the start of the feedback slide presentation. Inter-trial interval (ITI) was set at 4000-6000 ms. Participants completed 12 blocks of 10 trials each of the time estimation task. During the game, pictures of the three players were presented along with the experimental stimuli. Below each player's photo their individual score was displayed along with a number of stars reflecting performance (3 stars for the best player, 2 for the middle and 1 for the worst). The hierarchy and the scores were updated on each trial. For the first 5 blocks the participant's scores were manipulated so that he/she would have the highest score (high status blocks). From block 6 to 7 the participant would switch from the first to the second position in hierarchy (middle status blocks) and then to the third position from block 8 to 12 (low status blocks). The order of the high and low status blocks was reversed for half of the subjects so that they started in at the bottom of the hierarchy and ended at the top of it. At the end of each block, participants were asked to report how good they felt they performed on a visual analogic scale (VAS) ranging from 1 to 100.

Physiological Recording

Heart Rate was recorded with the CED Power1401 and 1902 amplifiers (Cambridge Electronic Design Limited, Cambridge, UK) at 1000 Hz sampling rate and was digitizes with Spike2 software (Cambridge Electronic Design Limited, Cambridge, UK). The raw signal was cleaned using the HumRemove Spike2 script to remove interference from the mains (i.e. 50 Hz) and visually inspected for artefacts. Interbeat intervals (IBIs) were extracted using Matlab (Mathworks, version 2017a). Following Crone and colleagues (Crone et al., 2003), we selected two IBIs during the presentation of the Blue slide (before the circle changes colour to Green; B1 and B2), the IBI around the Feedback slide presentation (F) and three IBIs following the Feedback slide (F+1, F+2, F+3). B2, F, F+1, F+2 and F+3 IBIs were standardised to (i.e.

subtracted from) B1. Although previous studies have used the IBI immediately preceding the Feedback presentation as a baseline, in our task participants were preparing to respond or were responding during this time interval. Therefore, we reasoned that the heart beats during the Green slide might have been contaminated by physiological activity related to motor preparation, and thus decided to use the beats before any change occurred.

Standardised IBIs were analysed with linear mixed models (LMM) including Status (High, Low), Feedback (Positive, Negative) and IBI (B2, F, F+1, F+2, F+3) as fixed factors. The random part included the random slopes of Status and Feedback over participants and the random intercept of Status and Feedback over participants.

. Statistical significance of fixed effects was determined using type III ANOVA test with the *mixed* function from *afex* R package. Post-hoc comparisons were performed with the 'Estimated Marginal Means' R package (version 1.3.3) via the *emmeans* and *emtrends* functions, respectively, and Tukey correction for multiple comparisons.

Preliminary Results

Model: IBI_difference ~ Status * Feedback * IBI + (1+ Status + Feeback | Subject)

Type III ANOVA (Status x Feedback x IBI) revealed a significant main effect of IBI ($F = 94.61$, $p < 0.0001$). Post Hoc tests showed that all IBIs were significantly different from each other. Specifically, IBI_B2 had smaller values than both IBI_F (estimate = - 0.01, SE = 0.002, z-ratio = - 8.20, $p < 0.0001$) and IBI_F+1 (estimate = - 0.007, SE = 0.002, z-ratio = - 3.48, $p = 0.004$), suggesting that the heart rate decelerated with respect to baseline following the Feedback presentation. Moreover, IBI_F+1, IBI_F+2 and IBI_F+3 were significantly smaller than both IBI_B2 and IBI_F (all Ps < 0.0001). This suggests that that the cardiac deceleration occurring in response to the feedback presentation was followed by an acceleratory pattern that lasted for at least three heart beats (see Fig. 1).

Type III ANOVA also revealed a significant main effect of Feedback (F = 4.34, p = 0.05) As shown in Fig. 2, although the heart rate decelerated in response to both Positive and Negative feedback, a stronger deceleration was observed after negative feedback (positive values indicate higher deceleration). The deceleration was observed in IBI_F, surrounding the Feedback presentation, and was followed by a subsequent acceleration in the heart rate, which was anticipated and more pronounced following Positive than Negative Feedback (see Fig. 2).

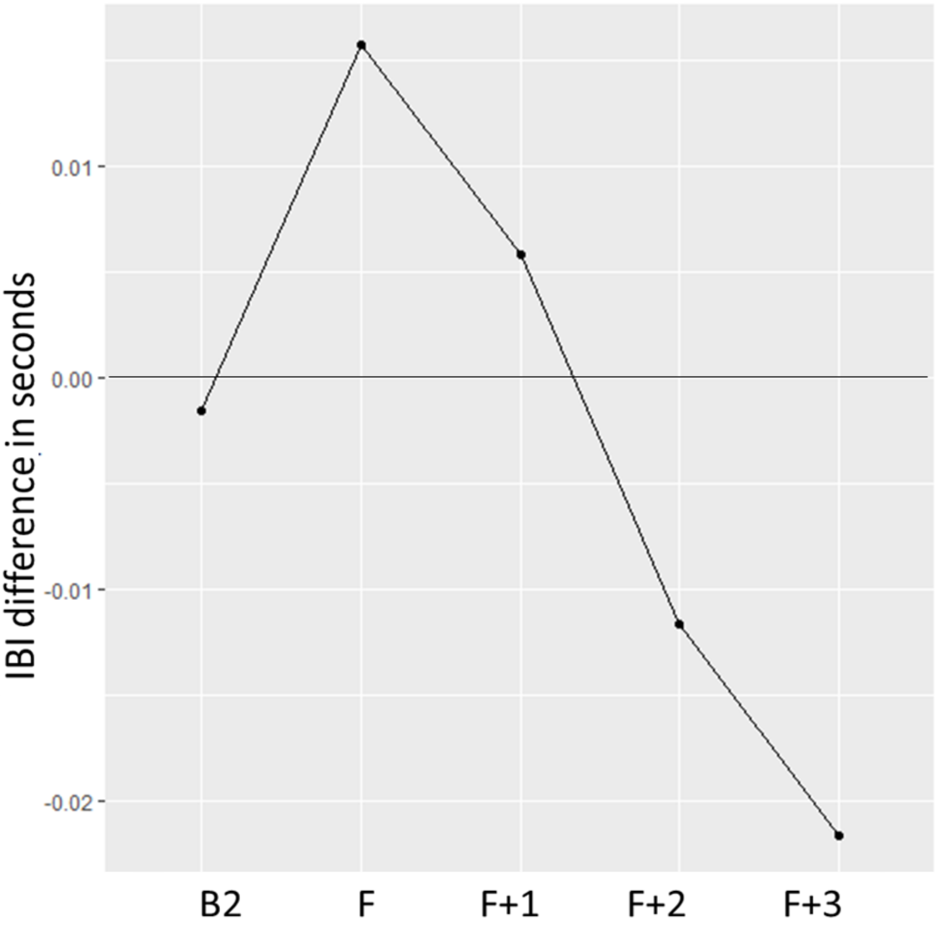


Fig. 1 - Heart rate variations in the 5 selected IBIs. Positive values indicate a deceleration and negative values an acceleration with respect to baseline (IBI B1).

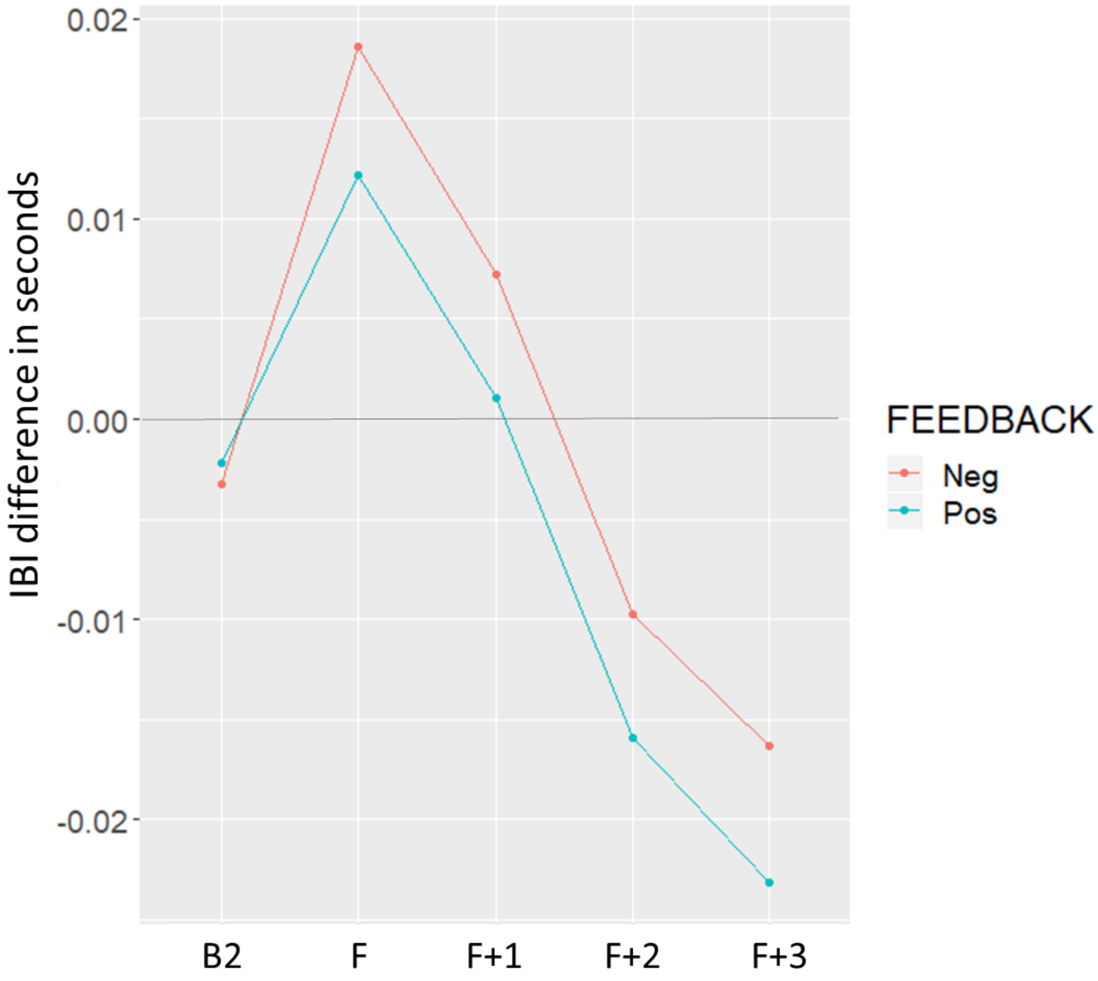


Fig. 2 – Heart rate variations associated with negative and positive feedback. Positive values indicate a deceleration and negative values an acceleration with respect to baseline (IBI B1).

Finally, there was a significant Status x Feedback (F = 6.15, p = 0.01) interaction. Post Hoc tests for the Status x Feedback interaction revealed a significant difference between Positive and Negative feedback only in the High-status condition (estimate = 7.32e-03, SE =

0.002, z-ratio = 3.096, p = 0.01), while all the other comparisons were not significant (all Ps > 0.63). As shown in Fig. 3, cardiac deceleration in response to the Feedback was present in all conditions and was equally followed by an acceleration in the subsequent IBIs. However, the deceleration-acceleration pattern seems to be influenced by both Status and Feedback valence. In the High Status_Positive condition, the cardiac deceleration at IBI_F seems reduced compared to the other conditions, while it appears to be maximal for the High Status_Negative. Furthermore, the acceleratory return to baseline appears stronger and more anticipated in the High Status_Positive condition, as it crosses the zero already at IBI F+1. Although the three-level Status x Feedback x IBI was nonsignificant (F = 1.55, p = 0.18), for exploratory purposes we ran Post Hoc tests to look at differences between conditions in the five IBIs. Post Hoc tests revealed that at IBI_B2 there was no significant difference between conditions (all Ps > 0.64), at IBI_F the IBI_difference was significantly higher in High status_Negative than in High status_Positive (estimate = 0.01, SE = 0.007, z-ratio = 2.55, p = 0.05), therefore indicating that in the High status condition participants showed a significantly higher deceleration following Negative than Positive Feedback; all the other comparisons at IBI_F were nonsignificant (all Ps > 0.69). At IBIs F+1 and F+2 there was no significant difference between conditions (all Ps > 0.12), while at IBI F+3 there was, again, a significant difference between High status_Negative and High status_Positive (estimate = 0.01, SE = 0.004, z-ratio = 2.51, p = 0.05), indicating that participants' heart rate in the High status condition was significantly more decelerated at IBI F+3 following Positive than Negative Feedback. All other comparisons at IBI F+3 were nonsignificant (all Ps > 0.16). Descriptive statistics (means and standard deviations) are reported in Table 1.

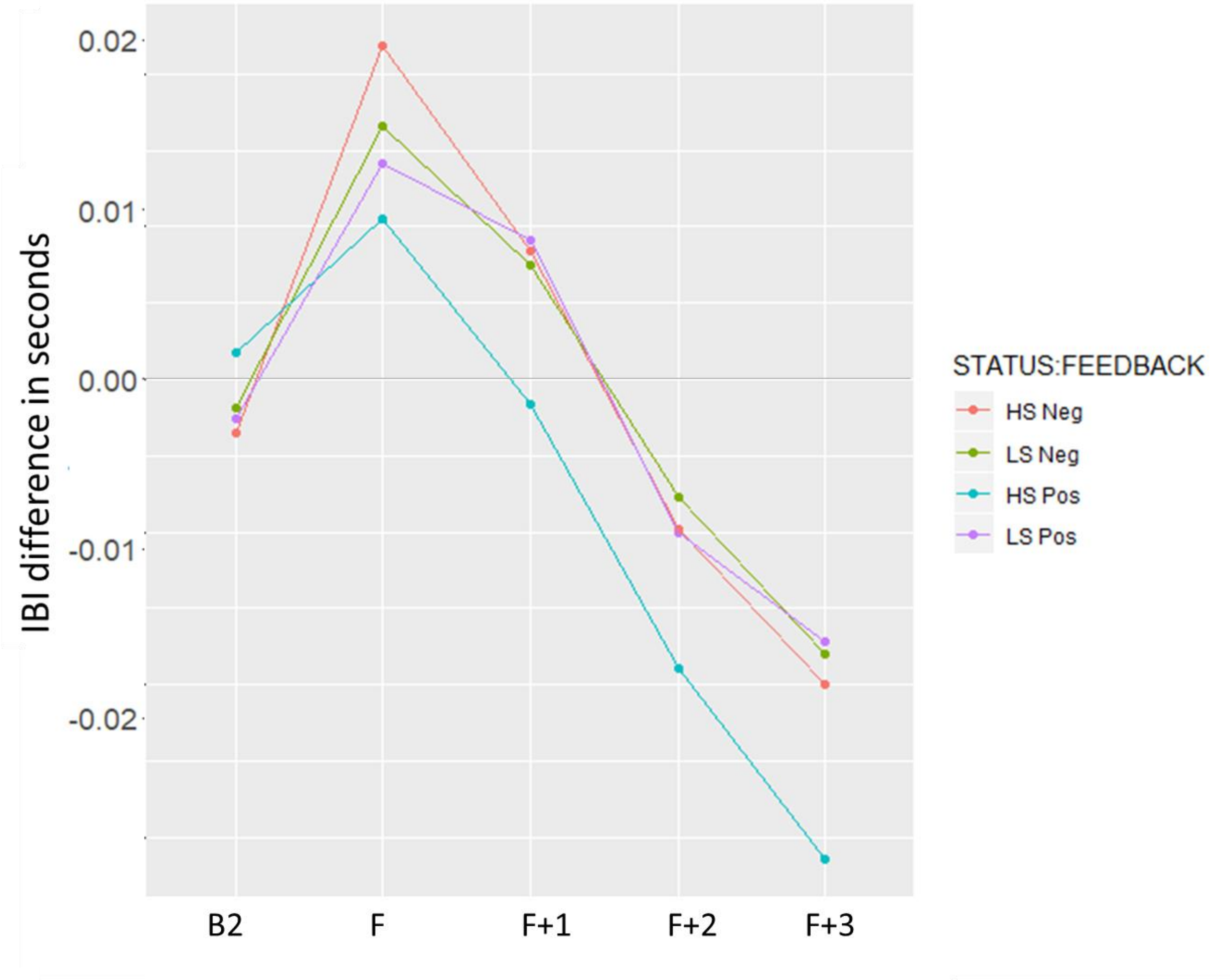
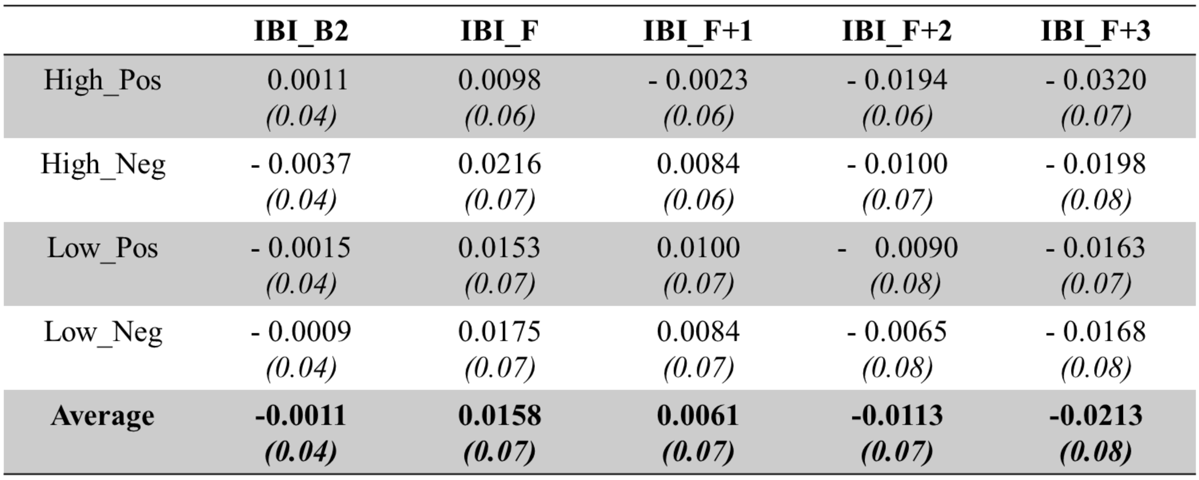


Fig. 3 - Heart rate variations associated with Negative and Positive feedback in the High and Low status conditions across IBIs. Positive values indicate a deceleration and negative values an acceleration with respect to baseline (IBI B1).



	IBI_B2	IBI_F	IBI_F+1	IBI_F+2	IBI_F+3
High_Pos	0.0011 *(0.04)*	0.0098 *(0.06)*	- 0.0023 *(0.06)*	- 0.0194 *(0.06)*	- 0.0320 *(0.07)*
High_Neg	- 0.0037 *(0.04)*	0.0216 *(0.07)*	0.0084 *(0.06)*	- 0.0100 *(0.07)*	- 0.0198 *(0.08)*
Low_Pos	- 0.0015 *(0.04)*	0.0153 *(0.07)*	0.0100 *(0.07)*	- 0.0090 *(0.08)*	- 0.0163 *(0.07)*
Low_Neg	- 0.0009 *(0.04)*	0.0175 *(0.07)*	0.0084 *(0.07)*	- 0.0065 *(0.08)*	- 0.0168 *(0.08)*
Average	**-0.0011** ***(0.04)***	**0.0158** ***(0.07)***	**0.0061** ***(0.07)***	**-0.0113** ***(0.07)***	**-0.0213** ***(0.08)***

Table 1 – Descriptive statistics of heart rate changes from baseline in the various condition combinations. Values represent mean(sd).

Discussion

In the present study, we examined whether individuals' competence-based hierarchical stance (i.e. social status) modulates cardiac responses when they receive negative and positive feedbacks concerning their performance in a social context. In line with previous findings (Crone et al., 2003; Hajcak et al., 2003; 2004; van der Veen et al., 2004), we observed that negative feedback elicited a stronger cardiac deceleration than positive feedback. Cardiac deceleration was followed by an acceleratory return to baseline that was reduced and delayed in response to negative, as compared to positive, feedback. That feedback valence modulates the cardiac acceleration pattern following deceleration has been also reported in previous studies (Crone et al., 2003; van der Veen et al., 2004; Kastner et al., 2017). In addition, we found that competence-based social status modulated the strength of cardiac deceleration following feedback. Specifically, our preliminary results show that the effect of Feedback valence (i.e. higher deceleration for negative than for positive feedback) was only significant in the high status condition. Moreover, participants in the high status condition showed a faster and more pronounced acceleratory return to baseline after positive feedback with respect to all the other conditions. The fact that cardiac deceleration following negative feedback was maximal in the high status is apparently at odds with the results reported in Boksem and colleagues' study (Boksem et al., 2012), where feedback-related medial frontal negativity (MFN) in response to negative feedback was enhanced in the low status condition. The authors discuss their results in terms of an increased activation of the performance monitoring system induced by the experience of a low hierarchical status. They suggest that since low status individuals are more likely to experience social evaluative threat (Anderson and Berdahl, 2002), they might be more engaged in monitoring their performance.

Conversely, our preliminary results seem to suggest that heart rate deceleration to negative feedback was increased in the high status condition. It should be noted that whether cardiac deceleration after negative feedback reflects the activation of a monitoring system that triggers the implementation of remedial actions (Somsen et al., 2000) or merely the representation of the motivational valence (van der Veen et al., 2000) is still an object of debate. Recent research showing that heart rate deceleration was sensitive to the violation of performance-based expectations (Kastner et al., 2017) seems to support the monitoring system hypothesis. At a first glance, our preliminary results appear more in line with the monitoring system account. Indeed, although the number of positive and negative feedback was equal in the high and low status conditions, during the low status blocks participants might have expected their performance to be worse than in the high status blocks, since they were at the bottom of the hierarchy. For that reason, if cardiac deceleration reflects a violation of feedback expectation one should expect it to be increased in the high status condition, where the participant is led to believe that he/she is the best player in the group. Following this interpretation, one should also expect to find a reduced deceleration for negative feedback in the low status condition (the one in which the participant is led to believe that he/she is the worst player in the group). Since this is not the case (see Fig. 3), it might be difficult to interpret the effect of status on cardiac deceleration in terms of expectation violation. However, it should be noted that at least some studied reported differential effects on neural signals reflecting positive prediction errors (i.e. when the outcome that is better than expected) and negative prediction errors (i.e. when the outcome is worst than expected) (e.g., Holroyd & Coles, 2002; 2006). In this vein, it is possible that the high and low status conditions represent two different predictions that, when violated, give rise to different responses according to outcome valence.

Another possibility is that negative feedback during the high status condition was experienced as more aversive because it reflected a potential threat to the acquired status. Indeed, being part of unstable hierarchies (where each member's position is often updated) elicits stronger activity in brain areas linked to social emotion (such as amygdala and medial prefrontal cortex) than being part of a stable hierarchy (Zink et al., 2008).

Further analysis on the final sample will reveal a complete picture of our results and will shed light on the relationship between social stance and cardiac reactivity to feedback. This will be accomplished also by examining the correlation between the actual performance (i.e. how accurate the time estimation was, considering the threshold) and the feedback-related cardiac deceleration. Further analysis will also take into account individual differences in subjective social status and anxiety.

In sum, our preliminary results confirm previous findings showing that cardiac deceleration is increased following negative, compared to positive, feedback. Moreover, our results expand on previous research by showing that not only neural (Boksem et al., 2012) but also autonomic responses to negative feedback are modulated by competence-based social status, although, apparently, in different ways.

5. Interim discussion on the effect of social status on affective evaluation, dyadic motor interactions and performance monitoring

The research described in chapters 2-4 investigated the effects of a status manipulation on implicit preference, dyadic motor interactions and performance monitoring. Overall, the three studies suggest that competence based social status modulates social cognition at different levels.

Study 1 used the AMP as a measure of implicit preference to test whether the competence-based hierarchical stance of two previously unacquainted individuals can influence participants' evaluation of neutral stimuli primed with the high- and low-status individuals' identity. Results show that, only after the status-inducing game, participants liked more neutral stimuli primed by the high than the low status player. In line with previous research showing that high status individuals are perceived as more rewarding, our results suggest that participants developed an implicit preference for the high status player. Study 2 used the same methodology as in Study 1, followed by a session in which participants were asked to coordinate their reach-to-grasp movements with those of the high and low status players. Behavioural and motion kinematics results indicate that the implicit preference toward the High and Low status players modulates participants' ability to coordinate with them to perform a joint action. Specifically, results showed that, when taking into account participants' implicit preference for the two players, synchrony performance was improved with the High, compared to the Low, status player. Moreover, participants were more likely to wait for the High status, compared to the Low, to decide where to grasp the object. While Study 1 has revealed the existence of an implicit positive bias towards highly competent individuals, Study 2 demonstrates that this bias can be transferred to the context of joint actions and modulate kinematic and behavioural parameters. This suggests that our implicit representation of high and low status individuals, along with the rewarding value we attach to them, is reflected in the way we interact with them. As stated in the Introduction, competence-based social status might have evolved as a mean to promote cultural transmission. From this perspective, it makes sense that highly competent individuals (and the interaction with them) are considered rewarding. Indeed, the pleasure experienced during the interaction with high status individuals might be another mean to further incentivise cultural transmission by seeking proximity with them. However, humans not only seek an interaction with the high status, they also strive to achieve a better stance for themselves. The goal of Study 3 was to reverse the perspective adopted in Studies 1 and 2 and investigate how the experience of high and low status modulates the autonomic correlates of performance monitoring. Results showed that heart rate deceleration was maximal following the presentation of negative feedback and minimal following the presentation of positive feedback when participants were experiencing a high status condition. This suggests that competence-based social status modulates the activity of the performance monitoring system in a social setting, possibly by creating different reward expectations.

6. Theta tACS over the frontal midline modulates behavioural adjustment during human-avatar motor interactions

Abstract

When engaging in joint actions, we need to continuously monitor our partner's movements and to predict their possible outcomes. Recent findings from our research group showed that motor interactions requiring moment-to-moment adaptation to the partner's actions elicit brain activity related to performance monitoring (i.e. enhancement of midfrontal Theta synchronisation). Importantly, this activity seems not associated to any explicit feedback concerning the interactive performance, but rather a response to observed violations to ones' expectation regarding the partner behaviour; in this sense it seems to mediate the process of adapting to a partner behavioural change. In the present study we explored the causal role of midfrontal Theta on behavioural adjustment during motor interactions by means of transcranial alternating current stimulation (tACS). Participants received Theta or Beta (between-subject) tACS at their individual frequency and Sham stimulation over the frontal midline (FCz) and parietal sites while coordinating their movements with those of a virtual partner to synchronously touch one of two different targets. Importantly, there were two experimental conditions that differed in the degree to which participants needed to adjust their movements to virtual partner's unexpected motor change. Results showed that, comparted to Beta tACS, Theta tACS improved synchronisation in all conditions and increased movement times after the virtual partner's motor change (making individuals' behaviour more synchronized with that of the partner), but only in the condition in which participants were asked to compensate that motor change.

Introduction

During motor interactions, in both cooperative and competitive settings, the ability to coordinate our actions with those of our conspecifics requires the continuous monitoring of owns and other's movements. This monitoring activity seems to be dependent on individuals' ability to predict the actions of the observed partner behaviour, namely the anticipation of the consequences of observed actions (Aglioti et al., 2008; Abreu et al., 2012), which is likely implemented through sensorimotor simulation processes that occur in the fronto-parietal mirror neurons system (Di Pellegrino et al., 1992; Rizzolatti and Craighero, 2004). Expectations about the unfolding of others' actions in a pure observational context are generated on the base of previous experience, knowledge about biological motion and intention understanding (Urgesi et al., 2010). Violations of our expectation regarding the fate of observed actions elicits error-related brain signatures. Error and conflict monitoring are two interrelated cognitive functions that contribute to improve adaptive behaviour during environmental and social demands. Mounting evidence from EEG and MEG studies revealed that the electrical correlates of error processing are characterized by specific neurophysiological signals, namely the Error Related Negativity (ERN, Gehring et al., 1993) and the positivity error (Pe, Falkenstein et al., 2000; Van Elk et al., 2012), likely generated in the anterior cingulate cortex (ACC, Ishii et al., 1999). These signatures are maximally distributed over the frontocentral and parietal (for Pe) areas of the cortex, sharing a common spectral signature in theta band (4-8 Hz), a frequency that correlates with the increment of need for control.

Studied have reported that observing a motor error from a first-person (Pavone et al., 2016; Spinelli et al., 2018; Pezzetta et al., 2018) and third person (van Schie et al., 2004; De Brujin & von Rhein, 2012; Pavone et al., 2016) perspective elicits the ERN, a phenomenon called observational ERN (oERN, Miltner et al., 2004; van Schie et al., 2004). Conversely, the enhancement in Theta power seems to be specific for one's own rather than for other's errors

(Pavone et al., 2016). At a behavioural level, observing an error in third-person perspective also induces a slowing in reaction times in the subsequent trial when participants are asked to grasp and move an object (Ceccarini and Castiello, 2018). This phenomenon is named post error slowing (PES) and is thought to reflect the implementation of adaptive adjustment to avoid further errors (Rabbitt, 1966; Notebaert et al., 2009; Danielmeier and Ullsperger, 2011). These findings suggest that the detection of committed and observed errors might rely on similar neural processes.

During motor interactions, action prediction also relies on knowledge about the interaction rules and shared goals (Sacheli et al., 2015). For a shared goal to be fulfilled, each part of a dyad needs to achieve its individual sub-goal while monitoring the other part's actions (Sebanz et al., 2006; Sacheli et al., 2012; 2018). When one of the two partners fails to comply with the interaction rules, the success of the joint action is jeopardized. Unexpected movements or changes in the context of motor interactions can therefore be considered as "errors", since they not only create a mismatch between expected and observed outcome, but also hinder the fulfilment of a shared goal. Indeed, error-related brain signatures are also elicited during motor interactions after observing a sudden change in partner's movement. In two recent studies, participants were asked to coordinate their reach-to-grasp (Moreau et al., 2020) and reach-to-press (Moreau et al., in preparation) movements with those of a virtual avatar to perform either complementary or imitative movements. In both studies, in 30% of the trials the virtual avatar suddenly changed its initial movement before reaching the target (i.e. from grasping the lower part of a bottle-shaped object (through a power grip) to grasping it upper part (through a precision grip) in the first study and from reaching and pressing a target button with the index to pressing it with the middle finger in the second one. The avatar's motor change required participants to promptly update their own motor plan in order to fulfil the common goal (i.e. performing an imitative or complementary movement). EEG results showed the presence of error-related brain activity both in the time domain (i.e. ERN) and in the frequency domain (i.e. increase in midline frontal Theta power) which was time-locked to the avatar's movement change (not to the corresponding change in the individual action). Interestingly, these brain signatures were absent in a control condition that was perceptually identical but did not require participants to adapt to the avatar's change because in this case they knew in advance which target they had to grasp or press.

Theories on error-related midfrontal theta activity posit that these brain oscillations may act as a nonspecific "alarm" signal that may be used to implement behavioural adjustment by synchronizing the simultaneous employment of the frontal (Hanslmayr et al., 2008), motor (Nigbur et al., 2012) and sensory (Van Driel et al., 2012) areas. Indeed, a Theta phase synchrony between the MFC and frontal sites has been repeatedly observed in various tasks eliciting the need for cognitive control (Cavanagh, 2015). Several studies have related midfrontal Theta power to PES, although with mixed results (Valadez and Simons, 2017; Van Driel et al., 2015; Fusco et al., 2018). Less clear is the relationship between midfrontal Theta and task performance. Since the implementation of cognitive control should serve the need of optimising behaviour, it should be expected that an increase in Theta power would produce an improvement in performance.

The present study aimed at investigating the causal role of midfrontal theta oscillation on behavioural adjustment to observed errors in a motor interaction context by means of Transcranial Alternating Current Stimulation tACS. To this end, we used a modified version of the task from Moreau and colleagues (in preparation) and asked participants to coordinate with a virtual partner to touch one of two targets. Importantly, in 30% of the trials the virtual partner would suddenly change its movement, therefore requiring participants to operate a motor correction. TACS is a non-invasive brain stimulation technique that can be used to target cortical oscillations by taking advantage of alternating current. A low intensity electric flow is delivered on the scalp through rubber-conductive electrodes. The oscillation frequency of the electric current can be set to mimic endogenous brain oscillations. Previous studies have shown that tACS is a viable tool to entrain endogenous rhythmic activity in a frequency-dependent manner (Helfrich et al., 2014; Neuling et al., 2013) and modulate behaviour (Feurra et al., 2013; Vosskhul et al., 2015). At the neurophysiological level, tACS enhances the power of existing brain oscillations, therefore acting as an “excitatory” neuromodulation. For the present study, we hypothesised that Theta (but not Beta) tACS would boost endogenous error-related Theta activity following an observed movement correction and facilitate behavioural adaptation (i.e. better synchrony performance in trials with a motor correction).

Methods

Participants

Forty-four (44) healthy participants without any declared neurological or psychiatric issues were recruited from Sapienza University. Suitability to receive non-invasive brain stimulation was assessed by a standardized questionnaire (Antal et al., 2017). All participants had normal or corrected-to-normal vision and were naïve as to the purpose of the experiment. Four subjects were excluded from the study because they reported: i) motion sickness induced by Immersive Virtual Reality (1 subject), ii) discomfort induced by tACS (2 subjects) or iii) anomalies in the resting-state EEG Alpha peak shape (1 subject). Our final sample comprised 40 right-handed subjects that were randomly assigned to receive either Theta (N=20 (10 Female) age = 25.4 ± 3.9) or Beta (N= 20 (8 Female) age = 23.3 ± 3.3) fronto-parietal tACS. Our sample size was determined from previous studies that employed tACS with a similar design (Van Driel et al., 2015 (20 subjects); Onoda et al., 2017 (15 subjects per group); Zaehle et al., 2010 (20 subjects per group). All participants gave written informed consent to participate in the study. The experimental procedure was approved by the Fondazione Santa Lucia (Rome) Ethics Committee and was performed in accordance with the 2013 Declaration of Helsinki.

Procedure

At their arrival at the laboratory, participants went through the EEG resting-state recording session (see details below) where they were asked to sit in a quiet room and stay still with their eyes closed for 5 minutes. Then, participants had a small break (around 20 minute), during which we extracted the individual-frequency information (see Fig. 1).

Prior to the stimulation session, subjects' scalp was measured to determine FCz and Pz positions according to the International 10-10 EEG layout. The areas of interest were cleaned with a cotton swab soaked in ethyl alcohol in order to reduce the skin's conductance and marked with a marker. The two tACS electrodes were then fitted through an EEG-cap over the head of the participants, with the side toward the skin coated with electro-conductive gel. The stimulation sessions started with a training phase so that participants could familiarize with the tACS-induced physical sensations (i.e. itching, heat). During this phase, participants received 15 seconds (5 ramp-up, 5 stimulation, 5 ramp-down) of tACS at 13 Hz and were asked to report physical sensation or discomfort. If no irregularities were reported, participants were asked to wear the Oculus Rift Head Mounted Display (HMD, www.oculus.com) where they would observe a virtual body in 1PP and the experimental scenario (see below). Participants underwent Calibration, Familiarization and Training phases in the virtual scenario before starting the experiment. In the Calibration phase, the perspective point-of-view of each participant was adjusted to match the virtual body with individual positioning in order to obtain the best spatial-match between the participant's real and virtual body. In the Familiarization phase, participants were invited to look both at the virtual body and at the environment, and to verbally describe what they were seeing (~30 sec) (Tieri et al. 2015b). During the Training phase, which was provided at the beginning of each of the two first blocks, participants completed 10 trials of the IVR Motor Interaction Task. The experimental phase consisted of two sessions (Theta/Beta tACS and Sham, order counterbalanced), each of which comprised two blocks (Interactive and Cued, order counterbalanced – see next section for a description of the tasks). At the end of each Session, participants completed the Embodiment Questionnaire, adapted from previous studies (Botvinick & Cohen, 1998; Tieri *et al.*, 2015a; Tieri *et al.*, 2017) and a standardized questionnaire measuring tES-induced physical sensations (Fertonani et al., 2015).

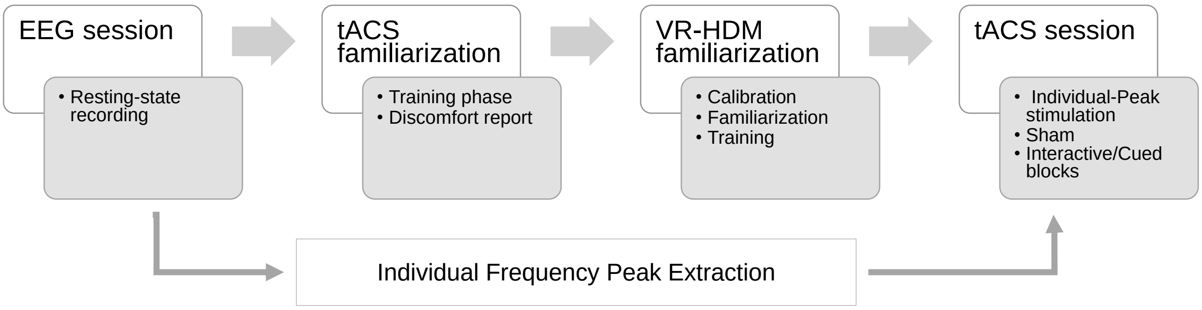


Fig. 1 – Timeline of the experimental procedure.

Electroencephalography (EEG) Protocol

EEG signals were recorded via Neuroscan SynAmps RT amplifier system, from an elastic headband (Electro-Cap International) EEG arranged according to the International 10-10 EEG System with 58 scalp electrodes (Compumedics, ltd). EEG was recorded using following channels: Fp1, Fpz, Fp2, AF3, AF4, F7, F5, F3, F1, Fz, F2, F4, F6, F8, FC5, FC3, FC1, FCz, FC2, FC4, FC6, T7, C5, C3, C1, Cz, C2, C4, C6, T8, TP7, CP5, CP3, CP1, CPz, CP2, CP4, CP6, TP8, P7, P5, P3, P1, Pz, P2, P4, P6, P8, PO7, PO3, PO1, POz, PO2, PO4, PO8, O1, Oz, O2. The amplifier hardware band-pass filter was 0.01–200 Hz and the sampling rate was 1000 Hz. Impedances were lowered below 5 kΩ using electrogel. Reference electrodes were applied to the left (digital reference) and right (physical reference) earlobes, and all electrodes were re-referenced offline to the average of both.

Transcranial Alternating Current Stimulation (tACS) protocol

Electrical stimulation was delivered via two circular sponge-based rubber electrodes (Sponstim, 25 cm , Neuroelectrics, Barcelona, Spain) soaked in saline water (NaCl) and connected to a rechargeable battery-operated stimulator system (Starstim/Enobio, Neuroelectrics, Barcelona, Spain) which in turn was controlled via Bluetooth by a dedicated software (Neuroelectrics Instrument Controller – NIC, Neuroelectrics, Barcelona, Spain). Electrodes were placed over the midline at FCz and Pz (International 10-20 System) beneath an EEG cap. Participants received sinusoidal alternating current (AC) of 1500 mA at their individual Theta (mean Hz = 5.5 ± 0.65) or Beta (mean Hz = 17.6 ± 2.54) frequency while engaged in the IVR-based Motor Interaction task. Impedance was kept below 5KΩ. Stimulation/task blocks lasted approximately from 9’ to 9’30’’. During each block, the current was ramped up for 5 seconds before starting the task and ramped down for 5 seconds after the task was completed. In half of the blocks, participants received sham stimulation which included 5 seconds of ramp up, 20 seconds of AC and 5 seconds of ramp down.

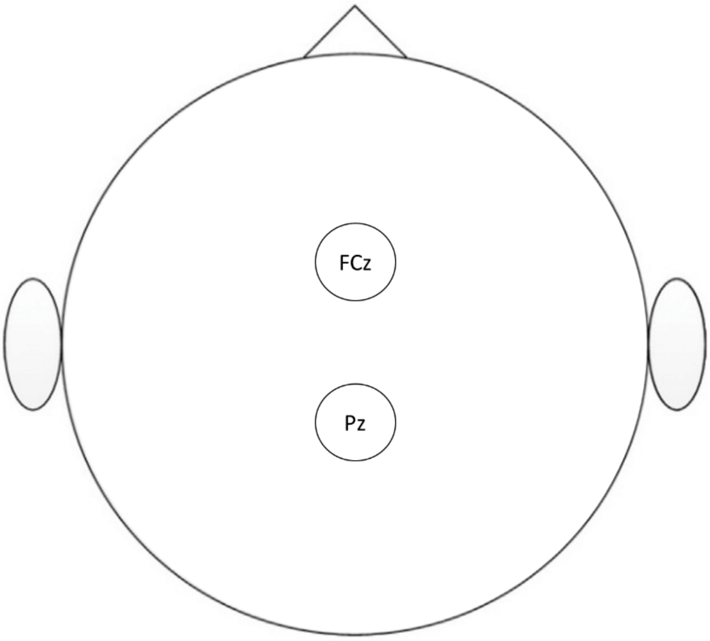


Fig. 2 – tACS electrodes placement

Experimental stimuli

The virtual scenario and avatars were designed by means of 3DS Max 2017 (Autodesk, Inc.) and IClone 7 (Reallusion, Inc.), respectively, and implemented in Unity 5 game software environment. The scenario was presented by means of the Oculus Rift Head Mounted Display (HMD; www.oculus.com) having 110° field-of-view (diagonal FOV) with a resolution of 2160 x 1200. The virtual scene consisted of a real-size room (1:1 scale), two virtual avatars sitting on opposite sides of a table and a virtual grey panel placed between the avatars that blocked their reciprocal view except for their hands, arms and lower part of the trunk. In front of both avatars, at the centre of the table, appeared the 3D model of two buttons, coloured purple and yellow and a LED light that could either turn red or green. Participants observed the virtual body from a first-person perspective (1PP) through HMD. A right Oculus Touch controller (www.oculus.com) was used in order to allow the participants to control the movement of the right arm of their avatar in real time, observed in 1PP. In particular, participants could i) move the avatar's hand forward in space by using the analogic stick of the Oculus touch controller with right thumb and ii) animate the right index or middle finger by pressing the Oculus touch controller's up and down trigger button, respectively. During the experiment, the virtual scenario was rendered in both HMD and a computer screen, such that the experimenter could observe and assist the participants.

IVR Motor Interaction task

The IVR Motor Interaction Task (Figure 3) comprised two conditions (blocks) that differed for the instruction received and for the type of interaction required. In the Interactive block, participants were asked to reach and press one of the two buttons as synchronous as possible with the virtual partner while performing either an imitative ('Same') or a complementary ('Opposite') movement with respect to the virtual partner's (e.g. if the instruction received is 'Opposite' and the virtual partner raises the index finger to press the purple button, the participant will need to raise the middle finger to press the yellow button). In the Cued block, participants still had to synchronize their reach-to-press movements with those of the virtual partner but were in this case instructed to press either the 'Purple' (index) or 'Yellow' (middle finger) buttons, regardless of which action the avatar was performing. In the Interactive condition participants needed to predict and monitor the action of the virtual partner in order to perform their own action, while action prediction and monitoring was not needed during the Cued condition, where participants already knew what action to perform. It is important to note that in the Interactive condition, Correction trials require participants to adapt their own behaviour to the observed change (i.e. change their own finger) in order to fulfil the request (e.g. to perform a complementary movement). In the Cued condition, instead, participants observed the avatar changing its initial behaviour but were not required to change and adapt their own behaviour.

Each trial started with an acoustic ‘go’ signal (“beep”) delivered by the Oculus headphones. Both avatars started with their hands closed and placed in the centre of table’s midline. After the go signal (“beep”) was delivered the participant and the virtual partner started moving (virtual-partner total movement time lasting 3170 ms). 1056 ms after it started moving (33% of the whole movement time), the avatar would raise a finger in order to press the associated button (index finger for purple button and middle finger for yellow button, see Fig 3). The participants was asked to control his/her avatar’s right hand with the Oculus touch controller to reach and press one of the two buttons as synchronously as possible with the virtual partner. With the analogic stick of the controller, participants could move their avatar’s arm forward and regulate its velocity (i.e. velocity was proportional to the force applied by their thumb) and, by pressing the index and middle trigger button of the controller, they could raise either the virtual index or the virtual middle finger of their avatar. Depending on the Asynchrony (i.e. absolute time difference between the two pressing times) the LED light could turn either green (‘win’ trial) or red (‘fail’ trial). A staircase procedure was adopted to make the task more challenging: after each ‘win’ trial the minimum time difference to turn the light green was reduced of 50 ms (e.g. from 200 ms to 150 ms), while in the case of ‘fail’ trials, the time window was increased of 50 ms (e.g. from 200 to 250 ms). The trial ended 2 seconds after the LED visual feedback. Importantly, in 30% of the trials the virtual partner changed its initial behaviour 2113 ms after starting its movement (66% of the total movement time), namely from using the middle to the index finger to press the button (Correction trials). The avatar’s total movement time (i.e. the time from start to touch) lasted approximately 3.2 seconds and did not vary through the task or in different conditions. Each of the two tasks (i.e. Cued and Interactive) comprised 68 trials, of which 20 were Corrections (10 Opposite, 10 Same) and 48 were NoCorrection (24 Opposite, 24 Same).

From the IVR Motor Interaction Task we extracted the following behavioural parameters: Asynchrony (absolute difference between the virtual partner's and subject's pressing times), Movement Times (time between subject's movement start and button press), Last Press Time (time of the last effector selection, note that in Correction trials the effector is selected twice, once before and once after the correction) and Reaction Times (time between the 'go' signal and subject's movement start), see Table 1.

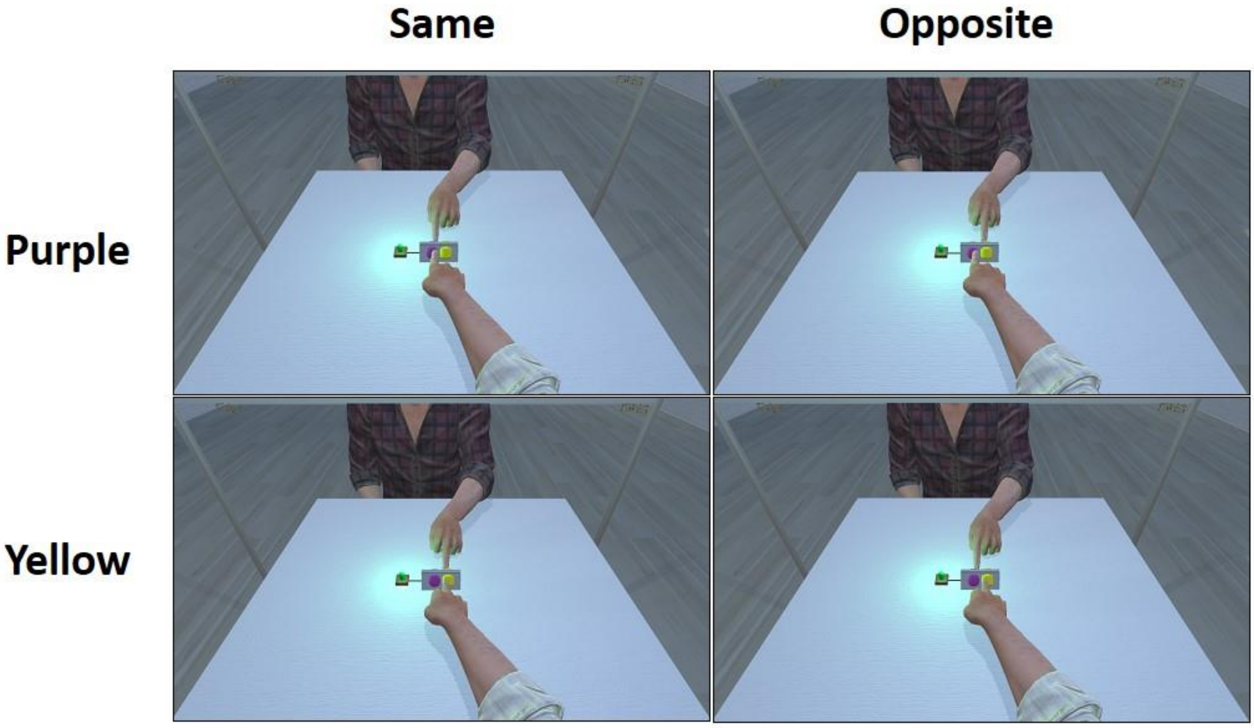


Fig 3– Motor Interaction Task. Participants were required to synchronise their reach-to-touch movements with those of the virtual partner to perform either an imitative (Same) or

complementary (Opposite) in the Interactive Blocks or to touch either the Purple or the Yellow button in the Cued Blocks.

Embodiment ratings

After each experimental session, a black panel with a horizontal green line (VAS scale, 60 cm length, left and right extremity marked as "0" and "100" respectively) was presented in the virtual scenario. In order to assess the degree to which participants experienced the illusory Feeling of Ownership (FO) and Agency (A) over the virtual right hand, a 6-item questionnaire (Table 2) was used. The questionnaire consisted of two blocks, each with three items concerning the FO (Q1–2 experimental, Q3 control) and Agency (Q4–5 experimental, Q6 control), respectively. Participants were asked to move a vertical bar along the horizontal VAS line by using the analogic stick of the right Oculus touch controller in order to answer the items reported in Table 2.

Behavioural variables	**Experimental design**
• Asynchrony (absolute difference between 1PP and 3PP touch time) • Movement Time (time from Start to Stop) • Motor Preparation Time (Time from 'go' signal to Start) • Last Press Time (time of last effector selection)	• Group (*Theta*, *Beta*) • Stimulation (*Real*, *Sham*) • Task (*Interactive*, *Cued*) • Trial (*NoCorrection*, *Correction*) • Movement (*Same*, *Opposite*)

Table 1 – List of behavioural variables and within/between subjects design.

Index	**Item**	
e-FO	**Q1**	I felt as if I were looking at my own hand
e-FO	**Q2**	I felt as if the Virtual Hand were my hand
c-FO	**Q3**	It felt as if I had more than one right hand
e-A	**Q4**	It felt as if the movements of the Virtual Hand were my own movements
e-A	**Q5**	I felt as if I could have caused a/the movement of the Virtual Hand
c-A	**Q6**	I felt as if the Virtual Hand were controlling me

Table 2 – Embodiment Questionnaire. Items Q1, Q2, Q4 and Q5 measure Feeling of Ownership (e-FO) and Agency (e-A), items Q3 and Q6 are control items.

tACS-induced sensations Questionnaire

After each experimental session, participants were asked to fill a questionnaire designed to measure the presence and intensity of physical sensations induced by electrical stimulation (Fertonani et al., 2015). Participants rated the intensity of each sensation (Itching, Pain, Burning, Warmth/Heat, Pinching, Metallic/Iron Taste, Fatigue) on a 5-points scale from None (0) to Strong (5). At the end of the experiment, participants were asked whether they believed to have received a placebo stimulation in the first or in the second stimulation session.

Resting EEG Data Analysis

The EEG data analysis was performed using the FieldTrip toolbox for EEG/MEG (Oostenveld et al, 2011; Donders Institute for Brain, Cognition and Behaviour, Radboud University, the Netherlands. See http://fieldtriptoolbox.org). In order to extract the individual peak frequencies, we segmented the five-minute resting state recordings into epochs of 4 seconds (Pahor & Jaušovec 2014). Independent Component Analysis was computed to identify and remove eye movements and muscular artifacts (ICA; Jung et al., 2000). An average of ~0.94 components (SD = 0.75) per subject was removed and ~ 69.53 artifact-free epochs (SD = 4.17) per participant was kept. Data were band-pass filtered at 1-70Hz and a Fast Fourier Transformation (FFT) with 0.25 Hz resolution was performed to derive estimates of absolute spectral power (Pahor & Jaušovec 2014). We first identified the individual Alpha peak frequency (IAF) (M_{IAF} = 10.64, SD_{IAF} = 0.66). Following Methods from Klimesch (1999), individual Theta frequency (ITF) was extracted by choosing the highest peak between IAF - 4.0 Hz - IAF - 6.0 Hz range (M_{ITF} = 5.5, SD_{ITF} = .65). For individual Beta frequency (IBF), the peak between 12.5 Hz and 22.5 Hz was chosen (M_{ITF} = 17.5, SD_{ITF} = 2.54). The calculated peaks were rounded-up to 0.5 Hz, and were visually inspected and confirmed, or changed when necessary (Klimesch 1999: van Driel et al 2015)

Data handling

Behavioural measures (Asynchrony, Movement Times, Motor Preparation Times, Last Press Times)

As a first step, for each behavioural variable we removed trials in which participants i) failed to follow the instructions (i.e. Same or Opposite for the Interactive Block and Purple or

Yellow for the Cued) or ii) failed to touch the target. From this new dataset, we removed trials that fell more than 2.5 standard deviations below or over the individual mean in the corresponding condition. Analysis on raw data (see Supplementary Materials) showed that the two groups (Theta and Beta) were significantly different between each other in many behavioural variables. In order to deal with between-subjects variability, we decided to perform data analysis on sham-corrected values. Then, for each participant values from each trial in the Real Stimulation condition were standardized by subtracting the corresponding average Sham Stimulation value in the same condition. For example, each trial in the Interactive Correction Opposite Real Stimulation condition was standardized by subtracting the mean value in the Interactive Correction Opposite Sham Stimulation condition (for results from raw data see Supplementary materials).

Statistical analyses

Data from the Embodiment Questionnaire (see Supplementary Materials) and behavioural measures (Asynchrony, Start – to Stop, Motor Preparation Times and Last Press Times) were analysed with Multilevel Linear Mixed Models using the software R and the packages lme4 (version 1.1 -21, Bates et al., 2015). For each model, the random part was selected using the principal component analysis (PCA) method (Bates et al., 2015). We kept all random factors that explained at least 1% of variance. Statistical significance of fixed effects was determined using type III ANOVA test with the *mixed* function from *afex* package. Post-hoc comparisons were performed with the ‘Estimated Marginal Means’ R package (version 1.3.3, Lenth, 2017) via the *emmeans* and *emtrends* functions, respectively, and Tukey correction for multiple comparisons.

For Asynchrony and Movement Times we ran LMM with Asynchrony values as our dependent continuous variable, *Frequency* (Theta, Beta), *Block* (Interactive, Cued), *Trial* (Correction, NoCorrection), *Movement* (Same, Opposite) and their respective interactions as our fixed effects, and *Participant:Block* (i.e., random intercept for each level of the Participant x Block interaction) as our random part.

For Motor Preparation Times we collapsed the Correction and NoCorrection trials, since at the moment in which participants start to move, they still do not know whether there will be a correction or not. Therefore our model included *Frequency* (Theta, Beta), *Block* (Interactive, Cued), *Movement* (Same, Opposite) and their respective interactions as our fixed effects and *Participant:Block* (i.e., random intercept for each level of the Participant x Block interaction) as our as our random part.

Since in the Cued block participants were not required to correct their movement and therefore Last Press Times were not informative, we decided to run LMM on Last Press Times only for the Interactive blocks. Moreover, we coded trials from the Interactive block as follows: NoCorrection (i.e. trials in which the avatar did not change its movement), Correction (i.e. trials in which the avatar changed its movement and the participant adapted) and FakeCorrection (i.e. i.e. trials in which the avatar changed its movement but the participant did not adapt). Our model for Last Press Times in the Interactive block included *Frequency* (Theta, Beta), *Trial* (Correction, NoCorrection, FakeCorrection), *Movement* (Same, Opposite) and their respective interactions as our fixed effects and *Participant:Block* (i.e., random intercept for each level of the Participant x Block interaction) as our as our random part.

tACS-induced physical sensations were analysed with non-parametric statistics. Embodiment ratings were analysed with LMM including Group (ThetaGroup, BetaGroup), Stimulation (Real, Sham) and Item (Experimental, Control) as fixed effects and Participant (i.e., random intercept) as our random part.

Results

Asynchrony

Model: Asynchrony ~ Frequency * Block * Trial * Movement + (1|Subject:Block)

Type III ANOVA on sham-corrected Asynchrony values with Block (Cued, Interactive), Trial (Correction, NoCorrection) and Movement (Opposite, Same) as within-subjects and Frequency (Beta, Theta) as between-subject factor revealed a significant main effect of Frequency (F = 3.81, p = 0.05). Indeed, Asynchrony values in the Theta group were smaller than in the Beta group (Theta M(SD) = -0.04 (0.17), Beta M(SD) = 0.02(0.23)), see Fig. 4. It should be noted that, given the standardisation over the sham condition, negative Asynchrony values indicate a better performance (i.e. smaller asynchrony) compared to baseline performance. Also, there was a significant interaction between *Frequency*, *Block*, *Trial* and *Movement* (F = 8.52, p < 0.01). Tukey-corrected post hoc test did not show any significant difference between conditions of this interaction (all ps > 0.1).

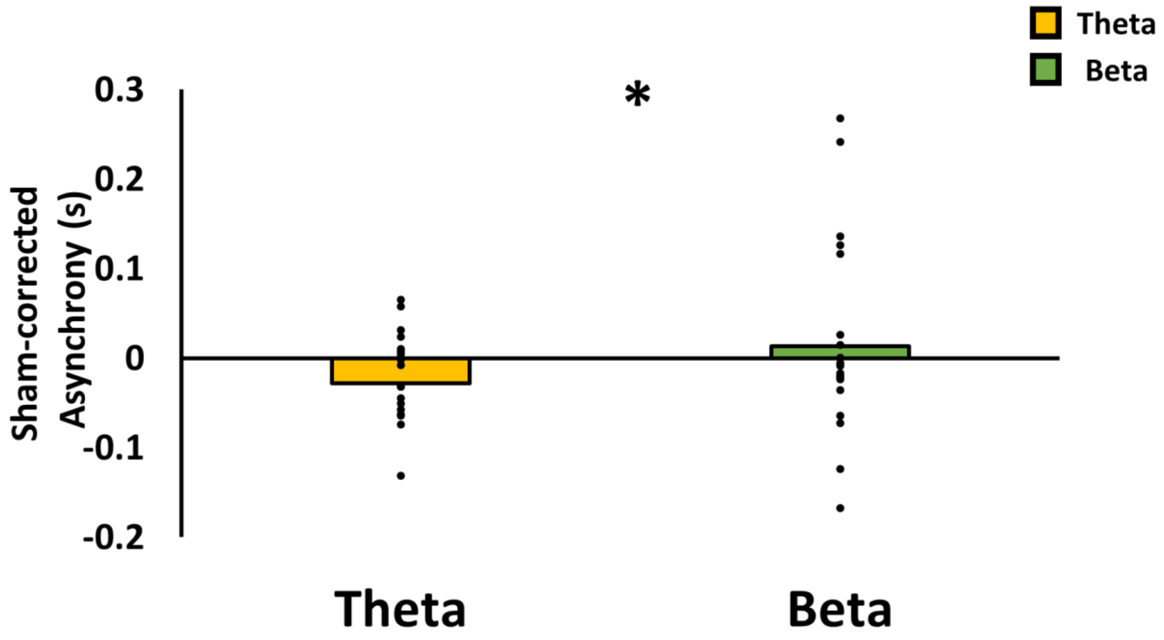


Fig. 4 - Main effect of Frequency for Asynchrony. Theta tACS reduced (and Beta tACS increased) Asynchrony across all conditions. Error bars indicate standard error (SE).

Movement Time (Time from Start to button press)

Model: MovTime ~ Frequency * Block * Trial * Movement + (1|Subject:Block)

Type III ANOVA on sham-corrected Movement Times values with Block (Cued, Interactive), Trial (Correction, NoCorrection) and Movement (Opposite, Same) as within-subjects and Frequency (Beta, Theta) as between-subject factor, revealed a main effect of Frequency (F= 6.28, p = 0.01), indicating that Movement Time values in the Theta group were significantly longer than in the Beta group and a 3-way interaction between *Frequency*, *Block* and *Trial* (*F* = 7.60, p = 0.006). Tukey-corrected post hoc tests showed that only in the Interactive block the contrast between Beta and Theta was significant for Correction trials (estimate = - 0.18, SE = 0.04, z-ratio = - 3.69, p = 0.001). Namely, Movement Times during

Correction trials were increased by Theta tACS and decreased by Beta tACS (see Fig. 5). None of the Frequency contrasts in the Cued block reached or approached significance. The ANOVA also revealed a significant main effect of Movement (F = 8.72, p = 0.003), indicating that Movement times were longer for Opposite than for Same trials and a 3-way interaction between *Block*, *Trial* and *Movement* (*F* = 13, p = 0.0003), which we further analysed with post hoc tests. Results showed that Movement Time values in the Interactive block when performing Opposite_Correction trials were higher than in Same_Correction trials (estimate = 0.02, SE = 0.02, z-ratio = 2.465, p = 0.06), while no difference was seen between Opposite_NoCorrection and Same_NoCorrection (estimate = 0.01, SE = 0.01, z-ratio = 0.10, p = 0.99). This means that in the Interactive block participants' reach-to-press movements were longer for Opposite than for Same trials only when the avatar changed its movement. Conversely, in the Cued block there was a significant difference between Opposite_NoCorrection and Same_NoCorrection (estimate = 0.07, SE = 0.01, z-ratio = 4.17, p < 0.0001) but not between Opposite_Correction and Same_Correction (estimate = -0.01, SE = 0.02, z-ratio = -0.63, p = 0.92), meaning that in the Cued block participants' reach-to-press movements were longer for Opposite than for Same trials only when the avatar did not change its movement.

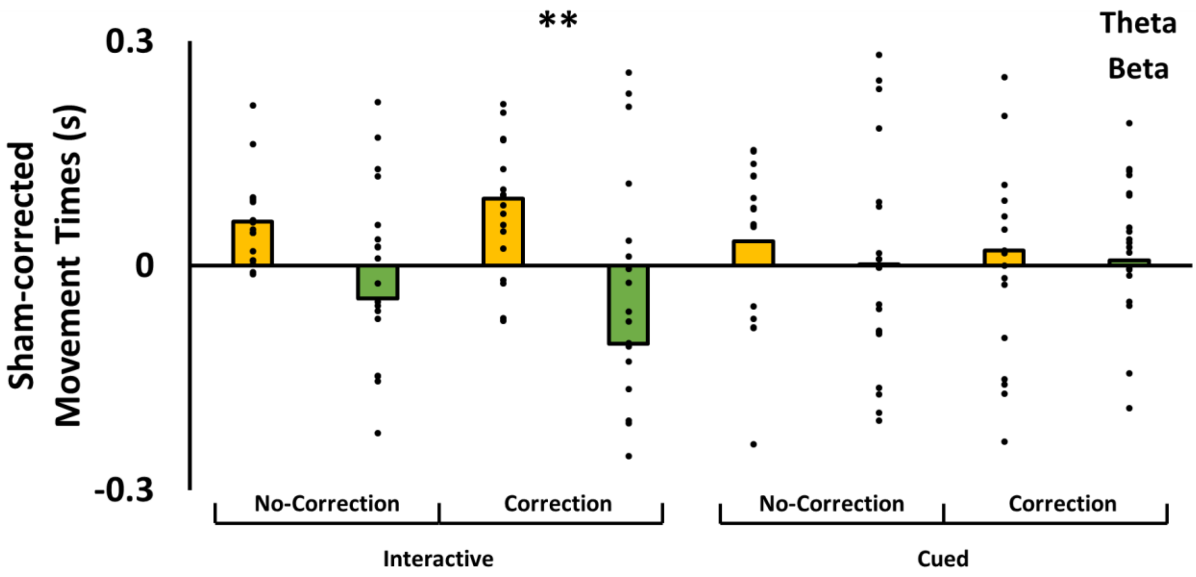


Fig. 5 – Frequency * Block * Trial Interaction for Movement Times. Theta tACS increased (and Beta tACS reduced) Movement Times during Correction trials in the Interactive Block.

Motor Preparation Times (Time from ‘Go’ signal to Start)

Model: MPT ~ Frequency * Block * Trial * Movement + (1|Subject:Block)

Type III ANOVA on sham-corrected values with Block (Cued, Interactive), Trial (Correction, NoCorrection) and Movement (Opposite, Same) as within-subjects and Frequency (Beta, Theta) as between-subject factor, revealed a significant Frequency * Block interaction (F = 4.53, p = 0.04). Post hoc analysis showed a marginally significant difference between Theta and Beta group in the Interactive Block (estimate = 0.07, SE = 0.03, z-ratio = 1.85, p = 0.06), suggesting that Theta tACS tended to reduce the Motor Preparation time only in the Interactive block, see Fig. 6.

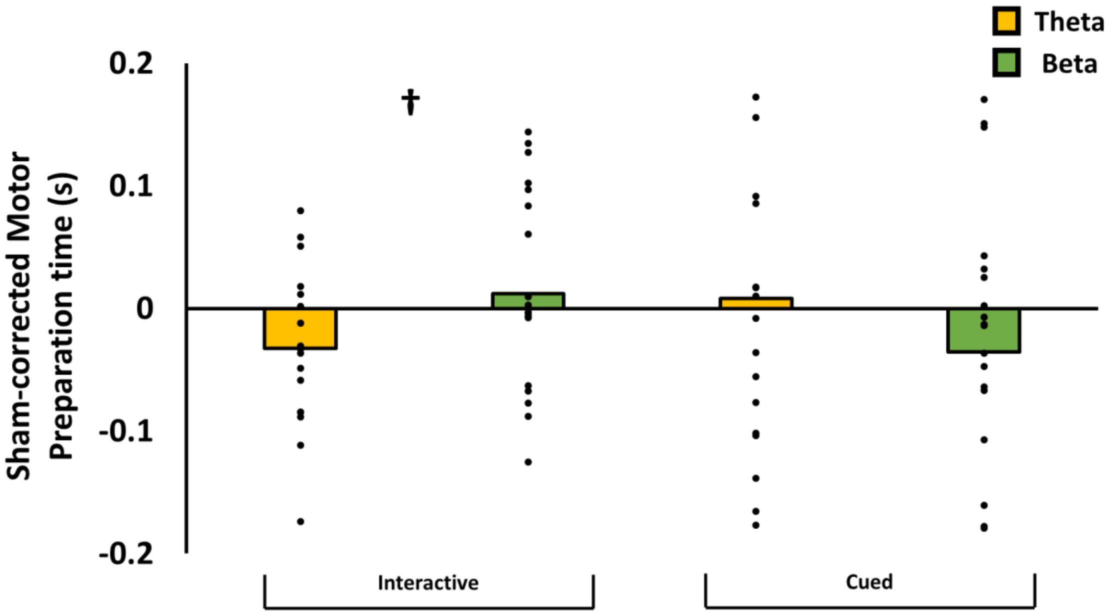


Fig. 6 - Frequency x Block interaction for Motor Preparation Times. Theta tACS reduced (and Beta tACS increased Motor Preparation Times in the Interactive Block.

Last Press Times (Interactive Block)

Model: LastPress ~ Frequency * Block * TypeTrial * Movement + (1|Subject:Block)

Type III ANOVA on sham-corrected values with Block (Cued, Interactive), TypeTrial (Correction, NoCorrection, FakeCorrection) and Movement (Opposite, Same) as within-subjects and Frequency (Beta, Theta) as between-subject factor, revealed no significant main effect or interaction (all Fs < 0.0, all ps > .99) suggesting that tACS didn’t have any effect on this variable.

Correlational analyses

Our results indicate that Theta tACS had the effect of reducing Asynchrony across all conditions and increasing Movement Times in Correction trials. Also, although not significant, an increase in Movement Times was found in NoCorrection trials during the Interactive Task (see Fig 7). We reasoned that longer Movement Times might have allowed participants to be more synchronous with the virtual partner in touching the targets. Indeed, we found that (across all conditions) the average participants' Movement Time was 2.65 (± 0.35), while the virtual partner's was 3.18 (± 0.01). This means that, on average, participants touched the target earlier than the virtual partner. In this vein, increasing Movement Times should allow participants to touch the target more in synchronous with the virtual partner. To test this hypothesis we ran correlation analysis between Asynchrony and Movement Times during the Interactive Block. We focused on the Interactive condition as the one in which a significant effect of tACS on Movement Times was found. Results showed a significant negative correlation between the two variables in all conditions (see Fig. 7) except for Theta_Correction. Specifically, Asynchrony and Movement Times were correlated in Theta_NoCorrection ($r = -0.53$, $p = 0.02$), Beta_NoCorrection ($r = -0.66$, $p < 0.01$) and Beta_Correction ($r = -0.63$, $p < 0.01$) but not in Theta_Correction ($r = 0.08$, $p = 0.73$).

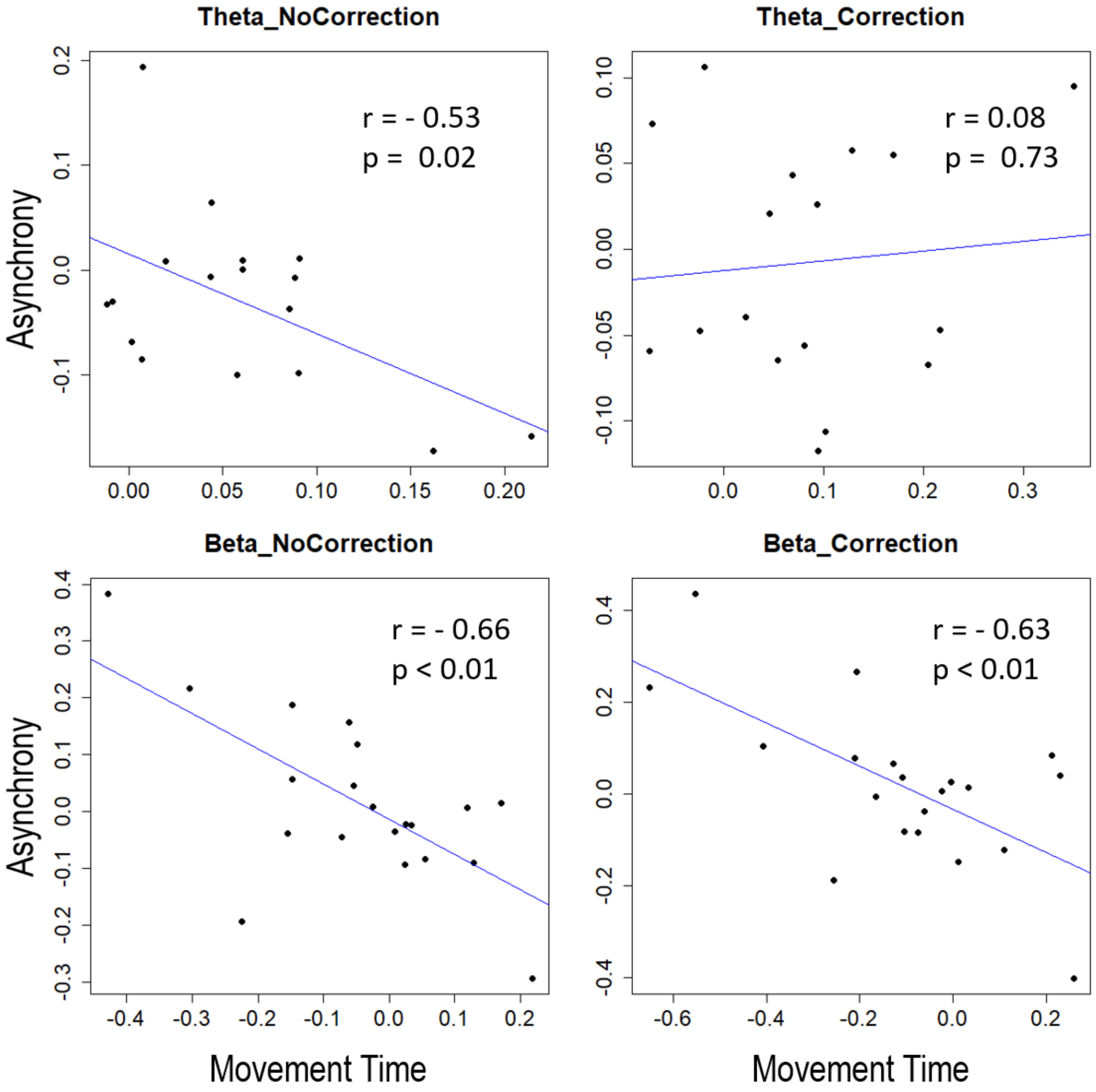


Fig. 7 – Correlations between Asynchrony and Movement Times in the Interactive Blocks.

Embodiment ratings

Experimental items of the Embodiment Questionnaire (Q1 and Q2 for Ownership, Q4 and Q5 for Agency) were collapsed.

For Ownership ratings, Type III ANOVA showed a significant main effect of Item (F = 65.82, p < 0.0001), indicating that participants gave higher ratings to the Experimental item compared to the Control ones. Analyses also showed a Group x Item interaction (F = 5.79, p = 0.02). Post hoc tests showed that both in the Theta and in the Beta group participants gave significantly higher ratings to the experimental than to the control item in the Questionnaire (Theta - estimate = - 18.52, SE = 4.62, t ratio = - 4.009, p = 0.0006; Beta - estimate = - 34.15, SE = 4.56, t ratio = - 7.48, p < 0.0001). Ownership ratings in the Theta group were not different from those in the Beta group (Experimental - estimate = 14.95, SE = 6.49, t ratio = 2.30, p = 0.10; Control - estimate = - 0.67, SE = 6.49, t ratio = - 0.10, p = 0.99).

For Agency ratings, Type III ANOVA showed a significant main effect of Item (F = 302.17, p < 0.0001), indicating that participants gave higher ratings to the Experimental item compared to the Control. No other main effect nor interaction was significant.

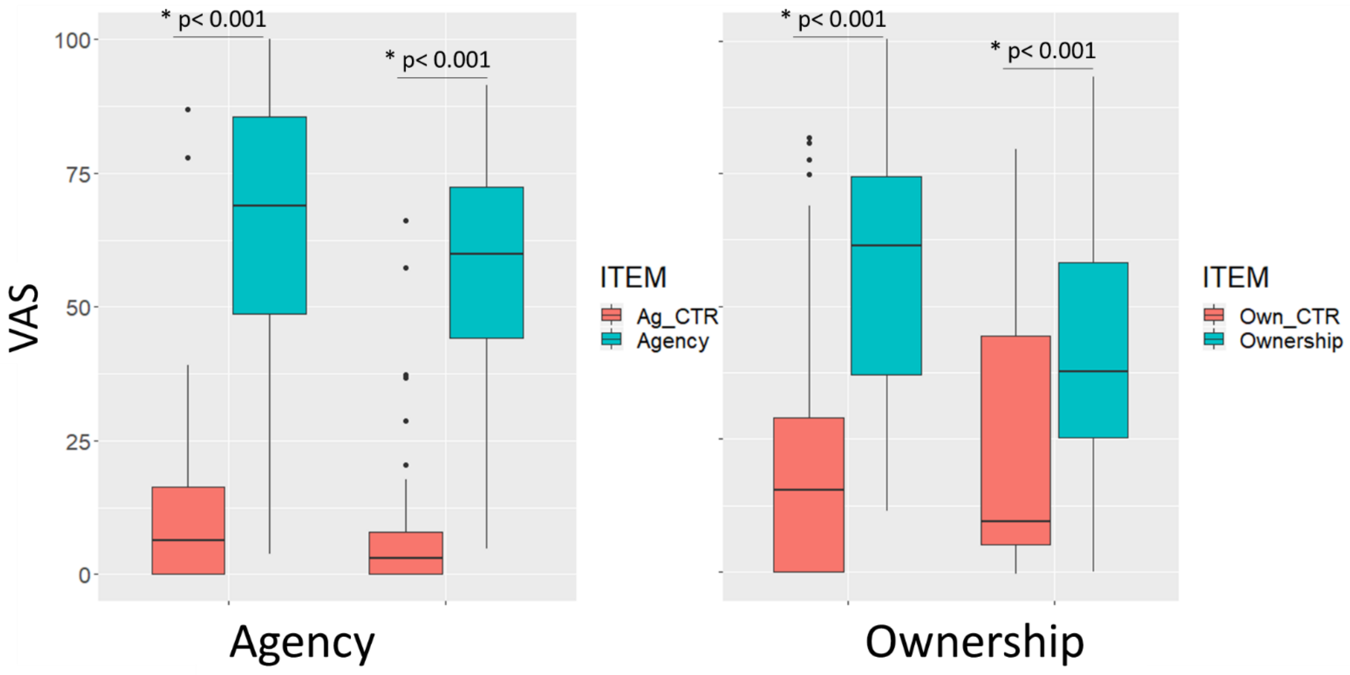


Fig. 8 - Group x Item interaction for Ownership and Agency ratings

tACS-induced sensations questionnaire

For each item of the TES-induced sensations questionnaire (Itching, Pain, Burning, Heat, Pinging and Fatigue) we first computed paired-sample Wilcoxon signed rank tests to check for within-subjects differences between Real and Sham stimulation conditions. Data from the Iron Taste item were not analysed, as only three responses in the whole dataset were higher than zero. We run these analyses separately in the Theta and Beta group. As a result, we found that in the Beta group the median rating for Fatigue after Real stimulation was significantly higher than the median rating after Sham stimulation (v = 27.5, p = 0.02). All the other comparisons were not significant (all ps > 0.1). Frequency-related effects on physical sensations were investigated with two-samples Wilcoxon tests (Mann-Whitney U-test) to compare each item’s rating (only for the Real stimulation condition) in the two groups. We found that median ratings of Pain were significantly higher in the Beta compared to the Theta (W = 288, p < 0.01). All the other comparisons were not significant (all ps > 0.1), see Fig. 9.

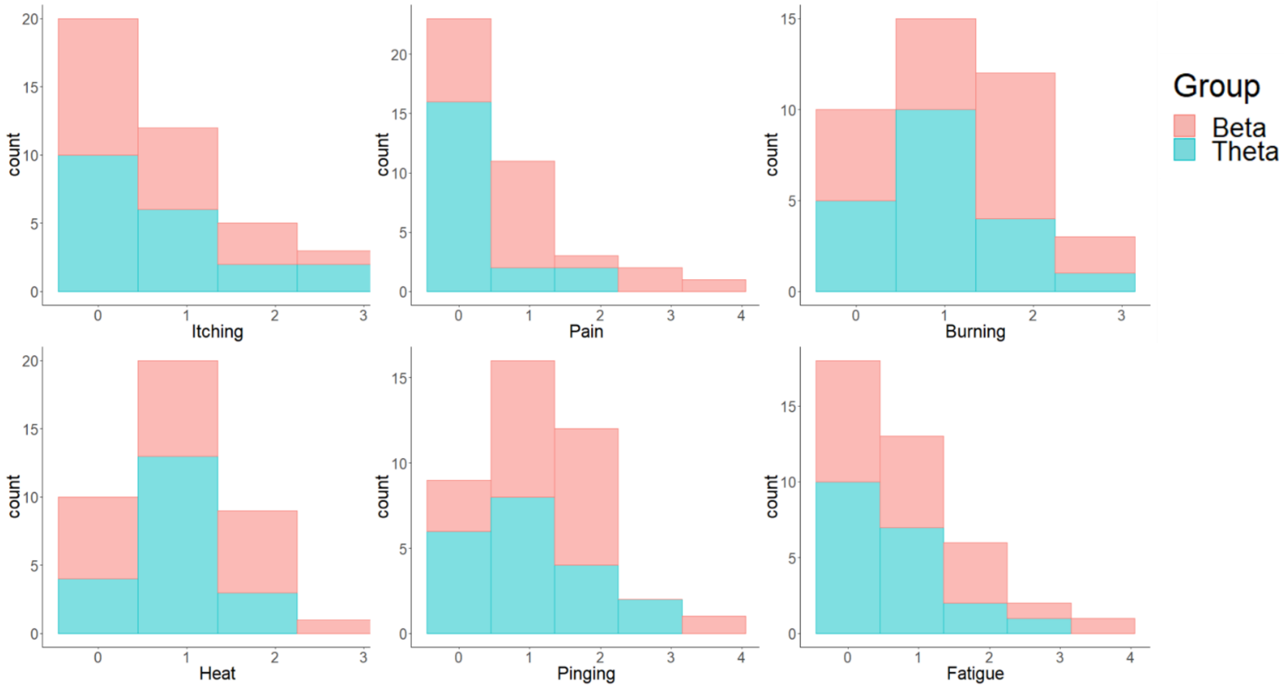


Fig. 9 - tACS-Induced sensations in the two groups.

Interactions between tACS-induced sensations and experimental effects

Statistical analyses on tACS-induced sensations revealed that participants in the Beta group, as compared to participants in the Theta group, experienced higher levels of Pain when receiving tACS. We decided to carry additional analyses to check whether the group-level effects of tACS on behaviour during the Motor Interaction Task might be accounted for by differences in experienced discomfort. To this end, we ran new LMMs for each variable (i.e. Asynchrony, Movement Time and Motor Preparation Time), this time including an index of difference (Real Stimulation – Sham) for each sensation as a covariate. Each model included one sensation index at time. Statistical significance of fixed effects and interactions was determined using Type III ANOVA. Results for each model (i.e. changes in the significance level with respect to the same models without the covariate and significant interactions between experimental factors and the covariate) are reported below. A typical model was:

Asynchrony ~ Frequency * Block * Trial * Movement + (Pain) + (1|Subject:Block)

Asynchrony models.

After the inclusion of Pain, the main effect of Frequency was no longer significant (F = 2.79, p = 0.10). Moreover, there was a significant Frequency x Block x Trial x Movement x Pain interaction (F = 4.79, p = 0.03). Simple slope analysis revealed that the slopes of Beta_Interactive_NoCorrection_Opposite (Pain trend = - 0.05) and Beta_Interactive_Correction_Same (Pain trend = - 0.07 were significantly different from zero. The negative trend suggests that Asynchrony *decreased* for each 1-unit increase in Pain. Namely, the more painful was the Real, compared to the Sham stimulation, the better were participants in the Beta group at synchronising their touch with the avatar in those conditions.

After the inclusion of Itching, the main effect of Frequency was no longer significant (F = 3.36, p = 0.07) and there was a significant Frequency x Block x Trial x Movement x

Itching interaction (F = 4.03, p = 0.04). Simple slope analysis revealed that none of the slopes was significantly different from zero.

After the inclusion of Burning, the main effect of Frequency was marginally significant (F = 3.56, p = 0.06). There was a significant Task x Trial x Burning_Ind (F = 11.90, p = 0.0006). Simple slope analysis revealed that the slope of Beta_Interactive_Correction_Same (Pain trend = - 0.07) was significantly different from zero. The negative trend suggests that Asynchrony *decreased* for each 1-unit increase in Burning. Namely, the stronger was the sensation of burning during the Real, compared to the Sham stimulation, the better were participants in the Beta group at synchronising their touch with the avatar in those conditions.

After the inclusion of Heat, the main effect of Frequency was no longer significant (F = 2.24, p = 0.14). Moreover, there was a significant Task x Trial x Heat interaction (F = 4.09, p = 0.04). Simple slope analysis revealed that the slopes of Beta_Interactive_Correction_Opposite (Heat trend = - 0.10), Beta_Interactive_NoCorrection_Opposite (Heat trend = - 0.08), Beta_Interactive_Correction_Same (Heat trend = - 0.10) and Beta_Interactive_NoCorrection_Same (Heat trend = - 0.05) were significantly different from zero. Again, the negative trend suggests that in these conditions Asynchrony *decreased* for each 1-unit increase in Heat. Namely, the stronger was the sensation of heat during the Real, compared to the Sham stimulation, the better were participants in the Beta group at synchronising their touch with the avatar in those conditions.

After the inclusion of Pinging, the main effect of Frequency was still significant (F = 3.96, p = 0.05). There was a significant Frequency x Block x Trial x Movement x Pain interaction (F = 9.19, p = 0.002). Simple slope analysis revealed that the slope of

Beta_Interactive_Correction_Opposite (Pinging trend = - 0.06) was significantly different from zero. The negative trend suggests that Asynchrony *decreased* for each 1-unit increase in Pinging. Namely, the stronger was the sensation of pinging during the Real, compared to the Sham stimulation, the better were participants in the Beta group at synchronising their touch with the avatar in those conditions.

After the inclusion of Fatigue, the main effect of Frequency was still significant (F = 5.57, p = 0.02). There was a significant Trial x Fatigue interaction (F = 5.87, p = 0.02). Simple slope analysis revealed that none of the slopes was significantly different from zero.

Movement Time models

After the inclusion of Pain, the main effect of Frequency (F = 6.51, p = 0.01) and the Frequency x Block x Trial interaction (F = 6.93, p = 0.009) were still significant. There was a Frequency x Trial x Pain interaction (F = 4.45, p = 0.03). Simple slope analysis revealed that none of the slopes was significantly different from zero.

After the inclusion of Itching, the main effect of Frequency (F = 5.44, p = 0.02) and the Frequency x Block x Trial interaction (F = 8.99, p = 0.003) were still significant. There were a Frequency x Block x Trial (F = 4.29, p = 0.04) and a Frequency x Block x Movement (F= 4.06, p = 0.04) significant interactions. Simple slope analysis for both interactions revealed that none of the slopes was significantly different from zero.

After the inclusion of Burning, the main effect of Frequency (F = 4.93, p = 0.03) and the Frequency x Block x Trial interaction (F = 5.99, p = 0.01) were still significant. There was a significant Trial x Movement x Burning interaction (F = 8.59, p = 0.003). Simple slope analysis revealed that none of the slopes was significantly different from zero.

After the inclusion of Heat, the main effect of Frequency (F = 4.23, p = 0.04) and the Frequency x Block x Trial interaction (F = 5.21, p = 0.02) were still significant. There was a Frequency x Block x Trial x Heat interaction (F = 4.12, p = 0.04). Simple slope analysis revealed that the slope of Beta_Interactive_Correction (Heat trend = 0.12) was significantly different from zero. The positive trend suggests that Movement Time *increased* for each 1-unit increase in Heat. Namely, the stronger was the sensation of heat during the Real, compared to the Sham stimulation, the longer was the movement time in the Interactive Correction condition for participants in the Beta group.

After the inclusion of Pinging, the main effect of Frequency (F = 6.69, p = 0.01) and the Frequency x Block x Trial interaction (F = 5.47, p = 0.02) were still significant. There was a significant Frequency x Block x Trial x Movement x Heat interaction (F = 4.16, p = 0.04). Simple slope analysis revealed that the slopes of Theta_Cued_Correction_Opposite (Pinging trend = 0.12) and Theta_Cued_NoCorrection_Same (Pinging trend = 0.09) were significantly different from zero. The positive trend suggests that Movement Time *increased* for each 1-unit increase in Heat. Namely, the stronger was the sensation of pinging during the Real, compared to the Sham stimulation, the longer was the movement time in those conditions for participants in the Theta group.

After the inclusion of Fatigue, the main effect of Frequency (F = 9.88, p = 0.002) and the Frequency x Block x Trial interaction (F = 7.07, p = 0.008) were still significant. There was a significant Frequency x Block x Movement x Fatigue (F = 8.86, p = 0.003). Simple slope analysis revealed that the slope of Theta_Cued_Opposite (Fatigue trend = 0.06) was significantly different from zero. Also, there was a significant Frequency x Trial x Movement x Fatigue interaction (F = 4.08, p = 0.04). Simple slope analysis revealed that the slope of Theta_NoCorrection_Opposite (Fatigue trend = 0.04) was significantly different from zero. Again, the positive value suggests that Movement Time *increased* for each 1-unit increase in

Fatigue. Namely, the stronger was the fatigue during the Real, compared to the Sham stimulation, the longer was the movement time in those conditions for participants in the Theta group.

Motor Preparation Time models

After the inclusion of Pain, the Frequency x Block interaction was still significant (F = 5.52, p = 0.02). There was a significant Frequency x Block x Movement x Pain interaction (F = 18.31, p < 0.0001). Simple slope analysis revealed that none of the slopes was significantly different from zero.

After the inclusion of Itching, the Frequency x Block interaction was still significant (F = 4.11, p = 0.05). There was no significant interaction between the experimental factors and Itching.

After the inclusion of Burning, the Frequency x Block interaction was still significant (F = 4.39, p = 0.04). There was no significant interaction between the experimental factors and Burning.

After the inclusion of Heat, the Frequency x Block interaction was still significant (F = 5.31, p = 0.02). There was a significant Frequency x Movement x Heat interaction (F = 14.98, p = 0.0001). Simple slope analysis revealed that none of the slopes was significantly different from zero.

After the inclusion of Pinging, the Frequency x Block interaction was still significant (F = 4.58, p = 0.04). There was no significant interaction between the experimental factors and Burning.

After the inclusion of Fatigue, the Frequency x Block interaction was still marginally significant (F = 3.55, p = 0.06). There was a significant Frequency x Block x Movement x

Fatigue interaction (F = 7.86, p = 0.005). Simple slope analysis revealed that none of the slopes was significantly different from zero.

Discussion

Motor and behavioural adjustment following observed errors in social contexts have been mainly investigated in turn-taking speeded reaction time (Schuch and Tipper, 2007, De Brujin et al., 2008) or grasping tasks (Ceccarini and Castiello, 2008). However, rather than "observing, then doing", the most part of everyday motor interactions require agents to "observe *while* doing", therefore involving a moment-by-moment integration of observed and executed movement. From this perspective, the most part of "joint errors" (i.e. errors occurring in the context of a joint action and influencing its success) can, and need to, be corrected online. Considering the classical example of two people moving a table together, if one of them accidentally loose his grip, the other will need to quickly implement a motor adjustment to compensate the other's failure and ensure the fulfilment of the joint action. Previous studies from our research group have shown that unexpected motor changes during motor interactions elicit error-related midfrontal Theta activity (Moreau et al., 2020, Moreau et al., in prep.), a neural marker of error and conflict detection. In the present study, we used a sham-controlled mixed design to test the hypothesis that boosting midfrontal Theta with tACS would modulate adaptive motor adjustments after the observation of a virtual partner's unexpected change.

Our results showed that Theta and Beta tACS had both general and condition-specific effects on performance in the motor interaction task. Participants' ability to synchronise their reach-to-press movements with those of the virtual partner was improved during Theta, compared to Beta, tACS, irrespective of the experimental condition. Synchronisation in motor interaction tasks requires the continuous monitoring of both the observed and the executed movements. Endogenous midfrontal Theta activity has been related to sustained attention during cognitive tasks (Sasaki et al., 1996; Onton et al., 2005) and meditation (Aftanas et al., 201, Tang et al., 2009). Since Theta tACS was delivered continuously, this improvement in synchrony performance might reflect an increased engagement of attentional systems. In this vein, Theta tACS might have helped participants to focus their attention on the motor task and to better control their own movements.

We also found an increase in movement time during Theta, compared to Beta tACS that was specific for Correction trials in the Interactive task, namely when participants observed a motor change in the virtual partner *and* needed to implement a motor correction. Midfrontal Theta activity has been related to both error detection (Cavanagh et al., 2009) and conflict resolution (Botvinick et al., 2007; Nigbur et al., 2011), two processes sharing the need of increased cognitive control. More generally, midfrontal Theta is elicited whenever a habitual response needs to be overcome (Cavanagh et al., 2013). In our task, when the virtual partner was correcting its movement, participants needed to inhibit their ongoing motor plan (e.g. pressing the button with the index finger) and to reprogram a different action (e.g. pressing the button with the middle finger). Motor inhibition involves movement slowing or stopping and has been associated with a brain network consisting of the lateral inferior frontal cortex (IFC), the presupplementary motor area (pre-SMA) and the subtalamic nucleus (STN) (Aron et al., 2007). Activity in this network has been associated with the implementation of PES (Danielmeier and Ullsperger, 2011). Interestingly, the STN is directly interconnected with the ACC (Orieux et al., 2002), where information about errors and conflict are processed and where Theta oscillations are putatively generated (Luu et al., 2004).

From this perspective, the Theta-tACS-induced increase in movement times during correction trials might reflect an enhanced activation of the performance monitoring system which in turn modulated the implementation of PES. Since in our task participants were not asked to be as fast as possible but, rather, as synchronous as possible, we did not expect to observe any slowing in reaction times in the following trial. Instead, we found an increase in movement times *during* the trial that could possibly reflect a phenomenon of motor inhibition (and movement slowing) induced by a response conflict. Interestingly, movement times during correction trials seemed to be reduced by Beta tACS. This result is particularly surprising, considering that increased EEG Beta power has been related to motor inhibition (Kuhn et al., 2004), movement slowing (Pogosyan et al., 2009) and PES (Marco-Pallares et al., 2008). However, since our participants were exerting a continuous force over the Touch controller button and since the velocity of the Avatar 1PP movements was directly related to the exerted force, it is possible that Beta tACS, rather than affecting motor control *per se*, has influenced the strength of the button press. Indeed, one study found that unexpected somatosensory and auditory events delivered while participants were performing an isometric task triggered an increase in force power that was paralleled by an enhancement in Beta EEG power recorded over the central electrodes (Novembre et al., 2019).

Correlation analyses showed that movement times were correlated to asynchrony. Namely, those participants who took more time to move their virtual arm to the target were also better at synchronising their reach-to-press movements with those of the virtual partner. The fact that, on average, participants’ movement times were shorter than the virtual partner’s ones might explain why their synchrony performance benefited from an increase in movement time. However, this was not true for correction trials in the Theta group, possibly because the increase in movement time elicited by Theta tACS was so large.

The application of electrical current for the modulation of brain activity elicits minimal discomfort sensations underneath the electrodes. Measuring the degree of discomfort induced by a specific stimulation protocol is important for two reasons. First, it allows the systematic investigation of tES-induced side effects, as reported for example in Fertonani et al., 2015, therefore promoting the use of safe and well-tolerated protocols for both clinical and research application. The second and more important reason is that the intensity of tES-induced discomfort might influence the behaviour at test. It is therefore important to disentangle the effects of the stimulation *per se* (i.e. whether verum and sham stimulation differently modulate the behaviour) from the effects induced by a different degree of experienced discomfort. In our study, we ran additional analyses in which we included as covariates the difference between Real and Sham stimulation in terms of experienced physical sensations. Our results suggest that the tACS induced sensations were indeed interacting with the experimental factors. The main effect Frequency for Asynchrony was in fact no longer significant when controlling for Pain, Itching and Heat. However, analysis of the interaction terms showed an effect of the discomfort only on some limited combinations of Block, Trial and Movement levels. The interpretation of this finding is quite tricky, as it would mean that an increase in discomfort affected the performance only during, say, opposite correction trials in the Interactive Block. Moreover, the results show that (surprisingly) such increase in discomfort led to an improvement in performance for the Beta group, which is the opposite of what the main analysis seems to suggest, namely that Beta tACS deteriorated performance. For what concerns Movement Time and Motor Preparation Time, the addition of tACS-induced sensation to the models did not bring substantial changes to the observed effects. Here too, we observed significant interactions between the experimental factors and the tACS-induced sensation, which, however, do not seem able to have determined the key group-level differences in the main analysis. Indeed, it seems that tACS-induced sensations (specifically heat, pinging and fatigue) had the effect of increasing movement times both in the Theta and in the Beta group. To conclude, although tACS-induced sensations might have interacted with the observed behaviour, we feel safe that the reported effects of different stimulation on movement time and motor preparation times cannot be accounted for by mere differences in discomfort levels.

Limits

There are potential limitations in this study that should be taken into account in the interpretation of the results. First, the time between the real and sham stimulation session might have been too short to cancel tACS aftereffects for those participants that received real tACS in the first session. This could explain why the two groups were showing differences in various kinematic parameters not only during real tACS but also (although to a lesser extent) during sham (see Supplementary Materials). There is still no consensus on the actual duration of tACS aftereffects, which seem highly dependent on the stimulation parameters (Veniero et al., 2015). However, the possibility that tACS effects might last after stimulation, especially for what concerns plasticity (Vossen et al., 2015) should be considered. Another potential limitation of our study is the absence of EEG recording during or after the stimulation, which prevents us to claim that we were, indeed, enhancing midfrontal Theta power. Future research should consider the potential benefits of concurrent EEG/MEG recording during Theta tACS stimulation.

Conclusion

In the present study we have addressed the causal role of midfrontal Theta oscillations in online motor adjustment to a “joint error”. To our knowledge, this is the first study investigating the causal role of the performance monitoring system in dyadic motor interactions. We showed that Theta tACS improved synchrony performance in all conditions and increased movement times when a motor correction was required. These results hint to a potential beneficial effect of combining tACS with motor interaction tasks for the treatment of motor impairments (e.g. Apraxia or Parkinson disease).

Supplementary Materials

Statistical Analyses on raw data

For Asynchrony and Movement Times we ran LMM with *Group* (Theta, Beta), *Stimulation* (Real, Sham), *Block* (Interactive, Cued), *Trial* (Correction, NoCorrection), *Movement* (Same, Opposite) and their respective interactions as our fixed effects, and *Stimulation* (i.e. random slope for each level of Stimulation over participants) and *Participant:Block* (i.e., random intercept for each level of the Participant x Block interaction) as our random part. For Motor Preparation Times we removed the Trial factor because when participants would start their movement, they could not know whether or not the avatar would correct its movement. Since in the Cued block participants were not required to correct their movement and therefore Last Press Times were not informative, we decided to run LMM on Last Press Times only for the Interactive blocks. For Last Press Time analyses, the factor Trial (which here we will call TrialType) had three levels: NoCorrection (i.e. trials in which the avatar didn't change his movement), RealCorrection (i.e. both the avatar and the participant changed their movements) and FakeCorrection (i.e. the avatar changed but the participant only chose the first finger and did not change his movement).Our model included *Group* (Theta, Beta), *Stimulation* (Real, Sham), *Block* (Interactive, Cued), *TypeTrial* (RealCorrection, FakeCorrection, NoCorrection), *Movement* (Same, Opposite) and their respective interactions as our fixed effects, and *Participant:TypeTrial* (i.e., random intercept for each level of the Participant x TypeTrial interaction) as our random part.

Results

Asynchrony

Model: Asynchrony ~ Group * Stimulation * Block * Trial * Movement +
(1+Stimulation|Subject:Block)

Type III ANOVA revealed significant main effects for Group (F= 8.52, p = 0.005) and Trial (F=7.58, p = 0.006), indicating that participants in the Theta group were more synchronous (i.e. smaller Asynchrony values) than those in the Beta group and that, across all conditions, participants were more synchronous in Correction compared to NoCorrection trials. Moreover, there was a significant Group x Stimulation interaction (F = 4.76, p = 0.03) which we further investigated with post hoc tests. Results showed that in the Real stimulation condition, participants in the Theta group were more synchronous (smaller Asynchrony values) than those in the Beta group (estimate = 0.13, SE = 0.03, z-ratio = 3.50, p = 0.002), while the comparison between Sham_Theta and Sham_Beta was marginally significant (estimate = 0.07, SE = 0.03, z-ratio = 2.01, p = 0.06), se Fig. S1. We also found a Group x Stimulation x Block x Trial x Movement interaction (F= 5.08, p = 0.02) which we further explored with post-hoc tests. Results showed only a marginally significant difference between Theta and Beta in the Cued_Opposite_Correction_RealStimulation condition. All the other comparisons were not significant (see Fig S2).

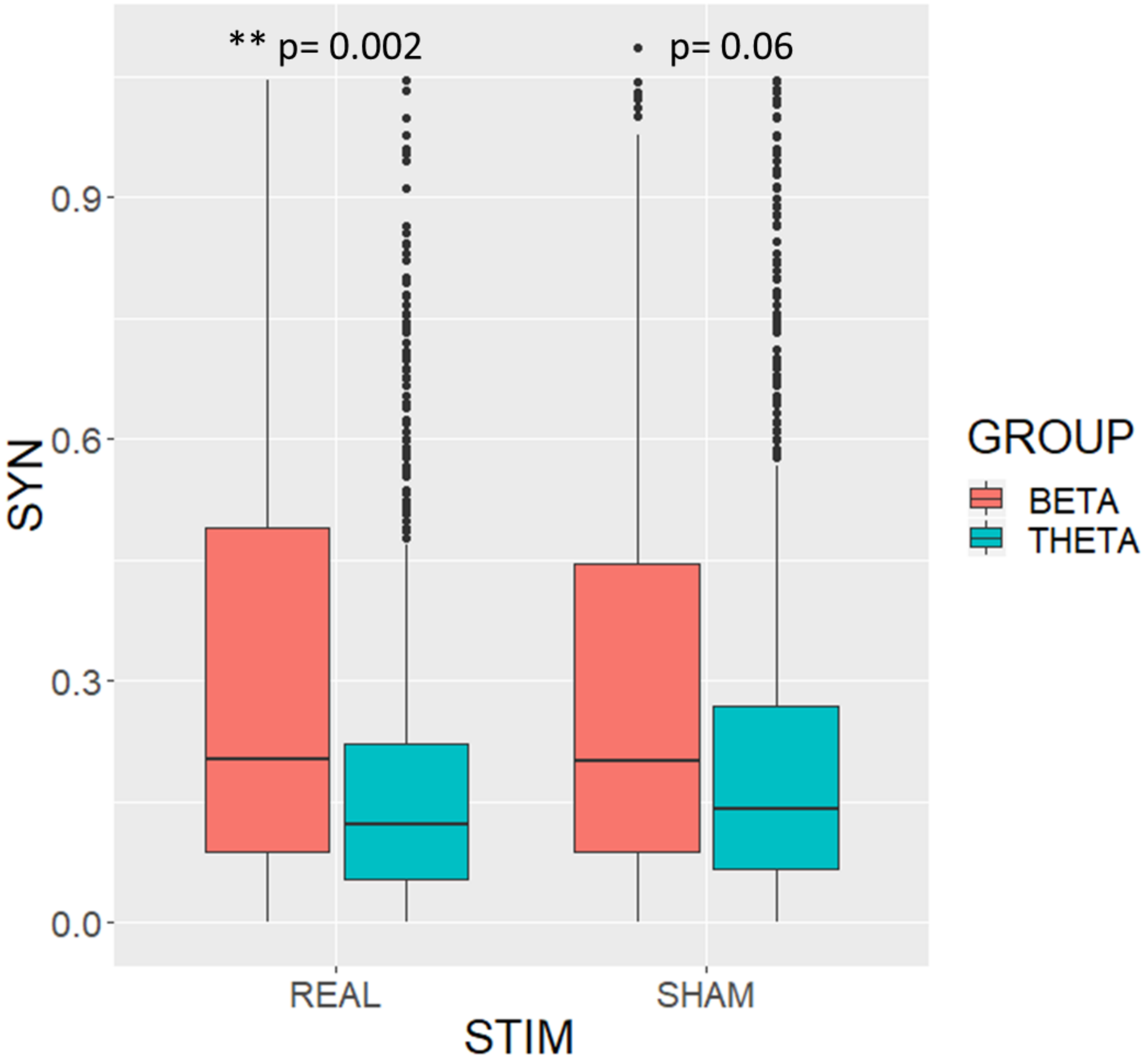


Fig. S1 – Stimulation x Group interaction for Asynchrony

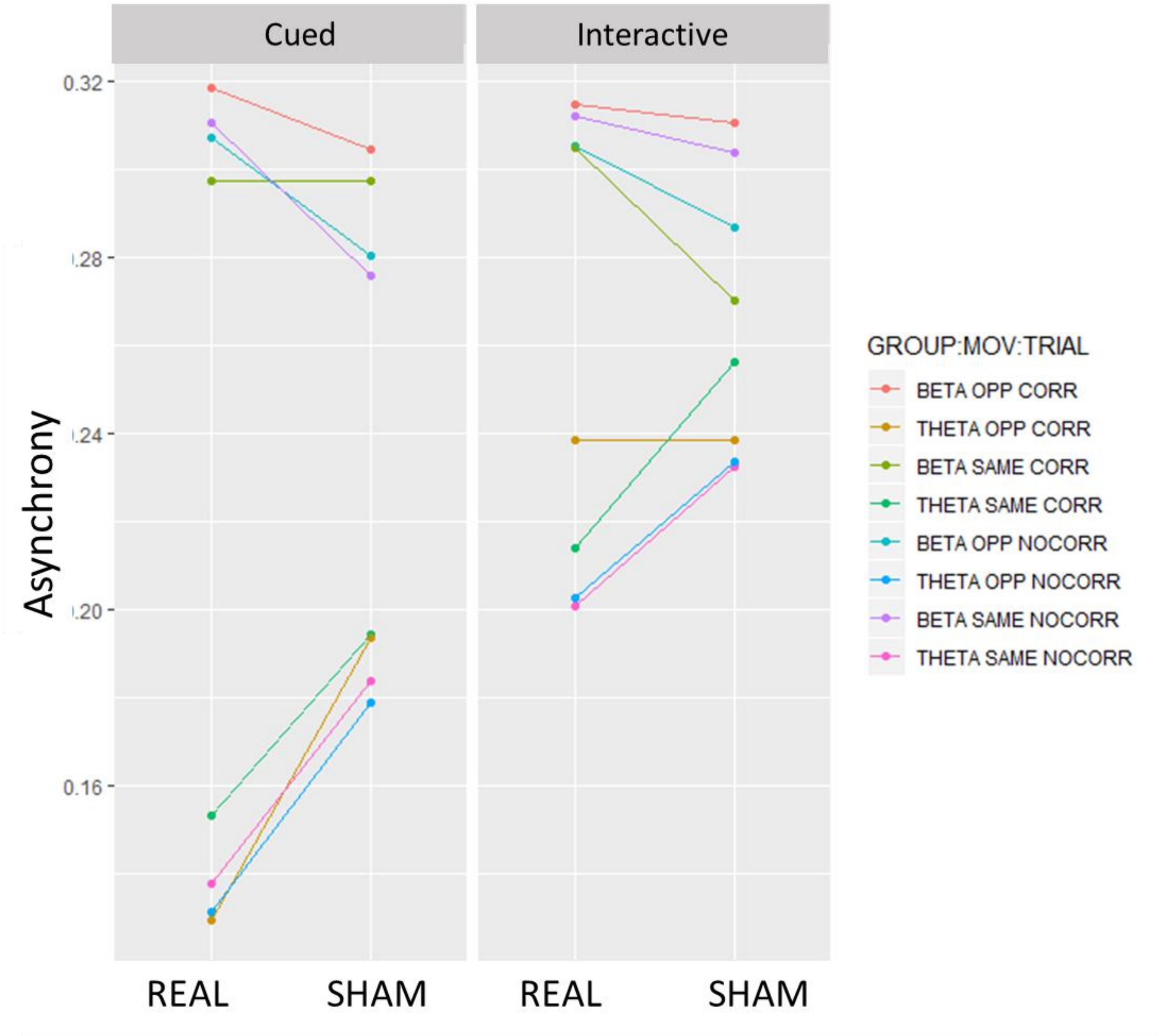


Fig. S2 Group x Stimulation x Block x Trial x Movement interaction for Asynchrony.

Movement Times

Model: MovTimes ~ Group * Stimulation * Block * Trial * Movement +
(1+Stimulation|Subject:Block)

Type III ANOVA revealed a Block x Trial interaction (F= 28.60, p < 0.0001). Post hoc tests indicated that Movement Times were significantly longer in Correction compared to NoCorrection trials, both in the Cued (estimate = 0.02, SE = 0.007, z-ratio = 3.36, p = 0.004) and in the Interactive (estimate = 0.08, SE = 0.05, z-ratio = 10.65, p < 0.0001) blocks. However, neither Correction nor NoCorrection trials were significantly different in the Cued compared to the Interactive blocks (all ps > 0.8). Moreover, there was a Group x Stimulation x Block x Trial interaction (F = 3.76, p = 0.05) which we further explored with post hoc tests. Results indicated that in the Interactive Block there was a significant group difference in Real_Correction (estimate = 0.31, SE = 0.07, z-ratio = 3.98, p = 0.001) but not in Sham_Correction (estimate = 0.13, SE = 0.07, z-ratio = 1.74, p = 0.65), namely participants in the Theta group had longer Movement Times for Correction trials only during real stimulation. The two groups failed to show any significant difference for NoCorrection trials, both in Real (estimate = 0.21, SE = 0.07, z-ratio = 2.71, p = 0.11) and Sham (estimate = 0.11, SE = 0.07, z-ratio = 1.54, p = 0.74) stimulation. In the Cued Block there was only a marginally significant group difference in the Real_Correction condition, with larger Movement Times for Theta compared to Beta (estimate = 0.22, SE = 0.07, z-ratio = 2.87, p = 0.07), while all other comparisons were not significant (all ps > 0.1) (see Fig S3). Comparisons between Correction and NoCorrection trials in the Interactive Block showed that participants in the Theta group had longer Movement Times in Correction than in NoCorrection trials during Real (estimate = 0.12, SE = 0.01, z-ratio = 8.33, p < 0.0001) and Sham (estimate = 0.09, SE = 0.01, z-ratio = 6.40, p < 0.0001) stimulation, while participants the Beta group showed longer Movement Times in Correction than in NoCorrection during Sham (estimate = 0.07, SE = 0.01, z-ratio =

5.21, p < 0.0001) but not during Real tACS (estimate = 0.02, SE = 0.01, z-ratio = 1.4, p = 0.85). All NoCorrection – Correction comparisons in the Cued Block were nonsignificant (all ps > 0.1). Furthermore, post hoc tests showed a marginally significant difference between Real and Sham stimulation in the Beta group for the Interactive_Correction condition. Specifically, Movement Times were longer in Sham than in Real stimulation (estimate = 0.10, SE = 0.03, z-ratio = 2.94, p = 0.06). All the other Real-Sham comparisons were not significant (all ps > 0.1). The ANOVA also revealed a significant Group x Block x Trial x Movement interaction (F = 5.03, p = 0.02). Post hoc tests showed that participants in the Beta group had longer Movement Times for Same than Opposite movements in Correction trials during the Interactive Block (estimate = 0.05, SE = 0.01, z-ratio = 3.17, p = 0.03). All the other Same-Opposite comparisons were not significant (all ps > 0.4). (See Fig. S4).

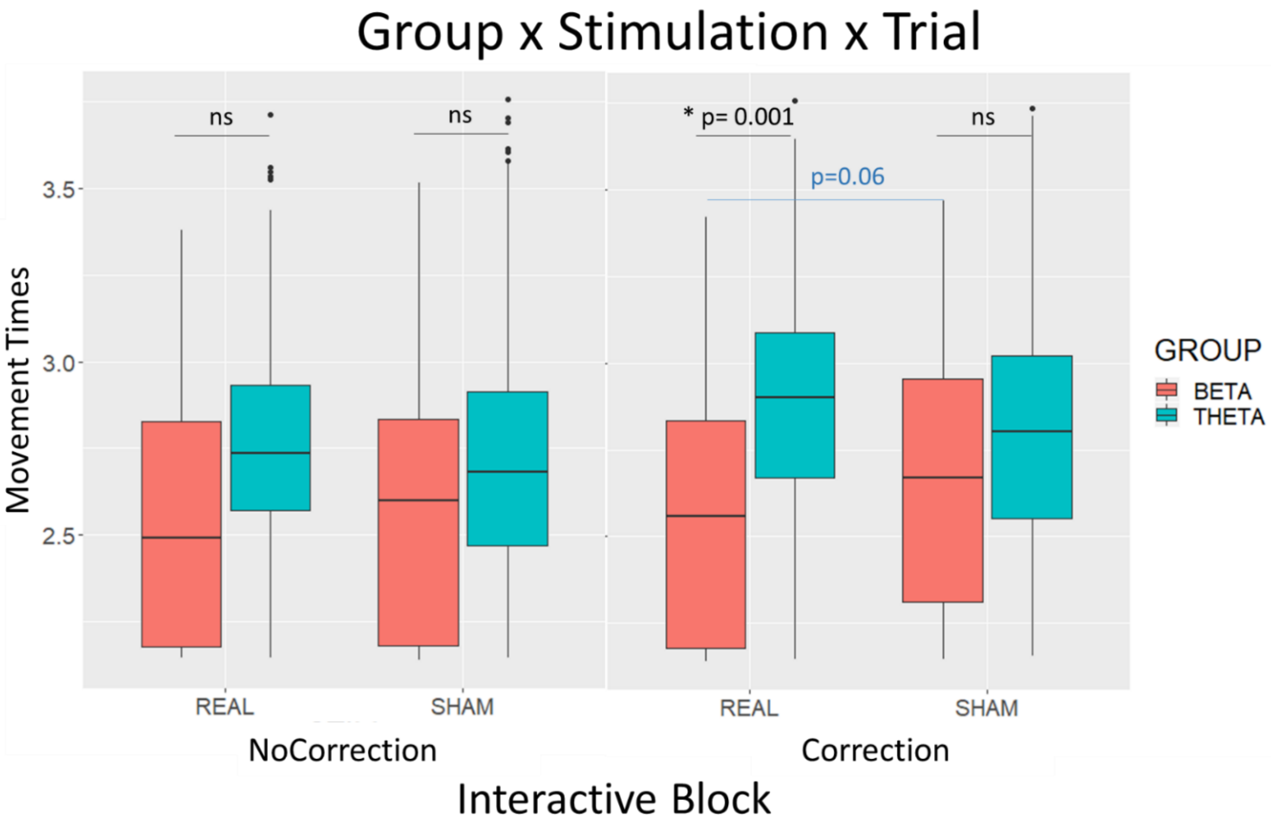


Fig. S3 Group x Stimulation x Trial interaction for Movement Times

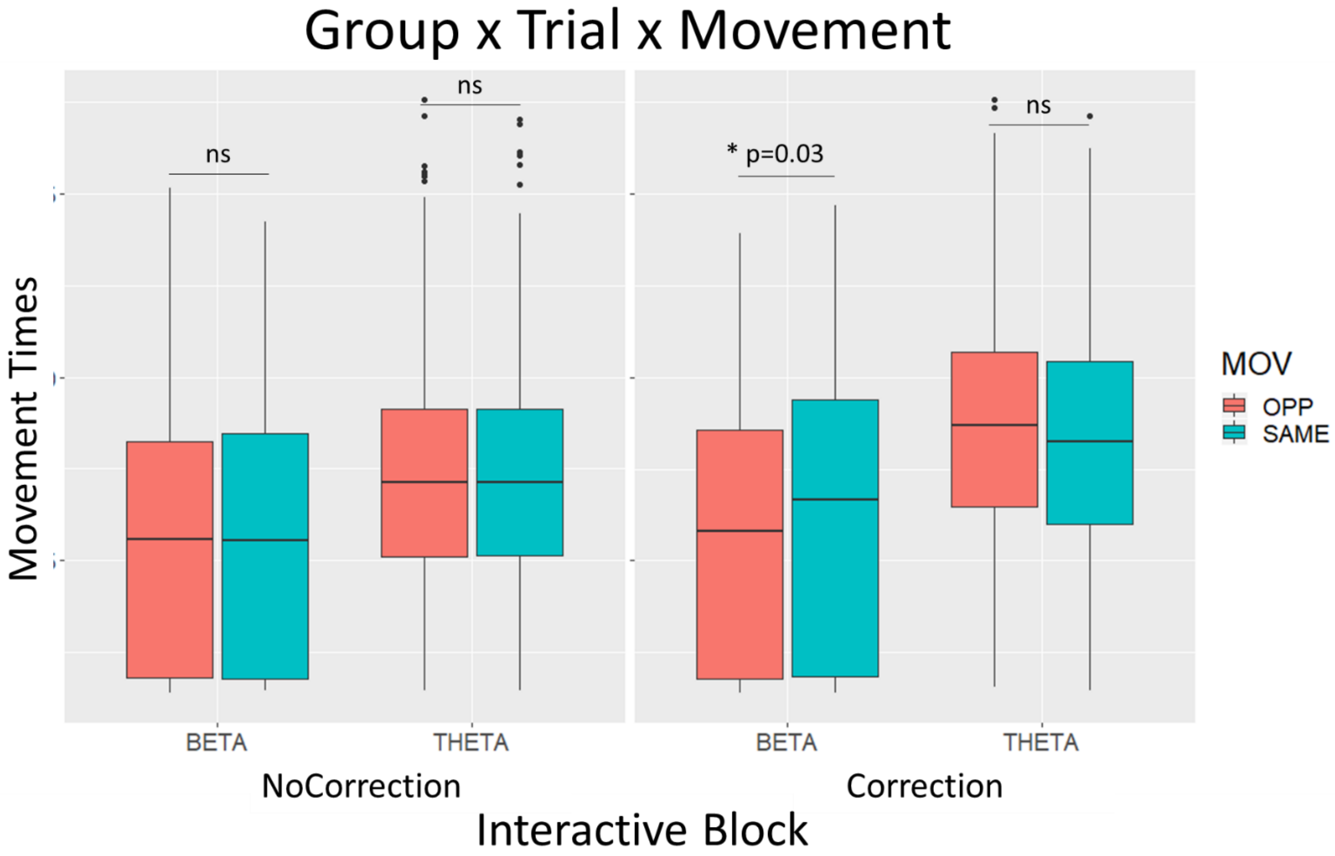


Fig. S4- Group x Trial x Movement interaction for Movement Times.

Motor Preparation Times

Model: MPT ~ Group * Stimulation * Block * Movement + (1+Stimulation|Subject:Block)

Type III ANOVA revealed a significant Group x Stimulation x Block interaction (F = 4.86, p = 0.03). Post hoc tests failed to reveal any significant difference (all ps >0.1). The ANOVA also revealed a significant effect of Movement (F = 9.88, p = 0.002) and a Block x Movement interaction (F= 18.65, p < 0.0001). Post hoc tests indicated that only in the Interactive block Motor Preparation Times were longer for Opposite than for Same trials (estimate = 0.05, SE = 0.03, z-ratio = 1.43, p < 0.0001), see Fig. S5.

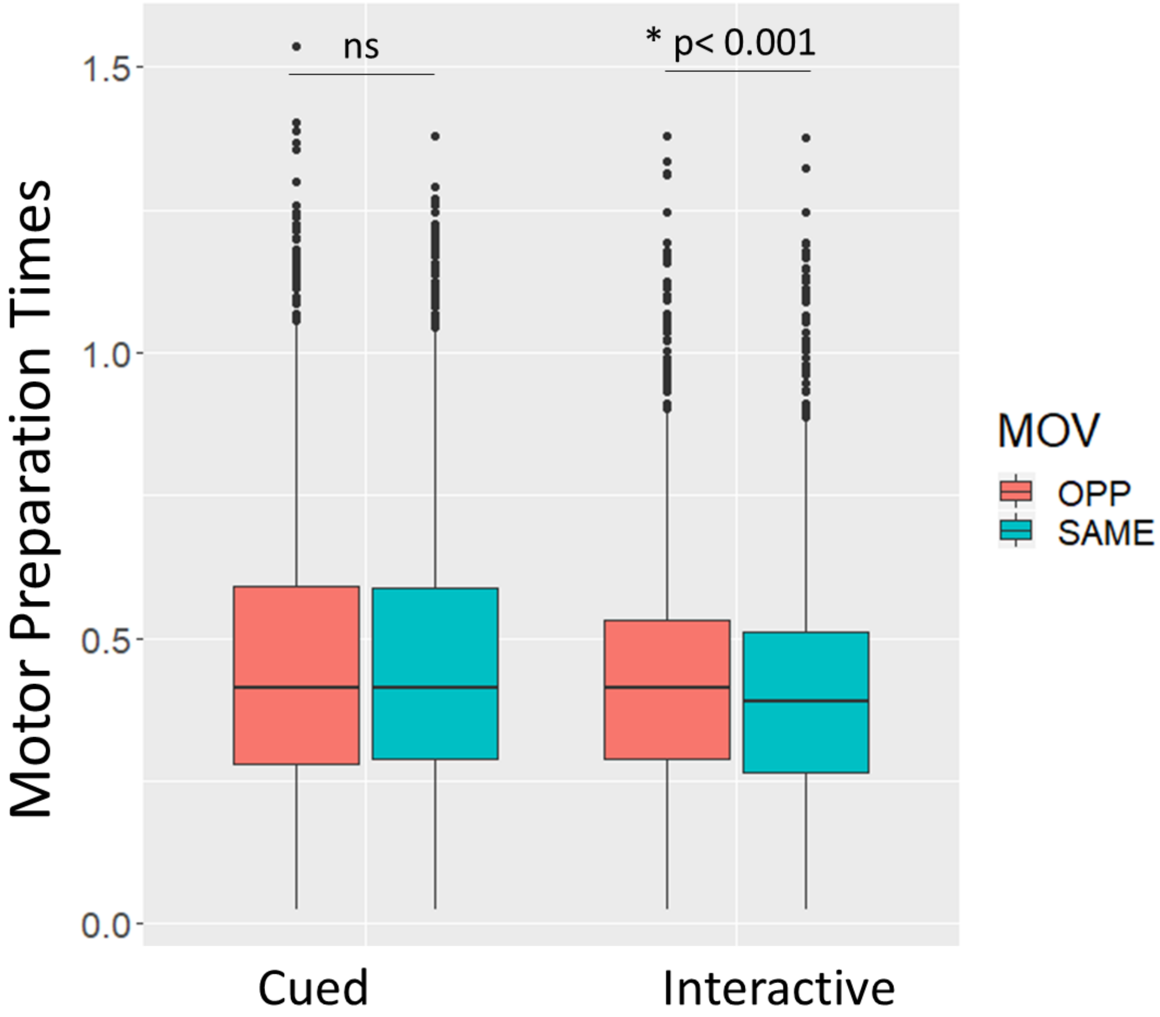


Fig. S5 – Block x Movement interaction for Motor Preparation Times.

Last Press Times

Model: LPT ~ Group * Stimulation * TypeTrial * Movement + (1+Stimulation|Subject:Block)

Type III ANOVA on Last Press Times in the Interactive Block revealed no significant effect of tACS stimulation. We found a significant main effect of Trial Type (F = 1773.55, p < 0.0001). Post hoc tests showed that Last Press Times were significantly higher for NoCorrection compared to RealCorrection (estimate = 0.55, SE = 0.06, z-ratio = 9.87, p <

0.0001) and to FakeCorrection (estimate = 0.62, SE = 0.06, z-ratio = 9.63, p < 0.0001). However, Last Press Times in RealCorrection trials were not significantly different from FakeCorrection trials (estimate = 0.06, SE = 0.06, z-ratio = 0.96, p 0.60) (Fig. S6).

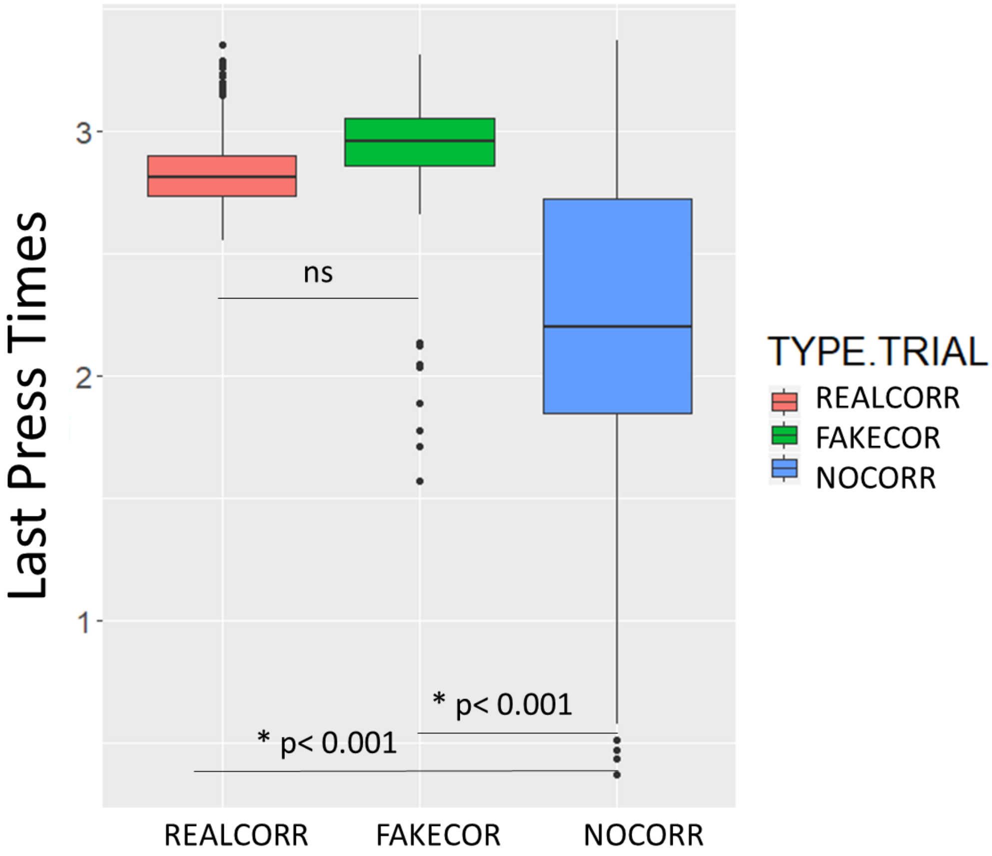


Fig. S6 – Last Press Times in RealCorrection, FakeCorrection and NoCorrection trials.

7. Interim discussion on the effects of Theta tACS on human-avatar motor interactions

The experiment reported in Chapter 6 tested the hypothesis that delivering Theta tACS over the frontal midline would modulate behavioural adaptation to unexpected motor changes during human-avatar motor interactions. Participants received Theta, Beta or Sham tACS while coordinating their reach-to-press movements with those of a virtual partner. Results showed that Theta tACS, compared to Beta, improved synchrony performance (i.e. reduced the time between participant's and avatar's press) and increased movement times when participants needed to adapt to an unexpected motor change in the avatar. Taken together, these results indicate tACS as a viable tool to improve motor interactions by up-regulating the performance monitoring system.

6. General Discussion

The studies reported in the present thesis investigated social interactions, with a particular focus on how hierarchical differentiation influences many aspects of interpersonal behaviour (Study 1 and 2). Another focus of the thesis was the investigation of performance monitoring in social settings (Study 4). These two research lines converged in Study 3, which examined the effects of social status on the autonomic correlates of performance monitoring.

Studies 1 and 2 showed i) that high status individuals are preferred over the low status both at the implicit and explicit level, ii) that the integration of owns' and others' actions during joint actions is easier when the co-agent is a high, as compared to low, status individual and iii) that participants are more likely to act as "followers" when interacting with a high status individual. These results expand on previous studies that investigated the effects of social status on motor resonance (Hogeveen et al., 2014) by showing that these effects also occur in the context of dyadic motor interactions. Future research might benefit from the reported procedure to investigate whether the same effects can be found in competitive (rather than cooperative) contexts. Also, it would be interesting to study whether also dominance-based social status modulates the ability to coordinate with a partner to perform a joint action. Finally, future research should investigate the neural bases of the positive bias for high status individuals both in the context of visual preference (as measured in Study 1) and motor interactions (as measured in Study 2). Indeed, while a great deal of research has investigated the neural correlates of perceived or experienced status, virtually no study has addressed the issue of how status-based differentiation is translated into perceptual or behavioural biases.

Study 3 showed that social status and feedback valence had additive effects on cardiac deceleration following feedback presentation. In line with previous findings (Boksem et al., 2011), results suggest that social status modulates the activity of the performance monitoring system not only at the neural but also at the autonomic level. However, the results from Study 3 seem to suggest that high, rather than low, status increases cardiac deceleration in response to negative feedback. Further analysis on the final sample size will clarify how social status modulates the performance monitoring system in a cooperative context. Again, future research is needed to study the effects of specific contexts (e.g. cooperative or competitive) and status dimensions (e.g. competence or dominance) on performance monitoring.

Finally, in Study 4 tACS was used to modulate endogenous brain oscillations associated with performance monitoring during human-avatar motor interactions. Results showed a frequency-specific effect of Theta tACS on behavioural adjustment to the interaction partner's sudden change, thus shedding new light on the role of performance monitoring during motor interactions. Research on joint actions has now started to investigate how people deal with "social errors" (see Moreau et al., 2020) and the role of the performance monitoring system in the point-by-point integration of observed and executed movements. Future studies will clarify the differences between solo and social errors at the kinematic, neural and affective levels. Combined neuroimaging and kinematic studies will also shed new light on how brain activity and the behaviour are related to each other. For what concerns Mifrontal Theta activity, future studies could benefit from in-phase/out-of-phase tACS protocols (in which two brain areas are stimulated at the same or at a different phase) to investigate how this oscillation supports complex behaviours by synchronising distant areas.

To conclude, the experiments reported in this thesis tackled different aspects of social cognition. The fil rouge connecting each other is the investigation of how cognitive and motor abilities can be modulated according to the specific social context. In the future, I would like to further integrate the different topics and methods covered in the present thesis, for example by recording autonomic activity during joint actions.

References

Abreu, A. M., Macaluso, E., Azevedo, R. T., Cesari, P., Urgesi, C., & Aglioti, S. M. (2012). Action anticipation beyond the action observation network: a functional magnetic resonance imaging study in expert basketball players. *European Journal of Neuroscience*, *35*(10), 1646-1654.

Adler, N. E., Epel, E. S., Castellazzo, G., & Ickovics, J. R. (2000). Relationship of subjective and objective social status with psychological and physiological functioning: Preliminary data in healthy, White women. Health Psychology, 19(6), 586-592.

Aftanas, L. I., & Golocheikine, S. A. (2001). Human anterior and frontal midline theta and lower alpha reflect emotionally positive state and internalized attention: high-resolution EEG investigation of meditation. *Neuroscience letters*, *310*(1), 57-60.

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

Anderson, C., & Kilduff, G. J. (2009). The pursuit of status in social groups. *Current Directions in Psychological Science*, *18*(5), 295–298. https://doi.org/10.1111/j.1467-8721.2009.01655.x

Anderson, C., & Berdahl, J. L. (2002). The experience of power: examining the effects of power on approach and inhibition tendencies. *Journal of personality and social psychology*, *83*(6), 1362.

Ansuini, C., Cavallo, A., Bertone, C., & Becchio, C. (2015). Intentions in the brain: the unveiling of Mister Hyde. *The Neuroscientist*, *21*(2), 126-135.

Ansuini, C., Santello, M., Massaccesi, S., & Castiello, U. (2006). Effects of end-goal on hand shaping. *Journal of neurophysiology*, *95*(4), 2456-2465.

Antal, A., Alekseichuk, I., Bikson, M., Brockmöller, J., Brunoni, A. R., Chen, R., ... & Fregni, F. (2017). Low intensity transcranial electric stimulation: safety, ethical, legal regulatory and application guidelines. *Clinical Neurophysiology*, *128*(9), 1774-1809.

Aquino, A., Paolini, D., Pagliaro, S., Migliorati, D., Wolff, A., Alparone, F. R., & Costantini, M. (2015). Group membership and social status modulate joint actions. *Experimental brain research*, *233*(8), 2461-2466.

Aron, A. R., Behrens, T. E., Smith, S., Frank, M. J., & Poldrack, R. A. (2007). Triangulating a cognitive control network using diffusion-weighted magnetic resonance imaging (MRI) and functional MRI. *Journal of Neuroscience*, *27*(14), 3743-3752.

Avenanti, A., Annella, L., Candidi, M., Urgesi, C., & Aglioti, S. M. (2012). Compensatory plasticity in the action observation network: virtual lesions of STS enhance anticipatory simulation of seen actions. *Cerebral cortex*, *23*(3), 570-580.

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

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.

Bargh, J. A., & Chartrand, T. L. (2000). Studying the mind in the middle: A practical guide to priming and automaticity research. Handbook of research methods in social psychology.

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

Baxter, M. G., & Murray, E. A. (2002). The amygdala and reward. *Nature reviews neuroscience*, *3*(7), 563.

Becchio, C., Sartori, L., Bulgheroni, M., & Castiello, U. (2008). The case of Dr. Jekyll and Mr. Hyde: a kinematic study on social intention. *Consciousness and cognition*, *17*(3), 557-564.

Berntson, G. G., Quigley, K. S., & Lozano, D. (2007). Cardiovascular psychophysiology. In J. T. Cacioppo, L. G. Tassinary, & G. G. Berntson (Eds.), *Cambridge handbook of psychophysiology* (3rd ed., pp. 182–210). Cambridge, UK: Cambridge University Press. doi: 10.1017/CBO9780511546396.008

Boksem, M. A., Kostermans, E., Milivojevic, B., & De Cremer, D. (2011). Social status determines how we monitor and evaluate our performance. *Social cognitive and affective* *neuroscience*, *7*(3), 304-313.

Botvinick, M. M. (2007). Conflict monitoring and decision making: reconciling two perspectives on anterior cingulate function. *Cognitive, Affective, & Behavioral Neuroscience*, *7*(4), 356-366.

Botvinick, M., & Cohen, J. (1998). Rubber hands 'feel' touch that eyes see. *Nature*, *391*(6669), 756.

Bourgeois, P., & Hess, U. (2008). The impact of social context on mimicry. *Biological psychology*, *77*(3), 343-352.

Bradley, M. M., Codispoti, M., Cuthbert, B. N., & Lang, P. J. (2001). Emotion and motivation I: defensive and appetitive reactions in picture processing. *Emotion*, *1*(3), 276.

Brass, M., Zysset, S., & von Cramon, D. Y. (2001). The inhibition of imitative response tendencies. *Neuroimage*, *14*(6), 1416-1423.

Breton, A., Jerbi, K., Henaff, M. A., Cheylus, A., Baudouin, J. Y., Schmitz, C., … Van Der Henst, J. B. (2014). Face the hierarchy: ERP and oscillatory brain responses in social rank processing. *PLoS ONE*, *9*(3). https://doi.org/10.1371/journal.pone.0091451

Calvo-Merino, B., Glaser, D. E., Grèzes, J., Passingham, R. E., & Haggard, P. (2004). Action observation and acquired motor skills: an FMRI study with expert dancers. *Cerebral cortex*, *15*(8), 1243-1249.

Calvo-Merino, B., Grèzes, J., Glaser, D. E., Passingham, R. E., & Haggard, P. (2006). Seeing or doing? Influence of visual and motor familiarity in action observation. *Current biology*, *16*(19), 1905-1910.

Candidi, M., Sacheli, L. M., & Aglioti, S. M. (2015). From muscles synergies and individual goals to interpersonal synergies and shared goals: mirror neurons and interpersonal action hierarchies: comment on "Grasping synergies: a motor-control approach to the mirror neuron mechanism" by D'Ausilio et al. *Phys. Life Rev*, *12*, 126-128.

Cannon, W. B. (1929). Organization for physiological homeostasis. *Physiological reviews*, *9*(3), 399-431.

Carter, C. S., Braver, T. S., Barch, D. M., Botvinick, M. M., Noll, D., & Cohen, J. D. (1998). Anterior cingulate cortex, error detection, and the online monitoring of performance. *Science*, *280*(5364), 747-749.

Cavallo, A., Koul, A., Ansuini, C., Capozzi, F., & Becchio, C. (2016). Decoding intentions from movement kinematics. *Scientific Reports*, *6*, 37036.

Cavanagh, J. F., & Shackman, A. J. (2015). Frontal midline theta reflects anxiety and cognitive control: meta-analytic evidence. *Journal of Physiology-Paris*, *109*(1-3), 3-15.

Cavanagh, J. F., Eisenberg, I., Guitart-Masip, M., Huys, Q., & Frank, M. J. (2013). Frontal theta overrides Pavlovian learning biases. *Journal of Neuroscience*, *33*(19), 8541-8548.

Ceccarini, F., & Castiello, U. (2018). The grasping side of post-error slowing. *Cognition*, *179*, 1-13.

Chan, M. Y., Na, J., Agres, P. F., Savalia, N. K., Park, D. C., & Wig, G. S. (2018). Socioeconomic status moderates age-related differences in the brain’s functional network organization and anatomy across the adult lifespan. *Proceedings of the National Academy of Sciences*, *115*(22), E5144-E5153.

Chapais, B. (2015). Competence and the Evolutionary Origins of Status and Power in Humans. *Human Nature*, *26*(2), 161–183. https://doi.org/10.1007/s12110-015-9227-6

Chaplin, W. F., Phillips, J. B., Brown, J. D., Clanton, N. R., & Stein, J. L. (2000). Handshaking, gender, personality, and first impressions. *Journal of personality and social psychology*, *79*(1), 110.

Chartrand, T. L., & Bargh, J. A. (1999). The chameleon effect: the perception–behavior link and social interaction. *Journal of personality and social psychology*, *76*(6), 893.

Cheng, J. T., Tracy, J. L., Foulsham, T., Kingstone, A., & Henrich, J. (2013). Two ways to the top: Evidence that dominance and prestige are distinct yet viable avenues to social rank and influence. *Journal of Personality and Social Psychology*, *104*(1), 103–125. https://doi.org/10.1037/a0030398

Chiesa, P. A., Liuzza, M. T., Acciarino, A., & Aglioti, S. M. (2015). Subliminal perception of others’ physical pain and pleasure. *Experimental Brain Research*, *233*(8), 2373–2382. https://doi.org/10.1007/s00221-015-4307-8

Chiao, J. Y., Adams Jr, R. B., Tse, P. U., Lowenthal, W. T., Richeson, J. A., & Ambady, N. (2008). Knowing who's boss: fMRI and ERP investigations of social dominance perception. *Group Processes & Intergroup Relations*, *11*(2), 201-214.

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.

Cloutier, J., & Gyurovski, I. (2014). Ventral medial prefrontal cortex and person evaluation: Forming impressions of others varying in financial and moral status. *NeuroImage*, *100*, 535–543. https://doi.org/10.1016/j.neuroimage.2014.06.024

Cooley, E., Payne, B. K., & Phillips, K. J. (2014). Implicit bias and the illusion of conscious ill will. *Social Psychological and Personality Science*, *5*(4), 500-507.

Critchley, H. D. (2005). Neural mechanisms of autonomic, affective, and cognitive integration. *Journal of comparative neurology*, *493*(1), 154-166.

Critchley, H. D., Corfield, D. R., Chandler, M. P., Mathias, C. J., & Dolan, R. J. (2000). Cerebral correlates of autonomic cardiovascular arousal: a functional neuroimaging investigation in humans. *The Journal of physiology*, *523*(1), 259-270.

Critchley, H. D., Elliott, R., Mathias, C. J., & Dolan, R. J. (2000). Neural activity relating to generation and representation of galvanic skin conductance responses: a functional magnetic resonance imaging study. *Journal of Neuroscience*, *20*(8), 3033-3040.

Critchley, H. D., Mathias, C. J., & Dolan, R. J. (2001). Neuroanatomical basis for first-and second-order representations of bodily states. *Nature neuroscience*, *4*(2), 207.

Critchley, H. D., Tang, J., Glaser, D., Butterworth, B., & Dolan, R. J. (2005). Anterior cingulate activity during error and autonomic response. *Neuroimage*, *27*(4), 885-895.

Critchley, H. D., Wiens, S., Rotshtein, P., Öhman, A., & Dolan, R. J. (2004). Neural systems supporting interoceptive awareness. *Nature neuroscience*, *7*(2), 189.

Crone, E. A., Van Der Veen, F. M., Van Der Molen, M. W., Somsen, R. J. M., Van Beek, B., & Jennings, J. R. (2003). Cardiac concomitants of feedback processing. *Biological Psychology*, *64*(1–2), 143–156. https://doi.org/10.1016/S0301-0511(03)00106-6

Curioni, A., Minio-Paluello, I., Sacheli, L. M., Candidi, M., & Aglioti, S. M. (2017). Autistic traits affect interpersonal motor coordination by modulating strategic use of role-based behavior. *Molecular autism*, *8*(1), 23.

Dalmaso, M., Pavan, G., Castelli, L., & Galfano, G. (2012). Social status gates social attention in humans. *Biology Letters*, *8*(3), 450–452. https://doi.org/10.1098/rsbl.2011.0881

Danielmeier, C., & Ullsperger, M. (2011). Post-error adjustments. *Frontiers in psychology*, *2*, 233.

De Bruijn, E. R., & von Rhein, D. T. (2012). Is your error my concern? An event-related potential study on own and observed error detection in cooperation and competition. *Frontiers in neuroscience*, *6*, 8.

Deaner, R. O., Khera, A. V., & Platt, M. L. (2005). Monkeys pay per view: adaptive valuation of social images by rhesus macaques. *Current Biology*, *15*(6), 543-548.

Demakakos, P., Biddulph, J., Tsakos, G., Marmot, M., & De Oliveira, C. (2018). The role of subjective social status in socioeconomic inequalities in mortality: Evidence from the English longitudinal study of ageing (ELSA). *Revue d'Épidémiologie et de Santé Publique*, *66*, S358.

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

Ell, K. (1984). Social networks, social support, and health status: A review. *Social Service Review*, *58*(1), 133-149.

Era, V., Boukarras, S., & Candidi, M. (2019). Neural correlates of action monitoring and mutual adaptation during interpersonal motor coordination: Comment on" The body talks: Sensorimotor communication and its brain and kinematic signatures" by G. Pezzulo et al. *Physics of life reviews*, *28*, 43.

Era, V., Candidi, M., & Aglioti, S. M. (2015). Subliminal presentation of emotionally negative vs positive primes increases the perceived beauty of target stimuli. *Experimental Brain Research*, *233*(11), 3271–3281. https://doi.org/10.1007/s00221-015-4395-5

Era, V., Candidi, M., Gandolfo, M., Sacheli, L. M., & Aglioti, S. M. (2018). Inhibition of left anterior intraparietal sulcus shows that mutual adjustment marks dyadic joint-actions in humans. *Social cognitive and affective neuroscience*, *13*(5), 492-500.

Eriksen, B. A., & Eriksen, C. W. (1974). Effects of noise letters upon the identification of a target letter in a nonsearch task. *Perception & psychophysics*, *16*(1), 143-149.

Fairhurst, M. T., Janata, P., & Keller, P. E. (2014). Leading the follower: an fMRI investigation of dynamic cooperativity and leader–follower strategies in synchronization with an adaptive virtual partner. *Neuroimage*, *84*, 688-697.

Falkenstein, M., Hoormann, J., Christ, S., & Hohnsbein, J. (2000). ERP components on reaction errors and their functional significance: a tutorial. *Biological psychology*, *51*(2-3), 87-107.

Farmer, H., Carr, E. W., Svartdal, M., Winkielman, P., & Hamilton, A. F. D. C. (2016). Status and power do not modulate automatic imitation of intransitive hand movements. *PloS one*, *11*(4), e0151835.

Ferguson, M. J., & Bargh, J. A. (2004). How social perception can automatically influence behavior. *Trends in cognitive sciences*, *8*(1), 33-39.

Ferguson, M. J., Mann, T. C., Cone, J., & Shen, X. (2019). When and How Implicit First Impressions Can Be Updated. *Current Directions in Psychological Science*, 0963721419835206.

Fertonani, A., Ferrari, C., & Miniussi, C. (2015). What do you feel if I apply transcranial electric stimulation? Safety, sensations and secondary induced effects. *Clinical Neurophysiology*, *126*(11), 2181-2188.

Feurra, M., Pasqualetti, P., Bianco, G., Santarnecchi, E., Rossi, A., & Rossi, S. (2013). State-dependent effects of transcranial oscillatory currents on the motor system: what you think matters. *Journal of Neuroscience*, *33*(44), 17483-17489.

Fiehler, K., Ullsperger, M., Grigutsch, M., & Cramon, D. Y. V. (2004). Cardiac Responses to Error Processing and Response Conflict. *Errors, Conflicts, and the Brain. Current Opinions on Performance Monitoring*, 135–147.

Fiske, S. T., & Dépret, E. (1996). Control, interdependence and power: Understanding social cognition in its social context. *European review of social psychology*, *7*(1), 31-61.

Fiske, S. T., Cuddy, A. J. C., Glick, P., & Xu, J. (2018). A model of (often mixed) stereotype content: Competence and warmth respectively follow from perceived status and competition. In *Social Cognition: Selected Works of Susan Fiske* (pp. 163–214). Taylor and Francis. https://doi.org/10.4324/9781315187280

Foulsham, T., Cheng, J. T., Tracy, J. L., Henrich, J., & Kingstone, A. (2010). Gaze allocation in a dynamic situation: Effects of social status and speaking. *Cognition*, *117*(3), 319–331. https://doi.org/10.1016/j.cognition.2010.09.003

Fragale, A. R., Overbeck, J. R., & Neale, M. A. (2011). Resources versus respect: Social judgments based on targets' power and status positions. *Journal of Experimental Social Psychology*, *47*(4), 767-775.

Fries, P. (2015). Rhythms for cognition: communication through coherence. *Neuron*, *88*(1), 220-235.

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

Gehring, W. J., Goss, B., Coles, M. G., Meyer, D. E., & Donchin, E. (1993). A neural system for error detection and compensation. *Psychological science*, *4*(6), 385-390.

Genschow, O., van Den Bossche, S., Cracco, E., Bardi, L., Rigoni, D., & Brass, M. (2017). Mimicry and automatic imitation are not correlated. *PloS one*, *12*(9), e0183784.

Green, A. R., Carney, D. R., Pallin, D. J., Ngo, L. H., Raymond, K. L., Iezzoni, L. I., & Banaji, M. R. (2007). Implicit bias among physicians and its prediction of thrombolysis decisions for black and white patients. *Journal of general internal medicine*, *22*(9), 1231-1238.

Greenwald, A. G., Poehlman, T. A., Uhlmann, E. L., & Banaji, M. R. (2009). Understanding and using the Implicit Association Test: III. Meta-analysis of predictive validity. *Journal of personality and social psychology*, *97*(1), 17.

Gruenewald, T. L., Kemeny, M. E., & Aziz, N. (2006). Subjective social status moderates cortisol responses to social threat. *Brain, behavior, and immunity*, *20*(4), 410-419.

Gunther Moor, B., Crone, E. A., & van der Molen, M. W. (2010). The heartbrake of social rejection: heart rate deceleration in response to unexpected peer rejection. *Psychological Science*, *21*(9), 1326-1333.

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.

Gyurovski, I., Kubota, J., Cardenas-Iniguez, C., & Cloutier, J. (2018). Social status level and dimension interactively influence person evaluations indexed by P300s. *Social Neuroscience*, *13*(3), 333–345. https://doi.org/10.1080/17470919.2017.1326400

Gyurovski, I., Kubota, J., Cardenas-Iniguez, C., & Cloutier, J. (2018). Social status level and dimension interactively influence person evaluations indexed by P300s. *Social neuroscience*, *13*(3), 333-345.

Hackman, D. A., & Farah, M. J. (2009). Socioeconomic status and the developing brain. *Trends in cognitive sciences*, *13*(2), 65-73.

Hajcak, G., McDonald, N., & Simons, R. F. (2003). To err is autonomic: Error-related brain potentials, ANS activity, and post-error compensatory behavior. *Psychophysiology*, *40*(6), 895-903.

Hajcak, G., McDonald, N., & Simons, R. F. (2004). Error-related psychophysiology and negative affect. *Brain and cognition*, *56*(2), 189-197.

Hajcak, G., Moser, J. S., Holroyd, C. B., & Simons, R. F. (2006). The feedback-related negativity reflects the binary evaluation of good versus bad outcomes. *Biological psychology*, *71*(2), 148-154.

Hamilton, A. F. D. C., & Grafton, S. T. (2006). Goal representation in human anterior intraparietal sulcus. *Journal of Neuroscience*, *26*(4), 1133-1137.

Hanslmayr, S., Pastötter, B., Bäuml, K. H., Gruber, S., Wimber, M., & Klimesch, W. (2008). The electrophysiological dynamics of interference during the Stroop task. *Journal of Cognitive Neuroscience*, *20*(2), 215-225.

Hardy, C. L., & Van Vugt, M. (2006). Nice guys finish first: The competitive altruism hypothesis. *Personality and Social Psychology Bulletin*, *32*(10), 1402-1413.

Haxby, J. V., Ungerleider, L. G., Horwitz, B., Maisog, J. M., Rapoport, S. I., & Grady, C. L. (1996). Face encoding and recognition in the human brain. *Proceedings of the National Academy of Sciences*, *93*(2), 922-927.

Helfrich, R. F., Knepper, H., Nolte, G., Strüber, D., Rach, S., Herrmann, C. S., & Engel, A. K. (2014). Selective modulation of interhemispheric functional connectivity by HD-tACS shapes perception. *PLoS biology*, *12*(12), e1002031.

Helfrich, R. F., Schneider, T. R., Rach, S., Trautmann-Lengsfeld, S. A., Engel, A. K., & Herrmann, C. S. (2014). Entrainment of brain oscillations by transcranial alternating current stimulation. *Current Biology*, *24*(3), 333-339.

Henrich, J., & Gil-White, F. J. (2001). The evolution of prestige: Freely conferred deference as a mechanism for enhancing the benefits of cultural transmission. *Evolution and Human Behavior*, *22*(3), 165–196. https://doi.org/10.1016/S1090-5138(00)00071-4

Herrmann, C. S., Murray, M. M., Ionta, S., Hutt, A., & Lefebvre, J. (2016). Shaping intrinsic neural oscillations with periodic stimulation. *Journal of Neuroscience*, *36*(19), 5328-5337.

Herrmann, M. J., Römmler, J., Ehlis, A. C., Heidrich, A., & Fallgatter, A. J. (2004). Source localization (LORETA) of the error-related-negativity (ERN/Ne) and positivity (Pe). *Cognitive Brain Research*, *20*(2), 294-299.

Herrmann, M. J., Römmler, J., Ehlis, A. C., Heidrich, A., & Fallgatter, A. J. (2004). Source localization (LORETA) of the error-related-negativity (ERN/Ne) and positivity (Pe). *Cognitive Brain Research*, *20*(2), 294-299.

Hogeveen, J., Inzlicht, M., & Obhi, S. S. (2014). Power changes how the brain responds to others. *Journal of Experimental Psychology: General*, *143*(2), 755.

Huo, Y. J., & Binning, K. R. (2008). Why the Psychological Experience of Respect Matters in Group Life: An Integrative Account. *Social and Personality Psychology Compass*, *2*(4), 1570–1585. https://doi.org/10.1111/j.1751-9004.2008.00129.x

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.

Imhoff, R., & Banse, R. (2009). Ongoing victim suffering increases prejudice: The case of secondary anti-Semitism. *Psychological Science*, *20*(12), 1443-1447.

Inzlicht, M., Gutsell, J. N., & Legault, L. (2012). Mimicry reduces racial prejudice. *Journal of Experimental Social Psychology*, *48*(1), 361–365. https://doi.org/10.1016/j.jesp.2011.06.007

Ishii, R., Shinosaki, K., Ukai, S., Inouye, T., Ishihara, T., Yoshimine, T., ... & Takeda, M. (1999). Medial prefrontal cortex generates frontal midline theta rhythm. *Neuroreport*, *10*(4), 675-679.

Jiang, J., Chen, C., Dai, B., Shi, G., Ding, G., Liu, L., & Lu, C. (2015). Leader emergence through interpersonal neural synchronization. *Proceedings of the National Academy of Sciences*, *112*(14), 4274-4279.

Jost, J. T., & Banaji, M. R. (1994). The role of stereotyping in system-justification and the production of false consciousness. *British journal of social psychology*, *33*(1), 1-27.

Jost, J. T., & Burgess, D. (2000). Attitudinal ambivalence and the conflict between group and system justification motives in low status groups. *Personality and Social Psychology Bulletin*, *26*(3), 293–305. https://doi.org/10.1177/0146167200265003

Jost, J. T., Banaji, M. R., & Nosek, B. A. (2004). A decade of system justification theory: Accumulated evidence of conscious and unconscious bolstering of the status quo. *Political psychology*, *25*(6), 881-919.

Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: a module in human extrastriate cortex specialized for face perception. *Journal of neuroscience*, *17*(11), 4302-4311.

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

Kiehl, K. A., Liddle, P. F., & Hopfinger, J. B. (2000). Error processing and the rostral anterior cingulate: an event-related fMRI study. *Psychophysiology*, *37*(2), 216-223.

Killgore, W. D., & Yurgelun-Todd, D. A. (2001). Sex differences in amygdala activation during the perception of facial affect. *Neuroreport*, *12*(11), 2543-2547.

Kilner, J. M., Paulignan, Y., & Blakemore, S. J. (2003). An interference effect of observed biological movement on action. *Current biology*, *13*(6), 522-525.

Klein, T. A., Endrass, T., Kathmann, N., Neumann, J., von Cramon, D. Y., & Ullsperger, M. (2007). Neural correlates of error awareness. *Neuroimage*, *34*(4), 1774-1781.

Kokal, I., Gazzola, V., & Keysers, C. (2009). Acting together in and beyond the mirror neuron system. *Neuroimage*, *47*(4), 2046-2056.

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

Koski, J. E., Xie, H., & Olson, I. R. (2015). Understanding social hierarchies: The neural and psychological foundations of status perception. *Social neuroscience*, *10*(5), 527-550.

Koul, A., Cavallo, A., Cauda, F., Costa, T., Diano, M., Pontil, M., & Becchio, C. (2018). Action observation areas represent intentions from subtle kinematic features. *Cerebral Cortex*, *28*(7), 2647-2654.

Kourtis, D., Sebanz, N., & Knoblich, G. (2010). Favouritism in the motor system: social interaction modulates action simulation. *Biology letters*, *6*(6), 758-761.

Krause, M. R., Vieira, P. G., Csorba, B. A., Pilly, P. K., & Pack, C. C. (2019). Transcranial alternating current stimulation entrains single-neuron activity in the primate brain. *Proceedings of the National Academy of Sciences*, *116*(12), 5747-5755.

Kreibig, S. D. (2010). Autonomic nervous system activity in emotion: A review. Biological psychology, 84(3), 394-421.

Kuhlen, A. K., & Brennan, S. E. (2013). Language in dialogue: when confederates might be hazardous to your data. *Psychonomic bulletin & review*, *20*(1), 54-72.

Levenson, R. W. (2014). The autonomic nervous system and emotion. Emotion Review, 6(2), 100-112.

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.

Liuzza, M. T., Cazzato, V., Vecchione, M., Crostella, F., Caprara, G. V., & Aglioti, S. M. (2011). Follow my eyes: The gaze of politicians reflexively captures the gaze of ingroup voters. *PLoS ONE*, *6*(9). https://doi.org/10.1371/journal.pone.0025117

Lord, R. G., De Vader, C. L., & Alliger, G. M. (1986). A meta-analysis of the relation between personality traits and leadership perceptions: An application of validity generalization procedures. *Journal of applied psychology*, *71*(3), 402.

Luu, P., Tucker, D. M., & Makeig, S. (2004). Frontal midline theta and the error-related negativity: neurophysiological mechanisms of action regulation. *Clinical Neurophysiology*, *115*(8), 1821-1835.

Ly, M., Haynes, M. R., Barter, J. W., Weinberger, D. R., & Zink, C. F. (2011). Subjective socioeconomic status predicts human ventral striatal responses to social status information. *Current Biology*, *21*(9), 794-797.

Marmot, M. G. (2006). Status syndrome: a challenge to medicine. *Jama*, *295*(11), 1304-1307.

Marmot, M. G., Stansfeld, S., Patel, C., North, F., Head, J., White, I., ... & Smith, G. D. (1991). Health inequalities among British civil servants: the Whitehall II study. *The Lancet*, *337*(8754), 1387-1393.

Marsh, A. a, Blair, K. S., Jones, M. M., Soliman, N., & Blair, R. J. R. (2009). Dominance and Submission: The Ventrolateral Prefrontal Cortex and Responses to Status Cues, *21*(4), 713–724. https://doi.org/10.1162/jocn.2009.21052.

Mattan, B. D., Kubota, J. T., & Cloutier, J. (2017). How Social Status Shapes Person Perception and Evaluation: A Social Neuroscience Perspective. *Perspectives on Psychological Science*, *12*(3), 468–507. https://doi.org/10.1177/1745691616677828

Mattan, B. D., Kubota, J. T., Li, T., Venezia, S. A., & Cloutier, J. (2019). Implicit Evaluative Biases Toward Targets Varying in Race and Socioeconomic Status. *Personality and Social Psychology Bulletin*, 0146167219835230.

Matthews, S. C., Paulus, M. P., Simmons, A. N., Nelesen, R. A., & Dimsdale, J. E. (2004). Functional subdivisions within anterior cingulate cortex and their relationship to autonomic nervous system function. *NeuroImage*, *22*(3), 1151–1156. https://doi.org/10.1016/j.neuroimage.2004.03.005

McIntosh, D. N. (2006). Spontaneous facial mimicry, liking and emotional contagion. *Polish Psychological Bulletin*, *37*(1), 31.

Melis, A. P., Hare, B., & Tomasello, M. (2006). Chimpanzees recruit the best collaborators. *Science, 311*(5765), 1297–1300. https://doi.org/10.1126/science.1123007

Mies, G. W., Van der Veen, F. M., Tulen, J. H., Hengeveld, M. W., & Van der Molen, M. W. (2011). Cardiac and electrophysiological responses to valid and invalid feedback in a time-estimation task. *Journal of Psychophysiology*.

Miles, L. K., Griffiths, J. L., Richardson, M. J., & Macrae, C. N. (2010). Too late to coordinate: Contextual influences on behavioral synchrony. *European Journal of Social Psychology*, *40*(1), 52-60.

Miltner, W. H. R., Brauer, J., Hecht, H., Trippe, R., & Coles, M. G. H. (2004). Parallel brain activity for self-generated and observed errors. In M. Ullsperger & M. Falkenstein (Eds.), *Errors, conflicts, and the brain: Current opinions on performance monitoring* (pp. 124– 129). Leipzig, Germany: MPI of Human Cognitive and Brain Sciences.

Molnar-Szakacs, I., Wu, A. D., Robles, F. J., & Iacoboni, M. (2007). Do you see what I mean? Corticospinal excitability during observation of culture-specific gestures. *PloS one*, *2*(7), e626.

Moreau, Q., Candidi, M., Era, V., Tieri, G., & Aglioti, S. M. (2020). Frontal and occipito-temporal Theta activity as marker of error monitoring in Human-Avatar joint performance. *Cortex*.

Morgan, D., Grant, K. A., Prioleau, O. A., Nader, S. H., Kaplan, J. R., & Nader, M. A. (2000). Predictors of social status in cynomolgus monkeys (Macaca fascicularis) after group formation. *American Journal of Primatology*, *52*(3), 115–131. https://doi.org/10.1002/1098-2345(200011)52:3<115::AID-AJP1>3.0.CO;2-Z

Munuera, J., Rigotti, M., & Salzman, C. D. (2018). Shared neural coding for social hierarchy and reward value in primate amygdala. *Nature neuroscience*, *21*(3), 415.

Murphy, S. T., & Zajonc, R. B. (1993). Affect, cognition, and awareness: AffectivePriming with optimal and suboptimal stimulus exposures. *Journal of Personality and Social Psychology*, *64*, 723–739.

Neuling, T., Ruhnau, P., Fuscà, M., Demarchi, G., Herrmann, C. S., & Weisz, N. (2015). Friends, not foes: magnetoencephalography as a tool to uncover brain dynamics during transcranial alternating current stimulation. *Neuroimage, 118*, 406-413.

Neuling, T., Ruhnau, P., Weisz, N., Herrmann, C. S., & Demarchi, G. (2017). Faith and oscillations recovered: on analyzing EEG/MEG signals during tACS. *Neuroimage*, *147*, 960-963.

Nigbur, R., Cohen, M. X., Ridderinkhof, K. R., & Stürmer, B. (2012). Theta dynamics reveal domain-specific control over stimulus and response conflict. *Journal of Cognitive Neuroscience*, *24*(5), 1264-1274.

Notebaert, W., Houtman, F., Van Opstal, F., Gevers, W., Fias, W., & Verguts, T. (2009). Post-error slowing: an orienting account. *Cognition*, *111*(2), 275-279.

Novembre, G., Ticini, L. F., Schütz-Bosbach, S., & Keller, P. E. (2012). Distinguishing self and other in joint action. Evidence from a musical paradigm. *Cerebral Cortex*, *22*(12), 2894-2903.

Novembre, G., Ticini, L. F., Schütz-Bosbach, S., & Keller, P. E. (2013). Motor simulation and the coordination of self and other in real-time joint action. *Social cognitive and affective neuroscience*, *9*(8), 1062-1068.

O'Connell, R. G., Dockree, P. M., Bellgrove, M. A., Kelly, S. P., Hester, R., Garavan, H., … Foxe, J. J. (2007). The role of cingulate cortex in the detection of errors with and without awareness: A high-density electrical mapping study. *European Journal of Neuroscience*, *25*(8), 2571–2579. https://doi.org/10.1111/j.1460-9568.2007.05477.x

Oldmeadow, J. A., & Fiske, S. T. (2010). Social status and the pursuit of positive social identity: Systematic domains of intergroup differentiation and discrimination for high-and low-status groups. *Group Processes & Intergroup Relations*, *13*(4), 425-444.

Onoda, K., Kawagoe, T., Zheng, H., & Yamaguchi, S. (2017). Theta band transcranial alternating current stimulations modulates network behavior of dorsal anterior cingulate cortex. *Scientific reports*, *7*(1), 3607.

Onton, J., Delorme, A., & Makeig, S. (2005). Frontal midline EEG dynamics during working memory. *Neuroimage*, *27*(2), 341-356.

Orieux, G., François, C., Féger, J., & Hirsch, E. C. (2002). Consequences of dopaminergic denervation on the metabolic activity of the cortical neurons projecting to the subthalamic nucleus in the rat. *Journal of Neuroscience*, *22*(19), 8762-8770.

Pavone, E. F., Tieri, G., Rizza, G., Tidoni, E., Grisoni, L., & Aglioti, S. M. (2016). Embodying others in immersive virtual reality: electro-cortical signatures of monitoring the errors in the actions of an avatar seen from a first-person perspective. *Journal of Neuroscience*, *36*(2), 268-279.

Payne, B. K., Cheng, C. M., Govorun, O., & Stewart, B. D. (2005). An inkblot for attitudes: Affect misattribution as implicit measurement. *Journal of Personality and Social Psychology*, *89*(3), 277–293. https://doi.org/10.1037/0022-3514.89.3.277

Pezzetta, R., Nicolardi, V., Tidoni, E., & Aglioti, S. M. (2018). Error, rather than its probability, elicits specific electrocortical signatures: a combined EEG-immersive virtual reality study of action observation. *Journal of neurophysiology*, *120*(3), 1107-1118.

Pezzulo, G., Donnarumma, F., Dindo, H., D'Ausilio, A., Konvalinka, I., & Castelfranchi, C. (2019). The body talks: Sensorimotor communication and its brain and kinematic signatures. *Physics of life reviews*, *28*, 1-21.

Pogosyan, A., Gaynor, L. D., Eusebio, A., & Brown, P. (2009). Boosting cortical activity at beta-band frequencies slows movement in humans. *Current biology*, *19*(19), 1637-1641.

Ponsi, G., Panasiti, M. S., Rizza, G., & Aglioti, S. M. (2017). Thermal facial reactivity patterns predict social categorization bias triggered by unconscious and conscious emotional stimuli. Proc. R. Soc. B, 284(1861), 20170908.

Porciello, G., Liuzza, M. T., Minio-Paluello, I., Caprara, G. V., & Aglioti, S. M. (2016). Fortunes and misfortunes of political leaders reflected in the eyes of their electors. *Experimental brain research*, *234*(3), 733-740.

Pryor, J. B., Reeder, G. D., Wesselmann, E. D., Williams, K. D., & Wirth, J. H. (2013). The influence of social norms upon behavioral expressions of implicit and explicit weight-related stigma in an interactive game. *The Yale journal of biology and medicine*, *86*(2), 189.

Rabbitt, P. M. (1966). Errors and error correction in choice-response tasks. *Journal of experimental psychology*, *71*(2), 264.

Ratcliff, N. J., Hugenberg, K., Shriver, E. R., & Bernstein, M. J. (2011). The allure of status: High-status targets are privileged in face processing and memory. *Personality and Social Psychology Bulletin*, *37*(8), 1003–1015. https://doi.org/10.1177/0146167211407210

Ridderinkhof, K. R., Ullsperger, M., Crone, E. A., & Nieuwenhuis, S. (2004). The role of the medial frontal cortex in cognitive control. *science*, *306*(5695), 443-447.

Rizzolatti, G., & Craighero, L. (2004). The mirror-neuron system. *Annu. Rev. Neurosci.*, *27*, 169-192.

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

Rohr, M., Degner, J., & Wentura, D. (2015). The “emotion misattribution” procedure: Processing beyond good and bad under masked and unmasked presentation conditions. *Cognition and Emotion*, *29*(2), 196–219. https://doi.org/10.1080/02699931.2014.898613

Sacheli, L. M., Arcangeli, E., & Paulesu, E. (2018). Evidence for a dyadic motor plan in joint action. *Scientific reports*, *8*(1), 5027.

Sacheli, L. M., Candidi, M., Era, V., & Aglioti, S. M. (2015). Causative role of left aIPS in coding shared goals during human–avatar complementary joint actions. *Nature Communications*, *6*, 7544.

Sacheli, L. M., Candidi, M., Pavone, E. F., Tidoni, E., & Aglioti, S. M. (2012). And yet they act together: interpersonal perception modulates visuo-motor interference and mutual adjustments during a joint-grasping task. *PloS one*, *7*(11), e50223.

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*, 8507.

Sacheli, L. M., Tidoni, E., Pavone, E. F., Aglioti, S. M., & Candidi, M. (2013). Kinematics fingerprints of leader and follower role-taking during cooperative joint actions. *Experimental brain research*, *226*(4), 473-486.

Santamaria-Garcia, H., Burgaleta, M., & Sebastian-Galles, N. (2015). Neuroanatomical Markers of Social Hierarchy Recognition in Humans: A Combined ERP/MRI Study. *Journal of Neuroscience*, *35*(30), 10843–10850. https://doi.org/10.1523/JNEUROSCI.1457-14.2015

Santamaría-García, H., Pannunzi, M., Ayneto, A., Deco, G., & Sebastián-Gallés, N. (2014). “If you are good, i get better”: The role of social hierarchy in perceptual decision-making. *Social Cognitive and Affective Neuroscience*, *9*(10), 1489–1497. https://doi.org/10.1093/scan/nst133

Sapolsky, R. M. (2005). The influence of social hierarchy on primate health. *Science*, *308*(5722), 648-652.

Sasaki, K., Tsujimoto, T., Nishikawa, S., Nishitani, N., & Ishihara, T. (1996). Frontal mental theta wave recorded simultaneously with magnetoencephalography and electroencephalography. *Neuroscience research*, *26*(1), 79-81.

Schilbach, L., Timmermans, B., Reddy, V., Costall, A., Bente, G., Schlicht, T., & Vogeley, K. (2013). Toward a second-person neuroscience 1. *Behavioral and brain sciences*, *36*(4), 393-414.

Sebanz, N., Bekkering, H., & Knoblich, G. (2006). Joint action: bodies and minds moving together. *Trends in cognitive sciences*, *10*(2), 70-76.

Shackman, A. J., Salomons, T. V., Slagter, H. A., Fox, A. S., Winter, J. J., & Davidson, R. J. (2011). The integration of negative affect, pain and cognitive control in the cingulate cortex. *Nature Reviews Neuroscience*, *12*(3), 154.

Shariff, A. F., & Tracy, J. L. (2009). Knowing who’s boss: Implicit perceptions of status from the nonverbal expression of pride. *Emotion*, *9*(5), 631.

Singer, T., Kiebel, S. J., Winston, J. S., Dolan, R. J., & Frith, C. D. (2004). Brain responses to the acquired moral status of faces. *Neuron*, *41*(4), 653-662.

Somsen, R. J., Van der Molen, M. W., Jennings, J. R., & van Beek, B. (2000). Wisconsin card sorting in adolescents: analysis of performance, response times and heart rate. *Acta psychologica*, *104*(2), 227-257.

Spinelli, G., Tieri, G., Pavone, E. F., & Aglioti, S. M. (2018). Wronger than wrong: Graded mapping of the errors of an avatar in the performance monitoring system of the onlooker. *NeuroImage*, *167*, 1-10.

Stanley, D., Phelps, E., & Banaji, M. (2008). The neural basis of implicit attitudes. *Current Directions in Psychological Science*, *17*(2), 164-170.

Tang, Y. Y., Ma, Y., Fan, Y., Feng, H., Wang, J., Feng, S., ... & Zhang, Y. (2009). Central and autonomic nervous system interaction is altered by short-term meditation. *Proceedings of the national Academy of Sciences*, *106*(22), 8865-8870.

Thayer, J. F., & Lane, R. D. (2000). A model of neurovisceral integration in ER and dysregulation. *Journal of Affective Disorders*, *61*, 201–216. https://doi.org/https://doi.org/10.1016/S0165-0327(00)00338-4

Thayer, J. F., Hansen, A. L., Saus-Rose, E., & Johnsen, B. H. (2009). Heart rate variability, prefrontal neural function, and cognitive performance: the neurovisceral integration perspective on self-regulation, adaptation, and health. *Annals of Behavioral Medicine*, *37*(2), 141-153.

Thomas, A. J., Thomsen, L., Lukowski, A. F., Abramyan, M., & Sarnecka, B. W. (2018). Toddlers prefer those who win but not when they win by force. *Nature Human Behaviour*, *2*(9), 662.

Tidoni, E., Borgomaneri, S., Di Pellegrino, G., & Avenanti, A. (2013). Action simulation plays a critical role in deceptive action recognition. *Journal of Neuroscience*, *33*(2), 611-623.

Tieri, G., Gioia, A., Scandola, M., Pavone, E. F., & Aglioti, S. M. (2017). Visual appearance of a virtual upper limb modulates the temperature of the real hand: a thermal imaging study in Immersive Virtual Reality. *European Journal of Neuroscience*, *45*(9), 1141-1151.

Tieri, G., Tidoni, E., Pavone, E. F., & Aglioti, S. M. (2015). Body visual discontinuity affects feeling of ownership and skin conductance responses. *Scientific reports*, *5*, 17139.

Tieri, G., Tidoni, E., Pavone, E. F., & Aglioti, S. M. (2015). Mere observation of body discontinuity affects perceived ownership and vicarious agency over a virtual hand. *Experimental brain research*, *233*(4), 1247-1259.

Tinio, P. P., & Leder, H. (2009). Just how stable are stable aesthetic features? Symmetry, complexity, and the jaws of massive familiarization. *Acta Psychologica*, *130*(3), 241-250.

Ullsperger, M., Harsay, H. A., Wessel, J. R., & Ridderinkhof, K. R. (2010). Conscious perception of errors and its relation to the anterior insula. *Brain Structure and Function*, *214*(5-6), 629-643.

Urgesi, C., Calvo-Merino, B., Haggard, P., & Aglioti, S. M. (2007). Transcranial magnetic stimulation reveals two cortical pathways for visual body processing. *Journal of Neuroscience*, *27*(30), 8023-8030.

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.

Van der Veen, F. M., Nieuwenhuis, S., Crone, E. A., & Van der Molen, M. W. (2004). Cardiac and electro-cortical responses to performance feedback reflect different aspects of feedback processing. In M. Ullsperger & M. Falkenstein (Eds.), *Errors, conflicts, and the brain. Current opinions on performance monitoring.* (pp. 140–147). Leipzig: Max Plank Institute for Human Cognitive and Brain Sciences.

van Driel, J., Ridderinkhof, K. R., & Cohen, M. X. (2012). Not all errors are alike: theta and alpha EEG dynamics relate to differences in error-processing dynamics. *Journal of Neuroscience*, *32*(47), 16795-16806.

van Driel, J., Sligte, I. G., Linders, J., Elport, D., & Cohen, M. X. (2015). Frequency band-specific electrical brain stimulation modulates cognitive control processes. *PloS one*, *10*(9), e0138984.

van Elk, M., Bousardt, R., Bekkering, H., & van Schie, H. T. (2012). Using goal-and grip-related information for understanding the correctness of other’s actions: an ERP study. *PloS one*, *7*(5), e36450.

Van Overwalle, F., & Baetens, K. (2009). Understanding others' actions and goals by mirror and mentalizing systems: a meta-analysis. *Neuroimage*, *48*(3), 564-584.

van Schie, H. T., Mars, R. B., Coles, M. G., & Bekkering, H. (2004). Modulation of activity in medial frontal and motor cortices during error observation. *Nature neuroscience*, *7*(5), 549.

Varnum, M. E. W. (2013). What Are Lay Theories of Social Class? *PLoS ONE*, *8*(7). https://doi.org/10.1371/journal.pone.0070589

Varnum, M. E., Blais, C., & Brewer, G. A. (2016). Social class affects Mu-suppression during action observation. *Social Neuroscience*, *11*(4), 449-454.

Veniero, D., Vossen, A., Gross, J., & Thut, G. (2015). Lasting EEG/MEG aftereffects of rhythmic transcranial brain stimulation: level of control over oscillatory network activity. *Frontiers in cellular neuroscience*, *9*, 477.

Vossen, A., Gross, J., & Thut, G. (2015). Alpha power increase after transcranial alternating current stimulation at alpha frequency (α-tACS) reflects plastic changes rather than entrainment. *Brain stimulation*, *8*(3), 499-508.

Vosskuhl, J., Huster, R. J., & Herrmann, C. S. (2015). Increase in short-term memory capacity induced by down-regulating individual theta frequency via transcranial alternating current stimulation. *Frontiers in human neuroscience*, *9*, 257.

Wang, X. J. (2010). Neurophysiological and computational principles of cortical rhythms in cognition. *Physiological reviews*, *90*(3), 1195-1268.

Willer, R. (2009). Groups reward individual sacrifice: The status so- lution to the collective action problem. American Sociological Review, 74, 23–43. Winter,. *American Sociological Review*, *74*(Winter), 23–43.

Wyer, N. A. (2010). You never get a second chance to make a first (implicit) impression: The role of elaboration in the formation and revision of

Zaehle, T., Rach, S., & Herrmann, C. S. (2010). Transcranial alternating current stimulation enhances individual alpha activity in human EEG. *PloS one*, *5*(11), e13766.

Zaki, J., Davis, J. I., & Ochsner, K. N. (2012). Overlapping activity in anterior insula during interoception and emotional experience. *Neuroimage*, *62*(1), 493-499.

Zink, C. F., Tong, Y., Chen, Q., Bassett, D. S., Stein, J. L., & Meyer-Lindenberg, A. (2008). Know Your Place: Neural Processing of Social Hierarchy in Humans. *Neuron*, *58*(2), 273–283. https://doi.org/10.1016/j.neuron.2008.01.025

Appendix: Overview of publication status of chapters in the thesis.

Chapter number and title	Original text (not published before)	Submitted	Published
1. Introduction	X		
2. Modulation of preference for visual stimuli following competence-based social status primes.			Experimental Brain Research
3. Hierarchical Interactions: competence-based social status and implicit preference shape hand kinematic and synchrony in joint actions	X (in preparation)		
4. Autonomic correlates of performance monitoring during a status-inducing procedure	X (in preparation)		
5. Interim discussion on the effect of social status on affective evaluation, dyadic motor interactions and performance monitoring	X		
6. Theta tACS over the frontal midline modulates behavioural adjustment during human-avatar motor interactions	X (in preparation)		
7. Interim discussion on the effects of theta tACS over the midline on motor interactions	X		
8. General Discussion	X		