UNIVERSITY OF PADOVA

Department of General Psychology

Master Degree in Cognitive Neuroscience and Clinical Neuropsychology

Final dissertation

Mirror Neurons and Empathy: A Biomarker for the Complementary System

Supervisor
Professor: Luisa Sartori

Co-supervisor
Professor / PhD: Silvia Guerra

Candidate: **Marith Jessica Carolina Ekström**
Student ID number: **2015703**

Academic Year: 2019-2022

Mirror Neurons and Empathy:

A Biomarker for the Complementary System

CONTENTS

DEDICATION

I would like to dedicate this dissertation to my parents, for their support to help me pursue my education, with a special feeling of gratitude for their encouragement. I also dedicated this dissertation to my many friends who always cheered and supported me throughout the process. With gratefulness to all, thank you.

Synopses

The discovery of the mirror neuron system gave rise to many new paths within neuroscience, psychology, kinematics and philosophy. This neurological system helped foster a broader understanding of social interaction, as these neurons fire in action observation and action performance. To this day, it is identified that the mirror neuron system is related to action understanding, comprehension of other's intentions and the ability to recognise another person's mental state. Furthermore, a link between the mirror neuron system, empathy and prosocial behaviour is also well-established, whereas the complementary system enables us to understand and complete other individual's actions. Hence, the objective of this study was to assess the relationship between the mirror neurons system, trait empathy and the ADM muscle activation in a complementary action setting, which is strongly related to the grasping movement within these contexts. Results revealed a relationship between low empathic traits and muscle activation in non-social conditions, suggesting that individuals scoring low on empathy seem less willing to help other people in a complementary action interplay.

The mirror neurons were first discovered in the brains of macaque monkeys in the early 1990s, in Parma, Italy, where they were located in the premotor cortex, which is also called area F5 (Di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti, Fogassi, & Gallese, 2001). Since the breakthrough discovery 30 years ago, much attention has been directed to this neural system in scientific literature and popular media (Kilner & Lemon, 2013). Many different names have been used to describe it; "communicative neurons" (Pier Francesco Ferrari, Gallese, Rizzolatti, & Fogassi, 2003), "audio-visual neurons" (Keysers et al., 2003), "neurons of imitation" (Tchernichovski & Wallman, 2008), "peripersonal" and "extra-personal" neurons (Caggiano, Fogassi, Rizzolatti, Thier, & Casile, 2009), where they all stress communication, social behaviour or interaction of some kind. It is argued that this mirror neuron system evolved into a complex neural system in humans, facilitating action-understanding, intention and the emotional states of others (Gallese, Keysers, & Rizzolatti, 2004). Nevertheless, monkeys are not the only species where mirror neurons have been identified. Evidence of mirror neuron activity is also known in songbirds, where the cells fire when the animal sings and when it hears another bird sing (Keysers, 2009; Miller, 2008). Although, most research has dominantly been human-based after the discovery (Bonini, Rotunno, Arcuri, & Gallese, 2022), showing that the mirror neuron system involves premotor cortex, inferior parietal lobe and motor and somatosensory cortex in the human brain (Newman-Norlund, van Schie, van Zuijlen, & Bekkering, 2007). It is suggested that the human mirror neuron system is the neural basis for intention and action-understanding, as this system is engaged both when one performs an action as well as observing another person performing a similar motor act (Rizzolatti et al., 2001; Rizzolatti & Sinigaglia, 2016). Activation of the mirror neuron system reflects a perceptual aspect of action performed by another subject, where the system comprehends the observed action, recruiting the required neural network to carry out the same action as you would mirror someone in front of you (Bonini et al., 2022). Therefore, this complex imitative neuronal mechanism was agreed to be named *mirror neurons* (Di Pellegrino et al., 1992).

However, most of our real-time social interactions are not imitative actions, but complementary (Iacoboni, 2009a; Redcay & Warnell, 2018). Therefore, a large portion of the neuroimaging research on the mirror neuron system involves communicative or joint actions (Ciaramidaro, Becchio, Colle, Bara, & Walter, 2014; Kokal, Gazzola, & Keysers, 2009). Handing over something to someone, such as a glass of water, is an example of joint action (Newman-Norlund et al., 2007), where it a complementary action is required a to complete the person's action whom you interact with (Iacoboni et al., 2005). The human mirror neuron system has been much researched in correlation to the complementary system, comparing imitating and complementary action (Newman-Norlund et al., 2007). Without this action understanding, social formation would be impossible (Rizzolatti & Craighero, 2004). Congruently, it is argued that the mirror neuron system is more active during complementary settings than in imitative actions context (Newman-Norlund et al., 2007). Hence, this indicates the mirror neuron system plays a fundamental role in action-understanding and comprehension of others' internal action.

Correspondingly, it is proposed that the mirror neuron system is heavily involved in decoding the emotional states of others (Jackson, Meltzoff, & Decety, 2005; Lawrence et al., 2006). It is also argued that empathy has a strong link to imitation (Iacoboni, 2009a). Findings show that imitation of facial emotional expression is linked to activation of brain areas interconnected with the mirror neuron system, along with the insula and amygdala, which is the emotional centre of the brain (Pfeifer, Iacoboni, Mazziotta, & Dapretto, 2008). Empathy is the ability to understand and accurately perceive the internal mental state experienced by another person (Lockwood, 2016; Vachon, Lynam, & Johnson, 2014).

Taken together, based on neuroscientific research, it is evident that mirror neurons react to elicitation of physical effects as well as an emotional reaction within the observer. That is, the mirror neurons acknowledge action-understanding and recognise intention and empathy. Hence, the neuronal relationship between action understanding and emotions within a complementary setting is clear.

CHAPTER 1

MIRROR NEURONS

The mirror neuron system appears to be the neurophysiological basis of the self/other understanding, as well as the intention of actions (Gallese et al., 2004). Perhaps, the reason why mirror neurons have gotten much attention is that they stand out from other neurons with the intriguing component that they are activated in both action execution and action observation (Fogassi et al., 2005; Rizzolatti & Craighero, 2004; Rizzolatti et al., 1996). An everyday life example of the active mirror neuron system would be seeing someone fall and hurt themselves; you might notice your body shudder or tremble a bit, making you feel uneasy. The system “mirrors” and empathises with what you see around you, embedded in a neurological system. This system is believed to be developed to empathises and understand the surroundings around us (Iacoboni, 2009a; Kilner & Lemon, 2013), since the mirror neurons fire when observing an action as it would be experienced by oneself (Heyes, 2010). It enables us to understand what actions the subject in front of us is carrying out.

Relatedly, communication primarily derives from gestural communication and arguably evolved into the language we have today. Gestures are fundamental in language (Prieur, Barbu, Blois-Heulin, & Lemasson, 2020). Neurobiological and behavioural research show that words and gestures are part of the same neurological system, as it is processed within the same brain area (Fröhlich, Sievers, Townsend, Gruber, & van Schaik, 2019; Gentilucci & Volta, 2008). The mirror neuron system provides new insights into the long puzzling question of the human communication and language evolution. In a finger-lifting experiment conducted by Iacoboni et al. (2001), it was found that the brain areas of the mirror neuron system were correlated to imitative actions. The regions activated during imitation, were anatomical homologous to the areas of the monkey brain. But one region in the frontal brain overlapped with the classical language area; Broca's area (Broadmann area 44), which is a premotor region (Heiser, Iacoboni, Maeda, Marcus, & Mazziotta, 2003). Thus, indicating that this area is essential for movement imitation, even for non-language tasks. Congruently, a TMS study conducted by Iacoboni (2007) showed that stimulation to Broca's area interfered with imitation, whereas every time interference occurred in the region, a performance reduction occurred. Furthermore, arm gestures are also shown to be correlated to language comprehension, to the extent that it can be used as a linguistic signal, the area responsible for both speech and gesture is Broca´s area (Gentilucci & Volta, 2008). Demonstrating that imitation and language exists in the same brain region.

Both behavioural and evolutionary theories have been trying to explore why this neural phenomenon exists and the underlying influence of correlated behaviours. It is evolutionary important for primates to understand the intention of another individual (Giacomo & Laila, 2004), and it is fundamental for social organisms and to associate and stick to the group (Brewer, 2007; Eisenberger & Lieberman, 2004; Over & Carpenter, 2013). Together, the benefits of these behaviours are critical for survival, where understanding your surroundings is crucial to cooperate with others. Mirror neurons provide new insight into the social nature of humans, as these neurons become activated as if one is watching oneself reflected by a mirror (Iacoboni, 2009b). Actions are almost always associated with some intention, either specific or general goals of the subject (Riva, Mantovani, Waterworth, & Waterworth, 2015). We can immediately recognise the actions of others, which is due to this higher-order cognition involvement, where the same machinery is involved the brain when we observe an action as when we perform the same actions (Iacoboni, 2011). Additionally, neuroscientific research shows that if the mirror neurons do not work to the full capacity, individuals have problems with social behaviours, such as action understanding and intention (Iacoboni, 2009b), which shines a light on the fundamental importance of this system with respect to social interactions.

Taken together, investigating the neuro-physiological mechanisms of these mirror behaviours at a neural and single-cell level, neuroscientific research has agreed that this system plays a fundamental role in social interaction, where mirror neurons become active when we watch somebody else making the same actions.

MIRROR NEURONS IN PRIMATES

"Monkey see, monkey do"

Mirror neurons were first discovered in monkeys, localised in the rostral division of the ventral premotor cortex and inferior parietal cortex of macaque monkeys (Di Pellegrino et al., 1992; Gallese et al., 1996). This area, also called F5, particularly controls hand and mouth movements, which are goal directed action movements (Rizzolatti & Arbib, 1998). To understand the motor activity, the experimenters tracked the neural activity using single-cell recordings of the monkeys' cortical neurons. To the experimenters surprise, these neurons would fire both when the monkey carried out an action and when the monkey passively observed the same action performed by the experimenter, such as picking up a peanut (Di Pellegrino et al., 1992). To confirm this, the experiment was repeated, using other food items. Remarkably, the neurons responded in the same order, as the neurons discharged when the animal carried out the goal-directed action such as grasping the item and also by simply observing the same action, even though the monkey was completely still (Baars & Gage, 2010; Di Pellegrino et al., 1992). Thus, the neuron empirically "mirrors" behaviours, just as the animal was itself acting.

Interestingly, these neurons were not like other neurons, as they would fire in both conditions. Which demonstrated that these cells are involved in grasping, observation and comprehension of actions (Castiello, 2005; Sheets-Johnstone, 2012; Tchernichovski & Wallman, 2008). These neurons play a more abstract role than other neurons, where they aim for meaning in the action context (Sartori, Betti, & Castiello, 2013). This complex imitation might be part of the developmental underpin of human language (Arbib, 2011). Additionally, mirror neurons are found in the insula of the primate's brain, which is part of the brain's emotional centre (Ehrenfeld, 2011). Findings show that this mechanism converts observed emotions as one's own (Fabbri-Destro & Rizzolatti, 2008). Collectively, recognition of other's emotional states is coded on a neural level.

MIRROR NEURONS IN HUMANS

Since the discovery of mirror neurons in the monkey brain, many scholars have become interested in the possibilities of the mirror neuron existence in humans (Baars & Gage, 2010). Today, there is plenty of evidence that mirror neurons also exist in humans, and their role in action understanding and intentions of others through matching actions (Pier F Ferrari & Coudé, 2018; Keysers & Gazzola, 2010; Praszkier, 2016; Redcay & Warnell, 2018). Transcranial magnetic stimulation (TMS) studies confirmed action observation causing subliminal activation of corresponding cortio-spinal pathways within the motor system (Sartori & Castiello, 2013). The mirror neuron system is considered to be part of a brain area called Broca´s area in humans (Ogura et al., 2014), which is made up of two areas, Broadmann area 44 and 45 and is located in the posterior inferior frontal gyrus in the left hemisphere (Sprung-Much, Eichert, Nolan, & Petrides, 2022). This area is found to be crucial in language processing and speech production (Heiser et al., 2003). It is specified that Broadman area 44 is involved in motor-related processes; in a functional magnetic resonance imagining (fMRI) study, Fadiga et al. (2006) demonstrated activation in this area while participants observed meaningful shadow hand gestures resembling animals. Additional scholars found neural activation in both movement production and observation in Broadmann area 44 (Lametti & Mattar, 2006). Congruently, neural activation was also discovered during the execution of grasping (Fadiga & Craighero, 2006). The grasping action is a fundamental core action for humans and occurs all the time in everyday life situations. Essentially when it comes to manipulating and communicating with our environment (Iacoboni et al., 2005). The F5 area in monkeys is similar to the human Broca´s area (Miall, 2003). Showing that the mirror neuron system is the neural correlate that codes goal-directed actions, in relation to language comprehension and gestures.

However, mirror neurons are somewhat limited to what we know ((Rizzolatti & Fogassi, 2007). To demonstrate this, a study was conducted on professional ballet dancers and non-ballet dancers, where they screened videos of ballet movements. Results disclose that ballet dancers showed significantly stronger mirror neurons activation in the premotor and parietal brain areas, and the STS region when watching the videos (Calvo-Merino, Glaser, Grèzes, Passingham, & Haggard, 2005; Shimada, 2022). A similar study was done on professional piano players, observing piano playing scenes. These individuals also showed greater activation in these areas compared to their control group (Haslinger et al., 2005). Similar studies investigated action-recognition and execution, where the participants observed a dog barking, a human talking and a monkey chattering (Bärthlein, 2021; Rizzolatti & Fogassi, 2007). Results showed activation in the human condition, less activation in the monkey condition and no activation at all in the dog condition, as dog barking cannot be performed by us humans (Arbib, 2005). Although showing images of the same animals biting a piece of food, an activation was present, regardless of animal, as this motor act is known to humans and can be performed (Buccino et al., 2004). Moreover, it is found that the mirror neurons system shows less activation during objectless action observation where the action was mimicked than to the identical movement including an object of interest (Holmes & Calmels, 2011). Together, this indicates that the mirror neurons are somewhat restricted to what humans know how to perform, as the observed action activates the mirror neuron system only when it is known to motor control of the individual. Indicating mirror neurons in actions that are observed are somewhat connected to the observers' motor repertoire and familiarity.

Additionally, links between the hormone oxytocin release and the mirror neuron system have been found to be important in social interactions (Ho, MacDonald, & Swain, 2014). EEG studies support this by clarifying that oxytocin significantly effects interpersonal coordination and relations (Mu, Guo, & Han, 2016; Patin, Scheele, & Hurlemann, 2017). Oxytocin is a nine-amino-acid peptide (nonapeptide) which is produced in the nuclei of the hypothalamus, released by the pituitary gland into the bloodstream, involving limbic areas such as the amygdala and hippocampus and brain regions associated with basic survival relevant behaviours (S. Kim & Strathearn, 2016). Furthermore, research shows that oxytocin improves mentalizing and theory of mind. This hormone heightens the capability to empathize in social and emotional cognitions (Ebert & Brüne, 2017; Schneider-Hassloff et al., 2016). Mentalizing is the ability to understand and interpret behaviours and the mental state of oneself as well as others (Freeman, 2016). Additional findings show an increase in oxytocin levels heighten the ability to empathize in participants with low empathy scores (Feeser et al., 2015). Together, oxytocin plays an essential role in social interactions, mentalizing and empathy.

Correspondingly, there is solid evidence that the areas in the human brain, such as the insula and the anterior cingulate that are involved in the integration and control of emotions (Pier Francesco Ferrari & Rizzolatti, 2014; Gallese et al., 2004; Singer et al., 2004). These areas, which is included in the mirror neuron system, play a fundamental role in action interpretation of others, action understanding, and sensory-motor transformation linked to imitation (Molnar-Szakacs & Overy, 2006). Collectively, the human mirror neuron system evolved into a comprehensive neural system, fostering the ability of action understanding, comprehension of action intentions, thoughts and feelings of other people (Rizzolatti, 2005).

MOTOR NEURONS

Hand movements have long been a focus of interest for many scholars within neuroscience (Castiello, 2005). Mirror neurons are classified as a separate class of motor neurons, as these neurons are activated both when individuals observe an action and perform a specific motor act (Rizzolatti & Craighero, 2004; Rodríguez, Cheeran, Koch, Hortobágyi, & Fernandez-del-Olmo, 2014). In motor skill learning, observation and execution of any action are critical to provide the capacity to accurately produce and reproduce voluntary actions (Williams & Gribble, 2012). As action understanding is fundamentally important for motor learning the mirror neurons system plays a big part in this process (Heyes & Catmur, 2022). It is even argued that the mirror neurons are formed through the course of human development, much like the learning process of Pavlovian conditioning (Heyes, 2010; Schultz & Dickinson, 2000).

The two major types of mirror neurons that are important to address are; *strictly congruent* and *broadly congruent* (Kosonogov, 2012). The strictly congruent neurons fire from an observed action that is the same as the coded action from a motor standpoint. That is, these type of mirror neurons are activated during a “whole-hand-grip” (WHG) action movement, which is used in grasping actions. They will also fire during the observation of a whole-grip action performed by someone else (Kilner & Lemon, 2013). The broadly congruent neurons, responsible for two-thirds of the mirror neuron population, respond to non-identical observed and executed actions and are essential for the flexibility of social interactions, especially complementary actions (Newman-Norlund et al., 2007). While social interactions include mirroring a person in front of oneself, the broadly congruent neurons play an essential role in predicting the actions of others. They then assist in the formation of the most suitable complementary action (Thompson, Bird, & Catmur, 2019). Moreover, a meta-analysis by Kilner and Lemon (2013) shows that mirror neurons are present in ventral and dorsal premotor cortices, primary motor cortex and other regions of the parietal cortex. This demonstrates that the mirror neurons system is present during the whole motor system.

However, mirror neurons are not only motor. Vision must also be considered (Perez, Sanguineti, Morerio, & Murino, 2020). The mirror neuron system has been studied mainly in two areas of interest; one is the motor system involved in language and speech production, and the other one is these motor regions responsible for coding and execution of action through observation (Ehrenfeld, 2011; Hickok, 2010; Meister, Wilson, Deblieck, Wu, & Iacoboni, 2007). The system can also be seen as an audio-visual motor unity embodied in two systems. In contrast, these neurons are activated when actions are performed and to the auditory stimuli of the motor act (Aziz-Zadeh, Iacoboni, Zaidel, Wilson, & Mazziotta, 2004; Fogassi & Ferrari, 2007; Kohler et al., 2002). Correspondingly, the neurotransmitter oxytocin is found to be released in activation of the primary motor cortex while observing another person's action grip (S. D. Muthukumaraswamy & B. W. Johnson, 2004; Perry et al., 2010), whereas changes in mu rhythm occurred in action observation of precision grip (S. D. Muthukumaraswamy & B. Johnson, 2004). Hence, the mirror neurons system is explained as the neurophysiological basis for visuo-motor and motor-visual in relation to motor learning processes. So to say, a bi-directional motor-related construct (Rodríguez et al., 2014), demonstrating the neurological mechanism in action understanding and motor learning.

IMITATION

Human social interaction has long been a phenomenon of interest. As the French phenomenological philosopher, Maurice Merleau-Ponty wrote in his book *Phenomenology of Perception* in the early 1900's; "it is as if the other person's intention inhabited my body and mine his" (Merleau-Ponty, 2013). Applying these motor-related movements to social contexts, a concept called *chameleon effect* may aid to an explanation of human social interactions (White, 2021), where individuals tend to imitate each other, such as mimicry of posture or facial expression even unconsciously to match their social environment (Yoon & Tennie, 2010). While there are personal differences among individuals, the tendency to imitate each other exists and comes natural to all humans (Byrne, 2005). Some neuroimaging research indicates that Broca´s area has a significant role in the imitation, comprehension and interpretation of gestures such as motor goal and intention (Buccino et al., 2013; Gentilucci, Bernardis, Crisi, & Volta, 2006).

Furthermore, it has been claimed that social exclusion shares somatosensory representations with physical pain (Block, Heathcote, & Burnett Heyes, 2018). Physical pain is defined as an unpleasant sensation that indicates actual or potential damage to body tissue or structure (Scholz et al., 2019). In contrast, social pain is the distressing experience associated with the perception of actual or potential psychological detachment from a social group or close others (Naomi, 2012). Probing from an evolutionary perspective, a separation from the group or caregiver often means a threat to the species' survival (Eisenberger & Lieberman, 2004). Social connection for a mammal species is equally crucial for our survival as the sensation of physical pain, in the forms of an alarm system telling us that something is wrong (Naomi, 2012). In order to prevent this separation, social rejection shares somatosensory representations with physical pain. Equally, the social bond resources are as crucial for survival as the mammal species are born entirely relying on caregivers to provide nourishment and protection. This collaborative neural network also helps with challenges such as hunting and predator defence, as well as increased access to mating (Chen, Williams, Fitness, & Newton, 2008; Eisenberger & Lieberman, 2004). Imitation in humans indicates that Brodmann area 44 has mirror neuron capacities where actions involving hand and arm movements (Baars & Gage, 2010; Iacoboni et al., 2005). Learning by imitation is the basis of human culture (Giacomo & Laila, 2004), where mirror neurons play a crucial role in explaining the social aspect of cognition through action understanding. These neurons are argued to be developed partly for this reason, as imitation neurons (Iacoboni, 2009b). This neurological mechanism is fundamental in both action understanding and imitation (Iacoboni et al., 2005). In addition to this, it is shown that when people start imitating each other, they start liking each other more, it is a powerful way where people connect with each other (Hansen, 2019; Iacoboni, 2009b). Returning to the oxytocin, it is shown to be associated with physiological and pathological functions such as heart rate, indicating it is a primal instinct. This hormone is also referred to as the “love hormone” or “bonding hormone”, due to the association between the release of oxytocin to reproduction and social bonding (Magon & Kalra, 2011; Neumann, 2009; Parmar & Malik, 2017). Hence, the mirror neuron system might provide a way to explain the human capacity to learn (Giacomo & Laila, 2004), indicating that it is fundamental in humans to imitate and tail individuals around.

Furthermore, neuroscience scholar highlights the neural process of imitation in human infants (Marshall & Meltzoff, 2014; Meltzoff et al., 2018), where it has been found that infants as young as 18 hours display imitation actions, such as mouth and face movements (Meltzoff & Moore, 1983, 1994). Emphasising the primal drive to understand and communicate with individuals in the form of motor imitations (Smith, 2006). From an evolutionary standpoint, human infants imitate in a social survival circuit matter, as it serves as the root of socio-culture evolution (LeDoux, 2012). Interestingly, human infants are not only imitating others, but they also have the awareness and recognition that they are being imitated (Meltzoff, Brooks, Shon, & Rao, 2010; Saby, Marshall, & Meltzoff, 2012). Stressing that also awareness of the environment is something fundamental in humans.

An experiment called “ the tea party” conducted by Iacoboni (2008), explains individual’s capacity to understand the intention of others. This fMRI study, had two conditions; one scene with a full cup of tea, milk and cookies, following a hand approaching the arrangement. The other scene was with empty cups, spilt milk and no cookies, following a hand approaching. In short, the experiment revealed that participants could distinguish between these two conditions. The first context is suggested to be a drinking or eating intention using a "whole-hand-grip" (WGH) action, whereas the second context suggest a clean-up action using a "precision-grip". Results disclose a significant fMRI increase in the posterior part of the inferior frontal gyrus in the drinking context (Iacoboni, 2011). This effect could arguably be because drinking is a more of a primal action than cleaning up. Therefore, the prediction was that the classical mirror neuron system in the frontal lobe was at higher activation before the tea party, where drinking was involved, in correlation to after the tea party where cleaning actions would occur (Baars & Gage, 2010).

Some studies suggest that the more people imitate one another, the more people tend to emphasise with one another (Hansen, 2019; Iacoboni, 2009b). To imitate and form an identity without the group is fundamentally crucial for social individuals, it is a powerful way to people connect, which enables us to gain an understanding of our environment and predict future consequences (Gallese, 2003; Iacoboni, 2009a). As imitation, the sincerest form of survival, as evolution has formed a system where the brain can gist the mental state of others, where imitating internal emotional states of others is part of a survival circuit to form a bond between individuals and the species around them (Hansen, 2019). Thus, the mirror neuron system seems to be designed as the neurological basis of social interactions (Iacoboni, 2009b).

THE COMPLEMENTARY SYSTEM

The meaning of collaboration and the underlying effect to explain it has long been an area of interest in evolutionary biology (Darwin, 1859). It has been argued that natural selection favours mirror neurons of action understanding and comprehension of goal-related behaviours

(Heyes, 2010), mainly through prosocial behaviours (Decety, Bartal, Uzefovsky, & Knafo-Noam, 2016). As stated earlier, it is clear that the act of imitation is a social act and to mirror actions formed by another subject is merely fundamental in humans. Nevertheless, it is not always appropriate to mimic each other all the time (Newman-Norlund et al., 2007), as interactions usually require complementary behaviours (Sartori, Betti, et al., 2013). Take an example of a baby crying. It would not be appropriate to just lay beside the baby and cry with it. It would be more apt to do something to comfort the baby. Actions that are formed to complete or correspond to another's subject's action are behaviours that are part of the complementary system (Iacoboni, 2009b; Newman-Norlund et al., 2007). From an evolutionary outlook, this system plays a role in a complex remapping from one situation to another in social interactions where the understanding of other individuals emotions are essential (Oberman & Ramachandran, 2008). Think of this system as a flexible coding scheme of action, where more complex, cooperative actions take play (Iacoboni, 2009a). As the action is observed and mapped into the observer's motor system, a complex switch from the imitative inclination to a more context-appropriate action response happens (Sartori, Betti, et al., 2013). Supporting evidence shows that in an fMRI study, the blood-oxygen-level-dependant (BOLD) signal in the right inferior frontal gyrus and bilateral inferior parietal lobes was greater during the complementary actions in comparison to imitative actions (Newman-Norlund et al., 2007). Together, the mirror neuron system may be essential for complementary actions, such as social situations, in coupling action observation to action execution and in human learning structure by imitation.

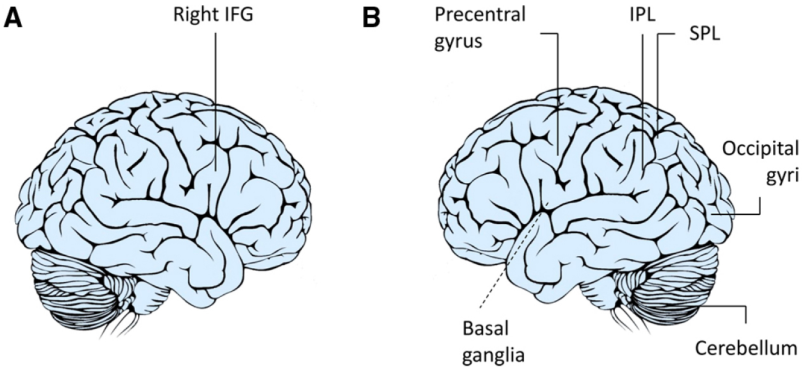


Figure 1. Neuroimaging studies of complementary actions, indicating the right inferior frontal gyrus (IFG) which is involved in imitation and complementary actions **(A)**. Additionally, areas such as inferior parietal lobule (IPL), superior parietal lobule (SPL), precentral gyrus, basal ganglia, middle and temporal occipital gyri and cerebellum are involved in coordination of actions in a complementary carried out action (Sartori & Betti, 2015).

CHAPTER 2

EMPATHY

Evidence show that the same brain regions overlap when individuals feel their own emotions and also the observed emotions of others (E. Kim et al., 2009). After the discovery of mirror neurons, the understanding of social interaction changed dramatically (Hamilton, 2013). It is claimed that the mirror neuron system is the humans can empathize with other individuals (Lamm & Majdandžić, 2015). Mirror neurons are connected to empathy; as Preston and De Waal (2002) state that empathy is the fundamental phenomenon of mirroring oneself in other individuals. Studies provide evidence that high social and emotional information processing is associated the processing of social skills (Oberman, Pineda, & Ramachandran, 2007), empathy and theory of mind (Ebert & Brüne, 2017; Lamm, Rütgen, & Wagner, 2019). Empathy crucial in our social and everyday lives (Preston & De Waal, 2002). It allows us to comprehend, understand and share other people's affective and sensory states, including pain (Decety et al., 2016; Preston & De Waal, 2002). Neuroscience literature divides empathy into two distinct components; affective empathy and cognitive empathy, as they are regionally and functionally specific. Cognitive empathy is a more intellectual understanding of another person's perspective, whilst affective empathy is the ability to experience the emotional state of another. (Shamay-Tsoory, Aharon-Peretz, & Perry, 2009; Shamay-Tsoory, Tomer, Goldsher, Berger, & Aharon-Peretz, 2004).

Hansen (2019) emphasises that emotions are evolutionary-orientated goals and derive from survival strategies, as empathy utilises the process of the information of affective and cognitive mental states (Preston & De Waal, 2002). Some even argue that humans are weird for empathy (Iacoboni, 2009a; Wittgenstein, 1965), which indicates that empathy is essential for social behaviour (Lamm et al., 2019). Interestingly, individuals scoring higher in empathy showed greater activation in areas correlated to pain, rostral anterior cingulate cortex, anterior insula, lateral cerebellum and brainstem while watching their partner in pain (Singer et al., 2004). Fascinating, these areas are activated when anticipating and experiencing pain (Decety et al., 2016), as the amygdala and the anterior insula are the brain regions facilitating the perception of emotions (Tippett et al., 2018). A wide range of literature points out that the core neural network involved in empathy for pain, anterior insula (AI) and anterior midcingulate cortex (MCC), sometimes also referred to as dorsal anterior cingulate cortex (dACC) (Bzdok et al., 2012; Lamm, Decety, & Singer, 2011; Timmers et al., 2018). Congruently, it has been shown that empathy develops earlier than mentalising, since the limbic structures are developed and mature earlier (Singer, 2006). Together, humans are evolutionary wired for empathy as our specie's biology is formed for to be social animals (Iacoboni, 2009b).

COGNITIVE EMPATHY

To “put yourself in someone else’s shoes”, explains the aspect of cognitive empathy, which is to see another person’s perspective and to engage in a mental representation without necessarily involving any emotions (Spaulding, 2017). This type of empathy can be viewed as more of a rational, logical empathy than getting any emotions evolved (Villadangos Fernández, Errasti Pérez, Amigo Vázquez, Jolliffe, & García Cueto, 2016). Pineda and Hecht (2009) conclude that the mirroring system is involves in judgement relating to emotions and person-object interactions. To understand and to read intentions of others around utilising a conceptual system (Bzdok et al., 2012), a term called ‘theory of mind’, refers to the ability to understand another person’s mental state (Premack & Woodruff, 1978), doing so by ascribing the mental state of other people (cite). This can also be referred to as *mentalising,* where another individual’s ability to understand the mental state of others as well as oneself, such as perception and experiences (Fu et al., 2022). Congruently, the brain region superior temporal sulcus (STS) has been discovered to be the core structure for the theory of mind and related mental tasks (Koster-Hale & Saxe, 2013; Otsuka, Osaka, Ikeda, & Osaka, 2009). This region is also significantly activated in human imitation behaviours, which share the mirror network basis of imitation, observation and execution (Molenberghs, Brander, Mattingley, & Cunnington, 2010). Cognitive empathy is considered a top-down process which the subject tries with a cognitive effort to represent the state of another person (Goldie, 1999). In everyday language, this phenomenon is sometimes discussed as *perspective-taking.* However, perspective-taking differs in how it includes both emotional and non-emotional.

Furthermore, an intriguing study done on teenagers in Singapore, investigated empathy and cyberbullying reveals that boys and girls who scored low on cognitive empathy scored higher on cyberbullying (Ang & Goh, 2010). Additionally, it is found that the neurotransmitter Oxytocin hormone improves the mentalising ability in humans (Domes, Heinrichs, Michel, Berger, & Herpertz, 2007). As stated earlier, oxytocin is related to the mirror neuron system in social interactions (Ho et al., 2014). Together, it is clear that cognitive empathy, mentalising, theory of mind and oxytocin release are all correlated to the mirror neuron system. The mirror neuron system seem to simply be designed for simulation of other individuals actions and to empathise with the surroundings (Iacoboni, 2009a).

AFFECTIVE EMPATHY

Affective empathy is explained as sharing the emotional state of another through the observed experience of others, such as joy or pain (Zaki & Ochsner, 2012). It can also be seen as more altruistic comportment of behaviour (Knafo & Israel, 2012). Some scholars even argue that this emotional experience is an automatic reaction, an impulsive convergence to the emotional state of others (Blakemore, Bristow, Bird, Frith, & Ward, 2005; Singer et al., 2004). Supporting research suggests that emotional empathy involves the motor and somatosensory system via thalamic-cortical modulations (Behrens et al., 2003). “I feel your pain” is a well-used phrase, as different languages across the globe use numerous pain-related words to describe emotional pain (Macdonald & Leary, 2005). This linguistic overlay found in common phrases like these might not be so far off from the truth, as this experience has been identified even neurologically related to social exclusion or rejection (Eisenberger, 2012). This painful experience due to loss or social exclusion might not merely be metaphorical, as it has been developed to be a fundamental evolutionary necessity to socially connect (Naomi, 2012). Imitating or sharing emotions and pain we never felt is called a “shared circuit” (Danziger, Faillenot, & Peyron, 2009).

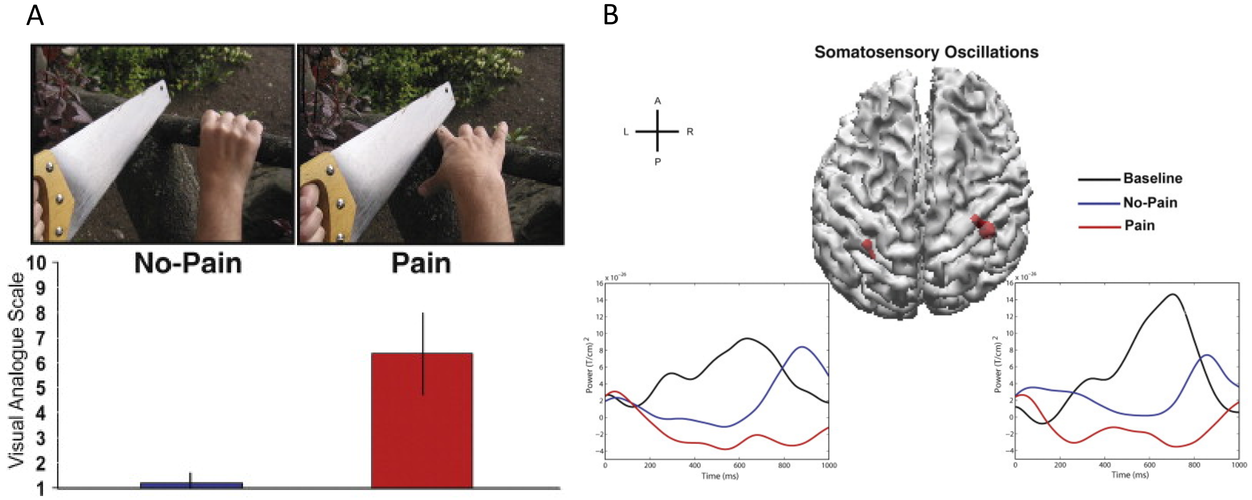


Figure 2. A study done on observed anticipated pain. The image on the left show the picture that the participants viewed **(A)**. The image to the right show an activation of the somatosensory oscillations which is associated with empathy for pain **(B)**. This study highlights the shared pain circuit of anticipated or observed pain and actual pain, as they share the same neural circuitry (Cheng, Yang, Lin, Lee, & Decety, 2008).

Additionally, it has been claimed that social exclusion shares somatosensory representations with physical pain (Block et al., 2018). Physical pain is the unpleasant sensation that indicates actual or potential damage to body tissue or structure (Scholz et al., 2019). In contrast, social pain is the distressing experience associated with perceiving actual or potential psychological detachment from a social group or close others (Naomi, 2012). The physical experience of pain is often subdivided into two components; the *sensory* component, which represents the discriminative aspect such as location or intensity and the *affective* component, which speaks for the unpleasant aspect such as distress or agony of pain (K. Davis & Panksepp, 2011). From an evolutionary perspective, this separation from the group or caregiver can threaten your survival (Eisenberger & Lieberman, 2004). Social connection for a mammal species is equally crucial for survival as the sensation of physical pain in the form of an alarm system telling us that something is fundamentally wrong (Naomi, 2012). Hence, social rejection shares somatosensory representations with physical pain to prevent this separation.

Returning to oxytocin, one prominent aspect of this neurotransmitter is that it produces a feeling of bonding in us when released, to focus on the person in front of us (Hansen, 2019). Scholars argue that this oxytocin release is due to avoid being excluded from the group, as social ties reduce morbidity and mortality (Berkman & Glass, 2000; Holt-Lunstad, 2021). Although, correlated studies show that oxytocin improves and enhances metalizing, the study implies that oxytocin levels strongly depend on social-cognitive skills such as empathy (Feeser et al., 2015). Hence, an investigation of this phenomenon considering affective empathy and the mirror neuron system may reveal something more evolutionary about human´s primary social connections (Naomi, 2012).

PROSOCIAL BEHAVIOUR

The meaning of collaboration, and the underlying effect to explain it, has long been an area of interest in evolutionary biology (Darwin, 1859). Natural selection favours mirror neurons in action understanding (Heyes, 2010), mainly through prosocial behaviours (Decety et al., 2016). Prosocial behaviour can be explained as an altruistic form of action performed to comfort another person's needs or improve their wellbeing (Decety et al., 2016). A transcranial magnetic stimulation (TMS) study shows that mirror neurons are driven by social reciprocity. They had their participants watch videos of an actor pouring coffee with a whole-hand-grip movement or pouring sugar into a cup with a precision grip hand movement, while recording their motor evoked-potential (MEP) (Sartori, Bucchioni, & Castiello, 2013). Interestingly, the participants showed a larger MEP when the actor in the video stretched towards the cup closest to the participant (Sartori, Bucchioni, et al., 2013). Concluding, the MEP response matched the socially appropriate response. That is, where the participant would pick the cup up and offer it to the actor, which could be performed action carried out in a live setting.

Empathy has been considered a driver of prosocial behaviour (Decety et al., 2016), although cooperation is a primary aspect of primates (Ohtsuki, Hauert, Lieberman, & Nowak, 2006). From a neurobiological point of view, oxytocin creates a feeling of bonding between people and that the individual is focusing on the person in front of you (Hansen, 2019), which shines a light on the neurological underpinning of this collaboration phenomenon, as it is associated with social behaviours such as social recognition (Choleris et al., 2003; Winslow & Insel, 2002), maternal attachment (Carter & Keverne, 2002; Strathearn, 2011) and social bonding (Hansen, 2019). This aids to an understanding of prosocial behaviours and how it is fundamentally rooted in us to bond and cooperating with people. As mentioned, mirror neurons are correlated to empathy and understanding of other's emotions and actions (Corradini & Antonietti, 2013), evidence highlights extremes of the distribution of some psychopathological disorders; very low levels or impaired empathy is often seen in autism spectrum disorder (Baron-Cohen & Wheelwright, 2004; Viding, 2004). Without mirror neurons, it is impossible to understand nor empathise with other people, making these individuals socially disconnected and withdrawn (Misra, 2014; Neta & Varanda, 2016). Supporting evidence show that impaired brain function involving mirror neurons has been identified in individuals with psychopathic personality traits (Mier et al., 2014), explaining why these individuals lack emotional sensitivity and empathy (Cummings, 2015). Additionally, as mentioned, social and physical pain are experiences crucial for our survival (Iannetti & Mouraux, 2011). The social bond resources are as crucial for survival as the mammal species are born entirely relying on caregivers to provide nourishment and protection.

Together, these marks confirm mirror neuron’s play in empathy and understanding of others. Hurlemann, Scheele, Maier, and Schultz (2017) indicate that oxytocin drives prosocial behaviour in favouring social bonds. It has been claimed this hormonal release is located in the brain’s reward system and serves some attachment qualities (Domes et al., 2007), demonstrating the neurological basis of social bonding. This collaborative network also helps with challenges such as hunting and predator defence and increased access to reproduce (Chen et al., 2008; Eisenberger & Lieberman, 2004). This emotional connection to others done by our brain cells is part of what makes us human (Pier F Ferrari & Coudé, 2018).

NEURAL CORRELATES

It has been proven through brain imaging studies that overlapping brain activation is evident when individuals feel their own emotions and when observing the same emotion of another individual. Two cortical regions anterior insula (AI) and the anterior cingulate cortex (ACC) showed activation (De Vignemont & Singer, 2006; Olsson & Ochsner, 2008), especially when it comes to pain (Bruneau, Pluta, & Saxe, 2012). This indicates a shared neuronal network, considering the mirror neuron systems appraisal. Probing from an evolutionary angle, pain equals fear, and fear is the most relevant feeling to our survival (Hansen, 2019). Empathy has a profound implication for survival, being able to tell if a person around is kind or not trustworthy (Clay, Palagi, & de Waal, 2018). Additionally, an highly empathic individual might challenge raised emotional states during social interaction (Gallese, 2007; Gallese et al., 2004). As indicated, pain comes with a strong emotional affective component, where the amygdala plays a crucial role in the emotional responses to pain (Butler, Oliver, Fadel, & Wilson, 2018). Consistently, further finding’s show similar results that networks of brain regions are associated with the affective component of physical pain; the dACC and the AI was also found to underlie the feeling of social rejection (Kross, Berman, Mischel, Smith, & Wager, 2011).

Similarly, activation overlap of the SII and PI was also found in the same study where participants were shown a social pain stimulus, pictures of their ex-partner from an unwanted breakup and a minor psychical pain condition such as a heat stimulus. These findings suggest that the experience of social pain may very well involve the somatosensory cortex (Kross et al., 2011). Furthermore, the amygdala is also shown to be a vital constituter of the relationship between the sensation of pain and negative affective such as fear (Bornhövd et al., 2002). Supporting research by Wang, Braun, and Enck (2017), found that the medial PFC was involved in regulatory functions of negative emotions/affect via the connections to the ACC and the amygdala.

As conveyed earlier, it is well-defined that observation and anticipation of another person's pain do prompt some emotional empathic response (Lamm et al., 2011). Even so, this emotional state automatically activates the autonomic and somatic responses during the observation (Preston & De Waal, 2002). In addition to the ACC, the right ventral prefrontal cortex (RVPFC) has also been found in an fMRI analysis to be activated in social exclusion compared to inclusion in a virtual ball-tossing experiment conducted by Eisenberger (2012). Chunlin and Jinglong (2012) findings show that in addition to those mentioned above as pain-related neural regions, the RVPFC is associated with regulating painful or negative affective experiences. Congruent research indicates that greater activity in the RVPFC is related to self-reported social distress during social rejection and reduced activity in the dACC (Eisenberger & Lieberman, 2004). Taken together, it seems possible that the RVPFC plays a role in a downregulation in the activity of the dACC and that the ACC is involved in distressing and emotional pain rather than the somatic sensory component of physical pain. Demonstrating the experience of pain is tangible when anticipating another person's pain.

CHAPTER 3

As emphasised, neuroimaging and neurophysiological studies provide evidence that the mirror neuron system is correlated to imitation, complementary actions, empathy and pro-social behaviour. Action observation in humans is relational and interpersonal, between the agent who is carrying out the action and the observer (Gallese, 2001). How humans coordinate complementary actions in a complex social situation is much on behalf of the mirror neuron system, where comprehension of one's own and other people's actions, intentions and emotions are gathered on a neurological basis.

Following this line of reasoning, empathic traits in individuals should be a biomarker for the complementary system and muscle activation within the mirror neuron system. The whole-hand-grip muscle activation including the MRI muscle, has not yet been studied compared to empathy and the complementary system, in relation to the mirror neuron system. Within this area of interest, there is a lack of studies identifying neural substrates responsible for complementary system correlated to empathy. Hence, the present study, is specified to fill the yet not empirically investigated area. This study will investigate the likely correlation between empathy, pro-social behaviour, MRI muscle activation and the complementary system.

The associative hypothesis is consistent with research showing that the mirror neurons system is considerably linked with anticipation of other's emotions, action understanding and complementary motor actions. Furthermore, the link between MRI muscle activation and the mirror neuron system is clear. Therefore, this study hypothesises that empathy is a biomarker for the complementary system, that is the more altruistic an individual is, the higher motor-evoked potential (MEP) in the MRI muscle, in correlation to the mirror neuron system.

CHAPTER 4

EXPERIMENT

The aim of this present experiment was to investigate a potential correlation and relationship between the activation of Pro-Social Behaviour and the Complementary Motor System. That is, to examine if the system underlying complementary actions can be considered a biological marker for pro-social behaviour. Thus, the main purpose of this experimental research was to understand if there are any differences in the activation of the complementary motor system associated with the amplitude of empathic behaviour, as previous research confirmed the correlation between pro-social behaviour and empathic traits (Lamm et al., 2019).

Hence, we hypothesise is that individuals with a strong amplitude of pro-social personality traits would have greater activation of the complementary motor system. With this means, it would be reasonable to attribute the complementary motor system as a biomarker for pro-social behaviour, as it would give a possible explanation of the differences in activation of the system based on high and low trait empathy. In this account, we assessed the corticospinal excitability (CE) modulations while participants were watching an actress on a screen performing a series of movements with her right hand, including social and non-social movements. These stimulations of movements by the actor produced imitative and complementary action activation in the observer. To that end, the Interpersonal Reactivity Index (IRI) (Keaton, 2017) and two scales (i.e., mrc3 and mrc5) of the Mental Representation of

Caregiving Scale (MRC) (Reizer & Mikulincer, 2007) questionnaires were used to investigate the relationship between complementary system activation and sensitivity to pro-sociality.

MATERIALS AND METHODS

Instrument preparation

Four sintered Ag/AgCI bipolar and one monopolar surface electrodes (15kΩ. 1.5 mm touch-proof safety socket) was connected with a sensory area (9 mm diameter) to an isolate, portable ExG input box linked to the main EMG amplifier via a twin fibre optic cable for signal transmission (Professional BrainAmp ExG MR, Munich, Germany). The raw myograpfic signals were band-pass filtered (20 Hz – 1 kHz), amplified before being digitalised (5 KHz sampling rate), and stored on a computer for offline analysis. A script for individual resting motor threshold (rMT) assessment was managed. Presentation of video stimuli and TMS stimulation synchronised with EMG registration by E-Prime presentation software running on a PC with a monitor (resolution 1,280 x 1,024 pixels), which was frequently refreshed. 75 Hz, background luminance of 0.5 cd/m2 was set at eye level. Any trails in which any EMG activity greater than 100 µV was present in the 100 ms window preceding the TMS pulse were discarded to prevent contamination of MEP measurements by background EMG activity. EMG data were collected for 300 ms after the MTS pulse by using Brain Vision Recorder software (Brain Products GmbH, Munich, Germany). Attaining an animation effect by selecting a series of signal frames (30 milliseconds each, 30 fpc) and the first and last frames lasting, respectively, 500 and 1,000 milliseconds.

Participants

Forty healthy participants, twenty-eight females and twelve males, aged 19-46 (mean ± SD age 23.4 ± 4.7 years for females and 23.8 ± 1.3 for males) took part in this experiment. Only right-handed participants with normal or corrected-to-normal vision were recruited. using the Standard Inventory questionnaire for handedness (Briggs & Nebes, 1975). All candidates were screened for TMS exclusion criteria for neurological, psychiatric and medical problems (Rossi, Hallett, Rossini, Pascual-Leone, & Group, 2009; E. M. Wassermann, 1998). Excluding subjects with higher than normal seizure risk (based on personal / family history of epilepsy, neurosurgery, brain injury) or receiving neuroactive medication since the principal known health risk of TMS in seizure induction. Also, excluding pregnant women, as the risks of TMS to an unborn fetus are unknown.

The participants were given basic information about the study and signed the written informed consent forms before the experiment. The candidates were asked to sit in the ergonomic armchair provided, to sit back and relax. The participant's arm was positioned on a full arm support and their head fixed on a headrest. The eye distance from the screen should be determined on the basis of the size of the stimulus presentation. All metal objects (earrings, necklaces, etc.) and objects sensitive to magnetic fields (mobile phones, credit cards) was removed from all the participants. This is due to the rapid rate of change of current in the coil is capable of inducing a change in a magnetic field. Ultimately, the candidates were instructed to observe the stimuli carefully and maintain a good attention level.

Experimental stimuli

The stimuli were two digitally recorded video clips showing an actress performing a series of movements with her right hand interacting with objects. One of the video clips was used for the social condition and the other for the non-social condition. The video setting of both of the clips consisted of two cups; one placed near the actress and the other more distant, closer to the observer´s point of view) along with a teaspoon full of sugar. The actress's face was cut out from the screen frame to prevent the observer from being influenced by the actress's intentions from her eye movements. Eliminate distracting elements and conditions unrelated to the experiment to avoid potential interference with the aimed experimental manipulation.

The videos were presented in randomised order for each participant. Each video was 7.2 seconds long and consisted of 25 frames per second. A 10-second resting interval between videos was inserted, with a message during the first five seconds of the rest intervals urging the participant to remain as still and relaxed as possible. Once the message disappears, arrange for a fixation cross to appear for the remaining five seconds. A white fixation cross on a black background was presented in the last 5 seconds of the rest interval to keep the participant's gaze and attention at the centre of the screen. This is to maintain a neutral position at the beginning of each video.

1. The Social condition: the actress grasped the teaspoon full of sugar with a precision grip (PG), lifted it and poured the content into the most proximal cup and then the actress continued the movement towards the cup that was strategically placed close to the observer, which was placed outside her reach. The fact that the actress cannot reach the cup close to the observer is an important segment in which it should elicit the participant to perform an approaching movement towards the cup to complete the movement of the actress. This means performing a complementary action by the observer towards the observed gesture through grasping the cup and performing a

Whole Hand Grasping (WHG) movement. Subsequently, this social condition will lead to a shift from an imitative setting to a complementary one. (See figure 3.)

2. The Non-Social/Individual condition: the actress grasped the teaspoon full of sugar with a precision grip (PG), lifted it, poured the content into the most proximal cup and then returned to the starting position. In this condition, the participants were requested to activate an imitative movement. (See figure 4.)

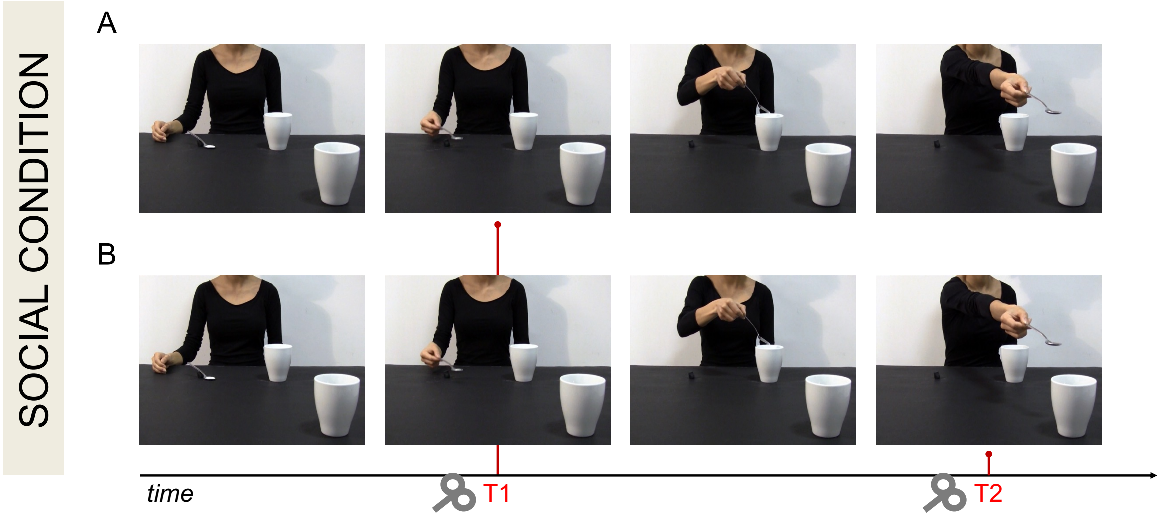


Figure 3. Social cognition where the actor is initiating a social act to elicit a complementary action from the participants. The T1 condition

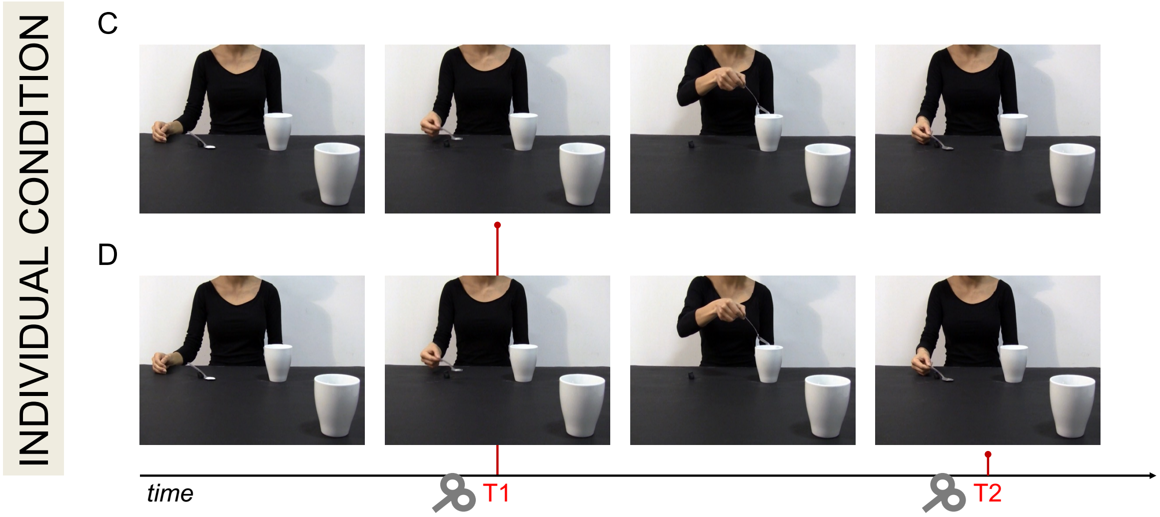


Figure 4. Non-Social cognition where the actor is not initiating any social contact.

Procedure

Participants were recruited to fill out two questionnaires online, such as the Interpersonal Reactive Index (IRI) (M. H. Davis, 1980; Keaton, 2017) and the scale mrc3 (e.g., perceived ability to help effectively) and mrc5 (e.g., altruistic reasons for helping) of the Mental Representation of Caregiving Scale (MRC) (Reizer & Mikulincer, 2007). Participants were tested individually in a single experimental session lasting for one hour and 30 minutes. Participants were asked to sit in a comfortable armchair in front of a 19° computer screen (i.e., 280 x 1024 pixels resolution, refresh rate of 75 Hz and background brightness of 0.5 cd / m2) at a distance of 80 cm. The participant's right arm was positioned on a pillow and head on in a fixed headrest. Participants were requested to stay as fixed and calm as possible during the whole experiment session. TMS-induced motor-evoked potentials (MEPs) were acquired from the participant's right dorsal interosseous (FDI) and abductor digiti minimi (ADM) muscles of the right hand. A single TMS pulse was released during each video presentation within two different timings; T1 and T2. The T1 resembles the delivery of the electromagnetic pulse when the actress performs a precision grip grasping the spoon (figure. 1 & 2). A total of 90 MEPs (i.e., 2 muscles x 2 conditions x 15 repetitions) were recorded for each participant. Each participant's baseline corticospinal excitability (CE) was assessed by acquiring 15 MEPs at the beginning and end of the experiment block. This was assessed while the participants passively watched a white fixation cross on a black background on the computer screen. The average MEP amplitude recorded during the two baseline periods (i.e., 30 MEPs in total) was used to set each individual's baseline for the data normalisation procedure. The fixation cross presented before each trial ensured that the participants always started the trail by observing the videos from a natural position. The order of the video clips was randomised across participants. Finally, at the end of the experiment, a brief interview was implemented, where the participants were asked to express their experiences and impression of watching the videos. Prepare the participants with detailed information about the experiment design at the end of the session. Acknowledgement for participation in the experiment, each individual received a stipend (13€).

DATA RECORDINGS

TMS Stimulation and MEP Recording

The electrodes were positioned over the right abductor digiti minimi (ADM) and the first dorsal interosseous (FDI) muscles by palpation during maximum voluntary muscle activation. The skin was cleaned thoroughly on and around the electrode locations. An abrasive skin prepping gel was applied to the entire site by using a clean gauze pad, it was then rubbed into the skin lightly, and any excess was removed with the gauze pad. Two surface electrodes were placed over each muscle and attached to the skin using self-adhering pads, containing a small amount of water-soluble EEG conductive paste. A belly-tendon montage was performed by placing the active electrodes over the muscle bellies of the right ADM and FDI. The reference electrodes were placed over the ipsilateral metacarpophalangeal joint. A single ground electrode containing conductive paste was then attached to the participant’s left wrist. The electrodes were connected to the standard input of the ExG input box. The impendence values were then checked (if the event is above the threshold (>5Ω), prepare and clean the skin again).

A single-pulse TMS was delivered to the scalp overlying the left primary motor cortex (M1) corresponding to the hand region using a 70mm figure-of-eight coil connected to a Magstim 200 stimulator (Magstim Co., Whitland, UK). It was ensured that the handle was pointing laterally and caudally to induce a posterior-anterior brain current through the precentral gyrus (Sommer & Paulus, 2008), in correspondence with the optimal scalp position (OSP) where MEPs with maximal amplitude were recorded simultaneously from FDI and ADM muscles from the participants right hand, with the maximum stimulation intensity. These muscles were chosen because of their activation differences during the observation of precision-grip (PG) and whole-hand-grasping (WHG) (Betti, Zani, Guerra, Castiello, & Sartori, 2018). The ADM is only activated for WHG, whereas FDI is modulated during both types of grasping (Gangitano, Mottaghy, & Pascual-Leone, 2001). The aspect of this is crucial for the manipulation since we expect a specific muscular activation for the ADM muscle when the video clip shows the hand reaching for the mug closer in respect to the participant's prospective (i.e., WHG). However, not in manipulation of the teaspoon, whereas the control muscle (FDI) should be activated in both cases.

The coil was placed 45° angle with respect to the interhemispheric fissure and positioned perpendicularly with respect to the central sulcus: the lowest motor threshold is achieved when the induced electric current in the brain is flowing approximately perpendicular to the central sulcus (Brasil-Neto et al., 1992; Mills, Boniface, & Schubert, 1992). During the experiment session, the coil was continuously checked by the experimenters to maintain a constant positioning with respect to the marked OPS. The OPS corresponding to the motor M1 was identified by moving 3 cm to the left and 1 cm forward from the vertex, which was obtained by crossing the distance between the nasion (i.e., median craniometrics point located on the naso-frontal suture) and the inion (i.e., top of the external occipital protuberance of the occipital lobe) with the median between the preauricular dimples (bony depression, immediately in front of the tragus). The OSP was then marked on a tight-fitting cap worn by the participant. Later the "individual resting motor threshold" (rMT) was determined. To determine rMT for each participant in the OPS, the minimum stimulation intensity necessary was detected to produce reliable MEPs (≥50 µV peak-to-peak amplitude) in a relaxed muscle in five out of ten consecutive trials. The rMT ranged from 30 to 60% (mean 60%; SD = 5.77) of the maximum stimulation output. The stimulation intensity was kept at a fixed value, 120% of the rMT during the entire recording session, to record a clear and stable MEP signal. EMG data were collected for 300 ms after the TMS pulse was delivered by using Brain Vision Recorder software (Brain Products GmbH, Munich, Germany).

Once located, the optimal scalp position (OPS) over pars opercularis of the inferior frontal gyrus, stimulate slightly suprathreshold intensity on the OSP invariability and produce the highest levels of MEP activity from the contralateral ADM and FDI muscles. A neuro-navigation system was used to maintain constant coil-positioning throughout the experiment and prevent any bias due to small movements of the participant's head during data collection. Three-dimensional online information with regard to the initial and actual coil placements was utilised to allow for the exact repositioning of the TMS coil in real-time during the experimental session, if and when needed. The marker positions were recorded using an optical digitiser in order to reproduce them on a screen. A bandpass filter (20 Hz-1 kHz) was used to record the raw myographic signals. The amplification digitised the signals (5 kHz sampling rate) and stored them in the computer for offline analysis. Ten MEPs were recorded while the participant passively watched a white-coloured fixation cross on a black background on the computer screen at the beginning of the experimental session. Ten more MEP was recorded at the end of the experimental session.

EMG data was recorded from the right ADM and FDI muscles after the TMS pulse at one of the four possible time points in the social condition (figure. 1), that is:

a) When the model’s hand first makes contact with the sugar spoon (T1),

b) When the model’s hand reaches the second cup, nearest to the camera (T2).

EMG data was recorded from the right ADM and FDI muscles after the TMS pulse at one of the four possible time points in the individual/non-social condition (figure. 2), that is:

a) When the model’s hand first makes contact with the sugar spoon (T1),

b) When the model finishes pouring sugar into the subject’s cup and returns to the starting point (T2).

Note: A basic TMS stimulator is composed of a power source, an energy storage element and a high-power switch precisely controlled by a processor that accepts control input from the equipment operator. The fundamental operating mechanism of a TMS simulator is to create a changing magnetic field that can induce a current in an adjacent conductive material (such as cortical tissue). Tissue stimulation is provoked by inducing a current of sufficient density in the tissue, which is proportional to the time rate of change of the magnetic flux density (E. Wassermann et al., 2008).

At low but supra-threshold stimulation intensities, the TMS-induced current excites preferentially axons of interneurons which project directly or indirectly on corticospinal neurons. Both inhibitory and excitatory synapses were activated, but at such stimulation intensities, the net effect is an excitatory post-synaptic potential in corticospinal neurons.

Figure 5. The image displays the TMS devices and equipment room which was used in the experiment. The ergonomic chair for the participants, positioned in the right distance to the computer screen. The pillows were aid for headrest and the pillow for resting the hand upon. To the right, the Transcranial Magnetic Stimulation (TMS) machine is positioned.

QUESTIONNAIRES

Interpersonal Reactivity Index (IRI) (M. H. Davis, 1980; Robinson, 2021).

IRI is a self-report questionnaire consisting of 28 items on a 5-point Likert scale (e.g. *1* would be "never true for me" to *5* "always true for me"). IRI is a widely used multidimensional measure of emphatic traits (e.g., effective and cognitive empathy) for adolescents and adults. The questionnaire consists of 4 subscales: (i) Perspective taking, which refers to people's ability to see another person's point of view (e.g., "When I´m upset at someone, I usually try to "put myself in his shoes" for a while"); (ii) Fantasy, which refers to the tendency of people to strongly empathise with characters in books, games or movies (e.g., "After seeing a play or a movie, I have felt as though I was one of the characters"); (iii) Empathic concern, which refers to the person's tendency to express compassion and concern for another person (e.g., "Other people's misfortune do not usually disturb me a great deal"); (iiii) Personal distress, which refers to the level of anxiety and person's ability to cope with a distressing situation experienced by the individual, or witnessing a painful/negative situation experienced by another individual (e.g., "I tend to lose control during emergencies").

Mental Representation of Caregiving Scale (MRC) (Reizer & Mikulincer, 2007).

MRC is a self-report questionnaire composed of five subscales measuring different aspects of the caregiving construct. In other words, the perceived ability to recognise the need of others, give effective help and evaluate others as worthy of help. Particularly, the participants were administrated only subscales mrc3 (e.g., perceived ability to give effective help) and mrc5 (e.g., altruistic motivations to help). Examples of the sample items: "I know I can help people in need" and "I feel that helping people in need is wonderful", for the mrc3 and mrc5 respectively.

DATA ANALYSES

The data was analysed offline, using Brain Analyzer software (Brain Products GmbH, Munich, Germany) for EMG data, R-Studio (a programming language for statistical computing and graphs) and the software SPSS (Statistical Package for Social Science) for statistical analysis. The motor evoked potential (MEP) peak-to-peak amplitude (mV) for the ADM and FDI muscles was determined as a measure of participants' CE. The MEP amplitude that deviated more than two standard deviations (SD) from the mean were considered outliers (<5%) of each experimental condition and trials where muscle pre-activation was recorded were excluded from the data analyses. Ratios were computed using the participant's individual baseline value (MEP ratio = MEP obtained/ MEP baseline) (Lepage, Tremblay, & Théoret, 2010). This comparison was made to determine the modulations in MEPs amplitudes due to the experimental manipulation and not to other influences. For each candidate and for each experimental condition (i.e., “social” and “non-social”) the mean absolute MEP amplitude was subjected to a normalising procedure by relating the MEP values to a correlating physiological baseline, separately for each muscle. A t-test was carried out for ADM activations compared to the two experimental conditions (i.e., “social” and “non-social”). The T1 and T2 stimulation times of the ADM muscles in the “social” and “non-social” conditions were also considered. The data analysis was confined to the ADM muscle only since it is the most involved in complementary actions. This grasping action implies a whole-handed-grip (WHG) involving the ADM muscle. In this study, the little finger muscle (ADM) is expected to be sensitive to the experimental manipulation, because it is mainly involved during WHG actions.

The delta ADM was calculated from the difference in ADM muscle activation in the different experimental conditions (social and non-social). The delta ADM represent an index of the differences of cortico-spinal activity in the “social” condition (i.e., complementary motor response activation) and “non-social” condition (i.e., imitative motor response activations), indicating the degree of activation of complementary motor system in the participants. Pearson’s R statistical index which calculated any linear relationship between statistical variables was used to calculate the correlation between physiological and empathy data. The significant threshold was set at $p < 0.05$ for all statistical analyses.

RESULTS

The repeated-measure ANOVA was carried out on the ADM muscle revealed a significant interaction between Condition and Time window ($p=0.054$). In particular, MEPs for ADM muscle were higher for the Social compared to the Non-Social condition, during the first time-window (p = 0.022; see Fig.6 and Fig.7). In fact, during the second-time window, MEPs were significantly decreased with respect to T_1 ($p < 0.001$). A statistically significant correlation was found between MRC5 and ADM muscle at T_2 (r= 0,330). In particular, the Linear Mixer Models revealed a statistically significant increase of ADM MEP amplitude at T_2 when the participants with Low MRC5 ratings observed a Non-social action, compared to when they observed a Social action (t = -2.253; p = 0.0262; see Fig.6 and Fig.7).

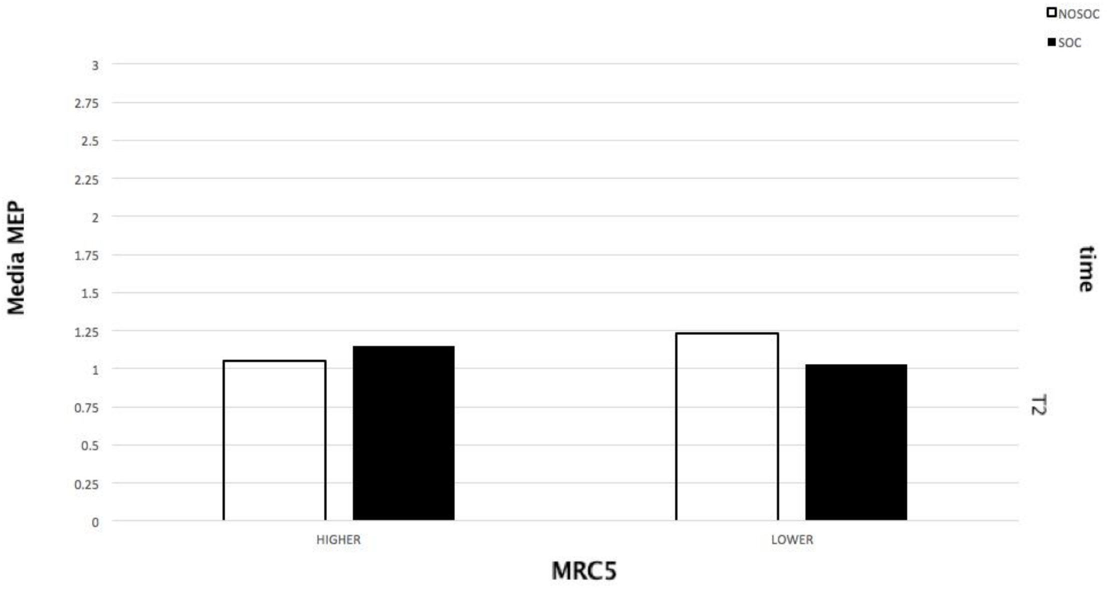


Figure 6. Median MEP in correlation to ADM muscle activation in two conditions (i.e., “Social” and “Non-social” conditions) for the two groups low and high responders within the MRC-5. Significance level *p < 0.05.

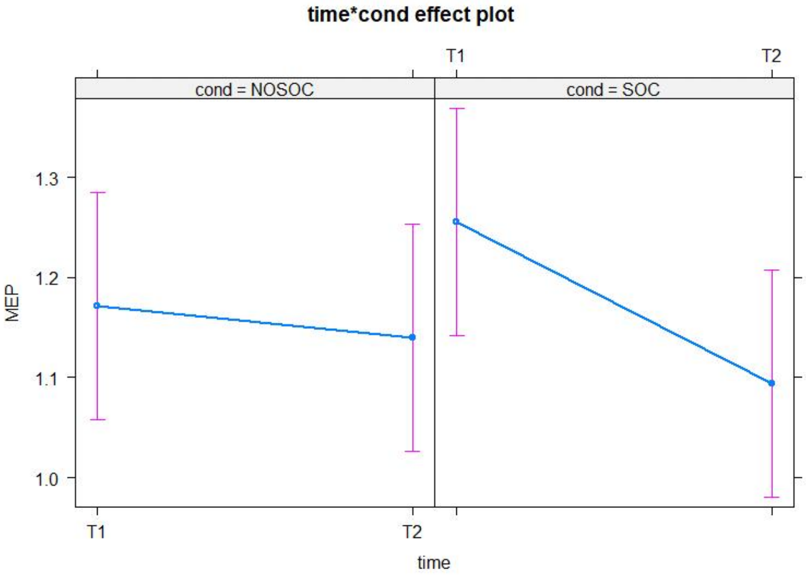
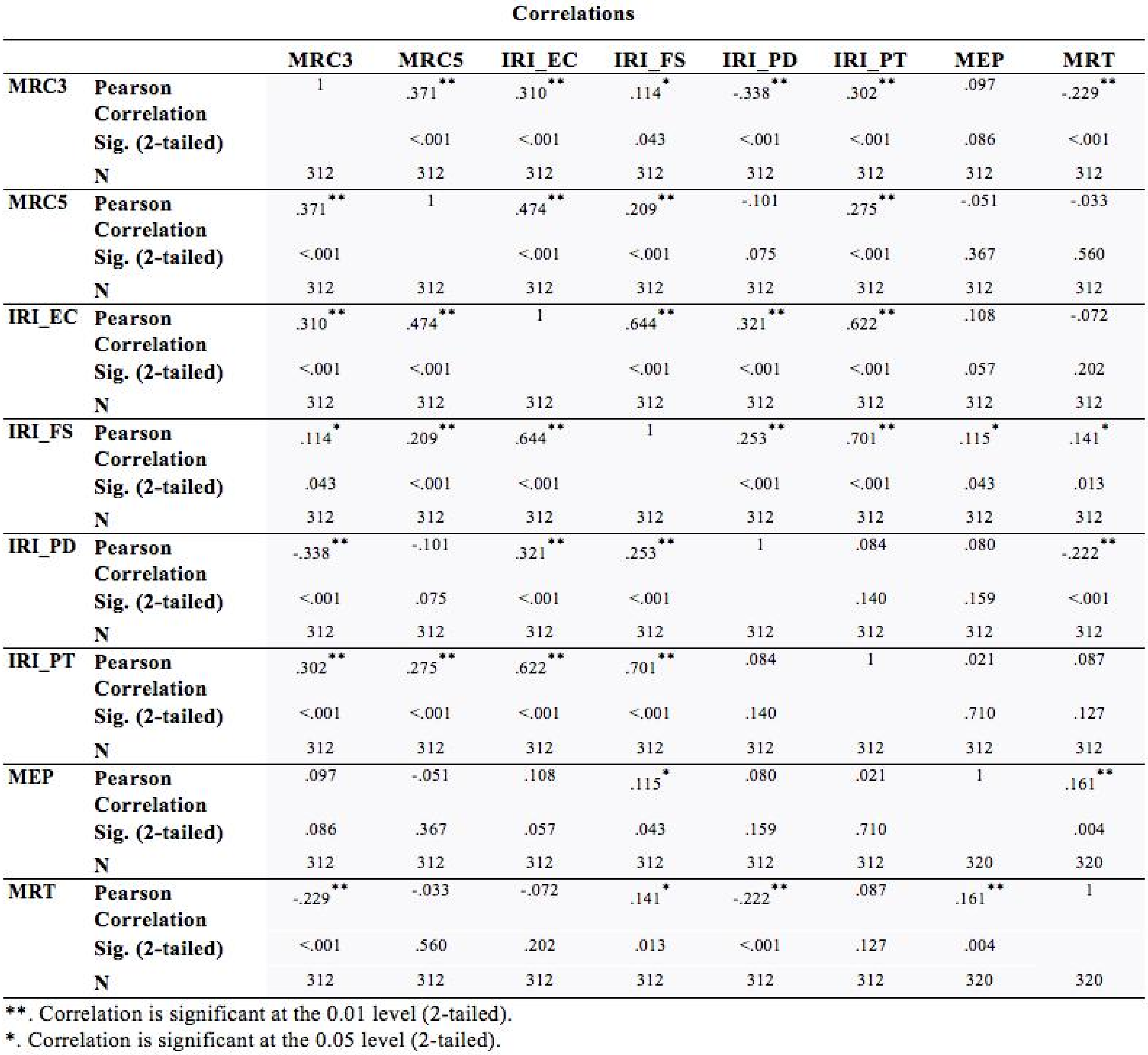


Figure 7. The figure shows the MEP value of ADM muscle activation in the two conditions; “non-social” to the left and “social” to the right, for T1 and T2. Indicate a significant level *p < 0.05.

Correlations

Results reveal a significant correlation between the Delta ADM and the fifth scale of Mental Representation of Caregiving Scale (MRC5; r= .01; p < .05), which investigates altruistic motivations to help. Correlations with the scales in the Interpersonal Reactive Index; personal distress (IRI_EC), perspective taking (IRI_PD), fantasy (IRI_FS) and the Mental Representation of Caregiving Test; perceived ability to help effectively (MRC3) were not significant (see Table 1.).



Correlations

		MRC3	MRC5	IRI_EC	IRI_FS	IRI_PD	IRI_PT	MEP	MRT
MRC3	**Pearson Correlation**	1	.371**	.310**	.114*	-.338**	.302**	.097	-.229**
	Sig. (2-tailed)		<.001	<.001	.043	<.001	<.001	.086	<.001
	N	312	312	312	312	312	312	312	312
MRC5	**Pearson Correlation**	.371**	1	.474**	.209**	-.101	.275**	-.051	-.033
	Sig. (2-tailed)	<.001		<.001	<.001	.075	<.001	.367	.560
	N	312	312	312	312	312	312	312	312
IRI_EC	**Pearson Correlation**	.310**	.474**	1	.644**	.321**	.622**	.108	-.072
	Sig. (2-tailed)	<.001	<.001		<.001	<.001	<.001	.057	.202
	N	312	312	312	312	312	312	312	312
IRI_FS	**Pearson Correlation**	.114*	.209**	.644**	1	.253**	.701**	.115*	.141*
	Sig. (2-tailed)	.043	<.001	<.001		<.001	<.001	.043	.013
	N	312	312	312	312	312	312	312	312
IRI_PD	**Pearson Correlation**	-.338**	-.101	.321**	.253**	1	.084	.080	-.222**
	Sig. (2-tailed)	<.001	.075	<.001	<.001		.140	.159	<.001
	N	312	312	312	312	312	312	312	312
IRI_PT	**Pearson Correlation**	.302**	.275**	.622**	.701**	.084	1	.021	.087
	Sig. (2-tailed)	<.001	<.001	<.001	<.001	.140		.710	.127
	N	312	312	312	312	312	312	312	312
MEP	**Pearson Correlation**	.097	-.051	.108	.115*	.080	.021	1	.161**
	Sig. (2-tailed)	.086	.367	.057	.043	.159	.710		.004
	N	312	312	312	312	312	312	320	320
MRT	**Pearson Correlation**	-.229**	-.033	-.072	.141*	-.222**	.087	.161**	1
	Sig. (2-tailed)	<.001	.560	.202	.013	<.001	.127	.004	
	N	312	312	312	312	312	312	320	320

**. Correlation is significant at the 0.01 level (2-tailed).
*. Correlation is significant at the 0.05 level (2-tailed).

Table 1. Correlation between Delta ADM and subscales

CHAPTER 5

DISCUSSION

The discovery of the mirror neuron system helped to gain a broader understanding of social interaction and action comprehension. However, the outcome of this research has provided new insight into interpersonal relationships and social settings, from a neurological investigation within action understanding through the mirror neuron system in correlation to empathy and prosocial behaviours. A wide range of behavioural and neuroscientific studies has supported evidence that a correlation exists between empathy and the mirror neuron system, and the link between the complementary system and the mirror neurons. With this taken into account, it implies that the human mirror neuron system is a critical component for the ability to understand actions, planning of actions and coordination of movements as response actions in a social situation in a highly flexible manner. Scholars agree that neural activity of brain regions correlated to the mirror neuron system is correlated to action observation and action performance (S. D. Muthukumaraswamy & B. Johnson, 2004; S. D. Muthukumaraswamy & B. W. Johnson, 2004). It is also evident that the mirror neuron system plays an integral role in facilitating empathy and pro-social behaviour.

Following that line of reasoning, the hypothesis of this study was to see if there was a correlation between empathic traits and the complementary system using muscle activation examinations. This study revealed muscle activation in the ADM muscle was higher for the Social compared to the Non-Social conditions during the first-time interval (T1). These results might be due to anticipating observed actions and mirror-effect such as imitation of the observed action.

Interestingly, a significant correlation was found between MRC-5 and the ADM muscle at the second-time interval (T2), in which participants with a lower score of MRC-5 rating observed a Non-social action in comparison to when they observed a Social action, which might be due to inhibition in second time interval (T2). As the MRC-5 measures altruistic motivations to help, this might imply the less altruistic an individual is, the less willing the person is to help.

The scientific and sociological relevance of this study shines a light on the understanding of action comprehension and how empathy and pro-social behaviour might influence social settings, gaining new social values of interactions and collective societal environments. Whichever could be applied to decision making, in the form of understanding intentions, and it might also be applied to occupational settings and relationship constellations. Building on this line of reasoning, social interactions in correlation to empathy could also be applied to reciprocity which is a mutual dependence of exchange and is used to explain prosocial behaviour among strangers (von Bieberstein, Essl, & Friedrich, 2021). Reciprocity is an essential element in social interaction is strongly liked to empathy. Hence, empathic traits play a crucial role in the complementary system in correlation to interpersonal interactions in everyday life.

Limitations to be addressed in this study are; using other types of questionnaires measuring empathy may be considered in future research, such as Toronto Empathy Questionnaire or Empathy Quotient (Muncer & Ling, 2006; Spreng*, McKinnon*, Mar, & Levine, 2009). As empathy is a broad phenomenon with a vast pool of surveys, choosing other scales might lead to different results. Another limitation of this study is covid-19 restrictions; the obligation of facemasks is known to impact individual's emotional recognition and trust attribution (Marini, Ansani, Paglieri, Caruana, & Viola, 2021). This is a direct effect on the altruistic motives within people to help other individuals, leading to inhibition of the willingness to help others. Last, the recognisable of the small sample is considered, as this study might not gain generalisability. Although, power-statistics were used to minimise this limitation factor.

CONCLUSION

In conclusion, it is well-established that the mirror neuron system has a strong link to action understanding, imitation and action intentions in social, as these neurons fire in action observation and action performance. Moreover, the link between the mirror neuron system, empathy and prosocial behaviour is also well-known. As most of the social interactions are mainly based on complementary action, the mirror neuron system plays an essential role in understanding another’s action. The system also assists in comprehending of forming the correct response-action to a complementary action in social settings. The present study assessed the relationship between trait empathy and ADM muscle activation within two conditions “social” and “non-social” conditions. The ADM muscle is strongly related to whole-hand-grip movement, which is frequently used in complementary action contexts. Higher muscle activation in participants scoring high in empathy was predicted in the social condition, which specifies high motivation to help others. An example from the questionnaire MRC-5 which examines empathic trait is “I´m good at recognising other person’s need and feelings, even when they are different from mine” represent appraisal of others as worthy of help (Reizer & Mikulincer, 2007).

The results revealed a significant interaction between conditions and time intervals with respect to the ADM during the second-time interval (T2). The motor evoked potentials (MEPs) were significantly decreased in the T1 intervals. The result show that there is a significant correlation between the social condition and MRC5 lower score individuals. Furthermore, a significant correlation was found between MRC-5 and muscle at T2, as the participants with a low score in MRC-5 observed the non-social actions, compared to when they observed a social action. As this scale measures the altruistic motivations to help, these results reveal a correlation between empathy and muscle activation in complementary action settings. Taken together, findings indicate that individuals scoring low on empathy seem less willing to help other people in a complementary action interplay, suggesting that trait empathy can be used as a biomarker for the complementary system in regard to the mirror neuron system.

References

Ang, R. P., & Goh, D. H. (2010). Cyberbullying among adolescents: The role of affective and cognitive empathy, and gender. *Child Psychiatry & Human Development, 41*(4), 387-397.

Arbib, M. A. (2005). From monkey-like action recognition to human language: An evolutionary framework for neurolinguistics. *Behavioral and brain sciences, 28*(2), 105-124.

Arbib, M. A. (2011). From mirror neurons to complex imitation in the evolution of language and tool use. *Annual Review of Anthropology, 40*, 257-273.

Aziz-Zadeh, L., Iacoboni, M., Zaidel, E., Wilson, S., & Mazziotta, J. (2004). Left hemisphere motor facilitation in response to manual action sounds. *European journal of neuroscience, 19*(9), 2609-2612.

Baars, B. J., & Gage, N. M. (2010). *Cognition, brain, and consciousness: Introduction to cognitive neuroscience*: Academic Press.

Baron-Cohen, S., & Wheelwright, S. (2004). The empathy quotient: an investigation of adults with Asperger syndrome or high functioning autism, and normal sex differences. *Journal of autism and developmental disorders, 34*(2), 163-175.

Bärthlein, J. (2021). *"Feeling into"and moral imagination: how the expression of empathy varies across different Corona-related dilemmas.* University of Twente.

Behrens, T. E., Johansen-Berg, H., Woolrich, M., Smith, S., Wheeler-Kingshott, C., Boulby, P., . . . Ciccarelli, O. (2003). Non-invasive mapping of connections between human thalamus and cortex using diffusion imaging. *Nature neuroscience, 6*(7), 750-757.

Berkman, L. F., & Glass, T. (2000). Social integration, social networks, social support, and health. *Social epidemiology, 1*(6), 137-173.

Betti, S., Zani, G., Guerra, S., Castiello, U., & Sartori, L. (2018). Reach-to-grasp movements: a multimodal techniques study. *Frontiers in psychology, 9*, 990.

Blakemore, S.-J., Bristow, D., Bird, G., Frith, C., & Ward, J. (2005). Somatosensory activations during the observation of touch and a case of vision–touch synaesthesia. *Brain, 128*(7), 1571-1583.

Block, P., Heathcote, L. C., & Burnett Heyes, S. (2018). Social interaction and pain: An arctic expedition. *Social science & medicine (1982), 196*, 47-55. doi:10.1016/j.socscimed.2017.10.028

Bonini, L., Rotunno, C., Arcuri, E., & Gallese, V. (2022). Mirror neurons 30 years later: implications and applications. *Trends in cognitive sciences*.

Bornhövd, K., Quante, M., Glauche, V., Bromm, B., Weiller, C., & Büchel, C. (2002). Painful stimuli evoke different stimulus-response functions in the amygdala, prefrontal, insula and somatosensory cortex: a single-trial fMRI study. *Brain : a journal of neurology, 125*(6), 1326. doi:10.1093/brain/awf137

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

Brewer, M. B. (2007). The importance of being we: human nature and intergroup relations. *American Psychologist, 62*(8), 728.

Briggs, G. G., & Nebes, R. D. (1975). Patterns of hand preference in a student population. *cortex, 11*(3), 230-238.

Bruneau, E. G., Pluta, A., & Saxe, R. (2012). Distinct roles of the ‘shared pain’and ‘theory of mind’networks in processing others’ emotional suffering. *Neuropsychologia, 50*(2), 219-231.

Buccino, G., Binkofski, F., Fink, G. R., Fadiga, L., Fogassi, L., Gallese, V., . . . Freund, H.-J. (2013). Action observation activates premotor and parietal areas in a somatotopic manner: an fMRI study *Social neuroscience* (pp. 133-141): Psychology Press.

Buccino, G., Lui, F., Canessa, N., Patteri, I., Lagravinese, G., Benuzzi, F., . . . Rizzolatti, G. (2004). Neural circuits involved in the recognition of actions performed by nonconspecifics: An fMRI study. *Journal of cognitive neuroscience, 16*(1), 114-126.

Butler, R. K., Oliver, E. M., Fadel, J. R., & Wilson, M. A. (2018). Hemispheric differences in the number of parvalbumin-positive neurons in subdivisions of the rat basolateral amygdala complex. *Brain research, 1678*, 214-219. doi:10.1016/j.brainres.2017.10.028

Byrne, R. W. (2005). Social cognition: Imitation, imitation, imitation. *Current Biology, 15*(13), R498-R500.

Bzdok, D., Schilbach, L., Vogeley, K., Schneider, K., Laird, A. R., Langner, R., & Eickhoff, S. B. (2012). Parsing the neural correlates of moral cognition: ALE meta-analysis on morality, theory of mind, and empathy. *Brain Structure and Function, 217*(4), 783-796.

Caggiano, V., Fogassi, L., Rizzolatti, G., Thier, P., & Casile, A. (2009). Mirror neurons differentially encode the peripersonal and extrapersonal space of monkeys. *Science, 324*(5925), 403-406.

Calvo-Merino, B., Glaser, D. E., Grèzes, J., Passingham, R. E., & Haggard, P. (2005). Action observation and acquired motor skills: an FMRI study with expert dancers. *Cerebral Cortex, 15*(8), 1243-1249.

Carter, C., & Keverne, E. (2002). The neurobiology of social affiliation and pair bonding *Hormones, brain and behavior* (pp. 299-337): Elsevier.

Castiello, U. (2005). The neuroscience of grasping. *Nature Reviews Neuroscience, 6*(9), 726-736.

Chen, Z., Williams, K. D., Fitness, J., & Newton, N. C. (2008). When Hurt Will Not Heal: Exploring the Capacity to Relive Social and Physical Pain. *Psychological science, 19*(8), 789-795. doi:10.1111/j.1467-9280.2008.02158.x

Cheng, Y., Yang, C.-Y., Lin, C.-P., Lee, P.-L., & Decety, J. (2008). The perception of pain in others suppresses somatosensory oscillations: a magnetoencephalography study. *NeuroImage, 40*(4), 1833-1840.

Choleris, E., Gustafsson, J.-Å., Korach, K. S., Muglia, L. J., Pfaff, D. W., & Ogawa, S. (2003). An estrogen-dependent four-gene micronet regulating social recognition: a study with oxytocin and estrogen receptor-α and-β knockout mice. *Proceedings of the National Academy of Sciences, 100*(10), 6192-6197.

Chunlin, L., & Jinglong, W. (2012). Activation of Right Ventral Prefrontal Cortex Using a Predictive Cue during Visual Spatial Orienting of Attentional Processes: An fMRI Study. *Neurology research international, 2012*(2012). doi:10.1155/2012/961342

Ciaramidaro, A., Becchio, C., Colle, L., Bara, B. G., & Walter, H. (2014). Do you mean me? Communicative intentions recruit the mirror and the mentalizing system. *Social cognitive and affective neuroscience, 9*(7), 909-916.

Clay, Z., Palagi, E., & de Waal, F. B. (2018). Ethological approaches to empathy in primates *Neuronal correlates of empathy* (pp. 53-66): Elsevier.

Corradini, A., & Antonietti, A. (2013). Mirror neurons and their function in cognitively understood empathy. *Consciousness and cognition, 22*(3), 1152-1161.

Cummings, M. A. (2015). The neurobiology of psychopathy: recent developments and new directions in research and treatment. *CNS spectrums, 20*(3), 200-206.

Danziger, N., Faillenot, I., & Peyron, R. (2009). Can we share a pain we never felt? Neural correlates of empathy in patients with congenital insensitivity to pain. *Neuron, 61*(2), 203-212.

Darwin, C. (1859). *The origin of species by means of natural selection* (Vol. 247): EA Weeks.

Davis, K., & Panksepp, J. (2011). The brain's emotional foundations of human personality and the Affective Neuroscience Personality Scales. *Neuroscience And Biobehavioral Reviews, 35*(9), 1946-1958. doi:10.1016/j.neubiorev.2011.04.004

Davis, M. H. (1980). Interpersonal reactivity index.

De Vignemont, F., & Singer, T. (2006). The empathic brain: how, when and why? *Trends in cognitive sciences, 10*(10), 435-441.

Decety, J., Bartal, I. B.-A., Uzefovsky, F., & Knafo-Noam, A. (2016). Empathy as a driver of prosocial behaviour: highly conserved neurobehavioural mechanisms across species. *Philosophical Transactions of the Royal Society B: Biological Sciences, 371*(1686), 20150077.

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.

Domes, G., Heinrichs, M., Michel, A., Berger, C., & Herpertz, S. C. (2007). Oxytocin improves “mind-reading” in humans. *Biological psychiatry, 61*(6), 731-733.

Ebert, A., & Brüne, M. (2017). Oxytocin and social cognition. *Behavioral Pharmacology of Neuropeptides: Oxytocin*, 375-388.

Ehrenfeld, T. (2011). Reflections on mirror neurons. *APS Observer, 24*.

Eisenberger, N. I. (2012). Broken Hearts and Broken Bones: A Neural Perspective on the Similarities Between Social and Physical Pain. *Current directions in psychological science : a journal of the American Psychological Society, 21*(1), 42-47. doi:10.1177/0963721411429455

Eisenberger, N. I., & Lieberman, M. D. (2004). Why rejection hurts: a common neural alarm system for physical and social pain. *Trends in cognitive sciences, 8*(7), 294-300. doi:10.1016/j.tics.2004.05.010

Fabbri-Destro, M., & Rizzolatti, G. (2008). Mirror neurons and mirror systems in monkeys and humans. *Physiology, 23*(3), 171-179.

Fadiga, L., & Craighero, L. (2006). Hand actions and speech representation in Broca's area. *cortex, 42*(4), 486-490.

Fadiga, L., Craighero, L., Fabbri Destro, M., Finos, L., Cotillon-Williams, N., Smith, A. T., & Castiello, U. (2006). Language in shadow. *Social neuroscience, 1*(2), 77-89.

Feeser, M., Fan, Y., Weigand, A., Hahn, A., Gärtner, M., Böker, H., . . . Bajbouj, M. (2015). Oxytocin improves mentalizing–pronounced effects for individuals with attenuated ability to empathize. *Psychoneuroendocrinology, 53*, 223-232.

Ferrari, P. F., & Coudé, G. (2018). Mirror neurons, embodied emotions, and empathy *Neuronal correlates of empathy* (pp. 67-77): Elsevier.

Ferrari, P. F., Gallese, V., Rizzolatti, G., & Fogassi, L. (2003). Mirror neurons responding to the observation of ingestive and communicative mouth actions in the monkey ventral premotor cortex. *European journal of neuroscience, 17*(8), 1703-1714.

Ferrari, P. F., & Rizzolatti, G. (2014). Mirror neuron research: the past and the future (Vol. 369, pp. 20130169): The Royal Society.

Fogassi, L., & Ferrari, P. F. (2007). Mirror neurons and the evolution of embodied language. *Current directions in psychological science, 16*(3), 136-141.

Fogassi, L., Ferrari, P. F., Gesierich, B., Rozzi, S., Chersi, F., & Rizzolatti, G. (2005). Parietal lobe: from action organization to intention understanding. *Science, 308*(5722), 662-667.

Freeman, C. (2016). What is mentalizing? An overview. *British Journal of Psychotherapy, 32*(2), 189-201.

Fröhlich, M., Sievers, C., Townsend, S. W., Gruber, T., & van Schaik, C. P. (2019). Multimodal communication and language origins: integrating gestures and vocalizations. *Biological Reviews, 94*(5), 1809-1829.

Fu, X., Hung, A., de Silva, A. D., Busch, T., Mattson, W. I., Hoskinson, K. R., . . . Nelson, E. E. (2022). Development of the mentalizing network structures and theory of mind in extremely preterm youth. *Social cognitive and affective neuroscience*.

Gallese, V. (2001). The'shared manifold'hypothesis. From mirror neurons to empathy. *Journal of consciousness studies, 8*(5-6), 33-50.

Gallese, V. (2003). The roots of empathy: the shared manifold hypothesis and the neural basis of intersubjectivity. *Psychopathology, 36*(4), 171-180.

Gallese, V. (2007). Before and below ‘theory of mind’: embodied simulation and the neural correlates of social cognition. *Philosophical Transactions of the Royal Society B: Biological Sciences, 362*(1480), 659-669.

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

Gallese, V., Keysers, C., & Rizzolatti, G. (2004). A unifying view of the basis of social cognition. *Trends in cognitive sciences, 8*(9), 396-403.

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

Gentilucci, M., Bernardis, P., Crisi, G., & Volta, R. D. (2006). Repetitive transcranial magnetic stimulation of Broca's area affects verbal responses to gesture observation. *Journal of cognitive neuroscience, 18*(7), 1059-1074.

Gentilucci, M., & Volta, R. D. (2008). Spoken language and arm gestures are controlled by the same motor control system. *Quarterly journal of experimental psychology, 61*(6), 944-957.

Giacomo, R., & Laila, C. (2004). The mirror-neuron system. *Annual review of neuroscience, 27*(1), 169-192.

Goldie, P. (1999). How we think of others' emotions. *Mind & Language, 14*(4), 394-423.

Hamilton, A. (2013). The mirror neuron system contributes to social responding. *cortex, 49*(10), 2957-2959.

Hansen, A. (2019). *Skärmhjärnan: hur en hjärna i osynk med sin tid kan göra oss stressade, deprimerade och ångestfyllda*: Bonnier fakta.

Haslinger, B., Erhard, P., Altenmüller, E., Schroeder, U., Boecker, H., & Ceballos-Baumann, A. O. (2005). Transmodal sensorimotor networks during action observation in professional pianists. *Journal of cognitive neuroscience, 17*(2), 282-293.

Heiser, M., Iacoboni, M., Maeda, F., Marcus, J., & Mazziotta, J. C. (2003). The essential role of Broca's area in imitation. *European journal of neuroscience, 17*(5), 1123-1128.

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

Heyes, C., & Catmur, C. (2022). What happened to mirror neurons? *Perspectives on Psychological Science, 17*(1), 153-168.

Hickok, G. (2010). The role of mirror neurons in speech perception and action word semantics. *Language and cognitive processes, 25*(6), 749-776.

Ho, S. S., MacDonald, A., & Swain, J. E. (2014). Associative and sensorimotor learning for parenting involves mirror neurons under the influence of oxytocin. *The Behavioral and brain sciences, 37*(2), 203.

Holmes, P., & Calmels, C. (2011). Mental practice: Neuroscientific support for a new approach. *Performance psychology: A practitioner's guide*, 231-244.

Holt-Lunstad, J. (2021). The major health implications of social connection. *Current directions in psychological science, 30*(3), 251-259.

Hurlemann, R., Scheele, D., Maier, W., & Schultz, J. (2017). Oxytocin drives prosocial biases in favor of attractive people. *Behavioral and brain sciences, 40*, e30.

Iacoboni, M. (2007). Face to face: The neural basis of social mirroring and empathy. *Psychiatric Annals, 37*(4), 236.

Iacoboni, M. (2008). The problem of other minds is not a problem: Mirror neurons and intersubjectivity *Mirror neuron systems* (pp. 121-133): Springer.

Iacoboni, M. (2009a). Imitation, empathy, and mirror neurons. *Annual review of psychology, 60*(1), 653-670.

Iacoboni, M. (2009b). *Mirroring people: The new science of how we connect with others*: Farrar, Straus and Giroux.

Iacoboni, M. (2011). Mirroring as a key neural mechanism of sociality. *Grounding sociality: Neurons, mind, and culture*, 13-26.

Iacoboni, M., Koski, L. M., Brass, M., Bekkering, H., Woods, R. P., Dubeau, M.-C., . . . Rizzolatti, G. (2001). Reafferent copies of imitated actions in the right superior temporal cortex. *Proceedings of the National Academy of Sciences, 98*(24), 13995-13999.

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.

Iannetti, G. D., & Mouraux, A. (2011). Can the functional MRI responses to physical pain really tell us why social rejection "hurts"? *Proceedings of the National Academy of Sciences of the United States of America, 108*(30), E343. doi:10.1073/pnas.1105451108

Jackson, P. L., Meltzoff, A. N., & Decety, J. (2005). How do we perceive the pain of others? A window into the neural processes involved in empathy. *NeuroImage, 24*(3), 771-779.

Keaton, S. A. (2017). Interpersonal Reactivity Index (IRI) (Davis, 1980). *The Sourcebook of listening research: Methodology and measures*, 340-347.

Keysers, C. (2009). Mirror neurons. *Current Biology, 19*(21), R971-R973.

Keysers, C., & Gazzola, V. (2010). Social neuroscience: mirror neurons recorded in humans. *Current Biology, 20*(8), R353-R354.

Keysers, C., Kohler, E., Umiltà, M. A., Nanetti, L., Fogassi, L., & Gallese, V. (2003). Audiovisual mirror neurons and action recognition. *Experimental brain research, 153*(4), 628-636.

Kilner, J. M., & Lemon, R. N. (2013). What we know currently about mirror neurons. *Current Biology, 23*(23), R1057-R1062.

Kim, E., Jung, Y.-C., Ku, J., Kim, J.-J., Lee, H., Kim, S. Y., . . . Cho, H.-S. (2009). Reduced activation in the mirror neuron system during a virtual social cognition task in euthymic bipolar disorder. *Progress in Neuro-Psychopharmacology and Biological Psychiatry, 33*(8), 1409-1416.

Kim, S., & Strathearn, L. (2016). Oxytocin and maternal brain plasticity. *New directions for child and adolescent development, 2016*(153), 59-72.

Knafo, A., & Israel, S. (2012). Empathy, prosocial behavior, and other aspects of kindness. *Handbook of temperament*, 168-179.

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

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

Kosonogov, V. (2012). Why the mirror neurons cannot support action understanding. *Neurophysiology, 44*(6), 499-502.

Koster-Hale, J., & Saxe, R. (2013). Theory of mind: a neural prediction problem. *Neuron, 79*(5), 836-848.

Kross, E., Berman, M. G., Mischel, W., Smith, E. E., & Wager, T. (2011). Social rejection shares somatosensory representations with physical pain. *Proceedings Of The National Academy Of Sciences Of The United States Of Ame, 108*(15), 6270-6275. doi:10.1073/pnas.1102693108

Lametti, D. R., & Mattar, A. A. (2006). Mirror neurons and the lateralization of human language. *Journal of Neuroscience, 26*(25), 6666-6667.

Lamm, C., Decety, J., & Singer, T. (2011). Meta-analytic evidence for common and distinct neural networks associated with directly experienced pain and empathy for pain. *NeuroImage, 54*(3), 2492-2502.

Lamm, C., & Majdandžić, J. (2015). The role of shared neural activations, mirror neurons, and morality in empathy–A critical comment. *Neuroscience Research, 90*, 15-24.

Lamm, C., Rütgen, M., & Wagner, I. C. (2019). Imaging empathy and prosocial emotions. *Neuroscience Letters, 693*, 49-53.

Lawrence, E. J., Shaw, P., Giampietro, V. P., Surguladze, S., Brammer, M. J., & David, A. S. (2006). The role of 'shared representations' in social perception and empathy: an fMRI study. *NeuroImage, 29*(4), 1173-1184.

LeDoux, J. (2012). Rethinking the emotional brain. *Neuron, 73*(4), 653-676.

Lepage, J. F., Tremblay, S., & Théoret, H. (2010). Early non-specific modulation of corticospinal excitability during action observation. *European journal of neuroscience, 31*(5), 931-937.

Lockwood, P. L. (2016). The anatomy of empathy: Vicarious experience and disorders of social cognition. *Behavioural brain research, 311*, 255-266.

Macdonald, G., & Leary, M. R. (2005). Why Does Social Exclusion Hurt? The Relationship Between Social and Physical Pain. *Psychological bulletin, 131*(2), 202-223. doi:10.1037/0033-2909.131.2.202

Magon, N., & Kalra, S. (2011). The orgasmic history of oxytocin: Love, lust, and labor. *Indian journal of endocrinology and metabolism, 15*(Suppl3), S156.

Marini, M., Ansani, A., Paglieri, F., Caruana, F., & Viola, M. (2021). The impact of facemasks on emotion recognition, trust attribution and re-identification. *Scientific Reports, 11*(1), 1-14.

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

Meister, I. G., Wilson, S. M., Deblieck, C., Wu, A. D., & Iacoboni, M. (2007). The essential role of premotor cortex in speech perception. *Current Biology, 17*(19), 1692-1696.

Meltzoff, A. N., Brooks, R., Shon, A. P., & Rao, R. P. (2010). "Social" robots are psychological agents for infants: A test of gaze following. *Neural networks, 23*(8-9), 966-972.

Meltzoff, A. N., & Moore, M. K. (1983). Newborn infants imitate adult facial gestures. *Child development*, 702-709.

Meltzoff, A. N., & Moore, M. K. (1994). Imitation, memory, and the representation of persons. *Infant behavior and development, 17*(1), 83-99.

Meltzoff, A. N., Ramírez, R. R., Saby, J. N., Larson, E., Taulu, S., & Marshall, P. J. (2018). Infant brain responses to felt and observed touch of hands and feet: an MEG study. *Developmental Science, 21*(5), e12651.

Merleau-Ponty, M. (2013). *Phenomenology of perception*: Routledge.

Miall, R. C. (2003). Connecting mirror neurons and forward models. *Neuroreport, 14*(17), 2135-2137.

Mier, D., Haddad, L., Diers, K., Dressing, H., Meyer-Lindenberg, A., & Kirsch, P. (2014). Reduced embodied simulation in psychopathy. *The World Journal of Biological Psychiatry, 15*(6), 479-487.

Miller, G. (2008). Mirror neurons may help songbirds stay in tune: American Association for the Advancement of Science.

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

Misra, V. (2014). The social brain network and autism. *Annals of neurosciences, 21*(2), 69.

Molenberghs, P., Brander, C., Mattingley, J. B., & Cunnington, R. (2010). The role of the superior temporal sulcus and the mirror neuron system in imitation. *Human brain mapping, 31*(9), 1316-1326.

Molnar-Szakacs, I., & Overy, K. (2006). Music and mirror neurons: from motion to'e'motion. *Social cognitive and affective neuroscience, 1*(3), 235-241.

Mu, Y., Guo, C., & Han, S. (2016). Oxytocin enhances inter-brain synchrony during social coordination in male adults. *Social cognitive and affective neuroscience, 11*(12), 1882-1893.

Muncer, S. J., & Ling, J. (2006). Psychometric analysis of the empathy quotient (EQ) scale. *Personality and Individual Differences, 40*(6), 1111-1119.

Muthukumaraswamy, S. D., & Johnson, B. (2004). Changes in rolandic mu rhythm during observation of a precision grip. *Psychophysiology, 41*(1), 152-156.

Muthukumaraswamy, S. D., & Johnson, B. W. (2004). Primary motor cortex activation during action observation revealed by wavelet analysis of the EEG. *Clinical neurophysiology, 115*(8), 1760-1766.

Naomi, I. E. (2012). The pain of social disconnection: examining the shared neural underpinnings of physical and social pain. *Nature Reviews Neuroscience, 13*(6), 421. doi:10.1038/nrn3231

Neta, M. G., & Varanda, C. (2016). The role of mirror neurons in autism impairment. *European Psychiatry, 33*(S1), S374-S375.

Neumann, I. D. (2009). The advantage of social living: brain neuropeptides mediate the beneficial consequences of sex and motherhood. *Frontiers in neuroendocrinology, 30*(4), 483-496.

Newman-Norlund, R. D., van Schie, H. T., van Zuijlen, A. M., & Bekkering, H. (2007). The mirror neuron system is more active during complementary compared with imitative action. *Nature neuroscience, 10*(7), 817-818.

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

Oberman, L. M., & Ramachandran, V. S. (2008). Reflections on the mirror neuron system: Their evolutionary functions beyond motor representation *Mirror neuron systems* (pp. 39-59): Springer.

Ogura, M., Watanabe, Y., Sanjo, Y., Edahiro, A., Sato, K., & Katakura, A. (2014). Mirror neurons activated during swallowing and finger movements: An fMRI study. *Journal of Oral and Maxillofacial Surgery, Medicine, and Pathology, 26*(2), 188-197.

Ohtsuki, H., Hauert, C., Lieberman, E., & Nowak, M. A. (2006). A simple rule for the evolution of cooperation on graphs and social networks. *Nature, 441*(7092), 502-505.

Olsson, A., & Ochsner, K. N. (2008). The role of social cognition in emotion. *Trends in cognitive sciences, 12*(2), 65-71.

Otsuka, Y., Osaka, N., Ikeda, T., & Osaka, M. (2009). Individual differences in the theory of mind and superior temporal sulcus. *Neuroscience Letters, 463*(2), 150-153.

Over, H., & Carpenter, M. (2013). The social side of imitation. *Child development perspectives, 7*(1), 6-11.

Parmar, M. P., & Malik, M. S. (2017). Oxytocin-The Hormone of Love. *IOSR Journal of Pharmacy and Byological Sciences (IOSR-JPBS), 12*(6), 1-9.

Patin, A., Scheele, D., & Hurlemann, R. (2017). Oxytocin and interpersonal relationships. *Behavioral Pharmacology of Neuropeptides: Oxytocin*, 389-420.

Perez, A., Sanguineti, V., Morerio, P., & Murino, V. (2020). *Audio-visual model distillation using acoustic images.* Paper presented at the Proceedings of the IEEE/CVF Winter Conference on Applications of Computer Vision.

Perry, A., Bentin, S., Shalev, I., Israel, S., Uzefovsky, F., Bar-On, D., & Ebstein, R. P. (2010). Intranasal oxytocin modulates EEG mu/alpha and beta rhythms during perception of biological motion. *Psychoneuroendocrinology, 35*(10), 1446-1453.

Pfeifer, J. H., Iacoboni, M., Mazziotta, J. C., & Dapretto, M. (2008). Mirroring others' emotions relates to empathy and interpersonal competence in children. *NeuroImage, 39*(4), 2076-2085.

Pineda, J., & Hecht, E. (2009). Mirroring and mu rhythm involvement in social cognition: are there dissociable subcomponents of theory of mind? *Biological psychology, 80*(3), 306-314.

Praszkier, R. (2016). Empathy, mirror neurons and SYNC. *Mind & Society, 15*(1), 1-25.

Premack, D., & Woodruff, G. (1978). Does the chimpanzee have a theory of mind? *Behavioral and brain sciences, 1*(4), 515-526.

Preston, S. D., & De Waal, F. B. (2002). Empathy: Its ultimate and proximate bases. *Behavioral and brain sciences, 25*(1), 1-20.

Prieur, J., Barbu, S., Blois-Heulin, C., & Lemasson, A. (2020). The origins of gestures and language: history, current advances and proposed theories. *Biological Reviews, 95*(3), 531-554.

Redcay, E., & Warnell, K. R. (2018). A social-interactive neuroscience approach to understanding the developing brain. *Advances in child development and behavior, 54*, 1-44.

Reizer, A., & Mikulincer, M. (2007). Assessing individual differences in working models of caregiving: The construction and validation of the Mental Representation of Caregiving scale. *Journal of Individual Differences, 28*(4), 227.

Riva, G., Mantovani, F., Waterworth, E. L., & Waterworth, J. A. (2015). Intention, action, self and other: An evolutionary model of presence *Immersed in media* (pp. 73-99): Springer.

Rizzolatti, G. (2005). The mirror neuron system and its function in humans. *Anatomy and embryology, 210*(5), 419-421.

Rizzolatti, G., & Arbib, M. A. (1998). Language within our grasp. *Trends in neurosciences, 21*(5), 188-194.

Rizzolatti, G., & Craighero, L. (2004). The mirror-neuron system.

Rizzolatti, G., Fadiga, L., Matelli, M., Bettinardi, V., Paulesu, E., Perani, D., & Fazio, F. (1996). Localization of grasp representations in humans by PET: 1. Observation versus execution. *Experimental brain research, 111*(2), 246-252.

Rizzolatti, G., & Fogassi, L. (2007). Mirror neurons and social cognition. *The Oxford handbook of evolufionary psychology*, 179-195.

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

Rizzolatti, G., & Sinigaglia, C. (2016). The mirror mechanism: a basic principle of brain function. *Nature Reviews Neuroscience, 17*(12), 757-765.

Robinson, T. (2021). Put yourself in their shoes: Empathy and thinking patterns.

Rodríguez, Á. L., Cheeran, B., Koch, G., Hortobágyi, T., & Fernandez-del-Olmo, M. (2014). The role of mirror neurons in observational motor learning: an integrative review. *European Journal of Human Movement*(32), 82-103.

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

Saby, J. N., Marshall, P. J., & Meltzoff, A. N. (2012). Neural correlates of being imitated: An EEG study in preverbal infants. *Social neuroscience, 7*(6), 650-661.

Sartori, L., & Betti, S. (2015). Complementary actions. *Frontiers in psychology, 6*, 557.

Sartori, L., Betti, S., & Castiello, U. (2013). When mirroring is not enough: that is, when only a complementary action will do (the trick). *Neuroreport, 24*(11), 601-604.

Sartori, L., Bucchioni, G., & Castiello, U. (2013). When emulation becomes reciprocity. *Social cognitive and affective neuroscience, 8*(6), 662-669.

Sartori, L., & Castiello, U. (2013). Shadows in the mirror. *Neuroreport, 24*(2), 63-67.

Schneider-Hassloff, H., Straube, B., Jansen, A., Nuscheler, B., Wemken, G., Witt, S. H., . . . Kircher, T. (2016). Oxytocin receptor polymorphism and childhood social experiences shape adult personality, brain structure and neural correlates of mentalizing. *NeuroImage, 134*, 671-684.

Scholz, B. J., Finnerup, I. N., Attal, D. N., Aziz, A. Q., Baron, N. R., Bennett, S. C. M., . . . Treede, W. S. R.-D. (2019). The IASP classification of chronic pain for ICD-11: chronic neuropathic pain. *PAIN, 160*(1), 53-59. doi:10.1097/j.pain.0000000000001365

Schultz, W., & Dickinson, A. (2000). Neuronal coding of prediction errors. *Annual review of neuroscience, 23*(1), 473-500.

Shamay-Tsoory, S. G., Aharon-Peretz, J., & Perry, D. (2009). Two systems for empathy: a double dissociation between emotional and cognitive empathy in inferior frontal gyrus versus ventromedial prefrontal lesions. *Brain, 132*(3), 617-627.

Shamay-Tsoory, S. G., Tomer, R., Goldsher, D., Berger, B., & Aharon-Peretz, J. (2004). Impairment in cognitive and affective empathy in patients with brain lesions: anatomical and cognitive correlates. *Journal of Clinical and Experimental Neuropsychology, 26*(8), 1113-1127.

Sheets-Johnstone, M. (2012). Movement and mirror neurons: a challenging and choice conversation. *Phenomenology and the Cognitive Sciences, 11*(3), 385-401.

Shimada, S. (2022). Multisensory and Sensorimotor Integration in the Embodied Self: Relationship between Self-Body Recognition and the Mirror Neuron System. *Sensors, 22*(13), 5059.

Singer, T. (2006). The neuronal basis and ontogeny of empathy and mind reading: review of literature and implications for future research. *Neuroscience & Biobehavioral Reviews, 30*(6), 855-863.

Singer, T., Seymour, B., O'doherty, J., Kaube, H., Dolan, R. J., & Frith, C. D. (2004). Empathy for pain involves the affective but not sensory components of pain. *Science, 303*(5661), 1157-1162.

Smith, A. (2006). Cognitive empathy and emotional empathy in human behavior and evolution. *The Psychological Record, 56*(1), 3-21.

Sommer, M., & Paulus, W. (2008). TMS waveform and current direction. *The Oxford handbook of transcranial stimulation. Oxford University Press, New York*, 7-12.

Spaulding, S. (2017). Cognitive empathy *The Routledge handbook of philosophy of empathy* (pp. 13-21): Routledge.

Spreng*, R. N., McKinnon*, M. C., Mar, R. A., & Levine, B. (2009). The Toronto Empathy Questionnaire: Scale development and initial validation of a factor-analytic solution to multiple empathy measures. *Journal of personality assessment, 91*(1), 62-71.

Sprung-Much, T., Eichert, N., Nolan, E., & Petrides, M. (2022). Broca's area and the search for anatomical asymmetry: Commentary and perspectives. *Brain Structure and Function, 227*(2), 441-449.

Strathearn, L. (2011). Maternal neglect: oxytocin, dopamine and the neurobiology of attachment. *Journal of neuroendocrinology, 23*(11), 1054-1065.

Tchernichovski, O., & Wallman, J. (2008). Neurons of imitation. *Nature, 451*(7176), 249-250.

Thompson, E. L., Bird, G., & Catmur, C. (2019). Conceptualizing and testing action understanding. *Neuroscience & Biobehavioral Reviews, 105*, 106-114.

Timmers, I., Park, A. L., Fischer, M. D., Kronman, C. A., Heathcote, L. C., Hernandez, J. M., & Simons, L. E. (2018). Is empathy for pain unique in its neural correlates? A meta-analysis of neuroimaging studies of empathy. *Frontiers in behavioral neuroscience, 12*, 289.

Tippett, D. C., Godin, B. R., Oishi, K., Oishi, K., Davis, C., Gomez, Y., . . . Hillis, A. E. (2018). *Impaired recognition of emotional faces after stroke involving right amygdala or insula.* Paper presented at the Seminars in speech and language.

Vachon, D. D., Lynam, D. R., & Johnson, J. A. (2014). The (non) relation between empathy and aggression: surprising results from a meta-analysis. *Psychological bulletin, 140*(3), 751.

Viding, E. (2004). Annotation: Understanding the development of psychopathy. *Journal of Child Psychology and Psychiatry, 45*(8), 1329-1337.

Villadangos Fernández, J. M., Errasti Pérez, J. M., Amigo Vázquez, I., Jolliffe, D., & García Cueto, E. (2016). Characteristics of empathy in young people measured by the Spanish validation of the Basic Empathy Scale. *Psicothema, 28 (3)*.

von Bieberstein, F., Essl, A., & Friedrich, K. (2021). Empathy: A clue for prosocialty and driver of indirect reciprocity. *PloS one, 16*(8), e0255071.

Wang, H., Braun, C., & Enck, P. (2017). How the brain reacts to social stress (exclusion) – A scoping review. *Neuroscience And Biobehavioral Reviews, 80*, 80-88. doi:10.1016/j.neubiorev.2017.05.012

Wassermann, E., Epstein, C., Ziemann, U., Walsh, V., Paus, T., & Lisanby, S. (2008). *Oxford handbook of transcranial stimulation*: OUP Oxford.

Wassermann, E. M. (1998). Risk and safety of repetitive transcranial magnetic stimulation: report and suggested guidelines from the International Workshop on the Safety of Repetitive Transcranial Magnetic Stimulation, June 5–7, 1996. *Electroencephalography and Clinical Neurophysiology/Evoked Potentials Section, 108*(1), 1-16.

White, A. B. (2021). How the Chameleon Effect Impacts Introverts and Extroverts in Social and Academic Settings. *Ursidae: The Undergraduate Research Journal at the University of Northern Colorado, 10*(1), 7.

Williams, A., & Gribble, P. L. (2012). Observed effector-independent motor learning by observing. *Journal of neurophysiology, 107*(6), 1564-1570.

Winslow, J. T., & Insel, T. R. (2002). The social deficits of the oxytocin knockout mouse. *Neuropeptides, 36*(2-3), 221-229.

Wittgenstein, L. (1965). I: A lecture on ethics. *The philosophical review, 74*(1), 3-12.

Yoon, J. M., & Tennie, C. (2010). Contagious yawning: a reflection of empathy, mimicry, or contagion? *Animal behaviour, 79*(5), e1-e3.

Zaki, J., & Ochsner, K. N. (2012). The neuroscience of empathy: progress, pitfalls and promise. *Nature neuroscience, 15*(5), 675-680.

Appendix

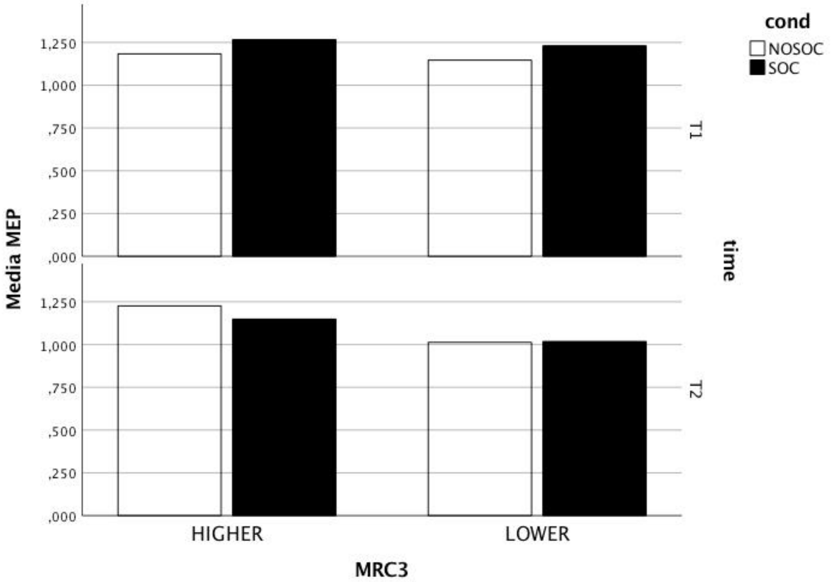


Figure 7. Median MEP in correlation to ADM muscle activation in two conditions (i.e., "Social" and "Non-social" conditions) for the two groups low and high responders within the MRC-3. Significance level *p < 0.05.

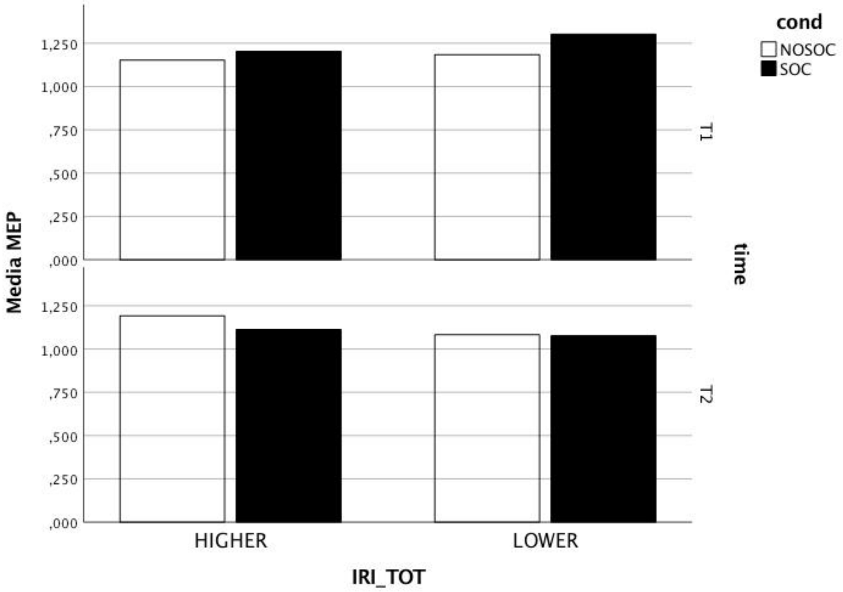


Figure 8. Median MEP in correlation to ADM muscle activation in two conditions (i.e., "Social" and "Non-social" conditions) for the two groups low and high responders within IRI (total subscales). Significance level *p < 0.05.