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The multi-actor mirror neuron system: Can individuals represent multiple observed movements simultaneously?

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Promoter: Prof. dr. Michael Andres

Supervisor: Lize De Coster

00901658

Emiel Cracco

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Abstract

A large body of research has provided evidence for the idea that individuals co-represent observed actions in their motor system. However, this research has focused almost exclusively on dyadic situations, hence ignoring the fact that social situations often require that the actions of multiple persons are monitored at the same time. The current thesis addresses this issue in two experiments. In the first experiment, an automatic imitation task is used to investigate how individuals are influenced by the movements of multiple observed actors. It is shown that individuals are able to co-represent the movements of two actors simultaneously. In extension, it is shown how individuals are influenced by the relationship between the movements of the actors. The results indicate that two identical observed movements activate the corresponding motor representation more strongly, whereas two different observed movements activate conflicting motor representations. In the second experiment, a motor TMS study is used to investigate at the neural level whether two identical observed movements activate the relevant motor representation more strongly than a single observed movement. Although no evidence was found for this hypothesis, it is argued that the power of the study was low and that more extensive testing will be necessary to resolve this question. In short, the current thesis extends research on action observation from situations where one actor is observed to situations where multiple actors are observed. This may allow for a better understanding of social interactions beyond the dyad.

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Introduction

The Perception-Action System

Over the past two decades, it has been investigated extensively how we represent the behavior of others. As a result of this research, it is now widely recognized that observed behavior is not only represented in the visual, but also in the motor system of the observer (reviewed in Heyes, 2011; Rizzolatti & Craighero, 2004; Rizzolatti & Sinigaglia, 2010). According to the ideomotor theory, this is due to the fact that perception and action share a representational domain (Greenwald, 1970; Hommel, 2009; Prinz, 1997; for a review see Shin, Proctor, & Capaldi, 2010). More specifically, this theory states that an action (e.g., switching on the light) is represented by the perceptual effects that result from that action (e.g., the sight of the light being on). As a result, actions can be triggered by seeing or hearing the perceptual effect related to that action. Because seeing an action corresponds to the perceptual effect of executing that action, it follows that an observed movement automatically activates the same movement in the motor cortex

Two distinct research lines have contributed to the idea of a shared representational domain for action observation and action execution. In what follows, these bodies of evidence will be discussed separately.

Automatic Imitation. A first type of research that speaks in favor of an intimate relation between action observation and action execution is research on automatic imitation. Automatic imitation refers to the tendency to imitate irrelevant observed movements and can occur on both the overt and covert level (see Heyes, 2011, for a review). On the overt level, automatic imitation has been studied as it occurs in daily social interactions. This has revealed that individuals often unintentionally copy the facial expression, behavior, and speech pattern of the person they interact with (e.g., Chartrand & Bargh, 1999; see Chartrand & van Baaren, 2009, for a review). On the covert level, automatic imitation has been investigated with stimulus-response compatibility tasks. In these tasks, often called imitation-inhibition tasks, subjects are required to make a certain finger movement in

response to a symbolic cue (e.g., 1 = lift index finger, 2 = lift middle finger) while a hand on the screen makes a compatible or incompatible movement. A typical effect of this procedure is that compatible observed movements facilitate responses, whereas incompatible observed movements impede responses (e.g., Bertenthal, Longo, & Kosobud, 2006; Brass, Bekkering, Wohlschläger, & Prinz, 2000; Catmur & Heyes, 2011; Liepelt, von Cramon, & Brass, 2008; Stürmer, Aschersleben, & Prinz, 2000). Notably, further studies have demonstrated the reliability of this effect by showing that it is not restricted to hand movements (e.g., feet: Gillmeister, Catmur, Liepelt, Brass & Heyes, 2008) and also occurs when the same predefined movement has to be executed throughout the experiment (e.g., Brass, Bekkering, & Prinz, 2001; Kilner, Paulignan, & Blakemore, 2003; Press, Bird, Walsh, & Heyes, 2008). Moreover, recent research convincingly supports the notion that automatic imitation reflects an automatic process by showing that imitative response tendencies occur even when they result in disadvantageous outcomes for the imitator (Cook, Bird, Lünser, Huck, & Heyes, 2012).

Apart from research on healthy individuals, automatic imitation has also been studied in patients. Luria (1966), for example, described ‘echopractic responses’ in patients with damage to the frontal lobe. In a task very similar to the imitation-inhibition task, he found that these patients often failed to overcome the urge to imitate when the required response did not match the observed movement. Later, Lhermitte, Pillon, and Serdaru (1986) linked frontal lobe damage to ‘imitation behavior’. Similar to echopractic response patients, imitation behavior patients would imitate the gestures of the experimenter even when explicitly asked not to (see also De Renzi, Cavalleri, and Facchini, 1996). More recently, this early evidence for imitative response tendencies amongst frontal lobe patients was confirmed by two studies that showed a larger interference effect on the imitation-inhibition task for these patients compared to healthy controls (Brass, Derrfuss, Matthes-von Cramon, & von Cramon, 2003; Spengler, von Cramon, & Brass, 2010) while posterior lobe patients did not differ from healthy controls (Brass et al., 2003). Furthermore, a larger imitation-inhibition interference effect was also observed in a sample of individuals with autism spectrum disorder and this was again linked to frontal brain dysfunctions (Spengler, Bird, & Brass, 2010). Interestingly, the role of the frontal cortex in the above disorders is

also supported by brain imaging studies that implicated the medial and lateral prefrontal cortex in the inhibition of imitative responses (e.g., Brass, Derrfuss, & von Cramon, 2005; Brass, Ruby, & Spengler, 2009; Brass, Zysset, & von Cramon, 2001)

To summarize, research on automatic imitation supports the idea of a common representational domain for action observation and action execution by showing that action observation is a strong trigger for action execution. Even though these observation induced actions can easily be inhibited by healthy individuals when they are inappropriate, damage to the prefrontal cortex may result in an irresistible urge to copy the movements of others.

The Mirror Neuron System. Another type of research that has contributed to the idea of a shared representational domain for action observation and action execution is research on the mirror neuron system (MNS). Mirror neurons are motor neurons that fire when an action is executed as well as when it is observed. While these neurons were originally discovered in the ventral premotor area (area F5) and the inferior parietal lobe of the monkey brain (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996; for reviews see Rizzolatti & Craighero, 2004; Rizzolatti & Sinigaglia, 2010), a large body of research has now provided support for the existence of similar neurons in humans.

In a first line of research, brain imaging techniques have been used to localize the regions of the human brain that contain mirror neuron properties. In accordance with research on monkeys, these studies have found an activation overlap between executed and observed movements in a fronto-parietal network of motor regions (e.g., Dinstein, Hasson, Rubin, & Heeger, 2007; Filimon, Nelson, Hagler, & Sereno, 2007; Gazzola & Keysers, 2009; Grèzes, Armony, Rowe, & Passingham, 2003; for meta-analyses see Molenberghs, Cunnington, & Mattingley, 2012; Morin & Grèzes, 2008). Furthermore, several studies have now applied a perception-action repetition suppression paradigm as a more direct test for mirror neuron properties. These studies rely on the well-established observation that the repetitive presentation of a stimulus leads to a diminished brain response towards that stimulus (see Grill-Spector, Henson, & Martin, 2006, for a review). While the precise mechanism behind this phenomenon is still under debate, it is commonly accepted that it is

based on changes in the response behavior of the neurons that are sensitive to the relevant stimulus (Grill-Spector et al., 2006). Consequently, if observed and executed movements are represented by the same neurons, repetition suppression effects should also be present when the execution of a certain action is followed by the observation of the same action and vice versa. In line with this idea, perception-action repetition suppression effects have been reported in the putative human homologues of the monkey mirror neuron regions: the inferior frontal gyrus (Kilner, Neal, Weiskopf, Friston, & Frith, 2009) and the inferior parietal lobe (Chong, Cunnington, Williams, Kanwisher, & Mattingley, 2008).

In a second line of research, electroencephalography (EEG; e.g., Lepage & Théoret, 2006; Zhu, Sun, & Fang Wang, 2013) and magnetoencephalography (MEG; e.g., Hari et al., 1998; Nishitani & Hari, 2000) have been used to show that action observation elicits motor-related brain activation. Importantly, the idea that this motor activation reflects the involvement of the MNS was recently strengthened by a study that indicated brain regions with mirror neuron properties to be at its origin (Arnstein, Cui, Maurits, & Gazzola, 2011).

In a last line of research, studies have investigated the effect of action observation on cortico-spinal excitability with transcranial magnetic stimulation (TMS). This technique relies on the fact that the premotor cortex, a key region in the MNS, has connections with the primary motor cortex (e.g., Muakkassa & Strick, 1979). As a result of these connections, action observation related activation in the premotor cortex should spread to the primary motor cortex. Although this spread of activation is not detectable under normal circumstances, it can be enhanced by providing magnetic stimulation to the primary motor cortex with TMS. In this case, the primary motor cortex response to observed movements can be measured by looking at the activation level of the muscles that are involved in the execution of the observed movement. In support of a human MNS, studies using this technique have shown that TMS elicits stronger motor-evoked potentials (MEPs) in conditions of action observation than in baseline conditions (e.g., Clark, Tremblay, & Ste-Marie, 2003; Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995; Maeda, Kleiner-Fisman, & Pascal-Leone, 2002; Schütz-Bosbach, Mancini, Aglioti, & Haggard, 2006; see Fadiga, Craighero, & Olivier, 2005, for a review), and that this is due to cortico-cortical connections from the premotor cortex to the primary motor cortex (Strafella & Paus, 2000).

To conclude, the discovery of the MNS has provided neural support for the idea of a shared representational format for action observation and action execution. Given that the aforementioned automatic imitation effects are usually explained in terms of such a shared representational format, it is therefore likely that automatic imitation is based on the MNS (Heyes, 2011). This is supported by a close overlap between the characteristics of the human MNS and the characteristics of automatic imitation. A first shared feature is that in humans both automatic imitation effects (e.g., Bertenthal, Longo, & Kosobud, 2006; Catmur & Heyes, 2011; Press et al., 2008) and mirror neuron activation (e.g., Clark et al., 2003; Lorey et al., 2013; Zhu et al., 2013) have been reported for intransitive movements (but see Jonas et al., 2007, for a more nuanced view), whereas in monkeys mirror neurons are known to respond only to transitive movements (e.g., Rizzolatti et al., 1996). A second shared feature relates to the fact that both automatic imitation and mirror neuron activation are specific for the observed movement. This is evidenced in a first way by the finding that automatic imitation effects (e.g., Gillmeister et al., 2008) as well as mirror neuron activation (Buccino et al., 2001; Wheaton, Thompson, Syngeniotes, Abbott, & Puce, 2004; but see Lorey et al., 2013, for counter-evidence) are specific to the observed limb. It is further supported by the correspondence between finger-specific automatic imitation effects (e.g., Bertenthal et al., 2006; Brass et al., 2000; Catmur & Heyes, 2011) and muscle-specific mirror activation (e.g., Maeda et al., 2002; Schütz-Bosbach et al., 2006). A final shared feature is that incompatible sensorimotor training (e.g., opening one's hand when seeing a hand closing) has shown to reduce or reverse both automatic imitation effects (e.g., Gillmeister et al., 2008; see Heyes, 2011, for an overview) and MNS activity (Catmur, Mars, Rushworth, & Heyes, 2010; Catmur, Walsh, & Heyes, 2007).

The Social Function of the Perception-Action System

Interestingly, several lines of research suggest that the perception-action system is crucial for successful social interaction. First, it is well established that being imitated during a social interaction increases the perceived smoothness of the interaction and induces positive feelings as well as pro-social behavior towards both the imitator and other

persons (e.g., Chartrand & Bargh, 1999; van Baaren, Holland, Kawakami, & van Knippenberg, 2004; see Chartrand & van Baaren, 2009, for an overview). Furthermore, these effects are not limited to the person being imitated, but can also be found in the person that is imitating (Stel & Vonk, 2010). Because the shared system for action observation and action execution causes individuals to automatically imitate one another, a first way in which it facilitates social interaction is by means of the positive effects related to imitation.

Second, research suggests that the MNS is related to several important social skills. One important social skill is the ability to understand the action goals and intentions of other persons (see Rizzolatti & Sinigaglia, 2010, for a review). When you see someone reaching, for example, it is relevant to know whether (s)he reaches for a coffee mug or for a knife (i.e., the action goal). Likewise, it is relevant to know whether the person reaches for the knife to slice vegetables or to stab you (i.e., the intention). Studies have shown that the MNS plays an important role in encoding action goals (e.g., Cattaneo, Caruana, Jezzini, & Rizzolatti, 2009; Hamilton & Grafton, 2006) and intentions (e.g., Iacoboni et al., 2005; Kaplan & Iacoboni, 2006). Understanding action goals and intentions, in turn, provides the basis for a number of other important social skills. One example of such a skill is the ability to perform tasks that require the cooperation of several persons. When carrying a couch downstairs with another person, for instance, it is important to take into account the movements, action goals, and intentions of your co-actor in order to avoid accidents (Knoblich & Sebanz, 2006). Indeed, in a recent EEG study it was confirmed that individuals employ the MNS to represent and anticipate the actions of their co-actor in joint action tasks (Kourtis, Sebanz, & Knoblich, 2013). A last social skill that has been linked to the perception-action system is empathy. More specifically, it has been argued that empathy is based on the co-representation of the actions and facial expressions of others in the MNS (e.g., Carr, Iacoboni, Dubeau, Mazziotta, & Lenzi, 2003). In accordance with this idea, it has been shown that individual differences in empathy are linked to individual differences in automatic imitation (e.g., Chartrand & Bargh, 1999; Müller, van Leeuwen, van Baaren, Bekkering, & Dijksterhuis, 2013) and in mirror brain activation (e.g., Gazzola, Aziz-Zadeh, & Keysers, 2006; Kaplan, & Iacoboni, 2006). The second line of research suggests, in other

words, that the MNS system allows us to understand observed actions from a first-person perspective. This, in turn, may allow us to understand the action goals and intentions of others, perform tasks with others, and empathize with others.

Finally, pathologies of social cognition have been linked to deficits in the perception-action system. In particular, it has been argued that social problems in autism spectrum disorder are caused by a disturbance of the MNS (Williams, Whiten, Suddendorf, & Perrett, 2001) or of brain regions modulating the MNS (Hamilton, 2013; Spengler et al., 2010). This is supported by findings of abnormal imitative behavior in these patients as expressed by a combination of decreased imitation accuracy (e.g., Stewart, McIntosh, & Williams, 2013; Williams, Whiten, & Singh, 2004) and increased imitation tendencies (e.g., Spengler et al., 2010; Williams et al., 2004). Interestingly, both types of imitation deficits have found to be related to the social difficulties experienced by individuals with autism spectrum disorder (Spengler et al., 2010; Stewart et al., 2013). These combined studies thus suggest that a disturbance of the MNS, be it directly or indirectly, can bring about profound social deficits as witnessed in autism spectrum disorder.

To conclude, evidence from different sources suggests that the shared system for perception and action serves an important social function. Not only does it smoothen social encounters, it also underlies several important social skills. This is corroborated by evidence for a disturbed MNS in individuals with autism spectrum disorder.

The Multi-Actor Mirror Neuron System

In the light of the research discussed above, it is warranted to say that individuals automatically co-represent the movements of others in their own motor system. However, the research conducted thus far has focused almost exclusively on the ability to represent the actions of a single agent. A fundamental, yet unanswered, question is therefore whether the MNS can also co-represent the movements of multiple agents. This is important because social interactions are seldom restricted to two people, but frequently include multiple actors whose behavior has to be monitored and understood. In a football game, for example, a striker often has to take into account the behavior of several defenders in order

to find a way to penetrate the defense. Given that the MNS plays an important role in social interaction, an intriguing possibility is that these multi-actor situations involve the online representation of multiple observed actions in the motor system.

Interestingly, some indirect evidence for the idea of a multi-actor MNS can be found in studies that investigated the effect of observing multiple movements onto one's own behavior. In one study, for instance, Tsai and colleagues (Tsai, Sebanz, & Knoblich, 2011) investigated imitative behavior at the inter-group level. More specifically, these authors examined how imitative responses were influenced by the overlap between the amount of actors and the amount of imitators. The results revealed that participants were faster to imitate the behavior when the amount of imitators matched the amount of actors (e.g., two actors and two imitators) compared to when they did not match (e.g., two actors and one imitator). This was interpreted as evidence for the idea that individuals include information regarding the amount of co-actors in the perception-action system.

In two other studies, the relation between the amount of actors and the probability of imitation was investigated. In an early study, Milgram, Bickman, and Berkowitz (1969) monitored the behavior of pedestrians as they passed by one to fifteen people looking at a sixth floor window. The results showed that pedestrians were more likely to copy this behavior as the sample of window watchers grew in number. Similarly, in a more recent study (Herrmann, Legare, Harris, & Whitehouse, 2013) it was shown that children are more likely to imitate observed behavior when it is demonstrated by two adult models at the same time compared to a single model or two consecutive models. Both these studies thus show that the probability of imitation is larger when the observed behavior is executed by multiple persons at the same time.

These preliminary studies show that automatic imitation is influenced by the amount of observed actors. A likely explanation for these findings is that the actions of the different actors were represented simultaneously in the motor system of the observer. In the current thesis, we aimed to investigate this possibility directly in a series of two experiments. In the first experiment, an automatic imitation task was used to investigate if and how individuals are influenced by multiple simultaneously observed movements. In the second experiment,

a motor TMS study was used to extend the multi-actor MNS account from the behavioral to the neural level.

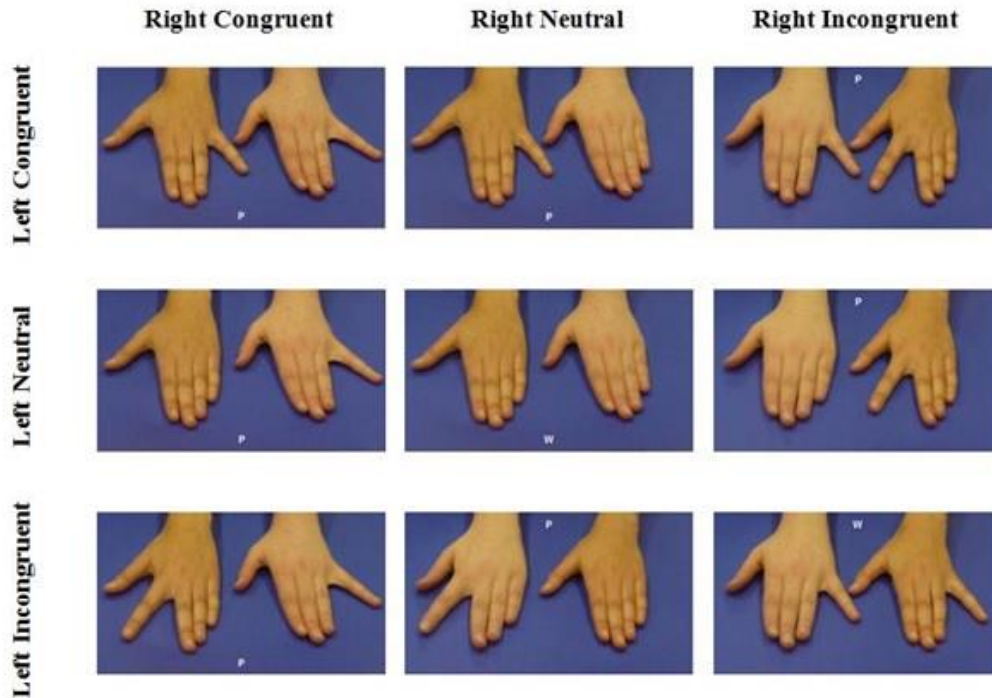


Figure 1. This figure represents the design of experiment 1. Each cell contains an example stimulus of the corresponding condition.

Experiment 1

Paradigm and Hypotheses

In the first study of this thesis, we used an adaptation of the imitation-inhibition paradigm to test whether human individuals can represent the movements of multiple actors simultaneously in their motor system. As discussed in the introduction, the imitation-inhibition paradigm is an automatic imitation task that is often used as a behavioral marker of MNS activation (Heyes, 2011). In contrast to the original paradigm, which includes only one hand, the current adaptation includes two different hands making a congruent (C), an incongruent (IC), or no (N) abduction movement with respect to the imperative cue (figure

1). This paradigm thus allows us to look at the congruency effect of both the hand on the left side (LC, LN, LIC) and the hand on the right side (RC, RN, RIC) of the screen. We can then investigate whether the movements of both hands are represented in the motor system of the observer by testing if a congruency effect is present for each of the two hands. Moreover, a congruency effect should be present for each hand independent of what the other hand is doing. That is, if two hand movements can be represented simultaneously in the MNS, the movements of each hand should be represented regardless of whether the other hand makes a movement and regardless of which movement the other hand makes.

If we manage to confirm that individuals are influenced by both hands at the same time, we can then also use this paradigm to investigate how individuals are influenced by the relationship between the actions of the two observed hands. That is, when two hands make a simultaneous movement, they can either make an identical movement or a different movement. When the two hands perform an identical movement, the multi-actor MNS account would predict that the actions of both hands are mapped onto the same motor representation. This account would thus predict increased activation of this motor representation. In other words, the multi-actor MNS account predicts a larger congruency effect for two identical observed movements than for a single observed movement. When the two hands perform a different movement, on the other hand, the multi-actor MNS account would predict that the two actions are mapped onto different motor representations. Translated to the imitation-inhibition task, the case of two different observed movements corresponds to the situation where one movement is congruent and the other movement is incongruent with respect to the imperative cue. Therefore, if the movements of both hands are represented in the motor system of the observer, one movement should cause facilitation and the other movement should cause interference. Because these effects are opposing forces, they should then cancel each other out.

Finally, it seems interesting to investigate how the multi-actor MNS relates to social cognition. As outlined in the introduction, the MNS may be crucial for the development of several important social skills. It is, however, not known whether the ability to represent multiple observed actions at the same time contributes to these skills. Nevertheless, this seems an important question given the fact that most social interactions exceed a dyadic

structure. Therefore, as a preliminary inquiry into the link between the multi-actor MNS and social cognition, we explored the relation between the ability to integrate multiple observed movements and empathy.

Method

Participants. 38 participants took part in the experiment ($M_{age} = 22.18$, $SD_{age} = 2.36$). All of them were right-handed females with good or corrected vision. Only female participants were included to optimize the overlap between the observed hands (i.e., two female hands) and the hands of the participants. Participants were paid 5 euro and signed an informed consent beforehand. The study was approved by the local Ethical Committee and all procedures were performed in accordance with the ethical standards laid down in the 1964 Helsinki Declaration.

Stimuli and Apparatus. The experiment was programmed in C with Tscope (Stevens, Lammertyn, Verbruggen, & Vandierendonck, 2006). Stimuli consisted of frames extracted from video clips (figure 1). These frames (1010 x 544 pixels) depicted two different female right hands, positioned next to each other on a blue background. The hands were positioned so they created mirror images of the participant's right hand (i.e., the response hand). To produce an illusion of movement, the hands were first presented in their neutral posture and were subsequently overwritten by a second picture of the hands in their final posture (see Catmur & Heyes, 2011, for a similar procedure). Both hands moved independently of one another and could either not move or perform an abduction movement of the index or little finger. Two types of video clips were created: one with hand A on the left side of the screen and hand B on the right side of the screen, and one the other way around. In order to record responses, a custom-made response box that detects when the finger leaves a sensor was used.

Empathy Questionnaire. Empathy was measured with the Interpersonal Reactivity Index (IRI) Measure of Empathy (Davis, 1983). According to the IRI, empathy is a

multidimensional construct that consists of perspective taking, empathic concern, fantasy, and personal distress. In agreement with previous research on automatic imitation (e.g., Chartrand & Bargh, 1999; Müller et al., 2013), we will only report relations with perspective taking (e.g., I sometimes try to understand my friends better by imagining how things look from their perspective) and empathic concern (e.g., I often have tender, concerned feelings for people less fortunate than me). These scales represent respectively cognitive and emotional empathy. Note, however, that relations with fantasy and personal distress never reached significance. Cronbach alpha coefficients in the current study were 0.85 for perspective taking and 0.73 for empathic concern.

Procedure. The experiment took about 30 minutes and consisted of two phases. To explore a possible influence of the imperative cue position, the cue was positioned at the top of the screen in one phase and at the bottom of the screen in the other phase. Each phase comprised a practice phase of 10 trials with feedback, followed by three blocks of each 90 trials without feedback. All of these blocks contained 10 trials of each condition within the left-side congruency (LC, LN, LIC) x right-side congruency (RC, RN, RIC) design, 5 of which were presented with W and 5 with P as imperative cue. After each block, participants had the opportunity to take a break. Trials were presented randomly, with the restriction that the same imperative cue could not appear on more than four consecutive trials. The position of the hands and the order of the phases was counterbalanced.

Each trial started with a picture of both hands in their neutral posture and a fixation cross for 500 ms. This was followed by the simultaneous presentation of the imperative stimulus and the hands in their final posture for a maximum of 2000 ms or until the response. After an inter trial interval of 1000 ms, the next trial started. Before the experiment, instructions appeared on the screen. The instructions requested participants to make an abduction movement with their right hand index finger when they saw W ('wijsvinger') and to make an abduction movement with their right hand little finger when they saw P ('pink'). Participants were asked to respond as fast as possible, but without making errors. After the experiment, participants were asked to complete the empathy questionnaire.

Data Analysis. All analyses were performed in R (R core team, 2013). Trials where no response was given before the response deadline (0.34%) were excluded from all analyses. Additionally, trials with a reaction time (RT) faster than 100 ms (0.05%) were considered as action slips and excluded as well. Finally, for the RT analyses, only correct trials were included and trials with a RT slower than 1000 ms (0.92%) were excluded to reduce the influence of outliers (see Catmur and Heyes, 2011, for a similar procedure). *T* tests represent two-tailed paired samples *t* tests. Correlation coefficients represent Pearson product-moment correlation coefficients. P-values of post-hoc tests were corrected for multiple testing (p_c) according to Holm's procedure (Holm, 1979). Cohen's *d* and partial eta squared (η_p^2) are reported as measures of effect size. Cohen's *d* is reported when the relevant analysis compares two means, whereas η_p^2 is reported when the relevant analysis compares more than two means.

To reduce the complexity of the data pattern, we will present three separate analyses that test our three main hypotheses. First, we test whether the left- and the right-side hand each have an independent influence. Second, we test whether a stronger congruency effect is observed when the two hands perform identical movements compared to when only one of the two hands moves. Finally, we investigate whether two different observed movements elicit opposing forces that cancel each other out.

Results

Representing two observed movements simultaneously. To determine whether a congruency effect was present for both hands, RTs and error rates were submitted to a 3 (left-side congruency: LC, LN, or LIC) x 3 (right-side congruency: RC, RN, or RIC) x 2 (imperative cue position: bottom or top) repeated measures MANOVA. The analysis of the RTs (figure 2a) revealed a main effect of left-side congruency, $F(2, 36) = 30.97$, $p < 0.001$, $\eta_p^2 = 0.63$, with faster RTs in LC (439 ms) than in LN (448 ms), $t(37) = -4.84$, $p_c < 0.001$, $d = 0.79$, and faster RTs in LN than in LIC (459 ms), $t(37) = -6.85$, $p_c < 0.001$, $d = 1.11$. Similarly, there was also a main effect of right-side congruency, $F(2, 36) = 22.91$, $p < 0.001$, $\eta_p^2 = 0.56$ with faster RTs in RC (438 ms) than in RN (450 ms), $t(37) = -5.83$, $p_c <$

0.001, $d = 0.95$, and faster RTs in RN than in RIC (457 ms), $t(37) = -3.39$, $p_c < 0.005$, $d = 0.55$. No main effect of imperative cue position was observed, $F(1, 37) = 2.38$, $p = 0.13$. The analysis also revealed an interaction between left-side congruency and right-side congruency, $F(4, 34) = 3.00$, $p < 0.05$, $\eta_p^2 = 0.26$. This seems at odds with the hypothesis that both hands have an influence irrespective of what the other hand is doing. However, an interaction does not necessarily imply that the presence of the congruency effect depends on the actions of the other hand. Instead, it could also imply that a congruency effect is always present for both hands, but varies in strength depending on the actions of the other hand. In line with this idea, simple main effect analyses indicated that a congruency effect was present for both the left-, $F(2, 36) \geq 8.39$, $p_c \leq 0.001$, $\eta_p^2 \geq 0.31$, and right-side hand, $F(2, 36) \geq 12.61$, $p_c < 0.001$, $\eta_p^2 \geq 0.41$, regardless of the action (C, N, or IC) of the other hand¹. No other two- or three-way interactions were observed, $p > 0.26$.

The error analysis (figure 2b) revealed a similar pattern with a main effect of left-side congruency, $F(2, 36) = 12.24$, $p < 0.001$, $\eta_p^2 = 0.41$, and right-side congruency, $F(2, 36) = 22.76$, $p < 0.001$, $\eta_p^2 = 0.56$. Post-hoc analyses revealed that the main effect of left-side congruency was due to lower error rates in LC (2.23%) than in LN (2.92%), $t(37) = -2.36$, $p_c < 0.05$, $d = 0.38$, and lower error rates in LN than in LIC (4.39%), $t(37) = -4.35$, $p_c < 0.001$, $d = 0.71$. Similarly, post-hoc analyses for the main effect of right-side congruency revealed lower error rates in RC (2.17%) than in RN (2.97%), $t(37) = -3.06$, $p_c < 0.005$, $d = 0.50$, and lower error rates in RN than in RIC (4.39%), $t(37) = -4.30$, $p_c < 0.001$, $d = 0.70$. There was no main effect of imperative cue position, $F < 1$. The interaction between left-side and right-side congruency was significant, $F(4, 34) = 3.15$, $p < 0.05$, $\eta_p^2 = 0.27$. Nevertheless, subsequent simple main effect analyses again revealed that a congruency effect was present for each of the two hands irrespective of what the other hand was doing (C, N, or IC). For the left-side hand, the congruency effect was significant under RN and RIC, $F(2, 36) \geq 4.63$, $p_c < 0.03$, $\eta_p^2 \geq 0.21$, and marginally significant under RC, $F(2, 36) = 2.79$, $p_c = 0.07$, $\eta_p^2 = 0.13$. For the right-side hand, the congruency effect was present under

¹ Please note that the pattern underlying the left-side congruency x right-side congruency interaction is not investigated here because it is complex and has no direct relevance to our research questions. The exploration of the interaction pattern would therefore only make the results section unnecessarily complicated. For completeness, the pattern behind the interaction is explored in appendix.

all levels of left-side congruency, $F(2, 36) \geq 4.05$, $p_c < 0.03$, $\eta_p^2 \geq 0.18^1$. Again, there were no other two- or three-way interactions, $p > 0.29$.

Finally, we examined whether individual differences in empathy were related to the magnitude of the RT congruency effect (IC – C) of both hands by computing correlations with the empathy scales referring to perspective taking and empathic concern. These analyses showed that higher scores on perspective taking were related to a larger congruency effect, both for the left-, $r = 0.46$, $p = 0.005$, and the right-side hand, $r = 0.48$, $p < 0.005$. Empathic concern, on the other hand, was not related to the congruency effect of either the left-, $r = 0.05$, $p = 0.76$, or right-side hand, $r = 0.15$, $p = 0.37$.

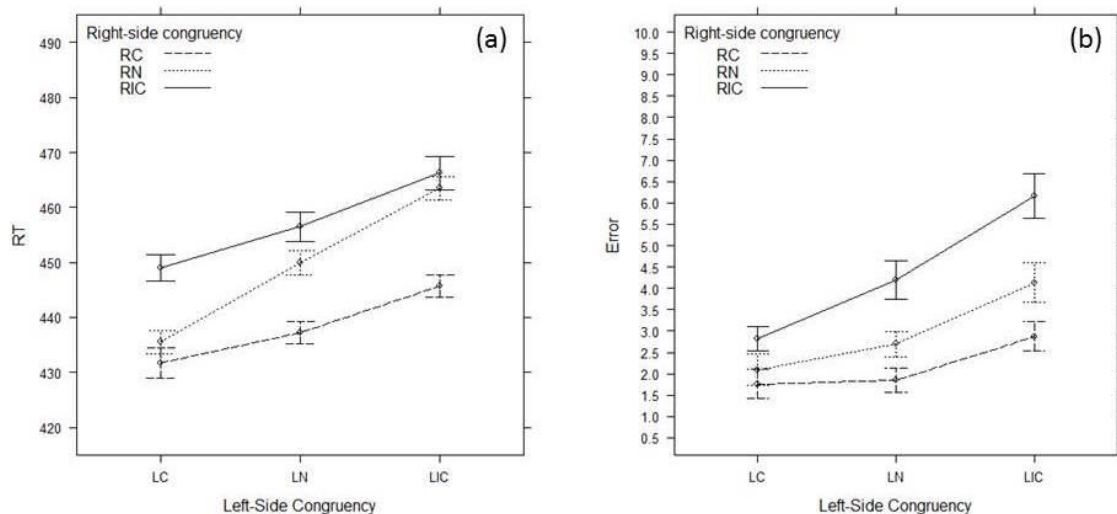


Figure 2. Reaction times (a) and error rates (b) of the left-side congruency x right-side congruency analysis. Error bars represent standard errors of the mean (SEMs) corrected for within-subject designs according to Morey (2008).

Representing two identical observed movements. Next, in order to determine whether seeing two identical actions results in a stronger activation of the corresponding motor representation, we took the relevant conditions (IC/IC, C/C, IC/N, N/IC, C/N, and N/C)² and submitted the RTs and error rates to a 2 (number of hand movements: one vs.

² Please note that these codes represent the following: MovementLeftSideHand/MovementRightSideHand. For example, IC/N means that the left-side hand performed an incongruent action while the right-side hand did not move.

two) x 2 (congruency: IC vs. C) repeated measures MANOVA. Because the effect of imperative cue position failed to reach significance in the previous analysis, this variable was no longer considered in this and further analyses. The RT analysis (figure 3a) revealed a main effect of congruency, $F(1, 37) = 65.67, p < 0.001, d = 1.32$, with responses in IC (463 ms) being slower than responses in C (434 ms), but no main effect of number of hand movements, $F < 1$. Crucially, the analysis also revealed an interaction between number of hand movements and congruency, $F(1, 37) = 6.91, p = 0.01, d = 0.43$, showing that the congruency effect was larger when two hands acted identically (IC – C = 34 ms) compared to when only one hand acted (IC – C = 24 ms).

The analysis of the errors rates (figure 3b) again showed a main effect of congruency, $F(1, 37) = 41.98, p < 0.001, d = 1.05$, with more errors in IC (5.16%) than in C (1.87%), but also a main effect of number of hand movements, $F(1, 37) = 6.25, p < 0.05, d = 0.41$, with more errors when two hands acted (3.96%) instead of one (3.07%). Importantly, the interaction between number of hand movements and congruency was again significant, $F(1, 37) = 14.02, p < 0.001, d = 0.61$, with a larger congruency effect when both hands acted identically (IC – C = 4.39%) compared to when only one hand acted (IC – C = 2.19%).

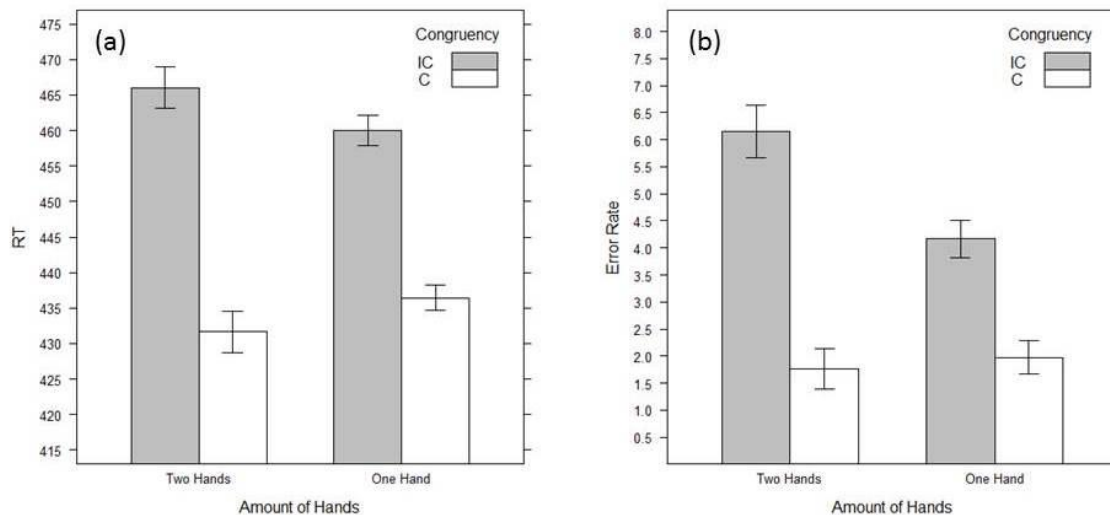


Figure 3. Reaction times (a) and error rates (b) of the number of hands x congruency analysis. Error bars depict SEMs corrected for within-subject designs according to Morey (2008).

Finally, we investigated whether individual differences in empathy were related to the capacity of representing two hands at the same time by calculating the partial correlation between empathy scores and the RT congruency effect of two identical hands (IC/IC – C/C) while controlling for the RT congruency effects of the left- (IC/N – C/N) and right-side hand (N/IC – N/C). This revealed that participants with higher scores on perspective taking experienced a larger influence from two hands acting identically, $r = 0.38$, $p < 0.05$. No correlation was observed for empathic concern, $r = 0.09$, $p = 0.61$.

Representing two different observed movements. Finally, we investigated whether the movements of both hands were represented when they acted differently. We reasoned that this should result in facilitation from the congruent hand and interference from the incongruent hand at the same time, cancelling each other out. To investigate this, we examined whether the RTs and error rates in the different movements conditions (MEAN C/IC)³ differed from the RTs and error rates in the no movements condition (N/N). Both for RTs (MEAN C/IC: 447 ms vs. N/N: 450 ms), $t < 1$, and error rates (MEAN C/IC: 2.85% vs. N/N: 2.69%), $t < 1$, no difference was observed between MEAN C/IC and N/N, suggesting that the facilitation and interference effects cancelled each other out.

However, an alternative explanation for this null effect could be that it reflects an inability to process two different movements simultaneously. In order to exclude this possibility, we performed additional analyses to test the alternative hypotheses that either none or only one of the two hands was processed when they performed different movements. First, to exclude the possibility that no processing occurred in the different movements conditions, we capitalized on the observation that some subjects were influenced more by congruent than by incongruent movements (and vice versa). Under the assumption that processing occurred when the two hands were moving differently, we expected that participants who showed a facilitation bias in the single movement conditions (N/N – MEAN C/N > MEAN IC/N – N/N) should also show a facilitation bias in the different movements conditions (N/N – MEAN C/IC > 0). A correlational analysis (figure

³ Please note that this code represents the fact that the C/IC and IC/C conditions were averaged. Similar codes will also be used further on in the text. For example, MEAN C/N means that the C/N and N/C conditions were averaged.

4a) confirmed this prediction, $r = 0.84$, $p < 0.001$, arguing against the idea that no processing occurred when both hands acted differently. Second, to rule out the possibility that only the left- or only the right-side hand was processed when the two hands acted differently, we computed the correlation between the facilitation bias in the C/IC condition ($N/N - C/IC$) and the facilitation bias in the IC/C condition ($N/N - IC/C$). If only one of the two hands was represented one should see a negative relation, whereas a positive relation should be observed if both hands were represented. For example, when only the left hand is represented, a facilitation effect should be apparent in the C/IC condition ($N/N - C/IC > 0$), but an interference effect should be apparent in the IC/C condition ($N/N - IC/C < 0$). When both hands are represented, on the other hand, a facilitation bias in the C/IC condition should still be apparent in the IC/C condition. The correlation analysis (figure 4b) between the two facilitation biases revealed a positive correlation, $r = 0.48$, $p < 0.005$, speaking against the possibility that participants represented only one hand when the hands performed different movements.

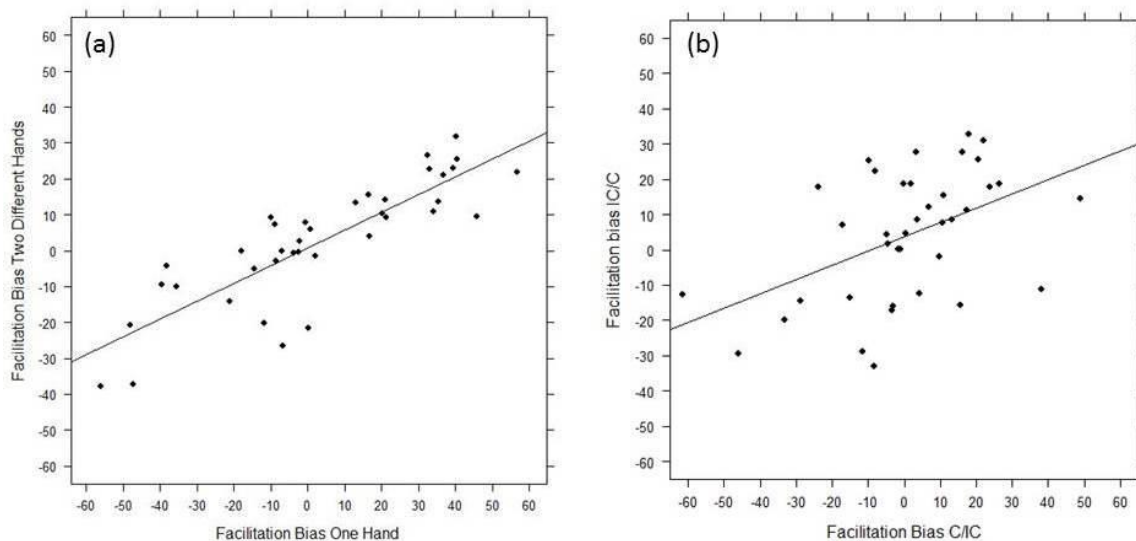


Figure 4. (a) Correlation between the facilitation bias in the single hand movement conditions and the different hand movements conditions, (b) correlation between the facilitation bias in the C/IC condition and the IC/C condition. The lines represent linear regression fit lines.

Discussion

In the current experiment, we set out to explore the possibility that the human MNS is not restricted to representing the movements of one actor, but is also capable of representing the movements of multiple actors simultaneously. For this purpose, we used an automatic imitation task that is often seen as a behavioral marker of MNS activation. More specifically, we adapted the imitation-inhibition paradigm to include two hands instead of one hand. We predicted to see a congruency effect for each of the two hands regardless of what the other hand did. It was found that both hands produced a congruency effect, but that these congruency effects were not independent of one another. In line with our hypothesis, however, follow-up analyses showed that it was the strength, but not the presence of the congruency effects that depended on the actions of the other hand. This suggests that both hands were always processed, albeit not entirely independent of one another.

To explore how individuals were influenced by the relation between the movements of the observed hands, we then zoomed in on two possible situations: two hands acting identically and two hands acting differently. When two identical movements were observed, a larger congruency effect was found compared to when a single movement was observed. Importantly, this additive effect cannot be explained by social facilitation (Zajonc, 1965). Social facilitation is the phenomenon that individuals perform a task better or worse in the presence of others. A social facilitation account would therefore predict that the influence of the number of observed movements is the same when the two hands act congruently and when the two hands act incongruently with respect to the required movement. The results of the current study, however, indicated an interaction between the number of observed movements and congruency. That is, an increased facilitation effect was found for two congruent observed movements, whereas an increased interference effect was found for two incongruent observed movements. This suggests that, instead of social facilitation, the corresponding motor representation was activated more strongly when the same action was seen twice.

When two different movements were observed, a congruent and an incongruent movement, the results indicated the presence of a concurrent facilitation and interference effect. Specifically, the results suggested that these two opposite effects cancelled each other out. Additional analyses further corroborated this idea by excluding the alternative explanations that neither or only one of the two hands was processed when the two hands acted differently. It thus appears that the actions of both hands were represented in the motor system even when they made different movements.

Finally, through correlations with empathy, we showed that the ability to represent multiple observed movements simultaneously was linked to differences in social cognition. First, it was shown that the congruency effects of both the left- and right-side hand were related to empathy. Second, it was shown that the congruency effect of two identical hand movements was related to empathy as well. Importantly, the relation with two identical movements was observed while the individual influence of the left- and right-side hand was controlled. This means that this relation cannot be reduced to the capacity of representing single hand movements. Instead, it suggests that the ability to adapt the perspective of another person is related to the specific ability of integrating the movements of multiple persons. These results indicate, in other words, that the ability to co-represent the movements of multiple actors simultaneously is related to social cognition. It is interesting to note, however, that the above relations were only found for the cognitive component (i.e., perspective taking), but not for the emotional component (i.e., empathic concern) of empathy. This is in correspondence with the study of Chartrand and Bargh (1999) in which it was found that perspective taking, but not empathic concern, was related to motor mimicry. Yet, other studies have linked automatic imitation to emotional empathy as well (Müller et al., 2013; Sonnby-Borgström, 2002; Sonnby-Borgström, Jönsson, & Svensson, 2003). The same distinction can be found in research on the MNS. While some studies have linked MNS activation to cognitive empathy (e.g., Gazzola et al., 2006; Milston, Vanman, & Cunnington, 2013), others have linked it to emotional empathy (e.g., Pfeifer, Iacoboni, Mazziotta, & Dapretto, 2008; Singer et al., 2004). A possible explanation for these contradictory results may be found in the different types of stimuli that were used in these studies. Whereas most studies that found a relation with emotional empathy used

emotionally laden stimuli (e.g., facial expressions), most studies that found a relation with cognitive empathy used neutral stimuli (e.g., hands). Since the current study also used neutral stimuli, this may explain why we observed a relation with cognitive empathy, but not with emotional empathy. Either way, it will be a task for further research to investigate explicitly how different forms of empathy are related to the perception-action system (see, Baird, Scheffer, & Wilson, 2011, for a similar proposal).

Implications. The findings of this study open up several new perspectives and research questions. First, the current study allows to integrate previous research on imitation in multi-actor situations (Tsai et al., 2011; Herrmann et al., 2013; Milgram et al., 1969). Each of these studies has found that automatic imitation tendencies are influenced by the amount of actors that perform a certain behavior. Despite the apparent similarity between these studies, however, each of them provided a different explanation for the obtained effect. The results of the current study, on the other hand, allow to put forward a shared underlying mechanism. Specifically, our results suggest that the findings of these previous studies were based on the capacity to represent the movements of multiple actors simultaneously in the motor system.

An interesting consequence of explaining multi-actor imitation effects in terms of a multi-actor MNS is that it allows to reinterpret the results that were obtained in earlier research. The multi-actor MNS account allows, for instance, to reinterpret of the finding that individuals are more likely to copy behavior when it is performed by multiple agents (e.g., Hermann et al., 2013; Milgram, Bickman, & Berkowitz, 1969). According to these studies, this phenomenon can be explained by interpretative processes. For example, when a group of people is looking in a certain direction, individuals are likely to copy this behavior because odds are that something interesting is happening there. The current study, on the other hand, suggests that an action performed by multiple people is imitated more often because this activates the corresponding motor representation to a greater extent. This mere motor activation could then trigger interpretative processes (e.g., “does the behavior make sense?”) that determine whether the evoked action is eventually executed or inhibited. In this view, several people looking in a certain direction would provide a strong

impetus for imitation, in advance to interpretative processes, because of the increased motor activation resulting from multiple action observation. Indeed, it seems evolutionary adaptive to have a mechanism that automatically increases imitative tendencies with the amount of observed actors. Not only may it allow to detect interesting things (e.g., when a group of people is looking at something), it may also allow to avoid danger (e.g., when a group of people is running in a certain direction).

In addition to the field of imitation, the results of the present study also have implications for the field of joint action. Research has shown that people represent both the task (e.g., Atmaca, Sebanz, & Knoblich, 2011; Sebanz, Knoblich, & Prinz, 2003) and the actions (e.g., Kourtis et al., 2013) of their co-actors when they perform a task together. Similar to research on the MNS, however, research on joint action has focused exclusively on dyadic situations. This stands in contrast with the fact that many tasks in daily life require the cooperation of multiple persons. Hence, an interesting possibility that follows from the current study is that tasks requiring the cooperation of multiple persons (e.g., a football game) rely on the ability to represent the tasks and actions of all these people.

Finally, the results of the present study may have implications for research on pathologies affecting social cognition, such as autism spectrum disorder. That is, we found that the ability of co-representing the movements of multiple actors simultaneously is related to the social skill of being able to take into account another's perspective. This suggests that individuals with poor social skills may have specific problems with monitoring the behavior of several persons simultaneously. It therefore seems interesting to investigate such problems in individuals with autism spectrum disorder, a condition that is characterized by social deficits and has been linked to the MNS (e.g., Spengler, Bird, & Brass, 2010; Williams, Whiten, & Suddendorf, 2001).

Limitations. The current study is also limited in several respects. First, it could be argued that the obtained results were due to spatial compatibility instead of imitative compatibility (e.g., Jansson, Wilson, Williams, & Mon-Williams, 2007). Imitative compatibility refers to whether the observed movement involves the same finger as the required movement. Spatial compatibility, on the other hand, refers to whether the observed

movement is in the same direction as the required movement. In the present experiment, however, an abduction movement of the index finger was always a movement to the left and an abduction movement of the little finger was always a movement to the right, both for the observed and executed movements. As a result, it is impossible to disentangle the influence of imitative and spatial compatibility. Nevertheless, a rising amount of studies has now shown that compatibility effects in automatic imitation studies reflect more than just spatial compatibility (see Heyes, 2011, for an overview). Especially relevant to the current experiment, is the study of Catmur and Heyes (2011), in which it was shown that both types of compatibility contribute independently to the pattern of response times in an abduction movement imitation-inhibition paradigm. Considering that these authors used the same task (i.e., imitation-inhibition task) and the same observed movements (i.e., abduction movement of the index or little finger), it seems unlikely that the results of the current study could be explained solely in terms of spatial compatibility. This interpretation is further strengthened by the fact that the congruency effects of both the left- and the right-side hand were correlated with empathy. That is, while it is well established that automatic imitation (e.g., Chartrand & Bargh, 1999) and MNS activation (e.g., Gazzola et al., 2006) are related to empathy, a relation between spatial compatibility and empathy has not been described yet. Indeed, it seems unlikely that a social skill like empathy would be related to a non-social effect like spatial compatibility. Notwithstanding these arguments, further research should try to disentangle imitative and spatial compatibility in an imitation-inhibition task with multiple observed movements.

Second, the current study only included females. This was done because previous research has shown that automatic imitation (e.g., Liepelt & Brass, 2010; Mondillon, Niedenthal, Gil, & Droit-Volet, 2007) and MNS activation (e.g., Buccino et al., 2004; Tai, Scherfler, Brooks, Sawamoto, & Castiello, 2004) is modulated by self-other overlap. Because the observed hands were female hands, the inclusion of only female participants increased the self-other overlap. This procedure thus optimized the paradigm for studying automatic imitation effects. However, a disadvantage of this approach is that it is not clear if the same effects can be obtained when there is no gender overlap between the observed

actors and the observer. Further research will be necessary to replicate the effects obtained in this study in mixed samples and in samples without actor-observer gender overlap.

Third, the method we employed is not a direct measure of MNS activation. Even though it is widely accepted that the imitation-inhibition task relies on the MNS (Heyes, 2011), the hypothesis of a multi-actor MNS is ideally investigated at the neural level. In an attempt to extend the multi-actor MNS account from behavioral measures to neural measures, we performed a motor TMS study.

Experiment 2

Paradigm and Hypotheses

In the second experiment of this thesis we designed a motor TMS study to investigate at the neural level whether two identical observed movements activate the corresponding motor representation more strongly than a single observed movement. As outlined in the introduction, motor TMS allows to measure the primary motor cortex activation in response to observed actions and hence provides a more direct test of the multi-actor MNS account. Similar to earlier research (e.g., Catmur et al., 2007, 2010), participants passively observed finger movements while TMS pulses were provided over the primary motor cortex. More specifically, participants saw two hands on the screen and either one or both hands made an abduction movement of the index or little finger. Importantly, the two hands always made an identical movement when they moved together (figure 5). To have a baseline, we also added a condition in which neither of the two hands moved. In line with the first experiment, we expect to see larger MEP deviations from the baseline when two hands act identically compared to when only one hand acts. Moreover, we expect these MEP deviations to be specific for the muscle that corresponds to the muscle involved in the observed action. An observed index finger abduction movement should thus selectively activate the index finger abductor muscle, whereas an observed little finger abduction movement should selectively activate the little finger abductor muscle.

It should be noted, however, that this study was primarily conducted as a pilot study and that its main aim was to validate the paradigm and the methods. Consequently, only a small sample of thirteen participants was included. Although this has proven to be sufficient for earlier research (e.g., Catmur et al., 2010), the results of experiment 1 suggest that the effect of interest is of small magnitude. That is, the comparison of the congruency effect for two identical observed movements with the congruency effect for a single observed movement yielded an effect size of $d = 0.43$. According to Cohen's rules of thumb this is a small effect size (Cohen, 1988). Assuming the same effect size for the current experiment, the statistical power to find the predicted effect at the 0.05 significance level is merely 0.30.

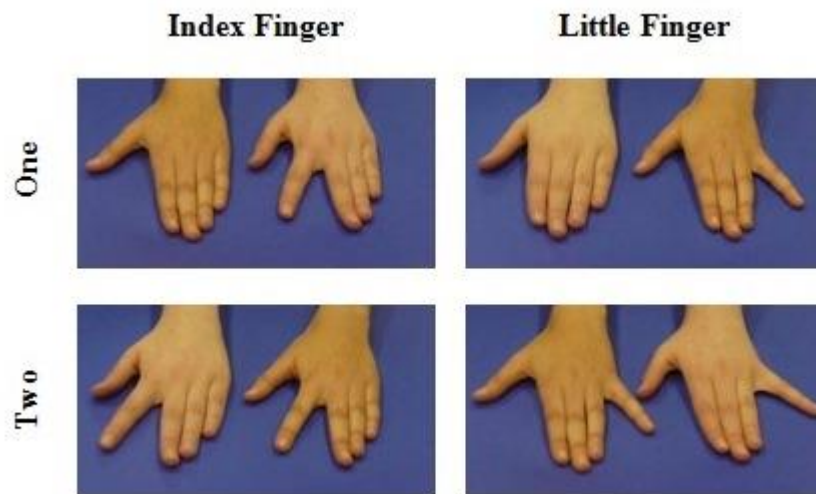


Figure 5. The design of experiment 2. Each cell represents an example stimulus for the corresponding condition. In addition to these four conditions, a baseline stimulus was included in which neither of the two hands moved.

Method

Participants. Thirteen right-handed persons ($M_{\text{age}} = 24.39$, $SD_{\text{age}} = 5.65$) participated in this study in exchange for 25 euros. Only male participants were included due to ethical reasons. All subjects had good or corrected vision, had no history of

neurological or psychiatric disorders, and complied to the TMS safety precautions (Rossi et al., 2009). Written informed consent was given before the start of the experiment. The study was approved by the Medical Ethic Review Board of the Ghent University Hospital and was conducted in accordance with the 1964 Helsinki Declaration.

Stimuli and Apparatus. The experiment was programmed in C with Tscope (Stevens et al., 2006). For this experiment, we selected the relevant stimuli from experiment 1. More specifically, we selected the stimuli in which both hands made an identical movement, the stimuli in which one hand made a movement, and the stimuli in which neither of the two hands made a movement. The experiment thus included seven possible final hand postures, namely Neutral/Neutral (N/N), IndexFinger/Neutral (I/N), Neutral/IndexFinger (N/I), Neutral/LittleFinger (N/L), LittleFinger/Neutral (L/N), IndexFinger/IndexFinger (I/I), and LittleFinger/LittleFinger (L/L). Note that these stimuli mirrored the hand from which the MEPs were recorded (i.e., the right hand).

Procedure. The experiment took about 40 minutes and consisted of three blocks. Each block contained 105 trials, distributed equally among the seven final hand postures. The position of the hands was counterbalanced.

Each trial started with a picture of both hands in their neutral posture and a fixation cross at the bottom of the screen for 500 ms. The hands were then presented in their final posture for a duration of 1000 ms. The TMS pulse was delivered at a variable moment (200, 300, or 400 ms) within this 1000 ms interval. The trial ended with the presentation of a white screen for a variable duration of 4000, 5000, or 6000 ms.

To maintain the attention of the participants, they were asked to monitor the two hands for the appearance of a flesh colored circle at the moment of the transition from the initial hand posture to the final hand posture (see Catmur et al., 2007, 2010, for a similar procedure). The color of the circle was different for each of the two hands and was determined by calculating the mean intensity of the red, green, and blue component of each pixel on the respective hand. In addition, the alpha value of the circle color was put at 80% to make it more transparent. The circle appeared in 20% of the trials and appeared an equal

amount of times for each final hand posture. Furthermore, the circle appeared equally on four possible locations, namely the two index fingers and the two little fingers (i.e., the fingers that could move). Each time a circle had appeared, the presentation of the hands in their final posture was followed by a screen that asked participants to indicate verbally on which of the four possible fingers the circle had been presented. In these trials, the white screen was presented after the experimenter had typed in the answer.

TMS and Electromyography. Single pulse TMS stimulation was applied with a biphasic magnetic stimulator (Rapid² Magstim, Whitland, UK) that was connected to a polyurethane-coated figure-of-eight coil (5.4-cm inner diameter windings). The coil was positioned tangentially over the hand area of the left primary motor cortex with a mechanical arm. The handle of the coil pointed backwards and formed an angle of 45 degrees with respect to the sagittal plane. Electromyographical (EMG) activity was recorded from the index finger abductor muscle (i.e., the first dorsal interosseus; FDI) of the right hand with the ActiveTwo system (BioSemi, Amsterdam, The Netherlands) using sintered 11 x 17-mm active Ag–AgCl electrodes. Note that, in contrast to earlier research (e.g., Catmur et al., 2007, 2010), we did not record MEPs from the little finger abductor muscle (i.e., the abductor digiti minimi; ADM). This was done because measuring MEPs simultaneously from both the FDI and the ADM requires compromises regarding the stimulation location and the stimulation intensity (e.g., Catmur et al., 2007, 2010). By restricting measurements to the FDI we could thus obtain finer MEP estimates.

Before the start of the experiment, the hotspot within the left primary motor cortex hand area was determined as the stimulation site that produced the largest MEPs in the FDI. When the hotspot was found, the motor threshold was determined as the stimulation intensity that produced an ≥ 50 μ V peak to peak MEP in the FDI in 50% of the pulses. Next, stimulation intensity was set at 110% of the motor threshold and was subsequently adjusted until stimulation resulted in an average peak to peak MEP of 1 mV in the FDI.

Data Analysis. All analyses were performed in R (R core team, 2013). First, trials in which a circle had appeared were excluded from the analysis. Next, we calculated the

root mean square (RMS) of the FDI background EMG signal in the 500 ms before the pulse. Trials in which the RMS exceeded 50 μV were excluded (0.51%). Furthermore, trials in which the FDI MEP amplitude was below 50 μV were excluded as well (1.10%). Finally, we excluded trials in which the FDI MEP amplitude was more than 2 SD above or below the individual mean from the remaining trials (5.12%). Note that the 2 SD criterion was applied separately for each block to account for variability in the MEPs due to differences in coil position and adaptation over blocks.

For the TMS analysis, we performed a 2 (moving finger: index finger or little finger) x 2 (number of movements: one or two) x 3 (pulse moment: 200, 300, or 400 ms) repeated measures MANOVA. To control for variability between individuals, the analysis was performed on the normalized MEPs. These were calculated by dividing the MEPs in each condition with the MEPs in the baseline condition (N/N) at the corresponding pulse moment. Cohen's d was used as a measure of effect size.

Results

Attentional task. The mean percentage of correct responses on the probe trials was 69% ($SD = 14\%$). To check whether accuracy on the attentional task was stable over the three blocks, we performed a one-way repeated measures MANOVA with block (one, two, or three) as a factor. This revealed that the attentional task performance did not differ between the blocks, $F < 1$, with a mean accuracy of 69% in all three blocks.

TMS data. The FDI MEP analysis (figure 6) revealed a marginally significant main effect of finger, $F(1, 12) = 3.46$, $p = 0.09$, $d = 0.52$, with larger MEPs when the index finger moved (1.04) compared to when the little finger moved (1.00). The main effect of number of movements was also marginally significant, $F(1, 12) = 3.34$, $p = 0.09$, $d = 0.51$, with larger MEPs when two fingers moved (1.04) compared to when one finger moved (1.01). The main effect of pulse moment did not reach significance, $F < 1$. The crucial finger x number of movements interaction did not reach significance, $F < 1$, and neither did the

three-way interaction finger x number of movements x pulse moment, $F(2, 11) = 1.44$, $p = 0.28$. None of the other interactions reached significance either, $F_s < 1$.

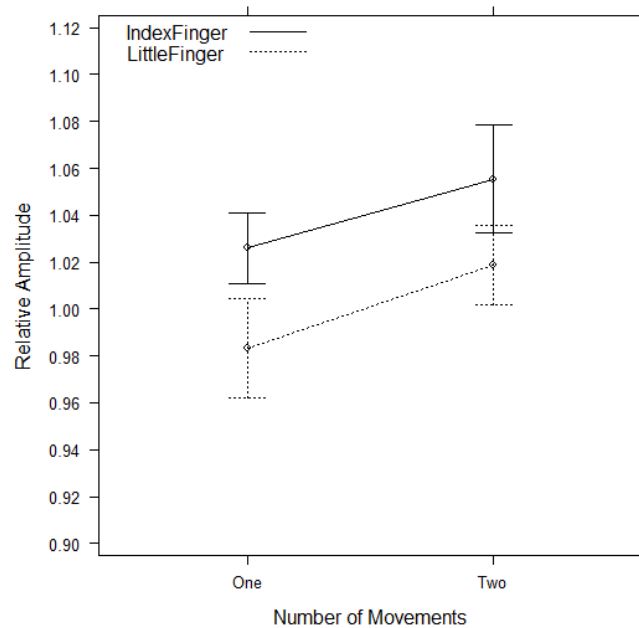


Figure 6. Relative amplitudes of the finger x number of movements analysis. Error bars depict SEMs corrected for within-subject designs according to Morey (2008).

Discussion

In the second study of this thesis we aimed to directly test the involvement of the MNS in representing simultaneous observed actions. More specifically, we aimed to test the idea that multiple identical observed movements activate the relevant mirror neurons to a greater extent than a single observed movement. To this end, we designed and piloted a motor TMS experiment in which participants saw two hands making finger movements. The results revealed that the MEPs in the index finger abductor muscle (i.e., the FDI) were larger when participants observed an index finger movement compared to when they observed a little finger movement. This is in line with the idea that observed movements selectively activate the neurons involved in the execution of that movement (e.g., Maeda et al., 2002; Schütz-Bosbach et al., 2006). Contrary to our expectations, however, this effect

was not modulated by the number of hands that made a movement. Instead, the FDI MEPs increased both when two identical index finger movements were observed and when two identical little finger movements were observed. This speaks against the idea of a specific increase in MNS activation when two identical movements are observed. If this were the case, an increase in FDI MEP amplitude should only have been present for observed index finger movements. The fact that FDI MEPs increased regardless of whether the hands made an index finger or little finger movement, on the other hand, may be explained as the result of expectancy violation. That is, stimuli in which a single hand moved (I/N, N/I, L/N, N/L) occurred twice as often as stimuli in which both hands moved (I/I, L/L). The larger MEPs when seeing a movement of both hands could thus reflect the unexpectedness of these stimuli. Since the two movements stimuli were equally unexpected when the two hands moved the index finger and when the two hands moved the little finger, this can explain the main effect of number of observed movements in the absence of an interaction with finger.

A possible explanation for the absence of the expected muscle-specific additive effect could be found in the literature on the rubber hand illusion. In this literature, it has been shown that it is possible to elicit the feeling of owning a supernumerary limb (e.g., two right hands; Ehrsson, 2009; Guterstam, Petkova, & Ehrsson, 2011; Newport, Pearce, & Preston, 2010). To explain this, it has been argued that the same neural population represents the original limb and the supernumerary limb by splitting up into two subpopulations (Ehrsson, 2009; Guterstam et al., 2011). Applied to the current experiment, it could be argued that the relevant mirror neurons split up into two subpopulations when the two hands made an identical movement. Indeed, in this case the neural output is expected to be the same for two hands making an identical movement and for a single hand making a movement. An alternative explanation could be that participants were not able to represent the movements of both hands when they acted together. Instead, they may have represented only the left-side hand or only the right-side hand. If this were the case, a muscle-specific additive effect is also not expected.

However, both explanations are in contrast with the results that were obtained in experiment 1. That is, in experiment 1 we found a larger congruency effect when two identical movements were observed compared to when a single movement was observed.

One possible explanation for this discrepancy could lie in the fact that experiment 2 only included males, whereas experiment 1 only included females. Because the observed hands belonged to females, the self-other overlap was lower for participants in experiment 2 than for participants in experiment 1. In accordance with research that has implicated self-other overlap as a moderator of automatic imitation (e.g., Liepelt & Brass, 2010; Mondillon, Niedenthal et al., 2007) and mirror brain activation (e.g., Buccino et al., 2004; Tai et al., 2004), it could be argued that the self-other overlap was insufficient in the current study to induce mirror activation.

Yet, an arguably more likely explanation for the disagreement between experiment 1 and 2 is that the sample size of the current study was too small to obtain meaningful results. That is, it is well known that the precision of statistical estimates is positively related with the sample size. This is especially relevant for small effects because imprecise estimates can easily render them invisible. With regard to the current study, the results of experiment 1 suggested that the effect of interest is likely to be of small magnitude ($d = 0.43$). The small sample of thirteen subjects may therefore have been too small to observe the predicted effect. In support of this idea, an a-priori power analysis identified that the statistical power of this study to detect an effect with a true effect size equal to the relevant effect size of experiment 1 was a mere 30 percent. In addition to the absence of the predicted effect, the poor power of the study may also explain why the two main effects did not reach the conventional levels of statistical significance (i.e., $p < 0.05$). In sum, the small sample of the current study makes it hard to make strong claims about the nature of the obtained results. Therefore, more participants will be needed before the results of this study can be interpreted with confidence.

Since this study was primarily intended as a pilot study, an important aim was to validate the experimental paradigm. A first aspect of the paradigm that required validation was the attentional task. The mean accuracy on this task (69%) suggests that the task was challenging, but not too hard (chance level = 25%). It is therefore likely that the task managed to maintain the attention of the participants to the hands. Importantly, the accuracy on the probe task proved to be constant over the three blocks, indicating that attention was sustained throughout the experiment. A second aspect that required validation

was the appropriateness of the stimulus material in a TMS context. The results indicated larger FDI MEPs in response to observed index finger movements than to observed little finger movements. This suggests that observed index finger movements activated the neurons involved in the execution of index finger movements to a greater extent than observed little finger movements did. The neural activation elicited by the stimuli thus appears to be specific to the stimulus that was presented, confirming the validity of the stimuli in a TMS context.

To conclude, the results of the current study do not support the idea that multiple identical observed movements activate the corresponding motor representation more strongly than a single observed movement. However, the fact that the study was underpowered makes it hard to interpret the results. More participants will have to be included in the study in order to obtain a clear view on the data.

Conclusion

The goal of this master thesis was to explore the possibility that human individuals are able to represent the movements of multiple actors simultaneously in their motor system. This proposition was investigated in a series of two experiments. In the first experiment, the imitation-inhibition paradigm was adapted so that participants saw two task-irrelevant hands making movements independent of one another. In line with the idea that the movements of two actors can be represented simultaneously in the motor system, it was shown that the response times and error rates of the participants were influenced by the movements of both hands. Moreover, it was shown that the influence of the hand movements was dependent on whether the two hands performed identical or different movements. Specifically, it was found that two identical observed movements had a larger influence than a single observed movement, whereas two different observed movements had an opposing influence. The larger influence of two identical hand movements was interpreted in terms of a relation between the number of observed identical movements and the amount of activation in the corresponding motor representation. The opposing influence

of two different movements was seen as an indication that two different motor representations were activated.

In the second experiment, we aimed to expand the multi-actor MNS hypothesis from the behavioral level to the neural level. In order to do this, we performed a motor TMS study that was designed to test whether two identical observed movements activate the relevant motor representation more strongly than a single observed movement. This study failed to show a specific increase in motor brain activation when two identical actions were observed compared to when a single action was observed. However, the study was underpowered, making it hard to interpret the absence of the expected effect.

To conclude, the current thesis provides the first evidence for the ability to represent the movements of multiple agents simultaneously from a first-person perspective. This ability may form the basis of social interaction with multiple agents, a fundamental aspect of daily life. As a result, the findings of the present study open up promising avenues for further research, both in the domain of action observation and in the broader field of social cognition.

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Appendix

In this appendix the left-side congruency x right-side congruency interaction obtained in experiment 1 will be explored. Note that there is no clear main variable and moderator variable in this analysis. It is therefore not clear in which direction the interaction should be interpreted. To compensate for this, the interaction will be explored in both ways. This means that both the influence of left-side congruency on right-side congruency and the influence of right-side congruency on left-side congruency will be investigated. In order to do this, the simple main effects of the left-side congruency effect will be compared for the different levels (C, N, and IC) of the right-side congruency effect and vice versa.

Reaction Times

First, the pattern behind the RT interaction will be discussed (figure 2a). With respect to the influence of right-side congruency on the left-side congruency effect, a simple main effects comparison revealed that the left-side congruency effect differed between RC and RN, $F(2,36) = 6.32$, $p_c = 0.01$, $\eta_p^2 = 0.26$. The left-side congruency effect did, however, not differ between RN and RIC, $F(2, 36) = 2.72$, $p_c = 0.16$, nor between RC and RIC, $F < 1$. These analyses thus indicate that the interaction was due to a difference in the nature of the left-side congruency effect between RN and RC. A visual inspection of figure 2a suggest that this difference reflected a stronger left-side congruency effect under RN than under RC. Indeed, post-hoc t tests showed that the left-side congruency effect (LIC – LC) was stronger under RN (28 ms) than under RC (14 ms), $t(37) = 3.59$, $p < 0.001$, $d = 0.58$.

With respect to the influence of left-side congruency on the right-side congruency effect, a simple main effects comparison did not show a difference in the right-side congruency effect between LC and LN, $F(2, 36) = 2.70$, $p_c = 0.16$, nor between LN and LIC, $F < 1$. The right-side congruency effect did, however, differ between LC and LIC, $F(2, 36) = 6.26$, $p_c = 0.01$, $\eta_p^2 = 0.26$. These analyses thus indicate that the interaction was

driven by a difference in the nature of the right-side congruency effect between LC and LIC. A closer look at figure 2a suggests that this difference was caused by a reversal of the right-side congruency effect for LC and LIC. That is, the RIC – RN difference was larger under LC (14 ms) than under LIC (3 ms), $t(37) = 2.14$, $p_c < 0.05$, $d = 0.35$, whereas the RN – RC difference was larger under LIC (18 ms) than under LC (4 ms), $t(37) = 3.59$, $p_c < 0.005$, $d = 0.58$.

Error Rates

Next, the interaction pattern will be discussed for the error rates (figure 2b). Pertaining to the influence of right-side congruency on the left-side congruency effect, a comparison of the simple main effects did not reveal a difference in the left-side congruency effect between RC and RN, $F < 1$, nor between RN and RIC, $F(2, 36) = 2.25$, $p_c = 0.24$. A difference in the left-side congruency effect was found, however, between RC and RIC, $F(2, 36) = 5.64$, $p_c < 0.05$, $\eta_p^2 = 0.24$. The analyses indicate, in other words, that the interaction was caused by a difference in the nature of the left-side congruency effect between RC and RIC. A visual inspection of figure 2b suggests that this difference reflected a stronger left-side congruency effect under RIC than under RC. Indeed, a t test revealed that the left-side congruency effect (LIC – LC) was larger under RIC (3.33%) than under RC (1.12%), $t(37) = 3.34$, $p < 0.005$, $d = 0.54$.

As regards the influence of left-side congruency on the right-side congruency effect, a simple main effects comparison revealed that the right-side congruency effect did not differ between LC and LN, $F(2, 36) = 1.72$, $p_c = 0.39$, nor between LN and LIC, $F < 1$. The right-side congruency effect did, however, differ between LC and LIC, $F(2, 36) = 5.69$, $p_c < 0.05$, $\eta_p^2 = 0.24$. This suggests that the interaction reflected a difference in the nature of the right-side congruency effect between LC and LIC. An examination of figure 2b suggests that this difference was caused by a stronger right-side congruency effect under LIC than under LC. A t test confirmed that the right-side congruency effect (RIC – RC) was indeed larger under LIC (3.27%) than under LC (1.06%), $t(37) = 3.34$, $p < 0.005$, $d = 0.54$.

Nederlandstalige Samenvatting

Het is ondertussen algemeen geweten dat individuen geobserveerde acties vanuit een eerste persoonsperspectief representeren in hun motorisch systeem. Dit onderzoek heeft zich echter uitsluitend toegespitst op de vraag hoe de acties van één enkele persoon worden gerepresenteerd. Dit staat in schril contrast met het feit dat sociale interacties gewoonlijk vereisen dat de acties van verschillende personen tegelijkertijd worden gemonitord. In een voetbalwedstrijd moet een spits bijvoorbeeld vaak het gedrag van verschillende verdedigers tegelijkertijd in rekening brengen om de defensie te kunnen omzeilen. Een open vraag is daarom of individuen in staat zijn om gelijktijdig de acties van meerdere personen te representeren in hun motorisch systeem. In onderhavige thesis werd deze vraag onderzocht aan de hand van twee experimenten. In het eerste experiment gebruikten we een automatische imitatietask om na te gaan hoe individuen worden beïnvloed door de geobserveerde acties van meerdere actoren. In overeenstemming met het idee dat individuen verschillende acties tegelijkertijd kunnen representeren in hun motorisch systeem, toonden de resultaten aan dat de participanten werden beïnvloed door de acties van beide handen. Daarenboven gaven de resultaten inzicht in hoe individuen worden beïnvloed door twee identieke en twee verschillende geobserveerde acties. Meer specifiek werd er gevonden dat twee identieke geobserveerde acties een grotere invloed uitoefenden dan één enkele geobserveerde actie, terwijl twee verschillende geobserveerde acties een tegengestelde invloed hadden op het gedrag van de participanten. De grotere invloed van twee identieke acties werd geïnterpreteerd als het gevolg van een relatie tussen het aantal geobserveerde identieke acties en de activatie van de overeenkomstige motorrepresentatie. De tegengestelde invloed van twee verschillende acties werd daarentegen geïnterpreteerd als een indicatie dat beide geobserveerde acties een verschillende motorrepresentatie activeerden.

In het tweede experiment gebruikten we een motor TMS studie om het multi-actor spiegelneuronsysteem te onderzoeken op het neurale niveau. Meer specifiek onderzochten we of twee identieke geobserveerde acties de bijhorende motorrepresentatie sterker activeren dan één enkele geobserveerde actie. In tegenstelling tot deze hypothese vonden

we geen specifieke toename van de motorische hersenactiviteit wanneer de deelnemers twee identieke acties zagen ten opzichte van één enkele actie. Het dient echter opgemerkt te worden dat deze studie voornamelijk bedoeld was als pilootstudie en bijgevolg een lage statistische power had. Verder onderzoek zal dus nodig zijn om duidelijke resultaten te verkrijgen.

Samengevat levert deze thesis als eerste steun voor het idee dat individuen in staat zijn om de acties van verschillende actoren tegelijkertijd te representeren vanuit een eerste persoonsperspectief. Deze vaardigheid ligt mogelijk aan de basis van sociale interacties die meerdere actoren omvatten. Bijgevolg kunnen de resultaten van deze thesis de aanleiding zijn van verder onderzoek in het domein van actie observatie en in het bredere domein van sociale cognitie.