FACULTY OF PSYCHOLOGY
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The multi-actor mirror neuron system: Can the human brain represent multiple actions simultaneously?

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Chapter 1

General Introduction[1]

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[1] This chapter is partly based on Cracco, E., Bardi, L., Desmet, C., Genschow, O., Rigoni, D., De Coster, L., Radkova, I., Deschrijver, E., & Brass, M. (in press). Automatic Imitation: A meta-analysis. *Psychological Bulletin*.

The Perception-Action Link

To understand social interaction, a fundamental question is how the actions of others are processed in the brain. Inspired by the neuroanatomical segregation of visual and motor functions (Power et al., 2011), traditional views have emphasized the dissociable nature of perception and action (Hurley, 2001). However, the past two decades have been characterized by a surge of research suggesting that both processes may be more closely connected than originally thought. In particular, there is now converging evidence from various domains that action observation recruits not only visual processes but also motor processes (Chartrand & Lakin, 2013; Chartrand & van Baaren, 2009; Cracco, Bardi, et al., 2018; Heyes, 2011; Rizzolatti & Sinigaglia, 2010, 2016). In other words, it appears from the literature that perception and action, rather than being two separate coins, are more like two sides of the same coin (Brass & Heyes, 2005). In this literature, there are currently three research lines supporting a relation between perception and action, namely research on motor mimicry (Chartrand & Lakin, 2013; Chartrand & van Baaren, 2009), research on automatic imitation (Cracco, Bardi, et al., 2018; Heyes, 2011), and research on the mirror neuron system (Rizzolatti & Sinigaglia, 2010, 2016). Therefore, in the first part of this introduction, these three research bodies will be discussed.

Motor Mimicry

The first line of evidence that perception and action are connected comes from social psychological research on motor mimicry. Motor mimicry is the observation that individuals tend to imitate each other during social encounters (Chartrand & Lakin, 2013; Chartrand & van Baaren, 2009). The first demonstration of motor mimicry can be traced back to Hull

(1933), who found that subjects inadvertently copied an experimenter reaching forward and backward during a series of psychological tests. However, the most well-known paradigm to study motor mimicry was conceived by Chartrand and Bargh (1999). These authors asked participants to take turns in describing photographs with a confederate who was, unbeknownst to the participant, instructed to either rub his face or shake his foot and to either smile or not smile throughout the interaction. Participants were found to shake their foot more often and rub their face less often when they were paired with a foot-shaking confederate than when they were paired with a face-rubbing participant. Likewise, participants smiled more often in the presence of a smiling confederate than in the presence of a non-smiling confederate. Critically, a subsequent debriefing revealed that participants had not noticed the mannerisms of the confederate, indicating that mimicry occurred without awareness.

The presence of motor mimicry in this paradigm has now been replicated across a multitude of studies (e.g., Castelli, Pavan, Ferrari, & Kashima, 2009; Genschow et al., 2017; Lakin & Chartrand, 2003; Marielle Stel et al., 2010; van Baaren, Maddux, Chartrand, de Bouter, & van Knippenberg, 2003; Yabar, Johnston, Miles, & Peace, 2006), which have been summarized in at least two major review papers (Chartrand & Lakin, 2013; Chartrand & van Baaren, 2009). Interestingly, these studies have argued that motor mimicry serves an important social function in the sense that it increases interpersonal rapport (Chartrand & Bargh, 1999; Lakin, Jefferis, Cheng, & Chartrand, 2003; Mariëlle Stel, van Dijk, & van Baaren, 2016; Wang & Hamilton, 2012). For example, Chartrand and Bargh (1999) showed in a second experiment that participants who were being imitated by a confederate liked the confederate more and rated the interaction as smoother than participants who were not being imitated, and these results have been replicated in subsequent work (Lakin & Chartrand, 2003; Mariëlle Stel & Vonk, 2010) as well as extended to prosocial behavior such as helpfulness (van Baaren, Holland, Kawakami, & van Knippenberg, 2004) and generosity (van Baaren et al., 2004; van Baaren, Holland, Steenaert, & van Knippenberg, 2003).

In sum, research on motor mimicry has revealed that people unconsciously imitate their interaction partner, and that this behavior acts as a social glue (Chartrand & Lakin, 2013; Chartrand & van Baaren, 2009). This indicates that seeing someone else perform an action triggers an involuntary imitative response, which, in turn, implies that perception and action are closely intertwined (Chartrand & Bargh, 1999).

Automatic Imitation

However, the finding that motor mimicry can occur without awareness does not necessarily imply that it is an involuntary process (Moors & De Houwer, 2006). For example, it has been argued in social reward theories that motor mimicry is used – be it consciously or unconsciously – as a means to obtain positive social consequences (Lakin et al., 2003; Mariëlle Stel et al., 2016; Wang & Hamilton, 2012). Instead, a process can be deemed involuntary if it cannot be controlled (Moors & De Houwer, 2006). Evidence that imitative tendencies are beyond voluntary control comes from research on automatic imitation. More specifically, this research has shown with stimulus-response compatibility tasks that observed actions are imitated even when imitation impairs task performance (Cracco, Bardi, et al., 2018; Heyes, 2011). For instance, in a seminal study, Brass et al. (2000) instructed participants to lift their index finger in response to the number “1” and their middle finger in response to the number “2”. At the same time, a hand on the screen also lifted its index finger, also lifted its middle finger, or did not move (Figure 1a). The results showed that, compared to when the hand did not move (neutral trial), responses were faster and more accurate when the observed action matched the instructed response (congruent trial), but slower and less accurate when the observed action did not match the instructed response (incongruent trial). The difference in reaction times and accuracy between incongruent and congruent trials is now widely used as a measure of automatic imitation (Cracco, Bardi, et al., 2018).

Following its initial demonstration (Brass, Bekkering, & Prinz, 2001; Brass, Bekkering, Wohlschlager, & Prinz, 2000; Sturmer, Aschersleben, & Prinz, 2000), automatic imitation has been studied extensively in the literature. This research has revealed that automatic imitation is a robust effect. For example, a recent meta-analysis identified 226 experiments conducted between 2000 and 2016, summing up strong average effect size of $g_z = 0.95$ (Cracco, Bardi, et al., 2018). Indeed, in addition to finger actions (Brass, Bekkering, Wohlschlager, Prinz, et al., 2000; Catmur & Heyes, 2011), automatic imitation has now been replicated across a wide range of effectors, including hand actions (Cracco, Genschow, Radkova, & Brass, 2018; Stürmer, Aschersleben, & Prinz, 2000), feet actions (Gillmeister, Catmur, Liepelt, Brass, & Heyes, 2008; Wiggett, Downing, & Tipper, 2013), arm actions (Kilner, Paulignan, & Blakemore, 2003; Stanley, Gowen, & Miall, 2007), and facial actions (Leighton & Heyes, 2010; Press, Richardson, & Bird, 2010).

However, an important question is also what causes automatic imitation. A critical view is that automatic imitation is merely an artefact of spatial compatibility (Aicken, Wilson, Williams, & Mon-Williams, 2007; Jansson, Wilson, Williams, & Mon-Williams, 2007). Spatial compatibility is the tendency to respond faster when the location of the stimulus corresponds to the location of the response (Hommel, 2011). In the Brass et al. (2000) study, spatial compatibility was confounded with imitative compatibility because the stimulus hand was a left hand mirroring participants' right response hand (Figure 1a). In other words, index finger stimulus movements were not only congruent with index finger responses in terms of imitation (i.e., see index finger, move index finger) but also in terms of location (i.e., see left finger, move left finger). A fundamental question is therefore whether automatic imitation (i.e., imitative compatibility) can be explained as a mere byproduct of spatial processing (i.e., spatial compatibility).

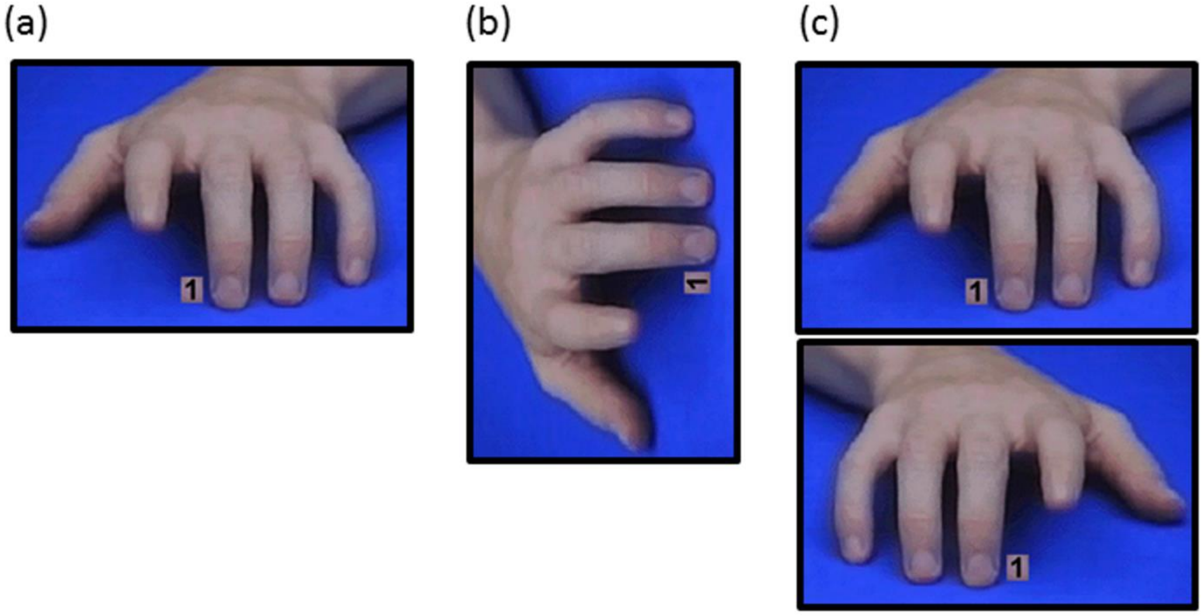

Figure 1. Examples of the stimuli used to study automatic imitation. In all three panels, participants have to lift their right index finger when the number 1 is presented and their right middle finger when the number 2 is presented. The first panel presents a case where imitative compatibility is confounded with spatial compatibility. The second panel presents a case where imitative compatibility is orthogonal to spatial compatibility. The third panel presents a case where the average performance across both trials provides a measure of imitative compatibility that is independent of spatial compatibility. See text for additional detail.

Two methods have been developed to rule out the confounding influence of spatial compatibility. In the first method, the stimulus hand is positioned orthogonal to the response hand (e.g., J. Cook & Bird, 2011, 2012). For example, in the Brass et al. (2000) study, spatial processes can be neutralized by rotating the stimulus hand 90° counterclockwise so that its fingers point to the right instead of downwards (Figure 1b). In this case, index finger stimulus movements are still compatible with index finger responses in terms of imitation (i.e., see index finger, move index finger), but no longer in terms of location (i.e., see lower finger, move left finger). However, a potential issue with this method is that there is a documented tendency to associate "down" with "left" and "up" with "right" (Weeks & Proctor, 1990). As a result, this method confounds automatic imitation with orthogonal spatial compatibility (Cracco, Bardi, et al., 2018; Heyes, 2011).

The second method solves this orthogonal spatial confound by independently manipulating imitative and spatial compatibility (Bertenthal, Longo, & Kosobud, 2006; Catmur & Heyes, 2011). For instance, using the stimuli of Brass et al. (2000), this means that a left stimulus hand is presented in one half of the trials and a right stimulus hand in the other half of the trials. This setup results in a positive relation between imitative and spatial compatibility in left hand trials and a negative relation in right hand trials, which makes it possible to calculate a main effect of imitative compatibility that is independent of spatial compatibility (Figure 1c). In a meta-analysis, we found that spatial compatibility inflates but cannot explain automatic imitation. More specifically, the results revealed that automatic imitation was robust even when both simple and orthogonal spatial compatibility were controlled (Cracco, Bardi, et al., 2018).

However, if automatic imitation is not spatial compatibility, then what is it? According to Heyes (2011), it is a combination of effector compatibility and movement compatibility. Given that effector is used as a synonym of body part in this context, effector compatibility is the overlap between the body part moved by the model and the body part that has to be moved by the participant (e.g., index or middle finger). In contrast, movement compatibility is the overlap between the type of movement made by the model and the type of movement that has to be made by the participant (e.g., lifting or tapping). Studies on effector compatibility manipulate effector overlap while keeping the movement constant (e.g., lift index finger or middle finger), whereas studies on movement compatibility manipulate movement overlap while keeping the effector constant (e.g., lift or tap index finger). Automatic imitation has been found in effector compatibility (e.g., Brass et al., 2000; Catmur & Heyes, 2011) as well as in movement compatibility tasks (e.g., Brass et al., 2001; Stürmer et al., 2000), and this has been confirmed by meta-analytic evidence of automatic imitation in both tasks (Cracco, Bardi, et al., 2018).

Like motor mimicry, automatic imitation has often been related to social processes (Brass, Ruby, & Spengler, 2009; Wang & Hamilton, 2012). For example, an important modulator of automatic imitation is the similarity between the actor and the imitator (Cracco, Bardi, et al., 2018; Press, 2011). That is, automatic imitation has shown to be stronger for humans than for robots (Kilner et al., 2003; Press, Bird, Flach, & Heyes, 2005; Press, Gillmeister, & Heyes, 2006) and more recently also for romantic partners than for close friends (Maister & Tsakiris, 2016). Nevertheless, in contrast to previous work (e.g., Gowen, Bolton, & Poliakoff, 2017; Liepelt & Brass, 2010), a recent meta-analysis found no evidence that automatic imitation is influenced by top-down beliefs about whether or not the actor is human (Cracco, Bardi, et al., 2018). Overall, the evidence thus shows that automatic imitation is tuned towards agents that are “like me”. This indicates that, similar to motor mimicry, automatic imitation is an inherently social process (Wang & Hamilton, 2012).

However, surprisingly, a recent study with 196 participants found no correlation between automatic imitation and motor mimicry (Genschow et al., 2017). Therefore, an important question is whether they share the same underlying mechanism, as has previously been suggested (Heyes, 2011). Although it is too early to tell, there is a striking overlap between the factors that modulate automatic imitation and the factors that modulate motor mimicry, suggesting that they tap into similar processes (Heyes, 2011). From this perspective, the absence of a correlation shows how methodological differences can blur the relation between two related concepts (Genschow et al., 2017). Whatever the reason, it is clear that care should be taken when equating automatic imitation with motor mimicry until further evidence has either confirmed or refuted the claim that they rely on similar mechanisms.

To conclude, research on automatic imitation has shown that imitative tendencies occur even when they impair task performance, demonstrating that imitation can occur even without intention. In line with the perception-action hypothesis, this indicates that action observation triggers not only the visual representation of the observed action, but also its motor representation, leading to an urge to imitate (Cracco, Bardi, et al., 2018).

The Mirror Neuron System

Nevertheless, perhaps the strongest evidence that perception is linked to action comes from research showing that observed actions are processed not only in the visual but also in the motor system of the brain (Rizzolatti & Sinigaglia, 2010, 2016). For example, single cell studies in the monkeys have revealed a subset of neurons in the ventral premotor cortex (Rizzolatti, Fadiga, Gallese, & Fogassi, 1996), the inferior parietal lobe (Rozzi, Ferrari, Bonini, Rizzolatti, & Fogassi, 2008), and the intraparietal sulcus (Fujii, Hihara, & Iriki, 2007) that fire both when an action is executed and when the same action is observed (Kilner & Lemon, 2013). These neurons were famously coined mirror neurons, indicating that they “mirror” observed actions in the motor system (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti et al., 1996).

The discovery of mirror neurons in monkeys was quickly followed by studies investigating whether similar neurons exist in humans as well. Supporting this hypothesis, functional magnetic resonance imaging (fMRI) research has revealed that action observation and action execution recruit an overlapping neural network (Caspers, Zilles, Laird, & Eickhoff, 2010; Molenberghs, Cunnington, & Mattingley, 2012). Similar to monkeys, this network extends the ventral premotor and inferior parietal cortex, as well as additional regions such as the superior parietal cortex and the cerebellum (Molenberghs et al., 2012). Yet, shared activation at the group level is not the same as shared activation at the individual level. For example, brain regions responding to action observation in some participants and to action execution in other participants would also appear to “share activation” across participants. However, while possible, there is now strong evidence that shared activation exists at the individual level as well (Gazzola & Keysers, 2009).

Nevertheless, fMRI still aggregates brain activation across several hundred thousand neurons. As a consequence, shared regions do not necessarily contain mirror neurons but could also contain a mixture of action observation and action execution neurons. Therefore, to demonstrate that mirror neurons exist, it has to be shown that observing and executing a specific action recruits the same neuronal population (Dinstein, 2008; Dinstein, Hasson, Rubin, & Heeger, 2007; Dinstein & Thomas, 2008). This can be done with cross-modal repetition suppression, which investigates whether brain activation during action observation is weaker when it is preceded by the execution of the same, as opposed to a different, action (and vice versa during action execution). Repetition suppression capitalizes on the fact that repeatedly presenting the same stimulus selectively suppresses neuronal firing in the neurons that code the presented stimulus (Malach, 2012). In other words, neuronal populations that show cross-modal repetition suppression can be considered to have mirror properties because they are responsive not only to observing but also to executing a specific action (Dinstein, 2008; Dinstein et al., 2007; Dinstein & Thomas, 2008). In line with a human mirror neuron system, cross-modal repetition suppression has now been reported across three studies in two key mirror regions, namely the inferior frontal gyrus (Kilner, Neal, Weiskopf, Friston, & Frith, 2009; Press, Weiskopf, & Kilner, 2012) and the inferior parietal lobe (Chong, Cunnington, Williams, Kanwisher, & Mattingley, 2008).

In addition to fMRI, a second technique to measure the human mirror neuron system is transcranial magnetic stimulation (TMS). TMS is a non-invasive technique to stimulate the human brain that works by passing an electric current through a magnetic coil. This current then generates a magnetic field perpendicular to the surface of the coil, which in turn causes an electric field perpendicular to the magnetic field that excites the neurons in the brain surface below the coil (Hallett, 2007). When the primary motor cortex (M1) is stimulated, a volley is sent down the corticospinal tract, resulting in a contraction of the muscles represented in the stimulated area. For example, stimulation of the M1 hand area will cause the contralateral hand muscles to contract. These TMS-induced muscle contractions are named motor evoked potentials (MEPs) and can be detected using electromyography (EMG). Mirror activation can be measured by applying TMS to M1 during action observation (Fadiga, Craighero, & Olivier, 2005; Naish, Houston-Price, Bremner, & Holmes, 2014). This was initially demonstrated by Fadiga et al. (1995) who found increased MEPs in two hand and two forearm muscles when participants observed an experimenter grasping an object but not when they observed an object that was not being grasped.

However, the strongest TMS evidence for mirror activation comes from studies showing a double dissociation between two muscles both during the observation and during the execution of two different actions (Naish et al., 2014). For example, two studies have now found that the first dorsal interosseous (FDI) and the abductor digiti minimi (ADM) muscles, which are respectively involved in index and little finger abduction, are differentially modulated during the execution and observation of index and little finger movements (Romani, Cesari, Urgesi, Facchini, & Aglioti, 2005; Urgesi, Candidi, Fabbro, Romani, & Aglioti, 2006). That is, MEPs were found to be stronger in the FDI than in the ADM during the execution and observation of index finger movements but weaker in the FDI than in the ADM during the execution and observation of little finger movements.

Nevertheless, the question remains whether increases in corticospinal excitability during action observation are indeed driven by activity in the mirror neuron system, as is typically assumed (Fadiga et al., 2005; Naish et al., 2014). Supporting this view, research has revealed that MEPs during action observation are decreased when a virtual lesion is applied to the ventral premotor cortex (Avenanti, Bolognini, Maravita, & Aglioti, 2007; Enticott et al., 2012) or to the inferior parietal cortex (Avenanti, Annella, Candidi, Urgesi, & Aglioti, 2013) using repetitive TMS or transcranial direct current stimulation (tDCS). Similarly, studies using a paired-pulse procedure have found stronger corticospinal excitability during action observation when the M1 pulse was preceded by a conditioning pulse to the premotor (Catmur, Mars, Rushworth, & Heyes, 2011; Koch et al., 2010) or anterior intraparietal cortex (Koch et al., 2010), indicating task-related facilitation of the connections between these two mirror regions and M1 (Koch et al., 2010).

Finally, a third method to investigate the human mirror neuron system is electroencephalography (EEG). More specifically, EEG research has focused on the mu rhythm, which is an alpha band (i.e., 8-13 Hz) brain oscillation thought to reflect sensorimotor processing (Fox et al., 2016). Indeed, it is well established that action execution leads to reduced power in the mu rhythm over central electrodes (Fox et al., 2016; Lepage & Théoret, 2006; Muthukumaraswamy & Johnson, 2004; Muthukumaraswamy, Johnson, & McNair, 2004). Interestingly, however, similar mu suppression has also been found during action observation (Fox et al., 2016; Lepage & Théoret, 2006; Muthukumaraswamy & Johnson, 2004; Muthukumaraswamy et al., 2004), and this has been taken as evidence for a human mirror neuron system (Fox et al., 2016). In line with this view, combined fMRI-EEG measurements have shown that mu-suppression is correlated with BOLD activity in the mirror neuron system both during action observation and during action execution (Arnstein, Cui, Keysers, Maurits, & Gazzola, 2011). Nevertheless, it has recently also been argued that methodological problems in the mu-suppression literature make it difficult to draw firm conclusions (Cuevas, Cannon, Yoo, & Fox, 2014; Hobson & Bishop, 2017). For example, the largest study to date that concluded that the presence of observation-induced mu-suppression critically depends on the baseline being used and can easily be confounded with alpha suppression (Hobson & Bishop, 2016). Similarly, a recent study revealed that mu-suppression during action observation reflects somatosensory rather than motor processes (Coll, Press, Hobson, Catmur, & Bird, 2017).

With regard to the function of the mirror neuron system, it has been argued that mirroring helps us to understand the behavior of others by making it possible to simulate observed actions in our own motor system (Gallese, 2007; Gallese, Keysers, & Rizzolatti, 2004; Keysers & Gazzola, 2006). In support of this view, research has shown that mirror activation is not only sensitive to action kinematics (Maeda, Kleiner-Fisman, & Pascual-Leone, 2002), but also action goals (Cattaneo, Caruana, Jezzini, & Rizzolatti, 2009; Hamilton & Grafton, 2006), action intentions (Cattaneo et al., 2007; Iacoboni, Molnar-Szakacs, Gallese, Buccino, & Mazziotta, 2005), and action outcomes (Aglioti, Cesari, Romani, & Urgesi, 2008; Hamilton & Grafton, 2008). Similarly, it has been found that virtual lesions to the inferior frontal gyrus disrupt performance on tasks requiring participants to infer the intention behind observed actions (Pobric & Hamilton, 2006; Tidoni, Borgomaneri, di Pellegrino, & Avenanti, 2013). Taken together, this work thus suggests that, similar to motor mimicry and automatic imitation, mirroring is an important social process.

In conclusion, there is now converging evidence from fMRI, TMS, and, to a lesser extent, EEG research that observed and executed actions are processed in shared neural networks. This mechanism is widely considered to be the neurophysiological basis of motor mimicry and automatic imitation (Catmur, Walsh, & Heyes, 2009; Cracco, Bardi, et al., 2018; Heyes, 2011) and as such makes it possible to develop a biologically plausible account of the relation between perception and action. Interestingly, research on the mirror neuron system has also extended beyond action observation. For example, it has been shown that action-related sounds likewise produce mirror activation (Etzel, Gazzola, & Keysers, 2008; Gazzola, Aziz-Zadeh, & Keysers, 2006) and that observing someone being touched (Keysers et al., 2004), someone in pain (Singer et al., 2004), or someone expressing an emotion (Wicker et al., 2003) activates the same brain regions as being touched, being in pain, or expressing the same emotion ourselves. This suggests, in other words, that mirroring is a general mechanisms that helps us to understand not only what other people do but also what they feel and think (Gallese, 2007; Gallese et al., 2004; Keysers & Gazzola, 2006).

Theories of Perception and Action

Having established that there is a connection between perception and action, an important question is also what causes this connection. Broadly speaking, theories on the perception-action link can be divided into specialist and generalist theories (Brass & Heyes, 2005). Specialist theories assume the presence of a special purpose mechanism that is uniquely dedicated to matching observed actions to motor representations (Gallese & Goldman, 1998; Simpson, Murray, Paukner, & Ferrari, 2014). Importantly, this mechanism is often held to be inborn (e.g., Meltzoff & Moore, 1983, 1989), consistent with evidence that imitation occurs already at birth (e.g., Meltzoff & Moore, 1983, 1989). However, recent work has called the evidence supporting neonatal imitation into question (Oostenbroek et al., 2016). Together with evidence that both mirror activation (Catmur, Walsh, & Heyes, 2007; Heyes, 2010) and automatic imitation (Cracco, Bardi, et al., 2018; Heyes, Bird, Johnson, & Haggard, 2005) are sensitive to sensorimotor learning, this supports the view that connections between perception and action might be acquired rather than inborn (R. Cook, Bird, Catmur, Press, & Heyes, 2014; Heyes, 2010, 2016; Keysers & Perrett, 2004).

The notion that perception-action links develop through domain-general learning mechanisms is at the core of two related yet distinct generalist theories (Brass & Heyes, 2005). The first theory is the associative sequence learning (ASL) theory (Brass & Heyes, 2005; R. Cook et al., 2014; Heyes, 2010; Ray & Heyes, 2011). This theory argues that the visual representation of an action is initially unconnected to its motor representations. Instead, it assumes that motor commands gradually become connected to their sensory consequences as a result of contingent co-activation. For example, when we grasp an object, we typically see how our hand grasps the object. Likewise, when we express an emotion, we tend to see the same emotion expressed on the face of others. These experiences lead to bidirectional connections between action perception and action execution. This, in turn, causes mirror activation (R. Cook et al., 2014; Heyes, 2010) and therefore also imitation (Cracco, Bardi, et al., 2018; Heyes, 2011).

The second theory, ideomotor theory (IM), extends ASL by assuming an additional mechanism (Brass & Heyes, 2005; Greenwald, 1970; Prinz, 1997; Shin, Proctor, & Capaldi, 2010). Like ASL, IM posits that associative learning leads to connections between visual and motor representations. However, IM also predicts that this learning process culminates in the development of ideomotor representations that code actions in terms of their anticipated sensory consequences (Greenwald, 1970). Given that the visual image of an action is part of its sensory consequences, seeing an action primes the ideomotor representation controlling that action. Thus, according to IM, mirror neurons are the neurophysiological manifestations of ideomotor representations (Brass & Muhle-Karbe, 2014), and priming these representations leads to imitation (Brass, Bekkering, Wohlschlager, & Prinz, 2000; Cracco, Bardi, et al., 2018). In other words, IM and ASL differ in whether or not they assume ideomotor representations, but agree in their emphasis on the role of motor learning (Brass & Heyes, 2005).

The Perception-Action Link in Multi-Agent Settings

While there is a large literature on the perception-action link in situations where a single person watches a single agent, virtually nothing is known about the perception-action link in multi-agent settings. In contrast, social interaction often exceeds a dyadic structure. Therefore, to understand social interaction, it is imperative to not only understand how others' actions are processed in single-agent but also in multi-agent settings. In particular, an interesting hypothesis is that observers can simultaneously represent the actions of multiple agents in their motor system. Indeed, considering the social function of the perception-action link, this could provide important insights into currently understudied social processes such as interaction representation (Quadflieg & Koldewyn, 2017; Quadflieg & Penton-Voak, 2017), group interactions (Ramenzoni, Sebanz, & Knoblich, 2014; Tsai, Sebanz, & Knoblich, 2011), and social contagion (Gallup et al., 2012; Hortensius & De Gelder, 2014; Latane, 1981; Milgram, Bickman, & Berkowitz, 1969).

Interaction Representation

A first process that could benefit from mirroring multiple agents is interaction representation. That is, in social life, we have to represent not only the actions but also the interactions of others. For instance, how do we decide whether two persons wrapping their arms around each other are hugging or wrestling? Recently, it has been argued that, in addition to high-level processes like mentalizing, interaction representation may also rely on low-level processes like motor simulation (Quadflieg & Koldewyn, 2017; Quadflieg & Penton-Voak, 2017). However, to simulate interactions, the actions of multiple agents have to be represented at the same time in the motor system.

Preliminary evidence that this is possible comes from research on interaction observation. In one relevant study, participants watched short video clips comprising two consecutive phases (Iacoboni et al., 2004). First, in the “alone phase”, a single actor appeared on the scene. Second, in the “relational phase”, this actor then started to interact with a second actor. In one of the videos, for instance, the actors played a couple looking at family photos. The results revealed that brain activation in two mirror neuron regions, namely the right premotor cortex and the right inferior frontal gyrus, was stronger in the relational phase than in the alone phase. In the same vein, a number of TMS studies have now demonstrated that corticospinal excitability is increased during interactive action observation compared with individual action observation (Aihara, Yamamoto, Mori, Kushiro, & Uehara, 2015; Bucchioni, Cavallo, Ippolito, Marton, & Castiello, 2013). For example, this research has shown that MEPs are stronger when participants see someone throwing a ball towards another person than when they see someone throwing a ball against a wall (Bucchioni et al., 2013). Finally, in two fMRI studies, observing two interacting persons was found to produce stronger motor activation than observing two independently acting persons (Centelles, Assaiante, Nazarian, Anton, & Schmitz, 2011; Georgescu et al., 2014).

Thus, taken together, these studies demonstrate that the motor system is activated more strongly during interaction observation than during action observation. However, it does not necessarily follow from an unspecific increase in motor activation that multiple observed actions were represented at the same time in the motor system. Instead, for this, it has to be shown that the corresponding motor representations were simultaneously activated.

Joint Action

In addition to interaction representation, the ability to mirror multiple observed actions might also play an important role in joint action. More specifically, joint actions are social interactions where two or more individuals coordinate their actions in space and time to achieve a common goal (Sebanz, Bekkering, & Knoblich, 2006). Importantly, this ranges from complex interactions such as dancing or playing football to simple interactions such as shaking hands or clinking glasses. However, to understand joint action, a key question is how individuals manage to synchronize their own actions with the actions of others (Sebanz et al., 2006), and previous work suggests that this relies in large part on mirror processes (Colling, Knoblich, & Sebanz, 2013; Hadley, Novembre, Keller, & Pickering, 2015; Kourtis, Sebanz, & Knoblich, 2013).

For example, Kourtis et al. (2013) developed a joint action task in which participants had to pick up and pass an object to another participant who then had to put it back to its original position. The results showed an increase in action coordination over time, and this increase was correlated with the degree to which receivers co-represented the actions of the givers in their motor system. Similarly, Hadley et al. (2015) found that disturbing the dorsal premotor cortex with repetitive TMS impaired interpersonal coordination in a musical duet task, suggesting that musical coordination relies at least in part on the mirror neuron system. However, joint action is not restricted to social interactions involving a single co-actor. For example, musicians in musical ensembles have to synchronize their actions not with one musician but with several musicians at the same time (Volpe, D’Ausilio, Badino, Camurri, & Fadiga, 2016). Therefore, considering past work, an interesting hypothesis is that this relies on the ability to simultaneously represent the actions of multiple co-actors in the motor system.

Indirect evidence supporting this possibility can be found in research on inter-group imitation. For instance, Tsai and colleagues (2011) investigated how overlap between the number of actors and the number of imitators influenced imitation. To this end, they presented two hands of which the left hand, the right hand, or both hands made an index finger movement. Participants sat on the left or right side of the screen and had to imitate the ipsilateral hand. Importantly, however, the task was performed together with a confederate who was sitting on the other side of the screen. In the compatible condition, the confederate also had to imitate the ipsilateral hand. In contrast, in the incompatible condition, the confederate had to imitate when one hand on either side of the screen made a movement but not when both hands made a movement.

In other words, there was a match between the number of actors and the number of imitators in the compatible condition but a mismatch in the incompatible condition. To give an example, when two hands made a movement, both the participant and confederate had to respond in the compatible condition, whereas only the participant had to respond in the incompatible condition. The results revealed that participants were slower on incompatible trials than on compatible trials. However, this was only true if the hands belonged to two different persons (“group condition”). Instead, if the hands belonged to the same person (“individual condition”), there was no compatibility effect. Overall, these results thus indicate that imitation was facilitated when the number of actors matched the number of imitators, namely in the compatible group condition.

In a follow-up study, using a continuous tapping paradigm, this finding was extended to synchrony (Ramenzoni et al., 2014). More specifically, in this study, two stimulus hands alternately tapped their index finger in a gradually increasing tempo, and participants had to imitate one of those hands either with (“joint condition”) or without (“solo condition”) another participant imitating the second hand. The results revealed that responses in the joint condition were more synchronized with the stimulus movements when the hands belonged to two different persons (i.e., group condition) than when they belonged to a single person (i.e., individual condition). In contrast, the opposite pattern was found in the solo condition. Taken together, research on inter-group imitation thus shows that imitation is facilitated when the number of actors matches the number of imitators. However, as with interaction observation, this does not necessarily mean that multiple observed actions were represented simultaneously in the motor system.

Social Contagion

Finally, the ability to simultaneously represent multiple observed actions in the motor system may have important implications for the social contagion literature. For example, in a seminal study, Milgram et al. (1969) monitored the behavior of pedestrians in a busy city street while they passed by a group of one to fifteen confederates looking at a sixth floor window. The results revealed that the likelihood that passers-by would also look up increased as the group of confederates grew in size. In other words, the probability of imitation depended on the number of actors, and this finding has since been replicated (Gallup et al., 2012; Knowles & Bassett, 1976), as well as extended to other behaviors such as applause contagion (Freedman & Birsky, 1980), queue formation (Mann, 1977), helping behavior (Darley & Latané, 1968), and action sequence imitation (Herrmann, Legare, Harris, & Whitehouse, 2013). However, these findings have mainly been explained in terms of interpretative processes. For instance, Milgram et al (1969) argued that imitation increased with group size because larger groups are more likely to be looking at something of interest. In contrast, an alternative explanation could also be that imitation increased with group size because the relevant motor representation was triggered more strongly when the action was executed by multiple persons.

Initial evidence that sensorimotor processes contribute to social group contagion was recently obtained in an fMRI study on the bystander effect (Hortensius & De Gelder, 2014). In this study, participants watched video clips showing zero to four bystanders walking past a person in need without intervening. The results showed that motor activation decreased as the number of bystanders increased, indicating that participants automatically embodied the bystanders' passive behavior, causing them to inhibit motor responses. These results suggest that social contagion phenomena such as bystander apathy might have a sensorimotor basis (Hortensius & De Gelder, 2014). However, despite the high degree of experimental control, it might still be argued that the relation between the number of bystanders and motor activation was driven by interpretative processes. For instance, it cannot be ruled out that participants inferred from the number of bystanders whether or not the victim was in need, and that this explains the relation with motor activation.

In sum, although previous research has already hinted towards the possibility of a multi-actor mirror mechanism, direct evidence is currently lacking. Therefore, the goal of the current PhD dissertation is to test whether multiple observed actions can be represented at the same time in the motor system. To this end, I will use a multi-method approach in which behavioral studies on automatic imitation are combined with TMS and fMRI studies on action observation so that informed conclusions can be reached on the basis of converging evidence from various sources. Together, this work offers an important contribution to the literature because it allows the role of perception-action processes to be extended beyond the dyad.

Outline of the Current Thesis

The overarching research question addressed in the current thesis is whether individuals can represent multiple identical and multiple different observed actions at the same time in their motor system. **Chapter 2** presents two automatic imitation experiments exploring both cases. That is, using automatic imitation (see Figure 1), this chapter investigates whether seeing two congruent or two incongruent actions produces a stronger motor trigger than seeing one congruent or incongruent action (i.e., identical actions) and whether seeing one congruent and one incongruent action produces concurrent facilitation and interference effects that cancel out each other (i.e., different actions). Furthermore, it also investigates whether these two effects are specific to human agents, or can be obtained with non-human agents as well. Indeed, research has shown that automatic imitation is stronger for human than for nonhuman agents (Cracco, Bardi, et al., 2018; Press, 2011). Therefore, if the hypothesized effects are caused by perception-action processes rather than by attentional or spatial processes, they should be sensitive to animacy.

In **Chapter 3**, I then use TMS to investigate motor co-representation of two identical observed actions during passive observation. More specifically, similar to Chapter 2, I investigate whether two identical observed actions produce stronger motor responses than a single observed action. As explained earlier, motor TMS can be used to measure mirror activation in the motor system (Naish et al., 2014). As such, Chapter 3 critically extends Chapter 2 by providing a more direct measure of mirror neuron activation.

The goal of **Chapter 4** is to address a confound present in the previous two chapters. That is, it could be argued that participants in Chapters 2 and 3 might randomly represent one hand on each trial. Indeed, this account also predicts stronger motor responses when seeing two identical actions because the probability to represent a moving hand would then be 100%

when both hands make a movement but only 50% when one hand makes a movement. In other words, the effects predicted in Chapters 2 and 3 do not necessarily arise within trials but could also arise across trials as a consequence of random sampling. Therefore, to address this issue, Chapter 4 investigates across four experiments whether the effects observed in Chapter 2 can be replicated when task requirements ensure that at least one action is represented on every trial.

In **Chapter 5,** I set out to investigate the hypothesis that sensorimotor processes contribute to social group contagion. That is, across seven experiments, I explore the relation between group size and automatic imitation while minimizing the role of interpretative processes. Specifically, I address the hypothesis that automatic imitation becomes stronger as the number of observed movements increases from one to four. Moreover, I explore whether this relation follows an asymptotic curve, in line with previous research on social contagion (Bond, 2005).

Chapter 6 provides a more direct test of the hypothesis that not only two identical but also two different observed actions can be represented in the motor system. In particular, Chapter 6 tests this hypothesis across three automatic imitation experiments including four stimulus hands. More specifically, in this chapter, I compare automatic imitation in a condition where three or four hands perform the same action with automatic imitation in a condition where three hands perform one action and the fourth hand performs a different action. If the actions of all four hands are represented in the motor system, automatic imitation should be weaker in the third condition, where the fourth hand counteracts the other two hands, than in the remaining two conditions. Furthermore, in this chapter, I also investigate if the ability to simultaneously represent two different observed actions in the motor system depends on whether or not these actions can be executed in parallel

Finally, in **Chapter 7**, I investigate the case of multiple different observed actions using fMRI instead of automatic imitation. More specifically, participants in this study passively observe two right hands performing sign language gestures. This allows me to address three questions. First, I can investigate whether two different observed actions produce stronger motor activation than a single observed action. Second, I can investigate whether it is possible to decode two observed actions at the same time from activation in the motor system using multivariate analysis techniques. Third, I can investigate whether seeing two different actions leads to motor conflict. Indeed, if participants represent two sign language gestures in their motor system, this should produce activation in brain areas associated with motor conflict because it is not possible to simultaneously execute two such gestures with a single hand.

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Chapter 2

Motor Simulation Beyond the Dyad: Automatic Imitation of Multiple Actors[1]

A large body of research has provided evidence for the idea that individuals simulate the actions of others 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 simulated simultaneously. In the current study, we addressed this issue by means of a widely used automatic imitation task. In Experiment 1, it is shown that individuals automatically imitate the actions of two agents at the same time. More specifically, the results indicate that two identical observed movements produce a stronger imitation effect, whereas two different observed movements produce two opposite imitation effects that cancel out each other. In Experiment 2, it is shown that the effects obtained in Experiment 1 cannot be explained in terms of attentional capture. Instead, the results point toward an explanation in terms of ideomotor theory. The finding that observers simultaneously represent the actions of multiple agents in their motor system allows for a better understanding of social interaction beyond the dyad.

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[1] Cracco, E., De Coster, L., Andres, M., & Brass, M. (2015). Motor Simulation Beyond the Dyad: Automatic Imitation of Multiple Actors. *Journal of Experimental Psychology: Human Perception and Performance, 41(6)*, 1488-1501.

Introduction

Motor Simulation

Social interaction often requires that individuals take into account the actions of the people they interact with. When two persons reach out to shake each other's hand, for example, the handshake will only succeed if they manage to coordinate their movements. To understand the mechanisms behind social interaction, it is therefore important to know how the actions of others are processed in the brain. According to ideomotor theory, action execution and action observation share a representational format (Greenwald, 1970; Hommel, 2009; Prinz, 1997). In particular, it is assumed that actions are represented in the motor system in the form of their anticipated sensory consequences. Because individuals often see the actions they perform, this implies that the visual image of an action is part of its motor representation. As a result, an important prediction of ideomotor theory is that observed actions should not only trigger the visual system but also the motor system.

Supporting the idea that observed actions trigger the motor system, research has revealed that individuals tend to automatically imitate the movements of others (reviewed in Heyes, 2011). Stimulus-response compatibility studies, for instance, have consistently shown that responses to a symbolic stimulus are facilitated by a compatible observed movement and impeded by an incompatible observed movement (e.g., Bertenthal, Longo, & Kosobud, 2006; Brass, Bekkering, Wohlschläger, & Prinz, 2000; Catmur & Heyes, 2011; Liepelt, Cramon, & Brass, 2008; Stürmer, Aschersleben, & Prinz, 2000). Similarly, research on social imitation has demonstrated that individuals often unintentionally copy the behavior, facial expression, and posture of their interaction partner (e.g., Chartrand & Bargh, 1999; Chartrand & van Baaren, 2009). Finally, patient studies have found that impaired inhibition due to frontal lobe damage can result in an irresistible urge to imitate the actions of others (Brass et al., 2003; De Renzi, Cavalleri, & Facchini, 1996; Lhermitte, Pillon, & Serdaru, 1986; Luria, 1966).

In addition to research on automatic imitation, ideomotor theory has recently gained support from neurophysiological data (reviewed in Rizzolatti & Craighero, 2004; Rizzolatti & Sinigaglia, 2010). Imaging studies, for instance, have identified brain areas within the motor system that are recruited both when individuals execute an action and when they observe the same action (e.g., Dinstein, Hasson, Rubin, & Heeger, 2007; Gazzola & Keysers, 2009; Kilner, Neal, Weiskopf, Friston, & Frith, 2009). This is supported by EEG (e.g., Lepage & Théoret, 2006; Zhu, Sun, & Wang, 2013) and TMS (e.g., Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995; Maeda, Kleiner-Fisman, & Pascual-Leone, 2002) research in which action observation was equally found to produce motor activation.

In summary, research from different sources has supported the idea that observed actions are simulated in the motor system. Interestingly, studies suggest that this intimate connection between action observation and action execution may play an important role in social interaction. Motor simulation has, for instance, been related to a variety of social skills such as empathy (Chartrand & Bargh, 1999; Gazzola, Aziz-Zadeh, & Keysers, 2006; Kaplan & Iacoboni, 2006), action goal inference (Cattaneo, Caruana, Jezzini, & Rizzolatti, 2009; Hamilton & Grafton, 2006), and intention inference (Iacoboni, Molnar-Szakacs, Gallese, Buccino, & Mazziotta, 2005; Kaplan & Iacoboni, 2006). Furthermore, it has been argued that social problems in autism spectrum disorder are caused by a deficit in the motor simulation mechanism (Williams, Whiten, Suddendorf, & Perrett, 2001) or by a deficit in the regulation of the motor simulation mechanism (Hamilton, 2013; Spengler, Bird, & Brass, 2010). Finally, motor simulation is assumed to be important for the execution of actions that require two or more individuals to coordinate their movements (Colling, Knoblich, & Sebanz, 2013; Knoblich & Sebanz, 2006). Specifically, it is thought that motor simulation enables individuals to anticipate the actions of their co-actor in joint action situations (Atmaca, Sebanz, & Knoblich, 2011; Kourtis, Sebanz, & Knoblich, 2013; Sebanz, Knoblich, & Prinz, 2003; Sebanz, Knoblich, Prinz, & Wascher, 2006), hence facilitating movement coordination (Kourtis et al., 2013).

Multi-Actor Motor Simulation

Despite the large body of research on motor simulation, however, most research has focused on how individuals process the actions of a single agent. This stands in contrast with the fact that individuals often engage in social interactions that involve multiple agents. When a large and heavy object has to be moved, for example, this may require the cooperation of more than two persons. To complete this task without accidents, it is imperative that the involved persons are able to coordinate their actions. This, in turn, requires that each of these persons is able to monitor and anticipate the actions of all the different co-actors. One possibility is that the latter relies on the ability to simulate the movements of multiple persons in the motor system.

Indirect evidence for the existence of a multi-actor motor simulation mechanism can be found in three earlier studies. In one study, 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 number of actors and the number of imitators. The results revealed that participants were faster to imitate when the number of imitators matched the number 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 motor simulation is sensitive to the number of co-actors.

In two other studies, the relation between the number of observed actors and the probability of imitation was investigated. In an early study, Milgram, Bickman, and Berkowitz (1969) registered 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 when 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 models at the same time compared to a single model or two consecutive models. Both studies show, in other words, that the probability of imitation is larger when the observed behavior is executed by multiple persons at the same time. However, these results were interpreted in terms of interpretive processes rather than in terms of a multi-actor motor simulation mechanism. For example, the tendency to look up may increase with the number of window watchers because the odds that something interesting is happening also increase with the number of window watchers. Nevertheless, an alternative explanation for the increased probability of imitation could be that the relevant motor representation was triggered more strongly when the action was executed by multiple persons.

To summarize, previous studies have shown that imitative tendencies can be modulated by the number of observed actors. While this suggests that motor simulation is sensitive to the number of actors, it is not yet known whether this also means that the actions of multiple observed actors can be simulated in the motor system at the same time. In the current study, we aimed to address this question by measuring automatic imitation in a situation where two observed actors are moving simultaneously. If the movements of both actors are indeed represented in the motor system at the same time, the automatic imitation effects should reflect a combination of these movements.

Experiment 1

In order to test the above prediction, we adapted a well-known automatic imitation paradigm in which individuals are required to make a finger movement in response to a symbolic cue while a hand on the screen makes a compatible or an incompatible movement (Bertenthal et al., 2006; Brass et al., 2000; Catmur & Heyes, 2011; Liepelt et al., 2008). In contrast to the original paradigm, in which a single hand appears on the screen, the current adaptation included two different hands next to each other making a congruent (C), an incongruent (IC), or no (N) abduction movement with respect to the imperative cue (figure 1). Consequently, this paradigm 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.

First, we can investigate *if* 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. Importantly, a congruency effect should be present for both hands irrespective of what the other hand is doing. That is, if the motor system is able to incorporate the movements of multiple actors simultaneously, the movements of each actor should result in an automatic imitation effect regardless of whether the other actor makes a movement and regardless of which movement the other actor makes.

Next, if we manage to confirm that individuals are influenced by the actions of both hands at the same time, we can use this paradigm to investigate *how* the movements of the two hands are represented in the motor system. More precisely, we can examine how individuals are influenced by two identical observed movements and how they are influenced by two different observed movements. When the two hands perform an identical movement, it can be expected that both hand movements are mapped onto the same motor representation. This should lead to increased activation of the corresponding motor representation and consequently to a larger congruency effect. Importantly, a larger congruency effect in the current study cannot be explained in terms of interpretive processes due to the fact that the observed movements are simple, meaningless movements that are irrelevant for the task at hand. When the two hands perform a different movement, the hand movements should trigger different motor representations. In terms of the automatic imitation task, this means that one hand movement should activate a congruent motor representation, while the other hand movement should activate an incongruent motor representation. As a result, a facilitation and an interference effect should be present at the same time. Because these effects are opposite forces, they should subsequently cancel each other out.

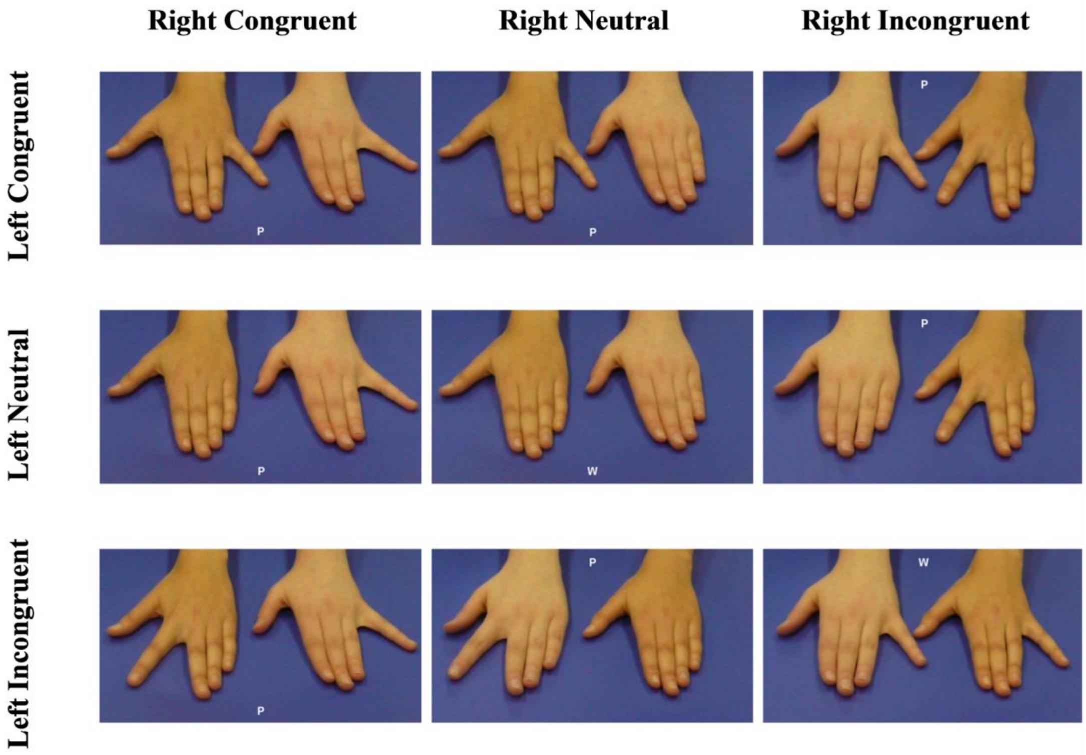

Figure 1. The design of experiment 1. Each cell contains an example stimulus for the corresponding condition.

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. 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 that were extracted from video clips (figure 1). These frames (1010 x 544 pixels) depicted two different female right hands (hand A and hand B), 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. 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. To record responses, we used an optical response box that detects when a finger leaves a sensor.

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 (left/right) and the order of the phases (cue bottom/cue top) was counterbalanced.

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. 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.

Data Analysis. All analyses were performed in R (R Development Core Team, 2013). Trials in which 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, erroneous trials (3.17%) and trials with a RT slower than 1000 ms (0.92%) were also excluded. Correlation coefficients represent Pearson product-moment correlation coefficients. *T* tests represent two-tailed paired samples *t* tests. *P*-values of post-hoc tests were corrected for multiple testing (p_c) according to Holm’s procedure (Holm, 1979) separately for each set of tests. When necessary, ANOVA degrees of freedom were corrected for violation of sphericity by applying the Greenhouse-Geisser correction. Partial eta squared (η_p^2) and Cohen’s *d* are reported as measures of effect size.

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 two identical observed movements produce a stronger congruency effect than a single observed movement. Finally, we investigate whether two different observed movements elicit opposing forces that cancel each other out.

Results

Motor simulation of two simultaneous observed movements. To determine whether a congruency effect was present for both hands, RTs and error rates were subjected 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 ANOVA. The analysis of the reaction times (figure 2a) revealed a main effect of left-side congruency, $F(1.47, 54.38) = 46.63$, $p < 0.001$, $\eta_p^2 = 0.56$, 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, $F(1.62, 59.86) = 31.59$, $p < 0.001$, $\eta_p^2 = 0.46$, 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), $t(37) = -3.39$, $p_c = 0.002$, $d = 0.55$. No main effect of imperative cue position was observed, $F(1, 37) = 2.38$, $p = 0.131$.

The analysis also revealed an interaction between left-side congruency and right-side congruency, $F(3.34, 123.76) = 3.36$, $p = 0.017$, $\eta_p^2 = 0.08$. This seems at odds with the hypothesis that a congruency effect should be present for both hands regardless of the action performed by the other hand. However, a left-side congruency x right-side congruency interaction does not necessarily imply that the presence of a left-side (right-side) congruency effect depended on right-side (left-side) congruency. It could, for instance, also indicate that the left-side (right-side) congruency effect was present for all levels of right-side (left-side) congruency but not with the same strength. To ensure that this was the case, we computed the left-side (right-side) congruency effect (IC – C) for the different levels of right-side (left-side) congruency. This confirmed that the congruency effect was present for both the left-side hand, all $t(37) \geq 4.15$, all $p_c < 0.001$, all $d \geq 0.67$, and the right-side hand, all $t(37) \geq 5.00$, all $p_c < 0.001$, all $d \geq 0.81$, regardless of the action (C, N, IC) performed by the other hand[2]. No other two- or three-way interactions were observed, all $p \geq 0.307$.

The analysis of the error rates (figure 2b) revealed a similar pattern with a main effect of left-side congruency, $F(1.61, 59.50) = 18.60$, $p < 0.001$, $\eta_p^2 = 0.33$, and right-side congruency, $F(1.87, 69.15) = 26.78$, $p < 0.001$, $\eta_p^2 = 0.42$. 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%), $t(37) = -2.36$, $p_c = 0.024$, $d = 0.38$, and lower error rates in LN than in LIC (4.39%), $t(37) = -4.35$, $pc < 0.001$, $d = 0.71$. 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%), $t(37) = -3.06$, $p_c = 0.004$, $d = 0.50$, 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 near significance, $F(3.46, 127.99) = 2.55$, $p = 0.051$, $\eta_p^2 = 0.06$. To ensure that the left-side (right-side) congruency effect was present for all levels of right-side (left-side) congruency, we again computed the left-side (right-side) congruency effect (IC – C) separately for the different levels of right-side (left-side) congruency. This confirmed that the congruency effect was present for both the left-side hand, all $t(37) \geq 2.25$, all $p_c \leq 0.031$, all $d \geq 0.37$, and the right-side hand, all $t(37) \geq 2.75$, all $p_c \leq 0.009$, all $d \geq 0.45$, irrespective of what the other hand was doing (C, N, IC)[2]. No other two- or three-way interactions were observed, all $p \geq 0.203$.

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[2] The precise pattern of the interaction is not further explored here because it is complex and not relevant to the research questions. A detailed description and interpretation of the interaction pattern can be found in appendix.

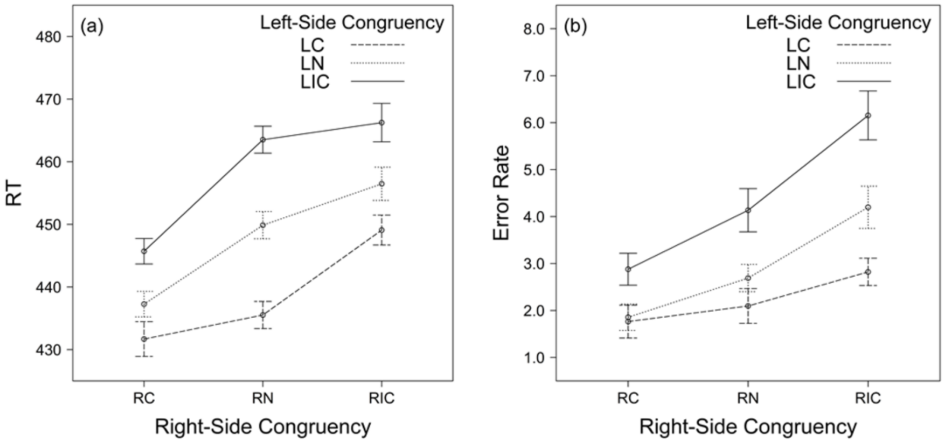

Figure 2. Reaction times in ms (a) and error rates in % (b) of the left-side congruency x right-side congruency analysis. Error bars represent standard errors of the mean (SEMs) corrected for within-subject designs according to Morey (2008).

Motor Simulation of two identical observed movements. Next, to determine whether two identical observed movements produced a stronger congruency effect, we took the relevant conditions (IC/IC, C/C, IC/N, N/IC, C/N, and N/C)[3] and submitted the RTs and error rates to a 2 (number of hand movements: one vs. two) x 2 (congruency: IC vs. C) repeated measures ANOVA. Because the effect of imperative cue position failed to reach significance in the previous analysis, this variable was no longer considered in this analysis or in further analyses. The reaction time analysis (figure 3a) revealed a main effect of congruency, $F(1, 37) = 65.67$, $p < 0.001$, $d = 1.32$, with RTs in IC (463 ms) being slower than RTs in C (434 ms), but no main effect of number of hand movements, $F < 1$. As predicted, the analysis also revealed an interaction between number of hand movements and congruency, $F(1, 37) = 6.91$, $p = 0.012$, $d = 0.43$. Follow-up tests showed that the congruency effect was present regardless of the number of hand movements, both $t(37) \geq 6.97$, both $p_c < 0.001$, both

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[3] 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.

$d \geq 1.13$, but the effect was stronger for two identical observed movements (34 ms) than for a single observed movement (24 ms).

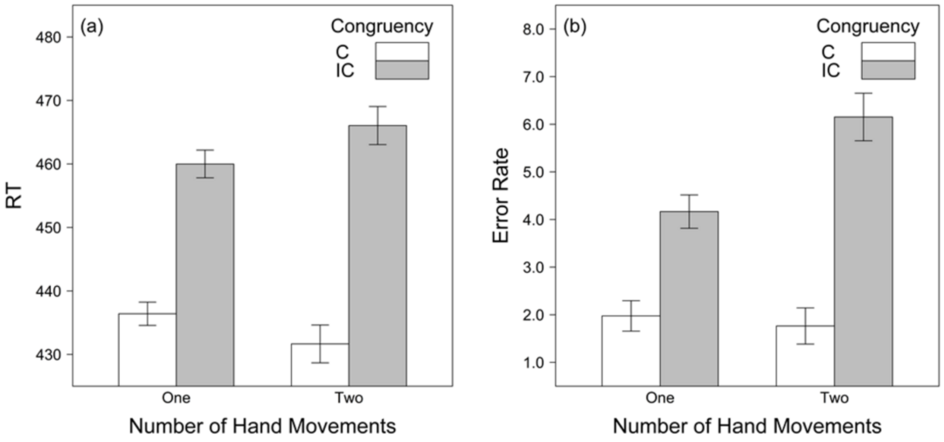

Figure 3. Reaction times in ms (a) and error rates in % (b) of the number of hand movements x congruency analysis. Error bars depict SEMs corrected for within-subject designs according to Morey (2008).

The analysis of the errors rates (figure 3b) again showed a main effect of congruency, $F(1, 37) = 41.89$, $p < 0.001$, $d = 1.05$, with more errors in IC (5.16%) than in C (1.87%), but also a main effect of number of hand movements, $F(1, 37) = 6.22$, $p = 0.017$, $d = 0.41$, with more errors when two hands made a movement (3.96%) instead of one (3.07%). Importantly, the interaction between number of hand movements and congruency was significant as well, $F(1, 37) = 14.02$, $p < 0.001$, $d = 0.61$. Follow-up tests showed that there was a congruency effect regardless of the number of hand movements, both $t(37) \geq 4.69$, both $p_c < 0.001$, both $d \geq 0.76$, but the effect was again stronger for two identical observed movements (4.39%) than for a single observed movement (2.19%).

Motor simulation of two different observed movements. Finally, we investigated the effect of seeing two different movements. We reasoned that this should result in facilitation from the congruent hand movement and interference from the incongruent hand movement. Because these effects are opposing forces, we hypothesized that they should cancel each other out. To investigate this, we examined whether the RTs and error rates were different when participants observed two different movements (MEAN C/IC)[4] compared to when participants observed no movement (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 capitalized on the observation that some subjects were influenced more by congruent than by incongruent movements (facilitation bias), whereas other subjects were influenced more by incongruent than by congruent movements (interference bias). To rule out the alternative hypotheses that neither movement or only one movement was processed when the two hands acted differently, we then 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 neither of the two movements was processed, no correlation should be observed between the two facilitation biases. This is due to the fact that the movements of at least one hand have to be processed in order for a facilitation (or interference) bias to occur. Alternatively, if only the movements of a single hand were processed, the facilitation biases should be correlated negatively. For example, if a certain participant processed only the movements of the left-side hand, 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). Finally, if the movements of both hands were processed, a positive relation should emerge because a facilitation bias in the C/IC condition should still be present in the IC/C

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[4] This code represents the fact that the C/IC and IC/C conditions were aggregated.

condition. The correlation analysis (figure 4) between the two facilitation biases revealed a positive correlation, r = 0.48, p = 0.002, suggesting that the movements of both hands were represented in the motor system even when they acted differently.

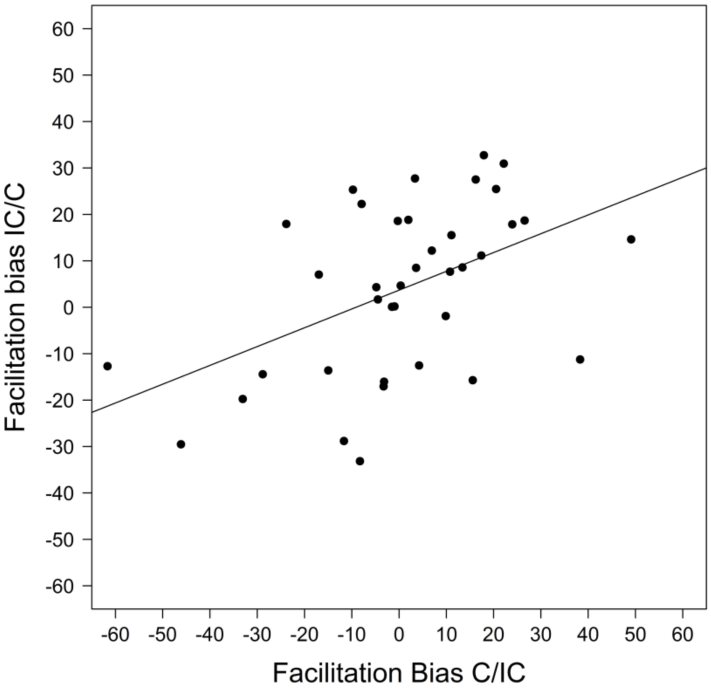

Figure 4. Correlation between the C/IC and IC/C facilitation bias in ms. The line represents a linear regression fit line.

Discussion

In the current experiment it was explored whether individuals automatically simulate the movements of multiple persons at the same time in their motor system. To this end, we investigated imitative tendencies in a situation where individuals saw two different hands making movements that were either congruent or incongruent with respect to the required response. It was hypothesized that automatic imitation should occur for both hands regardless of the action that was performed by the other hand. The results indicated that both hands produced a congruency effect, but also that these congruency effects were not independent of one another. Further analyses revealed that, despite the interaction, the congruency effect was always present for both hands irrespective of what the other hand did. This suggests that the actions of each hand influenced *how* the actions of the other hand were processed in the motor system, but not *if* the actions of the other hand were processed in the motor system.

Next, it was investigated how the motor system processes two simultaneously observed movements by zooming in on two specific situations, namely the situation in which the two hands made an identical movement and the situation in which the two hands made a different movement. When the two hands made an identical movement, a larger congruency effect was found as compared to when a single hand made a movement. This suggests that the movements of the two hands were mapped onto the same motor representation, causing the motor representation to be activated more strongly. When the two hands made a different movement, one congruent and one incongruent, 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 of the two movements was processed or that only one movement 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.

To summarize, the results of the current study suggest that the actions of multiple observed actors are automatically simulated in the motor system. Importantly, the results of the current study cannot be explained in terms of social facilitation (Zajonc, 1965), which is the phenomenon that individuals perform a task better or worse in the presence of others. That is, a social facilitation account would have predicted an influence of the number of observed actions independent of the content of these actions. The results of the current study, however, clearly showed that seeing two identical actions had a different effect than seeing two different actions. Moreover, a social facilitation account is not able to explain why the influence of seeing two identical actions was dependent on the congruency of these actions with the required response. It is, in other words, unlikely that social facilitation caused the effects described above.

Similarly, it is unlikely that the results of the current experiment can be reduced to general features of visual processing. For example, previous research has shown that reactions to bilateral redundant targets are faster than reactions to unilateral targets (e.g., Mooshagian, Kaplan, Zaidel, & Iacoboni, 2008). A crucial difference between these studies and the current study, however, is that these previous studies have investigated the influence of redundant task-relevant stimuli, whereas the current study investigated the influence of redundant task-irrelevant stimuli. That is, in the present study it was found that perceiving two identical movements facilitates motor responses even though the perceived movements were neither relevant nor informative for response selection. For these movements to influence the response selection process, it is necessary to assume a mechanism that automatically links perceived movements to motor responses. In line with previous work (Brass, Bekkering, & Prinz, 2001; Brass et al., 2000), we assume that this mechanism is the ideomotor mechanism.

It can, however, be argued that part of the results are due to the fact that two simultaneous observed movements are more salient than a single observed movement. Since earlier research has suggested that attention is an important modulator of automatic imitation (Aicken, Wilson, Williams, & Mon-Williams, 2007; Bach, Peatfield, & Tipper, 2007; Jansson, Wilson, Williams, & Mon-Williams, 2007), it is possible that the stronger congruency effect for two identical observed movements was caused by increased attentional orienting towards the hand stimuli rather than both hand movements activating the same motor representation.

Experiment 2

To rule out the possibility that the stronger congruency effect for two identical observed movements was caused by increased attentional orienting, experiment 2 tested if this effect depended on whether the hands belonged to a human agent or to a non-human agent. According to ideomotor theory, the connection between perception and action depends on the degree to which the observed agent is similar to oneself (Brass et al., 2001, 2000; Greenwald, 1972). In line with this idea, a number of studies have reported that automatic imitation is stronger for human agents than for non-human agents (Brass et al., 2001; Kilner, Paulignan, & Blakemore, 2003; Press, Bird, Flach, & Heyes, 2005; Press, Gillmeister, & Heyes, 2006, 2007) and for intentional agents than for non-intentional agents (Liepelt et al., 2008). Consequently, if the additive effect for two identical observed movements is the result of both movements activating the same motor representation, then this effect should be stronger for human agents than for non-human agents. On the other hand, if this effect is the result of increased attentional orienting, then it should not be different for human and non-human agents. Importantly, this is only the case if the movements of the human and non-human agents are matched on saliency. To account for this, we compared automatic imitation of human hands with automatic imitation of wooden hands (figure 5). Because the human and wooden hands were highly similar, differences between the two stimulus types cannot be explained in terms of attentional capture.

However, apart from the possibility that either motor simulation or attentional capture explains the additive effect of seeing two identical movements, it is also conceivable that both mechanisms play a role. To address this third option, we additionally examined whether the congruency effects produced by human and wooden hands followed the same time course. Because attentional capture is likely to operate at early time points (e.g., Klein, 2000) and motor simulation is known to operate primarily at later time points (e.g., Boyer, Longo, & Bertenthal, 2012; Brass et al., 2001; Catmur & Heyes, 2011; Cooper, Catmur, & Heyes, 2013), this analysis allows us to better understand their contribution in construing the obtained effects.

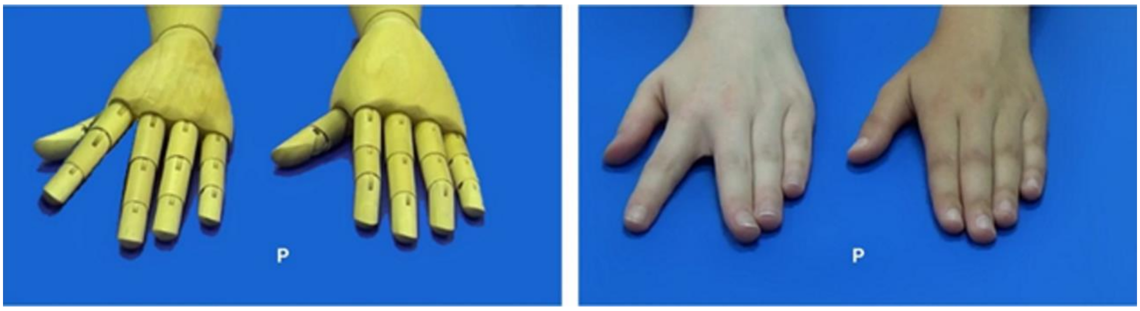

Figure 5. Example stimuli of experiment 2.

Method

Participants. 40 persons participated in the experiment (M_{age} = 24.52, SD_{age} = 6.36). All of them were right-handed females with good or corrected vision. 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 et al., 2006). In order to ensure that the human and the wooden hands were filmed from the same angle and with the same light exposure, we created new stimuli (1010 x 544 pixels) according to the procedure of experiment 1 (figure 5). An illusion of movement was again induced by overwriting a picture of the hands in their neutral posture with a picture of the hands in their final posture. Because the abduction movement was mechanically not possible for the wooden hands, they were manipulated digitally. Note that the wooden hands were manipulated in such a way that the abduction movements were of similar magnitude as the abduction movements of the human hands.

In contrast to experiment 1, we did not use the stimuli in which the two hands made a different movement and the stimuli in which neither of the two hands made a movement. The experiment thus included six possible final hand postures, namely C/N, N/C, IC/N, N/IC, C/C, IC/IC. In order to record responses, we used an optical response box that detects when a finger leaves a sensor.

Procedure. The experiment took about 20 minutes and consisted of two phases. In one phase the stimuli depicted two human hands and in the other phase the stimuli depicted two wooden hands. Each phase started with 10 practice trials with feedback, followed by three blocks of each 60 trials without feedback. Each final hand posture was shown 10 times per block, 5 times with W as imperative cue and 5 times with P as imperative cue. After each block, participants had the opportunity to take a break. Trials were presented at random, with the restriction that the same imperative cue could not appear on more than four consecutive trials. The position of the human hands (left/right), the position of the wooden hands (left/right), and the order of the phases (human hands first/wooden hands first) were counterbalanced.

Before the experiment, instructions appeared on the screen. The instructions differed slightly for the two phases. In the human hands phase, the participants were told that they would see two female hands and that these hands would make finger movements. In the wooden hands phase, the participants were told that they would see two wooden hands and that these hands were manipulated digitally to make it seem as if they made finger movements. The instructions further requested to make an abduction movement with the right hand index finger when W (‘wijsvinger’) appeared on the screen and to make an abduction movement with the right hand little finger when P (‘pink’) appeared on the screen. Participants were asked to respond as fast as possible, but without making errors.

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. 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.

Data Analysis. All analyses were performed in R (R Development Core Team, 2013). Trials in which the response deadline was exceeded (0.24%) were excluded from all analyses. Furthermore, trials with a RT faster than 100 ms (0.11%) were seen as action slips and were excluded as well. Finally, erroneous trials (4.62%) and trials with a RT slower than 1000 ms (0.59%) were excluded from the RT analysis. P-values of post-hoc tests were corrected for multiple testing (p_c) according to Holm’s procedure (Holm, 1979) separately for each set of tests. *T* tests correspond to two-tailed paired samples *t* tests. When necessary, ANOVA degrees of freedom were corrected for violation of sphericity by applying the Greenhouse-Geisser correction. Partial eta squared (η_p^2) and Cohen’s *d* are reported as measures of effect size.

Results

The RTs and error rates were subjected to a 2 (stimulus type: human vs. wooden hands) x 2 (number of hand movements: one vs. two) x 2 (congruency: C vs. IC) repeated measures ANOVA. The reaction time analysis (figure 6a, 6b) revealed a main effect of congruency, $F(1, 39) = 95.10$, $p < 0.001$, $d = 1.54$, with slower responses in IC (452 ms) than in C (419 ms). It also indicated a main effect of stimulus type, $F(1, 39) = 6.80$, $p = 0.013$, $d = 0.41$, with slower RTs for the wooden hands (440 ms) than for the human hands (431 ms).

The main effect of number of hand movements, however, had no effect on the RTs, $F < 1$. The interaction of stimulus type x number of hand movements was not significant, $F(1, 39) = 1.10$, $p = 0.309$. Furthermore, no interaction of stimulus type x congruency was found, $F < 1$, indicating no difference between the congruency effects produced by the human (35 ms) and the wooden hands (32 ms). In line with experiment 1, the interaction between number of hand movements and congruency was significant, $F(1, 39) = 19.10$, $p < 0.001$, $d = 0.69$. Follow-up tests indicated that the congruency effect was present regardless of the number of movements, both $t(39) \geq 7.94$, both $p_c < 0.001$, both $d \geq 1.26$, but the effect was stronger for two identical observed movements (40 ms) than for a single observed movement (27 ms). Importantly, the three-way interaction stimulus type x number of hand movements x congruency was also significant, $F(1, 39) = 5.50$, $p = 0.024$, $d = 0.37$. To further explore this three-way interaction, we analyzed the number of hand movements x congruency interaction separately for the two hand types. For the human hands, a significant interaction was observed, $F(1, 39) = 28.49$, $p_c < 0.001$, $d = 0.84$. Follow-up tests showed that there was a congruency effect regardless of the number of movements, both $t(39) \geq 6.53$, both $p_c < 0.001$, both $d \geq 1.03$, but the effect was stronger for two identical observed movements (45 ms) than for a single observed movement (25 ms). The same interaction did not reach significance for the wooden hands, $F(1, 39) = 2.84$, $p_c = 0.100$, $d = 0.27$, although there was a trend towards a stronger congruency effect for two identical observed movements (36 ms) than for a single observed movement (29 ms).

The error analysis (figure 6c, 6d) indicated a main effect of congruency, $F(1, 39) = 45.67$, $p < 0.001$, $d = 1.07$, with more errors in IC (7.19%) than in C (2.24%). The main effect of stimulus type and the main effect of number of hand movements, on the other hand, did not reach significance, both $F(1, 39) \leq 1.83$, both $p \geq 0.184$. The interaction between stimulus type and number of hand movements was not significant, $F(1, 39) = 2.16$, $p = 0.150$. In addition, the interaction between stimulus type and congruency did not show a difference between the congruency effect produced by the human hands (5.39%) and the wooden hands (4.52%), $F < 1$. The interaction between number of hand movements and congruency was again significant, $F(1, 39) = 15.01$, $p < 0.001$, $d = 0.61$. Follow-up analyses revealed the presence of a congruency effect independent of the number of movements, both $t(39) \geq 5.09$, both $p_c < 0.001$, both $d \geq 0.80$, but the effect was stronger for two identical observed movements (6.30%) than for a single observed movement (3.60%). The three-way interaction stimulus type x number of hand movements x congruency was, however, not significant, $F < 1$, indicating that two identical observed movements increased the congruency effect to the same extent for human and wooden hands.

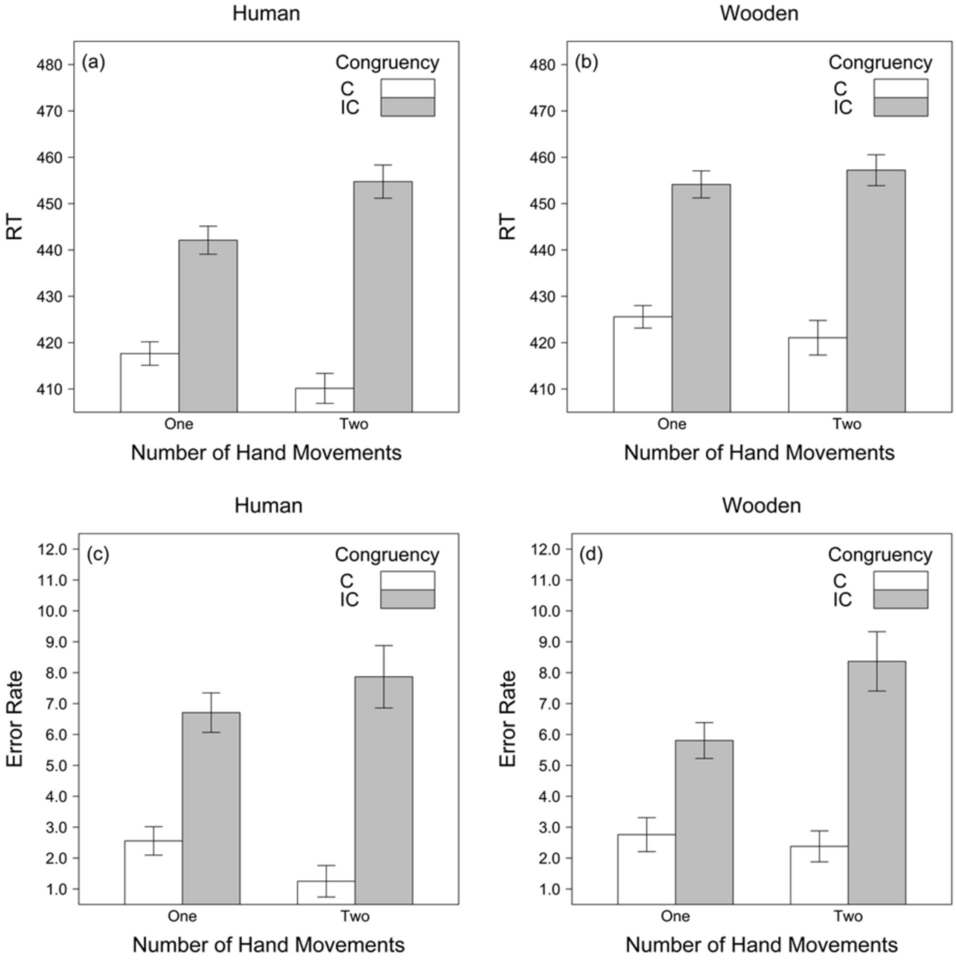

Figure 6. Reaction times in ms for the human (a) and wooden hands (b) and error rates in % for the human (c) and wooden hands (d). Error bars depict SEMs corrected for within-subject designs according to Morey (2008).

Finally, to better understand the obtained effects, we examined their time course by means of a quintile analysis (Ratcliff, 1979) on the RTs (figure 7). In this analysis, RTs are evenly divided into five bins ranging from fastest to slowest separately for each condition and for each participant. The congruency effects (IC – C) that resulted from this procedure were subjected to a 2 (stimulus type) x 2 (number of hand movements) x 5 (time bin) repeated measures ANOVA (table 1). Note that we will only report the results that relate to time bin because the remaining results were already discussed above. The main effect of time bin was significant, $F(1.60, 62.31) = 45.67$, $p < 0.001$, $\eta_p^2 = 0.54$, indicating that the congruency effect increased with each bin. The interaction between stimulus type and time bin was also significant, $F(1.83, 71.22) = 6.81$, $p = 0.003$, $\eta_p^2 = 0.15$, showing that the congruency effect increased more strongly with time bin for the human than for the wooden hands. The number of hand movements x time bin interaction was not significant, $F < 1$.

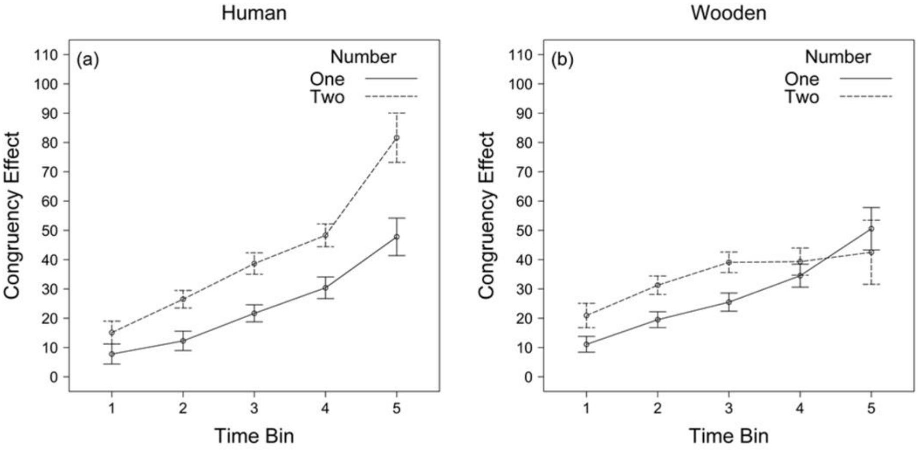

Figure 7. Reaction time congruency effects (IC – C) in ms for the human (a) and wooden hands (b) separately for each time bin. Error bars depict SEMs corrected for within-subject designs according to Morey (2008).

Interestingly, a near-significant stimulus type x number of hand movements x time bin three-way interaction was observed, $F(1.35, 52.66) = 3.41$, $p = 0.058$, $\eta_p^2 = 0.08$. To further explore this effect, we examined the stimulus type x time bin interaction separately for the condition in which a single movement was observed and the condition in which two identical movements were observed. This revealed that a stimulus type x time bin interaction was absent when a single movement was seen, $F < 1$, but present when two identical movements were seen, $F(1.53, 59.76) = 7.02$, $p_c = 0.008$, $\eta_p^2 = 0.15$. Additional analyses showed that the congruency effect increased with time bin both for human and wooden hands when a single hand made a movement, but not when both hands made an identical movement. Instead, when both hands made an identical movement, the congruency effect still increased with time bin for the human hands, but stabilized after the first three bins for the wooden hands. As a result of this pattern, the additive effect produced by two identical observed movements relative to a single observed movement was present in all but the first time bin when participants saw human hands, but only in the first three time bins when participants saw wooden hands.

Table 1.

Results of the quintile analysis.

	Bin 1		Bin 2		Bin 3		Bin 4		Bin 5
Human Hands									
One	7.78	†	12.27	***	21.69	**	30.41	**	47.79
			**		**		**		**
Two	15.12	**	26.50	**	38.68	**	48.32	***	81.64
Wooden Hands									
One	11.10	**	19.51	*	25.50	***	34.53	*	50.55
	†		*		*				
Two	20.94	*	31.28	**	39.10		39.34		42.53

Note. Each cell displays the mean congruency effect (IC – C) in ms. In between the cells is shown whether the respective conditions differ significantly after applying Holm's correction for multiple testing (Holm, 1979) separately for each set of tests. Significance is denoted as follows: †$p < 0.10$, *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.

Discussion

Experiment 1 revealed a stronger congruency effect when individuals saw two identical movements compared to when they saw a single movement. It was argued that two identical observed movements trigger the same motor representation and therefore produce a stronger automatic imitation effect. However, an alternative explanation is that two simultaneous observed movements are more salient than a single observed movement and hence attract more attention. To exclude the latter possibility, we conducted a second experiment in which the additive effect of seeing two identical movements was compared for human and wooden hands. Specifically, it was reasoned that human and wooden hands are highly similar and that their movements should therefore not differ with respect to attentional capture. Following this line of reasoning, it was argued that the specified additive effect should be equally strong for the two hand types if it is driven by saliency. If it is driven by motor simulation, however, it should be stronger for human hands. That is, ideomotor theory states that the influence of perception on action depends on the degree to which the observed agent resembles the observer. Because wooden hands are non-intentional (e.g., Liepelt et al., 2008) and non-biological (e.g., Press et al., 2006, 2007) agents, they are expected to produce less automatic imitation than human hands (Brass et al., 2001, 2000; Greenwald, 1972). The results of experiment 2 replicated the finding that two identical observed movements produce a stronger congruency effect than a single observed movement. Importantly, the RT additive effect was found to be present for human hands, but not for wooden hands. This finding speaks against the saliency account and instead suggests that two identical observed movements activate the corresponding motor representation more strongly than a single observed movement.

However, we were not able to replicate previous reports of an overall weaker congruency effect for non-biological agents (e.g., Brass et al., 2001; Kilner et al., 2003; Press et al., 2005, 2006, 2007). Furthermore, a discrepancy was observed between the RT additive effect and the error rate additive effect. That is, whereas the RT additive effect distinguished between human and wooden hands, this was not the case for the error rate additive effect. To better understand the obtained pattern, we therefore studied the time course of the congruency effect separately for human and wooden hands by means of a time bin analysis (Ratcliff, 1979). This analysis revealed that the time course was similar when a single movement was observed, but not when two simultaneous movements were observed. While the congruency effect evoked by seeing a single movement increased with response time for both human and wooden hands, the congruency effect evoked by seeing two identical movements increased consistently only for human hands. For wooden hands, the congruency effect first increased with response time but then stabilized. As a consequence of this pattern, the additive effect of seeing two identical movements was observed regardless of response time when the hands were human, but only at early response times when the hands were wooden. To summarize, the results of the time bin analysis suggest that human and wooden hand movements were processed differently when two simultaneous movements were observed. As a result, the additive effect of seeing two identical movements followed a different pattern for the two hand types. Specifically, the time course suggests that the additive effect was driven by saliency for the wooden hands, but by automatic imitation for the human hands. Indeed, previous work has shown that the deployment of attention to salient stimuli occurs very rapidly and decreases over time (e.g., Klein, 2000). Automatic imitation, on the other hand, is known to be weak at early response times and to build up over time (e.g., Boyer et al., 2012; Brass et al., 2001; Catmur & Heyes, 2011; Cooper et al., 2013).

In contrast to the congruency effect produced by multiple agents, however, the congruency effect produced by a single agent appeared to be driven by the same mechanism for human and wooden hands. Specifically, the finding that the congruency effect increased in strength with response time is consistent with the idea that it reflected automatic imitation (e.g., Boyer et al., 2012; Brass et al., 2001; Catmur & Heyes, 2011; Cooper et al., 2013). In conclusion, Experiment 2 shows that human hand movements were simulated regardless of the number of observed movements, whereas wooden hand movements were only simulated when a single movement was observed. The fact that automatic imitation of a single wooden hand was unimpaired is in line with a number of previous studies in which reduced automatic imitation for humanlike non-biological agents was also not found. Press and colleagues (Press et al., 2006), for example, compared automatic imitation of human hand movements with automatic imitation of robot hand movements. When the robot hand was constructed as a human hand with a metal wire wrist, no difference in automatic imitation was found. When the robot hand was constructed as a gripper, however, automatic imitation was stronger for the human hand. Similarly, Longo and Bertenthal (2009) found no difference in automatic imitation of human and computer-generated hand movements unless attention was directed towards the non-biological character of the computer-generated hand. Finally, in a study by Liepelt, Prinz, and Brass (2010) automatic imitation was only stronger for human hand movements than for wooden hand movements when the hands performed communicative gestures. Adding to these findings, the results of the current study suggest that differences in motor simulation between biological and humanlike non-biological agents might only become visible in complex social situations where the actions of multiple agents have to be integrated.

The question still remains, however, why the error rate additive effect was not different for human and wooden hands. A likely explanation is that this is due to differences in response time between error and correct responses. That is, errors are known to coincide with early responses (e.g., Rabbitt, 1966) as they often reflect impulsive responses delivered before the relevant stimulus was completely processed (Botvinick, Braver, Barch, Carter, & Cohen, 2001; Gratton, Coles, Sirevaag, Eriksen, & Donchin, 1988). In the current study, RTs of erroneous responses (398 ms) were indeed significantly faster than RTs of correct responses (439 ms), $t(39) = -5.16$, $p < 0.001$. Given that the additive effect of seeing two identical movements only differentiated between human and wooden hands for later responses, it is probable that the error rate analysis was unable to detect this difference.

To conclude, the findings of experiment 2 replicate the findings of experiment 1 and show that the stronger congruency effect for two identical observed movements is possibly driven by saliency on fast responses but by automatic imitation on late responses. As such, experiment 2 further supports the idea that the movements of multiple agents are automatically simulated in the motor system of the observer.

General Discussion

The aim of the current study was to investigate whether individuals automatically simulate the actions of multiple agents in their motor system. In order to address this question, we adapted a well-known automatic imitation paradigm to include two observed hands instead of one. In experiment 1, it was found that individuals automatically imitated the movements of both hands. In addition, it was found that two identical observed movements produced a stronger automatic imitation effect than a single observed movement and that two different observed movements produced a concurrent facilitation and interference effect that cancelled each other out.

However, an alternative explanation for the finding that two identical observed movements produced a stronger automatic imitation effect is that two simultaneous observed movements attract more attention than a single observed movement. To exclude an explanation in terms of salience, experiment 2 examined if the additive effect of seeing two identical movements differed between human and wooden hands. It was reasoned that the effect should be equally large if it was driven by saliency, but smaller for the wooden hands if it was driven by motor simulation. In line with the motor simulation explanation, the results demonstrated that the additive effect of seeing two identical movements was stronger for human than for wooden hands. This supports the idea that two identical observed movements are mapped onto the same motor representation and therefore activate this representation more strongly.

Parameters of Multi-Actor Motor Simulation

While the current study provides support for the idea that the actions of multiple individuals are simulated automatically in the motor system, important questions remain with respect to the different parameters that influence the involvement of the motor system in multi-actor situations. For example, one important question is whether the motor system differentiates between two observed actions performed by different individuals and two observed actions performed by the same individual (e.g., bimanual actions). While this is the first study to investigate how the actions of multiple actors are processed in the motor system, two studies have already investigated the involvement of the motor system in bimanual action observation. In one study, it was compared how the brain responds to unimanual and bimanual observed actions (Heitger, Mace, Jastorff, Swinnen, & Orban, 2012). It was found that bimanual observed actions activate the motor system with the same strength as unimanual observed actions, but do so more bilaterally. In another study, weak bilateral motor activation was observed when the involvement of the motor system was measured with TMS while participants observed symmetrical bimanual language signs (Möttönen, Farmer, & Watkins, 2010). These studies thus suggest that the observation of bimanual actions affects the lateralization of the motor response rather than its strength. Given the different methods and paradigms, it is not evident to compare these results with the results of the current study. Nevertheless, the fact that the current study revealed an influence of the number of observed agents on the strength of the motor response may point towards differences in processing multiple simultaneous actions of the same individual and multiple simultaneous actions of different individuals. Further research should directly compare these two situations to better understand if and how the brain distinguishes between them.

Another parameter that may influence the activation in the motor system is the synchronicity of the observed movements. Herrmann and colleagues (2013), for example, observed that children have an increased tendency to imitate behavior when the behavior is demonstrated by two models compared to a single model. Interestingly, two models increased imitative tendencies both when the models performed the behavior in synchrony and when they performed the behavior consecutively, but the effect was stronger for two synchronous models. This suggests that identical actions trigger the motor system more strongly when they are performed without delay.

Finally, the activation of the motor system may depend on the number of observed actors. In the study of Milgram and colleagues (1969), for example, it was shown that the probability of imitation increased with the number of observed actors. However, the degree to which an additional actor increased the probability of imitation decreased when the group of observed actors became larger. This suggests that a saturating curvilinear relation may exist between the number of observed actors that perform an identical movement and the activation in the motor system.

Implications of Multi-Actor Motor Simulation

The finding that individuals simultaneously simulate the actions of multiple agents in their motor system may have important implications for the understanding of the neurocognitive mechanisms that support social interaction. That is, while previous work has ascribed an important role to motor simulation in social interaction (e.g., Knoblich & Sebanz, 2006), its social function has so far only been investigated in dyadic situations. The findings of the current study allow us to extend the social function of motor simulation to multi-actor social situations.

An important social skill that relies on motor simulation, for instance, is the ability to execute joint actions (e.g., Colling et al., 2013; Knoblich & Sebanz, 2006). In joint action tasks, it is imperative that individuals are able to adapt their behavior to the actions of others. In a tennis game, for example, a player can anticipate the end location of the ball by combining information about the kinematics and the strength of his opponent’s shot. An efficient way to do this is to simulate the actions of the opponent in the motor system. However, a tennis game can also be played in teams. In such games, each player has to take into account the actions of three other players, namely one team member and two opponents. To decide where to run when an opponent hits the ball, it is now not only important to monitor the kinematics and strength of the opponent’s shot, but also to monitor the behavior of the team member. The current study opens up the possibility that multi-actor joint action tasks, such as doubles tennis games, depend on the ability to simulate the movements of multiple agents simultaneously in the motor system. An interesting avenue for further research is therefore to explore the involvement of the motor system in joint action tasks that exceed a dyadic structure.

In addition to the field of joint action, the current study may also have implications for imitation research. While most research on imitation has examined imitation in a context where one imitator copies the actions of one agent, some studies have now also investigated imitation in a context with multiple agents (Herrmann et al., 2013; Milgram et al., 1969; Tsai et al., 2011). In two of these studies, it was found that that the probability of imitation is related to the number of observed actors (Herrmann et al., 2013; Milgram et al., 1969). As an explanation, these studies argued that interpretive processes mediate the effect of the number of observed actors on imitative tendencies. The current study, on the other hand, suggests that these effects are not mediated by interpretive processes but by the degree to which the relevant motor representation is activated. That is, in the current study the relation between the number of agents and imitative tendencies was explored in a situation where interpretive processes are unlikely to have played a role. Nevertheless, automatic imitation was found to depend on the number of agents that performed a certain movement. The current study thus suggests that an action performed by multiple people is imitated more often because this activates the corresponding motor representation more strongly. This mere motor activation could then trigger interpretive processes (e.g., “does the behavior make sense?”) that determine whether the evoked action is eventually executed or inhibited. However, in this view, interpretive processes are not the antecedent but the consequence of imitative tendencies.

To conclude, the current study provides evidence for the idea that individuals automatically simulate the actions of multiple agents in their motor system. Given the fact that motor simulation is deeply rooted in social cognition (Knoblich & Sebanz, 2006), this finding may increase our understanding of the neurocognitive mechanisms that support multi-agent social interactions.

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Appendix

In this appendix, we will explore the left-side congruency x right-side congruency effect reported in experiment 1 separately for RTs and error rates. In addition, we will provide an interpretation for the obtained pattern.

Reaction Times

With regard to the RTs, it appears from figure 2a that the interaction was driven by a stronger left-side congruency effect under RN than under RC or RIC. This was supported by post-hoc analyses that confirmed the presence of a stronger left-side congruency effect (LIC – LC) under RN (28 ms) than under RC (14 ms), $t(37) = 3.58$, $p_c = 0.003$, $d = 0.58$, and a trend towards a stronger left-side congruency effect under RN than under RIC (17 ms), $t(37) = 2.14$, $p_c = 0.078$, $d = 0.35$, but no difference between the left-side congruency effect under RC and under RIC, $t < 1$.

Error Rates

With regard to the error rates, figure 2b suggests that the left-side congruency effect was stronger under RIC than under RC or RN and that the right-side congruency effect was stronger under LIC than under LC or LN. Follow-up tests for the left-side congruency effect partially supported this visual analysis by showing a stronger left-side congruency effect (LIC – LC) under RIC (3.33%) than under RC (1.11%), $t(37) = 3.34$, $p_c = 0.006$, $d = 0.54$. However, no stronger left-side congruency effect was found under RIC than under RN (2.03%), $t(37) = 1.93$, $p_c = 0.122$, $d = 0.31$. Likewise, the left-side congruency effect did not differ between RC and RN, $t(37) = 1.24$, $p_c = 0.225$, $d = 0.20$. Similar to pattern for left-side congruency, exploration of the right-side congruency effect revealed that it (RIC – RC) was stronger under LIC (3.27%) than under LC (1.06%), $t(37) = 3.34$, $p_c = 0.006$, $d = 0.54$, but not stronger under LIC than under LN (2.34%), $t(37) = 1.23$, $p_c = 0.226$, $d = 0.20$. No difference was observed between the right-side congruency effect under LC and under LN, $t(37) = -1.87$, $p_c = 0.139$, $d = 0.30$.

Interpretation

A possible explanation for the RT interaction pattern could be that there was a processing bias for the right-side hand. That is, it was found that the left-side congruency effect was strongest when the right-side hand did not move. This suggests that the actions of the right-side hand hindered the processing of the left-side hand. One reason for such a right-side hand bias could be that the right-side hand was more similar to the response hand (i.e., the right hand). This could have caused the actions of the right-side hand to attract more attention than the actions of the left-side hand, leading to a reduced left-side congruency effect when the right-side hand moved.

This interpretation can, however, not easily explain the interaction pattern for the error rates. That is, for the error rates we found a stronger congruency effect when the other hand performed an incongruent action compared to when the other hand performed a congruent action. A look at figure 2b suggests that this was mainly driven by an imbalance in the additive effect produced by seeing two identical movements (see also figure 3b). That is, while there was a strong additive effect for two identical incongruent movements (IC/IC) compared to a single incongruent movement (IC/N or N/IC), $t(37) = 3.60$, $p < 0.001$, $d = 0.58$, there was virtually no additive effect for two identical congruent movements (C/C) compared with a single congruent movement (C/N or N/C), *t* < 1. A likely explanation for this finding is that there was a floor effect: two congruent movements may not have decreased the error rate because it was already very low for a single congruent movement.

The interaction thus appears to have a different cause for RTs and error rates. While the RT interaction seems to reflect a right-side hand bias, the error rate interaction seems to reflect an imbalance in the additive effect produced by two identical observed movements.

Chapter 3

Mirroring Multiple Agents: Motor Resonance During Action Observation is Modulated by the Number of Agents[1]

Although social situations regularly involve multiple persons acting together, research on the mirror neuron system has focused on situations in which a single agent is observed. Therefore, the goal of the current study was to explore the role of the mirror mechanism in situations involving multiple agents. Specifically, we used transcranial magnetic stimulation (TMS) to investigate whether mirror activation is modulated by the number of observed agents. Based on group contagion research, we hypothesized that multiple agents would provide a stronger trigger to the motor system and would therefore produce a stronger mirror response than a single agent. Participants observed movements performed by a single hand or by two hands while TMS was applied to the primary motor cortex. The results confirmed that activation in the motor system was stronger for two hands. This suggests that input to the motor system increases as the number of agents grows. Relating back to group contagion, our study suggests that groups may be more contagious simply because their actions resonate louder. Given that the mirror mechanism has been linked to a variety of social skills, our findings additionally have important implications for the understanding of social interaction at the group level.

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[1] Cracco, E., De Coster, L., Andres, M., & Brass, M. (2016). Mirroring multiple agents: motor resonance during action observation is modulated by the number of agents. *Social Cognitive and Affective Neuroscience, 11(9)*, 1422-1427.

Introduction

Since their discovery in the monkey brain (Gallese et al. 1996; Rizzolatti et al. 1996), mirror neurons have been studied extensively in the literature. As a result of this research, it is now well established that a shared system for perception and action does not only exist in monkeys but can be found in humans as well (Molenberghs et al. 2012; Rizzolatti & Sinigaglia 2010). A useful technique to study the human mirror neuron system is transcranial magnetic stimulation (TMS). Numerous studies have now shown that the application of TMS to the primary motor cortex increases corticospinal excitability of the muscles involved in executing the observed movement (Fadiga et al. 1995, 2005; Maeda et al. 2002; Naish et al. 2014). Furthermore, it has been shown that these effects rely on input from regions within the frontoparietal mirror neuron network such as the premotor and intraparietal cortex (Avenanti et al. 2007, 2013; Catmur et al. 2011; Enticott et al. 2012; Koch et al. 2010). Interestingly, it has been argued that this mirror mechanism facilitates social interaction because it allows individuals to obtain first-person knowledge on the actions of others (Rizzolatti & Fabbri-Destro 2008). In line with this argument, studies have shown that motor resonance does not only reflect the kinematics (Maeda et al. 2002), but also the intention (Cattaneo et al. 2007; Tidoni et al. 2013), the goal (Cattaneo et al. 2009), and the outcome (Aglioti et al. 2008) of an observed action. This is further supported by evidence suggesting that motor activation is facilitated when an observed action is produced by another person but suppressed when it is produced by oneself (Schütz-Bosbach et al. 2006).

However, research on the mirror neuron system has so far mainly focused on situations in which a single agent is observed. It is therefore largely unknown how this system behaves in situations that include multiple agents. If the mirror system is involved in multi-agent interactions, activation in this system should be sensitive to the number of observed agents. In support of this idea, research in social psychology has shown that the behavior of groups is more contagious than that of a singleton. For example, Milgram et al. (1969) monitored the behavior of pedestrians as they passed by one or multiple confederates looking at a sixth floor window. It was shown that the tendency of passers-by to copy this behavior was stronger when the confederates formed a group (see also: Gallup et al. 2012; Knowles & Bassett 1976). In other work, similar effects were also obtained in the context of applause contagion (Freedman & Birsky 1980), queue formation (Mann 1977), helping behavior (Latané & Darley 1968), and action imitation (Herrmann et al. 2013). However, these findings have mainly been explained in terms of high-level interpretive processes. In the study of Milgram et al. (1969), for instance, it was argued that the gaze of a group is followed more often because groups are more likely to be attending something of interest. In contrast to this idea, we have recently shown that imitative tendencies increase for multiple agents in a simple movement paradigm where interpretive processes are unlikely to contribute (Cracco et al. 2015). Given that motor resonance is considered to be at the basis of automatic imitation (Bien et al. 2009; Catmur et al. 2009; Heyes 2011), this suggests that activation in the mirror neuron system might be sensitive to the number of observed agents. Specifically, multiple agents may provide a stronger trigger to the mirror system and hence produce a stronger motor response. As a result, groups could be more contagious simply because their actions resonate louder (Raafat et al. 2009).

To test the hypothesis that multiple agents evoke a stronger mirror response, the current study measured corticospinal excitability by means of TMS while participants passively observed two agents of whom a single agent or both agents performed a movement. To eliminate the influence of interpretive processes, the social context was minimized by reducing the agents to two hands making an index or little finger abduction movement (Cracco et al. 2015). Based on previous TMS research, we expected that action observation would enhance corticospinal excitability of the action relevant muscles but not of the action irrelevant muscles (Fadiga et al. 2005; Naish et al. 2014). In addition, we expected this effect to be stronger when the observed action was performed by two agents instead of a single agent.

Materials and Methods

Participants

Thirty-six right handed males (M_{age} = 22.25, SD_{age} = 3.06) participated in the study in exchange for 25 euros. However, as described below, two participants were excluded from analysis. This resulted in a sample of thirty-four participants (M_{age} = 22.27, SD_{age} = 3.14). All subjects had good or corrected vision, had no history of neurological or psychiatric disorder, 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 with Tscope (Stevens et al. 2006). Stimuli consisted of frames that were extracted from video clips (figure 1). The stimuli (1010 x 568 pixels) depicted two different male right hands. The hands were presented next to each other on a blue background from a first person perspective. The position (left/right) of the hands on the screen was counterbalanced. To produce an illusion of movement, a picture of the hands in their end posture was superimposed on a picture of the hands in their starting posture (see also: Catmur et al. 2007, 2011). The hands could either not move or abduct the index or little finger. Importantly, when both hands made a movement they always performed the same movement. As a result, the experiment included seven possible end postures: Static-Static, IndexFinger-Static, Static-IndexFinger, LittleFinger-Static, Static-LittleFinger, IndexFinger-IndexFinger, and LittleFinger-LittleFinger.

Task and Procedure

The experiment took about 45 minutes and consisted of four blocks of 105 trials each. All end postures were presented an equal number of times in each block in a random order. The experimental task required participants to monitor a cue (N, W, or P) appearing at the top of the screen simultaneously with the presentation of the end posture. Participants were instructed to abduct the index finger when W (10%) was presented and to abduct the little finger when P (10%) was presented. When N (80%) was presented, no action was required. The movement (W or P) and no-movement (N) trials were distributed equally among the seven possible end postures. On the movement trials, the cue was chosen randomly so that W and P appeared an equal number of times. This resulted in 14% neutral movement trials, 44% congruent movement trials, and 42% incongruent movement trials. The rationale behind the task was twofold. First, we wanted to maintain the attention of the participants. Second, we wanted to ensure that the relevant motor representations remained active throughout the experiment. Note that analyses were restricted to the N trials. As a result, motor execution processes could not influence the results.

Each trial started with a picture of the hands in their starting posture and a fixation cross at the top of the screen for 500 ms. The hands were then presented in their end posture for a duration of 1000 ms together with the cue. A TMS pulse was delivered on every trial. The pulse was delivered randomly at 300, 400, or 500 ms after the presentation of the end posture. The pulses were distributed equally among the three stimulation moments. The trial ended with the presentation of a black screen for a jittered duration of 4000, 5000, or 6000 ms.

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. 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 first dorsal interosseous (FDI) and the abductor digiti minimi (ADM) of the right hand with the ActiveTwo system (BioSemi, Amsterdam, The Netherlands) using sintered 11 x 17-mm active Ag–AgCl electrodes. The FDI is involved in abducting the index finger and the ADM is involved in abducting the little finger.

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 motor evoked potentials (MEP) in both the FDI and ADM. When the hotspot was found, the motor threshold was determined as the minimal stimulation intensity that produced a peak-to-peak MEP of 50μV or more in both muscles in 50% of the pulses. The stimulation intensity was set at 110% of the motor threshold during the experiment.

Data Analysis

The MEP peak-to-peak amplitude was computed in MATLAB. All statistical analyses were performed in R (R Development Core Team 2013). Two participants were excluded because their accuracy rate on the movement trials (75% and 80%) was more than 2.5 median absolute deviations (MADs) away from the median (Leys et al. 2013). Note, however, that including these two participants did not have an influence on the results.

For the remaining participants, only trials in which no movement was required were included in the analysis. Trials in which a movement was nonetheless produced were excluded (1.48%). To account for noise, we additionally removed trials in which the root mean square of the EMG signal was above 50μV in the 100 ms before the pulse (0.49%) and trials in which the MEP was below 50μV (4.13%). Finally, we excluded trials in which the MEP was more than 2.5 MADs away from the median (6.56%) to remove outliers (Leys et al. 2013). In total, 12.17% of the no-movement trials were excluded.

Data analysis was performed on the percentage of change in the MEPs with respect to the Static-Static baseline condition. The obtained change scores were subjected to a 2 (muscle: action relevant or action irrelevant) x 2 (number: one or two) x 3 (pulse moment: 300, 400, or 500 ms) repeated measures MANOVA. On each trial, the action relevant muscle was defined as the muscle involved in executing the observed movement and the action irrelevant muscle as the muscle not involved in executing the observed movement. For example, the FDI was defined as action relevant when an index finger abduction movement was observed but as action irrelevant when a little finger abduction movement was observed (and vice versa for the ADM).

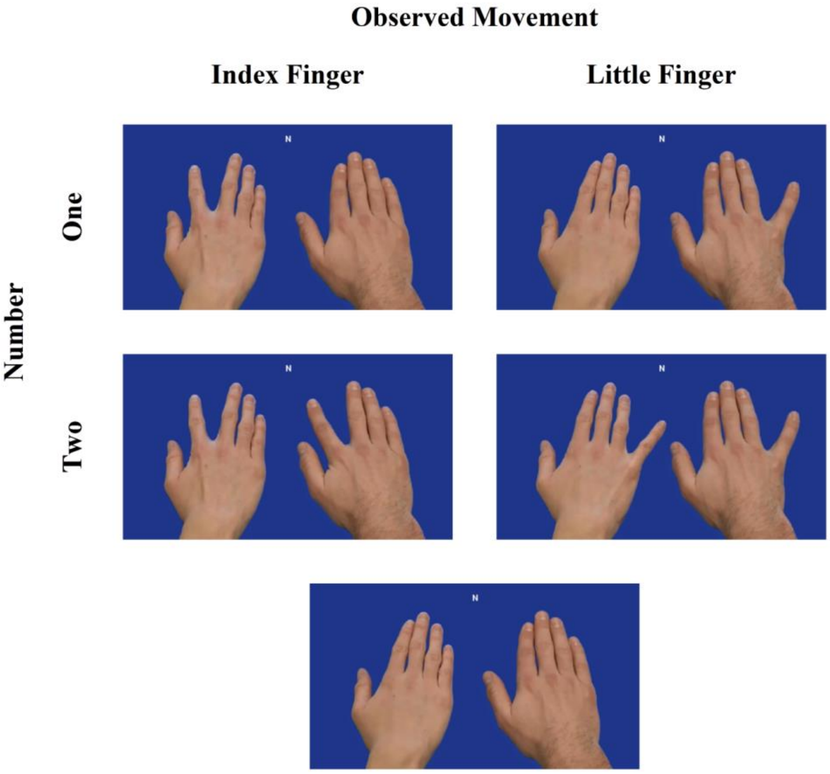

Figure 1. Design of the experiment. TMS was applied over the left primary motor cortex while participants observed two hands. Either a single hand made a movement or both hands made an identical movement. Two static hands were used as a baseline condition.

Results

The behavioral data revealed a mean response time of 632 ms (SD = 127 ms) and an accuracy rate of 95% (SD = 4%) on the movement trials. As can be seen in figure 2, the TMS results on the no-movement trials confirmed that MEPs in the action relevant muscle were stronger than MEPs in the action irrelevant muscle, $F(1, 33) = 22.80$, $p < 0.001$, $\eta_p^2 = 0.41$, $d = 0.82$. As expected, this effect was modulated by the number of observed movements, $F(1, 33) = 8.25$, $p = 0.007$, $\eta_p^2 = 0.20$, $d = 0.49$, with a larger difference between the action relevant and action irrelevant muscle when two movements were observed, $t(33) = 4.87$, $p < 0.001$, $d = 0.84$, compared with when a single movement was observed, $t(33) = 2.70$, $p = 0.011$, $d = 0.46$. Importantly, follow-up two-tailed t tests revealed that seeing two identical movements compared with a single movement increased MEPs in the action relevant muscle, $t(33) = 2.50$, $p = 0.018$, $d = 0.43$, but did not modulate MEPs in the action irrelevant muscle $t(33) = -1.37$, $p = 0.181$, $d = -0.24$. The analysis additionally revealed a significant Muscle x Pulse interaction, $F(2, 32) = 3.37$, $p = 0.047$, $\eta_p^2 = 0.17$, indicating that the difference between the action relevant and action irrelevant muscle was stronger when the pulse was delivered at 400 ms, $t(33) = 5.18$, $p < 0.001$, $d = 0.89$, than at 300 ms, $t(33) = 2.53$, $p = 0.016$, $d = 0.44$, or at 500 ms, $t(33) = 2.15$, $p = 0.039$, $d = 0.37$ (table S1). None of the other main or interaction effects reached significance, all $F \leq 0.70$, all $p \geq 0.503$.

Discussion

The goal of the current study was to study the role of the mirror neuron system in situations that involve multiple agents acting at the same time. Based on group contagion research in social psychology (e.g., Milgram et al., 1969; Knowles and Bassett, 1976; Gallup et al., 2012), it was hypothesized that multiple agents would provide a stronger trigger to the mirror system and would therefore produce a stronger mirror response. To test this hypothesis, we conducted a TMS study in which participants passively observed two hands of which a single hand made a movement or both hands made an identical movement. As predicted, a stronger mirror response was found when two identical movements were observed. This finding extends previous TMS research on the mirror neuron system (Fadiga et al. 1995, 2005; Naish et al. 2014) by showing that the mirror mechanism does not only play a role in dyadic interactions but also in multi-agent interactions (Raafat et al. 2009).

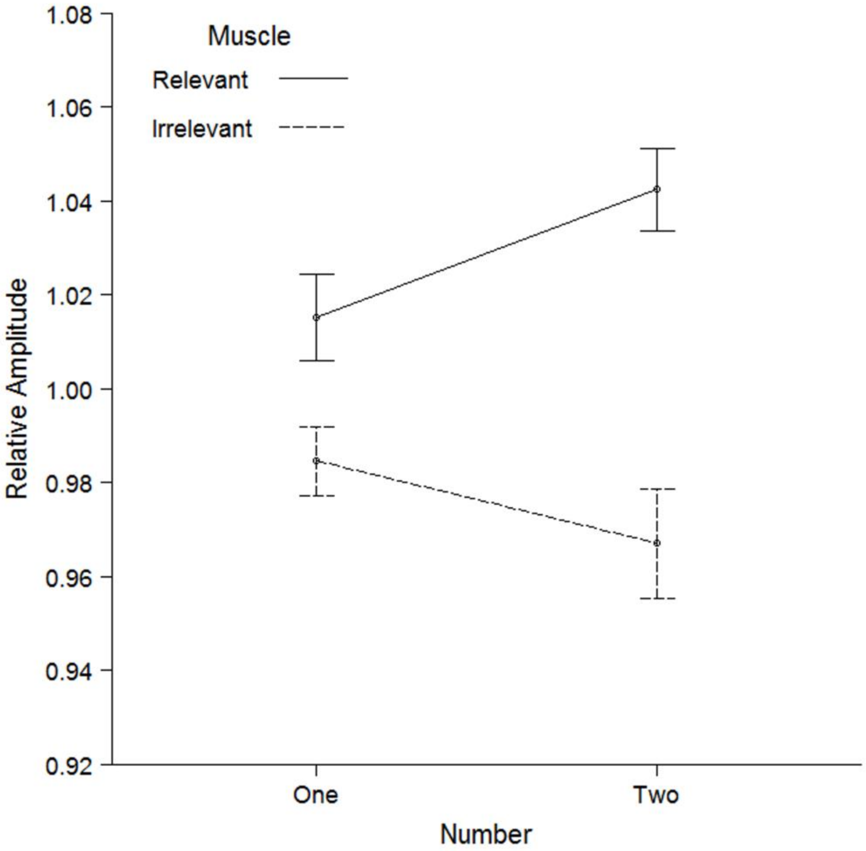

Figure 2. TMS results of the experiment. The two lines depict the MEP amplitude relative to the static hands condition in the action relevant muscle and in the action irrelevant muscle. The action relevant muscle was defined as the muscle involved in executing the observed movement and the action irrelevant muscle as the muscle not involved in executing the observed movement. Error bars represent standard errors of the mean corrected for within-subject designs according to Morey (2008). The TMS results for the two separate muscles are available in supplementary material (fig S1).

Importantly, the obtained results cannot easily be explained in terms of attentional facilitation or motor inhibition. With regard to attentional facilitation, it could be argued that two simultaneous movements attracted more attention and therefore produced a stronger mirror response. However, orienting responses are known to be fast and transient. That is, studies on inhibition of return have consistently shown that attention does not remain at the location where it has previously been drawn by a salient stimulus (Klein 2000). In particular, these studies have demonstrated that the facilitatory influence of attention on both sensory and motor processes (Tian et al. 2008, 2011) disappears around 250-300 ms (Klein 2000; Samuel & Kat 2003). Because TMS was applied at 300, 400, or 500 ms following movement observation, attentional influences were likely to have tapered off at the time of stimulation. Instead, research suggests that TMS at these time points is optimal to study muscle-specific modulations of motor resonance (Naish et al. 2014).

With regard to motor inhibition, it could be argued that the static hand triggered an inhibition response when there was only one hand making a movement. According to this account, the results of the current study should not be interpreted as an increase in MEPs in the two movement condition but as a decrease in MEPs in the one movement condition. However, previous work has shown that the observation of passive body parts results in excitation rather than inhibition of corticospinal excitability (Borgomaneri et al. 2012; Mattiassi et al. 2014; Schütz-Bosbach et al. 2006). Moreover, because a static hand is not linked to a particular movement, inhibition of this hand should target both the FDI and ADM. As a result, the motor inhibition account predicts that MEPs in the one movement condition should be smaller than MEPs in the two movement condition both for the action relevant and action irrelevant muscle. Because the number of observed movements only influenced MEPs in the action relevant muscle, it is unlikely that inhibition of the static hand can explain the obtained results.

By showing that the mirror neuron system is sensitive to the number of observed agents, the current study sheds light on the neurocognitive mechanisms underlying multi-agent interactions. While it is broadly accepted that the mirror system supports social interaction (Keysers & Gazzola 2006; Knoblich & Sebanz 2006; Rizzolatti & Fabbri-Destro 2008), previous work has mainly focused on situations in which a single agent is observed. The finding that motor resonance is sensitive to the number of observed agents opens up the possibility that the mirror system is also involved in social situations involving multiple agents. In particular, it provides an alternative explanation for the phenomenon that groups are more contagious than individuals (e.g. Gallup et al. 2012; Knowles & Bassett 1976; Milgram et al. 1969). While previous studies on this phenomenon have mostly explained their findings in terms of high-level interpretive processes, our results indicate that groups may instead be more contagious simply because they trigger the motor system more strongly. This sensorimotor interpretation fits well with recent work in which we showed that imitative tendencies are stronger for multiple agents even when the influence of interpretive processes is minimized (Cracco et al., 2015). Adding to this work, the current study identifies the mirror mechanism as a possible neural mechanism behind these effects.

Nevertheless, it should be noted that the account outlined above does not necessarily exclude an influence of interpretive processes at later stages of processing. When motor resonance produces the urge to imitate, interpretive processes could for instance be recruited to decide if the evoked behavior is reasonable given the context. Such an evaluative process could then determine whether the prepared action is eventually executed or inhibited. However, in this view, interpretive processes are not the antecedent but the consequence of imitative tendencies. In support of this proposition, research has shown that the conscious decision to imitate is driven by the gating of mirror activation (Bien et al. 2009). Similarly, interpretive processes could serve as a gating mechanism to regulate imitative tendencies in social group situations (Freedman & Birsky 1980; Gallup et al. 2012; Herrmann et al. 2013; Knowles & Bassett 1976; Latané & Darley 1968; Mann 1977; Milgram et al. 1969).

To conclude, the finding that motor resonance is modulated by the number of observed agents suggests that the mirror system is involved in social interactions that go beyond a dyadic structure. In particular, it opens up the possibility that groups are more contagious not because of interpretive processes (Freedman & Birsky 1980; Gallup et al. 2012; Herrmann et al. 2013; Knowles & Bassett 1976; Latané & Darley 1968; Mann 1977; Milgram et al. 1969) but because they produce a stronger mirror response. Given that the mirror mechanism has been linked to a variety of social skills, among which theory of mind (Keysers & Gazzola 2006) and empathy (Carr et al. 2003; Gazzola et al. 2006), our findings may additionally have important implications for the understanding of social interaction at the group level.

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Supplementary Material

Table S1.

Relative MEPs (M ± SD) for the different conditions of the experiment.

	Relevant		Irrelevant	
	One	Two	One	Two
300 ms	1.00 (0.10)	1.02 (0.11)	0.98 (0.10)	0.95 (0.15)
400 ms	1.04 (0.15)	1.07 (0.15)	0.99 (0.14)	0.96 (0.18)
500 ms	1.01 (0.14)	1.05 (0.22)	0.99 (0.19)	1.00 (0.16)

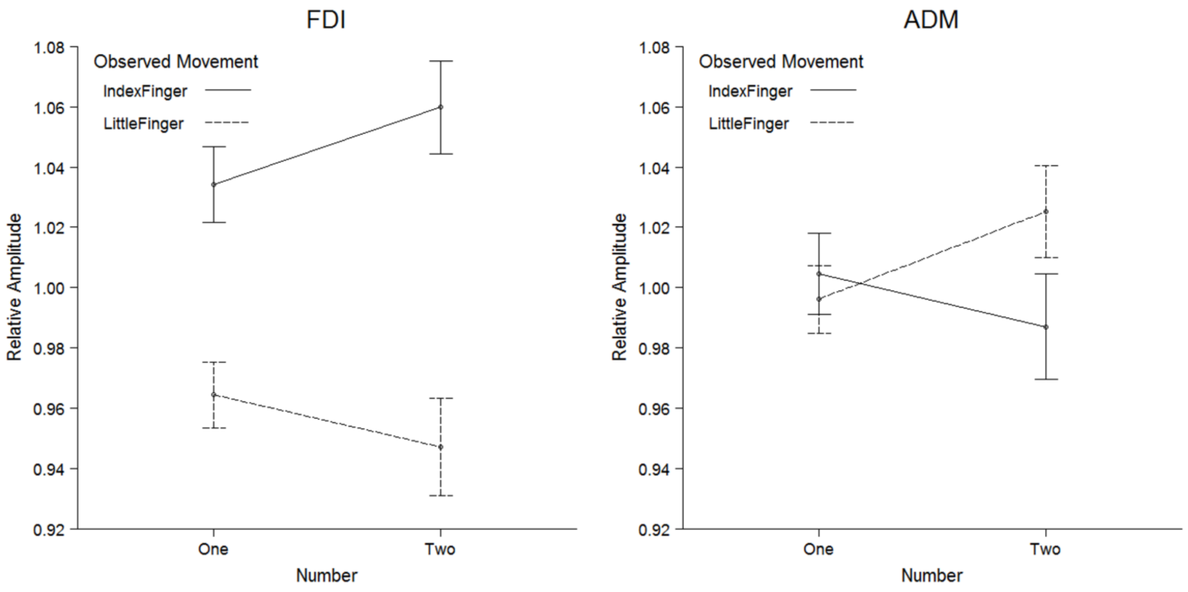

Fig S1. TMS results separately for the FDI and the ADM. A Muscle (FDI or ADM) x Number (one or two) x Observed Movement (index finger or little finger) x Pulse (300, 400, or 500 ms) repeated measures MANOVA indicated a Muscle x Number x Observed Movement interaction, F(1, 33) = 8.25, p = 0.007.

Chapter 4

Automatic Imitation of Multiple Agents: Simultaneous or Random Representation?[1]

Research has shown that the observation of another's movement activates the corresponding motor representation in the observer. However, it is largely unknown how activation of these shared representations is influenced by the number of observed agents. In recent work, we have studied automatic imitation while participants saw two hands of which either one hand or both hands made a movement. These studies found that two hands produced a stronger imitative response than a single hand when the hands made an identical movement but not when they made different movements. It was argued that identical movements were mapped onto the same motor representation and therefore produced a stronger motor response. Nevertheless, an alternative explanation is that participants randomly represented 1 hand on each trial. The goal of the current study was to disentangle these two hypotheses. In Experiments 1 and 2, we replicate our results using a stimulus setup that made random sampling unlikely. In Experiment 3, we show that an additive effect was still present when attention was directed to 1 hand that always made a movement. Finally, in Experiment 4, we show that intentional imitation of 1 hand did not preclude automatic imitation of a second hand. Together, these findings support the hypothesis that the actions of multiple persons can be represented together in the motor system.

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[1] Cracco, E., & Brass, M. (2017). Automatic Imitation of Multiple Agents: Simultaneous or Random Representation? *Journal of Experimental Psychology: Human Perception and Performance*, Advance online publication.

Introduction

There is strong evidence from cognitive and social psychology that people sometimes inadvertently imitate the behavior of others (Chartrand & van Baaren, 2009; Heyes, 2011). For example, it has often been shown that responses to symbolic stimuli such as numbers are facilitated when a hand on the screen makes a compatible movement and impeded when it makes an incompatible movement (Bertenthal, Longo, & Kosobud, 2006; Brass, Bekkering, & Prinz, 2001; Brass, Bekkering, Wohlschlager, & Prinz, 2000; Catmur & Heyes, 2011; Heyes, 2011; Heyes, Bird, Johnson, & Haggard, 2005). Moreover, studies in naturalistic settings have demonstrated that interaction partners tend to copy each other's mannerisms, postures, and speech patterns (Chartrand & Bargh, 1999; Chartrand & van Baaren, 2009; Stel & Vonk, 2010). According to a dominant theoretical view, automatic imitation is the result of learned associations between visual and motor representations that develop as a consequence of self-observation (Brass & Heyes, 2005; Heyes, 2011). In particular, it is assumed that actions have perceivable consequences that over time become associated with the motor command that produced them. As individuals often look at the actions they perform, this mechanism leads to a connection between the visual image of an action and its motor program, which in turn leads to automatic imitation. In line with this view, brain imaging studies have uncovered a network of motor regions that are not only activated when an action is executed but also when the same action is observed (Caspers, Zilles, Laird, & Eickhoff, 2010; Cook, Bird, Catmur, Press, & Heyes, 2014; Heyes, 2010; Molenberghs, Cunnington, & Mattingley, 2012; Rizzolatti & Sinigaglia, 2010). Together, this research has been interpreted as evidence that people use their own motor system to simulate the behavior of others via shared representations for action observation and action execution (Brass & Heyes, 2005; Jeannerod, 2001; Keysers & Gazzola, 2006).

As motor simulation allows observed behavior to be translated into motor programs (Brass & Heyes, 2005), it is widely regarded as an important social process (Colling, Knoblich, & Sebanz, 2013; Knoblich & Sebanz, 2006; Rizzolatti & Fabbri-Destro, 2008; Sebanz, Bekkering, & Knoblich, 2006). In accordance with this view, studies have shown that shared action representations support interpersonal coordination in joint action tasks (Colling et al., 2013; Kourtis, Sebanz, & Knoblich, 2013) by enabling co-actors to anticipate each other's movements (Aglioti, Cesari, Romani, & Urgesi, 2008; Colling, Thompson, & Sutton, 2014; Kourtis, Knoblich, Woźniak, & Sebanz, 2014; Kourtis et al., 2013). However, research in this domain has focused mainly on interactions between two persons even though naturalistic social interactions often require individuals to coordinate their movements with multiple persons at the same time. For example, the outcome of a tug-of-war game strongly depends on how well the players of each team are able to synchronize their movements. Likewise, the creation of a harmonious sound in musical ensembles requires a high degree of coordination among the different musicians (Volpe, D'Ausilio, Badino, Camurri, & Fadiga, 2016). A focus on the neurocognitive mechanisms of social group interaction is furthermore relevant considering that synchronous group behavior is known to foster social bonds (Cohen, Ejsmond-Frey, Knight, & Dunbar, 2010; Tarr, Launay, Cohen, & Dunbar, 2015), cooperation (Davis, Taylor, & Cohen, 2015; Reddish, Fischer, & Bulbulia, 2013; Wiltermuth & Heath, 2008), interpersonal memory (Woolhouse, Tidhar, & Cross, 2016), and trust (Launay, Dean, & Bailes, 2013). In other words, in order to comprehend the social behavior that emerges from group dynamics, it is important to understand how the sensorimotor processes involved in social interaction can be extended from dyads to triads, tetrads, or even pentads.

To address this question, recent work has explored the hypothesis that the actions of multiple persons can be represented together in the motor system of the observer (Cracco, De Coster, Andres, & Brass, 2015, 2016; Ramenzoni, Sebanz, & Knoblich, 2014; Tsai, Sebanz,

& Knoblich, 2011). For example, research on joint action has looked at inter-group imitation and found that it is facilitated when the number of imitators matches the number of agents (Ramenzoni et al., 2014; Tsai et al., 2011). In addition, as a more direct test, we measured automatic imitation with a stimulus-response compatibility task while participants observed two hands of which neither hand made a movement, one hand made a movement, both hands made identical movements, or both hands made different movements (Cracco et al., 2015). The results revealed that automatic imitation was stronger when two identical movements were observed compared to when a single movement was observed, and subsequent work confirmed that this was due to an increase in corticospinal excitability (Cracco et al., 2016). In contrast, no imitation was found when two different movements, one congruent and one incongruent, were observed. These findings support the simultaneous representation hypothesis. In particular, they suggest that identical movements triggered the same motor representation and therefore produced a stronger imitative response, whereas different movements triggered a distinct congruent and incongruent motor representation whose output cancelled each other out (Cracco et al., 2015).

Nevertheless, an alternative hypothesis is that the above effects did not arise within the context of a single trial but instead developed over the course of many trials. For example, it could be argued that participants did not represent both hands at the same time but rather represented one hand at random. According to this hypothesis, the likelihood that participants represented a moving hand on a particular trial depended on the number of hands that made a movement. That is, if both hands made a movement, then there was a 100% probability to represent a moving hand. However, if just one hand made a movement, then there was a 50% probability to represent a moving hand. This difference in the likelihood to represent a movement leads to a difference in the likelihood to imitate and as such to more automatic imitation on average in the condition where both hands made an identical movement. The same mechanism can then also explain why automatic imitation disappeared when two different movements were observed because a random sampling mechanism assumes that in this condition participants imitated a congruent movement in one half of the trials and an incongruent movement in the other half of the trials.

In the current study, we aimed to distinguish between the simultaneous and random representation accounts of multi-actor imitation. In Experiments 1 and 2, we first attempted to replicate the finding of Cracco et al. (2015) that two identical observed movements produced stronger automatic imitation, using a stimulus setup that put the two stimulus hands close together in the center of the screen. This setup made it unlikely that participants sometimes did not represent the hand movement(s) and therefore that a random sampling mechanism could lead to an additive imitation effect. In Experiment 3, we further ensured that at least one hand movement was represented on each trial by directing attention to one particular hand that always made a movement (Bach, Peatfield, & Tipper, 2007; Chong, Cunnington, Williams, & Mattingley, 2009). Since the random representation account assumes that participants are unable to represent the movements of multiple hands simultaneously, it no longer predicts an additive imitation effect in this situation. The simultaneous representation account, on the other hand, predicts an additive imitation effect regardless of whether attention was cued to a particular hand or not. Finally, in Experiment 4, participants were instructed to imitate one of the two hands. Given that not only automatic but also intentional imitation relies on motor simulation (Bertenthal et al., 2006; Bien, Roebroeck, Goebel, & Sack, 2009; Brass et al., 2000; Caspers et al., 2010; Hamilton, 2015; Heyes, 2011; Iacoboni et al., 1999), the random representation account predicts that intentional imitation of one hand will preclude automatic imitation of a second hand. In contrast, the simultaneous representation account predicts that automatic imitation will persist because motor simulation is not restricted to a single agent.

Experiment 1

Method

Participants. In accordance with best practice guidelines, we will report for all experiments how we determined our sample size, all data exclusions (if any), all manipulations, and all measures (Simmons, Nelson, & Simonsohn, 2011, 2012). The sampling goal of all experiments was to collect 50 participants in keeping with our recent research on automatic imitation (Cracco & Brass, submitted). A sample size of 50 participants results in 93% power to detect a medium-sized effect of $d_z = 0.50$ (Cohen, 1988). Data from 50 participants was collected for Experiment 1 (42 female, $M_{\text{age}} = 19.28$, $SD_{\text{age}} = 3.27$). Participants were excluded if their overall reaction time (RT) or error rate (ER) exceeded the sample mean by more than 3 *SD*. This resulted in the exclusion of two participants with an ER of respectively 33.51% and 25.67%. As a consequence, the final sample consisted of 48 participants (41 female, $M_{\text{age}} = 19.33$, $SD_{\text{age}} = 3.33$). All participants were right-handed and had self-reported normal or corrected-to-normal vision. An informed consent was signed before the experiment and partial course credit was provided in return for participation. The study was approved by the local ethical committee and all procedures were performed in accordance with the 1964 Helsinki Declaration.

Stimuli, Task, and Apparatus. The experiment was programmed in C with Tscope5 (Stevens, Lammertyn, Verbruggen, & Vandierendonck, 2006). The stimuli (1379 x 776 pixels) consisted of a left and right hand printed on a blue background in horizontal position with the fingers pointing towards each other (Figure 1). To ensure that the two hands were conceived as belonging to different persons, we used one male and one female hand. This was furthermore explicitly communicated to the participants in the instruction phase. The position of the hands on the screen was counterbalanced across participants. The hands could lift the index finger, lift the middle finger, or not move. Importantly, when both hands moved, they always performed the same movement. As a result, the experiment consisted of six possible stimulus configurations: left index and right neutral, left neutral and right index, left middle and right neutral, left neutral and right middle, left index and right index, and left middle and right middle. Movements were presented as a sequence of two frames so that a picture of the hands in their neutral position was replaced with a picture of the hands in their final position.

Together with the presentation of the stimulus movement(s), a letter appeared between the two hands in the center of the screen. Participants had to lift their right index finger when W ("wijsvinger") was presented and their right middle finger when M ("middelvinger") was presented. This letter will be referred to as the "imperative cue". The instructed response could be congruent (C) or incongruent (IC) with respect to the imperative cue. That is, a congruent trial was a trial in which participants were instructed to lift the same finger as the stimulus hand(s) and an incongruent trial was a trial in which participants were instructed to lift the opposite finger as the stimulus hand(s). In accordance, automatic imitation was operationalized as faster and more accurate responses on congruent trials than on incongruent trials. However, a trial could not only be congruent or incongruent with respect to the observed movement (i.e., lift index or middle finger) but also with respect to the stimulus hand that made the movement (i.e., left or right hand). In this sense, for right-handed participants, a movement of the right stimulus hand was "hand congruent" and a movement of the left stimulus hand was "hand incongruent". Importantly, this type of congruency was not confounded with movement congruency because each of the six possible stimulus configurations occurred equally often with both imperative cues. Together with the fact that we did not have specific hypotheses regarding hand congruency, we therefore decided to not analyze hand congruency but to instead restrict our analyses to movement congruency. As a result, the term congruency will refer exclusively to movement congruency in what follows. Responses were recorded with an optical sensor box that contained four sensors organized from left to right. Participants were asked to put the index and middle finger of their dominant hand on the two middle sensors. A response was registered as soon as the finger moved away from the sensor.

Procedure. The total duration of the experiment was about 20 minutes and started with the instructions being presented on the computer monitor. The instructions explained that a letter would be presented in the center of the screen together with two hands of two different persons lifting either the index or middle finger. Participants were asked to respond to the letter as fast as possible but without making errors. After the instructions, 12 practice trials with performance feedback were performed. This was followed by four experimental blocks of 96 trials without feedback for a total of 384 trials. Participants were allowed to take a break after each block. All conditions occurred equally often per block and were presented in a random order with the restriction that the same imperative cue could not appear more than four times in a row. Trials started with a picture of the two hands in neutral position together with a fixation cross in the center of the screen. After 500 ms, the picture was overwritten by a picture of the hands in final position. At the same time, the fixation cross was replaced with the imperative cue (W or M). These stimuli remained on the screen until the response for a maximum of 2,000 ms and were followed by a black screen for 1,000 ms to signal the end of the trial. The experiment was concluded with a questionnaire measuring social susceptibility. The questionnaire was included for exploratory purposes and will not be reported here.

Data Analysis. All analyses were performed in R (2013). Trials without a response before the response deadline were excluded (0.05%). Furthermore, trials with a RT faster than 100 ms were considered action slips and were excluded as well (0.04%). Finally, error trials (5.75%) and trials in which the RT deviated from the participant’s mean by more than 3 *SD*

(1.65%) were excluded from the RT analysis but not from the ER analysis. The latter criterion was applied to reduce the impact of RT outliers on the mean RT and for that reason was restricted to the RT analysis. The data was analyzed with a 2 x 2 repeated measures MANOVA with number (one vs. two) and congruency (congruent vs. incongruent) as within-subject factors. Effect sizes and their 95% confidence interval (*CI 95%*) will be reported for all effects (Lakens, 2013). The stimuli, code, data, and analyses from all experiments are available at the Open Science Framework: https://osf.io/p3a6w/.

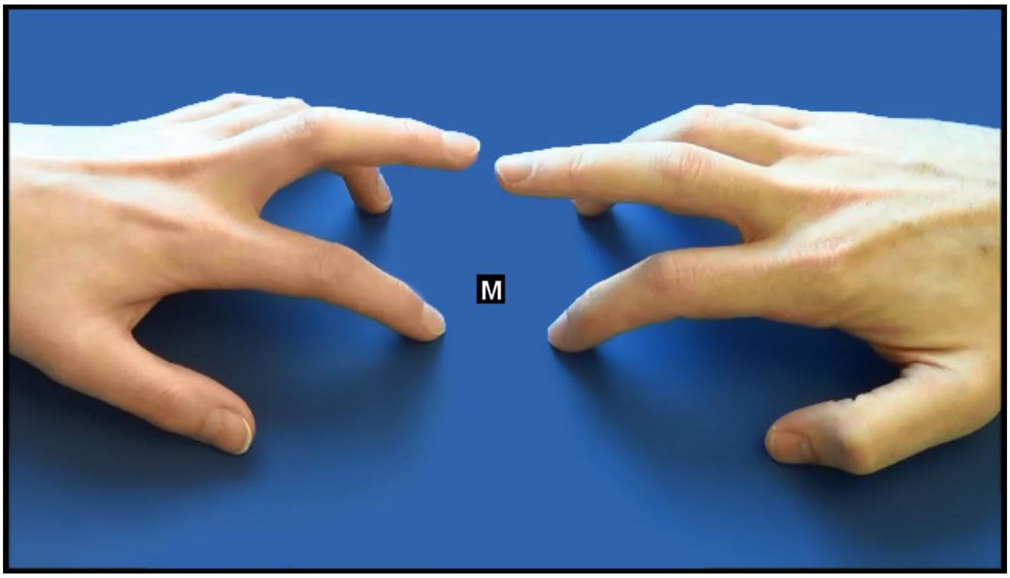

Figure 1. Example of the stimuli used in Experiments 1 and 2. Participants had to respond to the letter in the center of the screen while either one hand or both hands made a congruent or incongruent movement.

Results and Discussion

The RT analysis revealed a significant main effect of congruency with faster responses on congruent than on incongruent trials, $F(1, 47) = 23.53$, $p < .001$, $d_z = 0.70$, *CI 95%* = [0.38, 1.01], but no main effect of number, $F(1, 47) = 0.34$, $p = 0.563$ $d_z = 0.08$, *CI 95%* = [-0.20, 0.37]. In contrast to our expectations, we did not find an interaction between number and congruency, *F*(1, 47) = 1.93, *p* = .171, d_z = 0.20, *CI 95%* = [-0.09, 0.49] (Figure 2a). Similar to the RT analysis, the ER analysis indicated a significant main effect of congruency with fewer errors on congruent than on incongruent trials, *F*(1, 47) = 18.62, $p < .001$, d_z = 0.62, *CI 95%* = [0.31, 0.93], and no main effect of number, *F*(1, 47) = 0.58, *p* = .451, d_z = 0.11, *CI 95%* = [-0.18, 0.39]. In addition, the ER analysis also found a number x congruency interaction, *F*(1, 47) = 6.52, *p* = .014, d_z = 0.37, *CI 95%* = [0.07, 0.66], with a stronger congruency effect (IC - C) when two identical movements were observed, *t*(47) = 4.60, $p < .001$, d_z = 0.66, *CI 95%* = [0.35, 0.97], than when a single movement was observed, *t*(47) = 2.42, *p* = .020, d_z = 0.35, *CI 95%* = [0.06, 0.64] (Figure 2b).

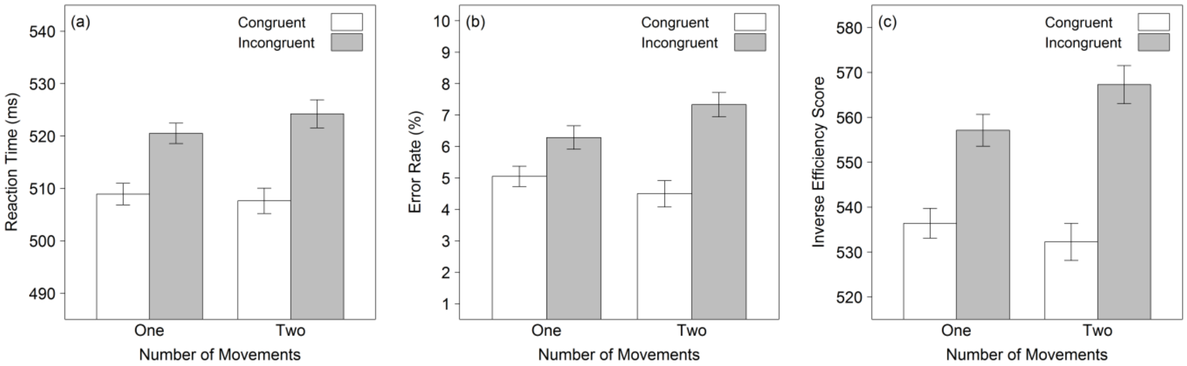

Figure 2. Results of the number x congruency analysis of Experiment 1 for (a) reaction times, (b) error rates, and (c) inverse efficiency scores. Error bars are standard errors of the mean (SEMs) corrected for within-subject designs (Morey, 2008).

In summary, Experiment 1 found an additive imitation effect for ERs but not for RTs. However, an inspection of Figure 2 showed that RTs were in the same direction as ERs. We therefore combined RTs and ERs into the inverse efficiency score (IES). The IES is defined as $RT/(1-ER)$ and can be used as a compound measure of task performance (Bruyer & Brysbaert, 2011). The IES analysis confirmed the presence of a number x congruency interaction, *F*(1, 47) = 8.90, *p* = .005, d_z = 0.43, *CI 95%* = [0.13, 0.73], with a stronger congruency effect when two identical movements were observed, $t(47) = 5.11$, $p < .001$, $d_z = 0.74$, *CI 95%* = [0.42, 1.05], than when a single movement was observed, $t(47) = 3.81$, $p < .001$, $d_z = 0.55$, *CI 95%* = [0.24, 0.85] (Figure 2c). Taken together, the data thus indicated that two identical observed movements produced a stronger imitation effect than did a single observed movement. Nevertheless, we expected but did not find an additive imitation effect for RTs. We therefore decided to replicate Experiment 1 with Experiment 2. Experiment 2 was identical to Experiment 1 in all respects, except that the size of the stimulus display was slightly reduced.

Experiment 2

Method

Participants. A new sample of 50 participants was collected for Experiment 2 (40 female, $M_{\text{age}} = 20.78$, $SD_{\text{age}} = 4.01$). Participants were excluded if their overall RT or ER exceeded the sample mean by more than 3 *SD*. As a result, one participant with an ER of 20.57% was removed and the final sample consisted of 49 participants (39 female, $M_{\text{age}} = 20.73$, $SD_{\text{age}} = 4.04$). All participants were right-handed and had self-reported normal or corrected-to-normal vision. Subjects received partial course credit or a reward of 5 euro in return for participation.

Stimuli, Task, Apparatus, and Procedure. The method of Experiment 2 was identical to the method of Experiment 1. However, the size of the stimuli was reduced to 1226 x 690 pixels.

Data Analysis. The data analysis of Experiment 2 was identical to that of Experiment 1. Trials without a response (0.09%) and trials with a RT faster than 100 ms (0.04%) were excluded from both the RT and ER analysis. For the RT analysis, we additionally excluded error trials (6.50%) and trials with a RT exceeding the participant's mean by more than 3 *SD* (1.51%).

Results and Discussion

The RT analysis revealed a significant main effect of congruency with faster responses on congruent than on incongruent trials, $F(1, 48) = 18.76$, $p < .001$, $d_z = 0.62$, *CI 95%* = [0.31, 0.92], and a significant main effect of number with faster responses when one hand made a movement than when two hands made a movement, $F(1, 48) = 12.23$, $p = .001$, $d_z = 0.50$, *CI 95%* = [0.20, 0.79]. Importantly, we also found a significant number x congruency interaction, $F(1, 48) = 10.51$, $p = .002$, $d_z = 0.46$, *CI 95%* = [0.17, 0.76], indicating a stronger congruency effect when two identical movements were observed, $t(48) = 4.31$, $p < .001$, $d_z = 0.62$, *CI 95%* = [0.31, 0.92], than when a single movement was observed, $t(48) = 2.30$, $p = .026$, $d_z = 0.33$, *CI 95%* = [0.04, 0.62] (Figure 3a). The ER analysis also revealed a main effect of congruency with fewer errors on congruent than on incongruent trials, $F(1, 48) = 16.06$, $p < .001$, $d_z = 0.57$, *CI 95%* = [0.27, 0.87], and a main effect of number with more errors when one hand made a movement than when two hands made a movement, $F(1, 48) = 5.22$, $p = .027$, $d_z = 0.33$, *CI 95%* = [0.04, 0.61]. As predicted, the number x congruency interaction was significant as well, $F(1, 48) = 4.75$, $p = .034$, $d_z = 0.31$, *CI 95%* = [0.02, 0.60]. In line with the RT data, the congruency effect was stronger when two identical movements were observed, $t(48) = 3.63$, $p < .001$, $d_z = 0.52$, *CI 95%* = [0.22, 0.82], than when a single movement was observed, $t(48) = 1.91$, $p = .062$, $d_z = 0.27$, *CI 95%* = [-0.01, 0.56] (Figure 3b). Finally, we also performed an IES analysis for comparison with Experiment 1. In line with RTs and ERs, this analysis revealed a significant number x congruency interaction, $F(1, 48) =$

11.97, *p* = .001, d_z = 0.49, *CI 95%* = [0.20, 0.79], with a stronger congruency effect when two identical movements were observed, *t*(48) = 4.36, *p* < .001, d_z = 0.62, *CI 95%* = [0.31, 0.93], than when a single movement was observed, *t*(48) = 3.10, *p* = .003, d_z = 0.44, *CI 95%* = [0.15, 0.73] (Figure 3c).

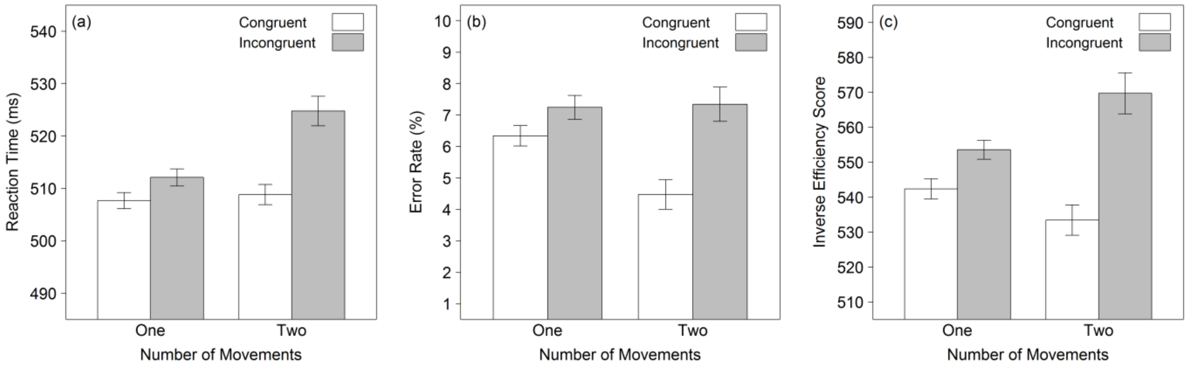

Figure 3. Results of the number x congruency analysis of Experiment 2 for (a) reaction times, (b) error rates, and (c) inverse efficiency scores. Error bars are SEMs corrected for within-subject designs (Morey, 2008).

The results of Experiment 2 confirmed that automatic imitation was stronger in the condition with two identical observed movements than in the condition with a single observed movement. To explore potential differences between Experiment 1 and 2, we furthermore conducted a repeated measures MANOVA with number and congruency as within-subject factors and experiment as a between-subject factor. This revealed a significant number x congruency interaction for RTs, *F*(1, 95) = 10.67, *p* = .002, d_z = 0.33, *CI 95%* = [0.13, 0.54], ERs, *F*(1, 95) = 10.47, *p* = .002, d_z = 0.33, *CI 95%* = [0.13, 0.53], and IES, *F*(1, 95) = 20.36, *p* < .001, d_z = 0.46, *CI 95%* = [0.25, 0.67]. Follow-up paired *t* tests further showed that the congruency effect was stronger when two identical movements were observed, *t*(96) ≥ 5.71, *p* < .001, d_z ≥ 0.58, than when a single movement was observed, *t*(96) ≥ 3.08, *p* ≤ .003, d_z ≥ 0.31, for all three outcome measures (Figure 4). Finally, the experiment x number x congruency interaction did not reach significance for either RTs, *F*(1, 95) = 1.66, *p* = .201, d_s

= 0.26, *CI 95%* = [-0.14, 0.66], ERs, *F*(1, 95) = 0.11, *p* = .741, d_s = 0.07, *CI 95%* = [-0.33, 0.47], or IES, *F*(1, 95) = 1.53, *p* = .219, d_s = 0.25, *CI 95%* = [-0.15, 0.65], indicating that the strength of the additive imitation effect did not differ between the two experiments.

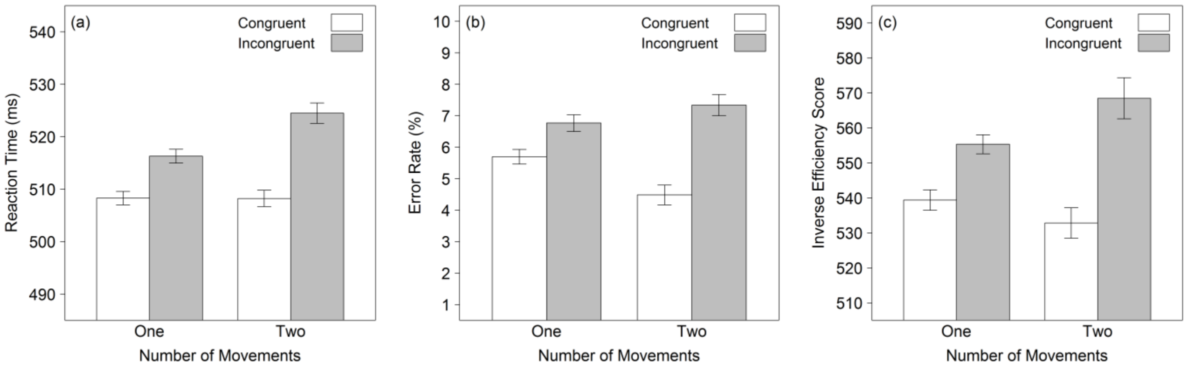

Figure 4. Results of the number x congruency analysis of Experiments 1 and 2 combined for (a) reaction times, (b) error rates, and (c) inverse efficiency scores. Error bars are SEMs corrected for within-subject designs (Morey, 2008).

To conclude, Experiments 1 and 2 replicated the additive imitation effect reported in Cracco et al. (2015) with a different stimulus setup. The setup of the current experiments put the two hands close together in the center of the screen and therefore made it unlikely that participants sometimes did not represent at least one hand movement. As a result, these experiments speak against the hypothesis that participants randomly represented one hand on each trial. Instead, they suggest that both movements activated the same motor representation and therefore produced a stronger imitative response (Cracco et al., 2015, 2016). In Experiment 3, we further distinguished between the random and simultaneous representation account by putting the imperative cue either on the left hand or on the right hand. This manipulation directed attention to one particular hand and thus increased the likelihood that it was processed (Bach et al., 2007; Chong et al., 2009). Furthermore, the hand on which the cue was positioned always made a movement. Given that participants processed a moving stimulus hand on each trial in this experiment, the random representation account predicts that participants should not be influenced by the movements of the non-cued hand. In contrast, the simultaneous representation account predicts stronger automatic imitation in the condition where both hands made a movement regardless of whether attention was directed to a particular hand or not.

Experiment 3

Method

Participants. A new sample of 50 participants was collected for Experiment 3 (41 female, $M_{\text{age}} = 22.06$, $SD_{\text{age}} = 3.94$). Participants were excluded if their overall RT or ER exceeded the sample mean by more than 3 *SD*. This resulted in the exclusion of one participant with a mean RT of 708 ms and another participant with an ER of 21.62%. The final sample therefore consisted of 48 participants (39 female, $M_{\text{age}} = 21.98$, $SD_{\text{age}} = 3.98$). All participants were right-handed, had self-reported normal or corrected-to-normal vision, and received 5 euro in return for participation.

Stimuli, Task, Apparatus, and Procedure. The method of Experiment 3 was identical to that of Experiment 2 except that the imperative cue was no longer positioned in the center of the screen but instead between the index and middle finger of either the left or right stimulus hand (Figure 5). The experiment consisted of 384 trials divided into two phases, each with two blocks of 96 trials in which all conditions were presented equally often in random order with the restriction that the same imperative cue could not appear more than four times in a row. The cue was positioned on the left stimulus hand in one phase and on the right stimulus hand in the other phase. The order of the two phases was counterbalanced across participants. Both phases were preceded by 8 practice trials with performance feedback. Importantly, the hand on which the cue was placed always made a movement. The other hand either made no movement or made the same movement. As a result, the number of possible stimulus configurations was now four instead of six: cue index and non-cue neutral, cue middle and non-cue neutral, cue index and non-cue index, and cue middle and non-cue middle.

Data Analysis. The analysis of Experiment 3 was identical to that of Experiment 1. Trials without a response (0.02%) and trials with a RT faster than 100 ms (0.01%) were excluded from both the RT and ER analysis. For the RT analysis, we additionally excluded error trials (4.80%) and trials with an RT deviating from the participant's mean by more than 3 *SD* (1.39%).

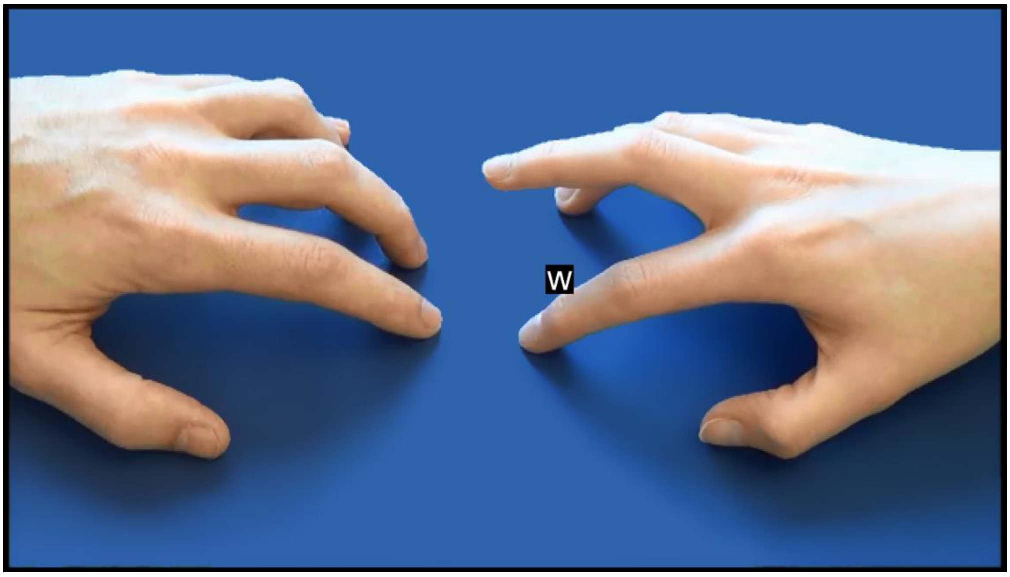

Figure 5. Example of the stimuli used in Experiments 3 and 4. In Experiment 3, participants had to respond to the letter. In Experiment 4, the letter was replaced with a fixation cross and participants had to imitate the hand on which the cross was located. The cued hand always made a movement. In Experiment 3, the non-cued hand either made no movement or the same movement. In Experiment 4, the non-cued hand made no movement, the same movement, or a different movement.

Results and Discussion

The RT analysis revealed a main effect of congruency with faster responses on congruent than on incongruent trials, *F*(1, 47) = 53.34, $p < .001$, $d_z = 1.05$, *CI 95%* = [0.70, 1.40], but no main effect of number, *F*(1, 47) = 0.15, $p = .696$, $d_z = 0.06$, *CI 95%* = [-0.23, 0.34]. As predicted by the simultaneous representation hypothesis, there was a significant number x congruency interaction, *F*(1, 47) = 5.83, $p = .020$, $d_z = 0.35$, *CI 95%* = [0.06, 0.64], with a stronger congruency effect when two identical movements were observed, *t*(47) = 8.49, $p < .001$, $d_z = 1.23$, *CI 95%* = [0.85, 1.60], than when a single movement was observed, *t*(47) = 5.34, $p < .001$, $d_z = 0.77$, *CI 95%* = [0.45, 1.09] (Figure 6a). The ER analysis indicated a main of effect of congruency with fewer errors on congruent than on incongruent trials, *F*(1, 47) = 26.83, $p < .001$, $d_z = 0.75$, *CI 95%* = [0.42, 1.07], but no main effect of number, *F*(1, 47) = 0.22, $p = .639$, $d_z = 0.07$, *CI 95%* = [-0.22, 0.35]. The number x congruency interaction was again significant, *F*(1, 47) = 5.00, $p = .030$, $d_z = 0.32$, *CI 95%* = [0.03, 0.61], indicating that the congruency effect was stronger when two identical movements were observed, *t*(47) = 5.63, $p < .001$, $d_z = 0.81$, *CI 95%* = [0.48, 1.14], compared with when a single movement was observed, *t*(47) = 3.70, $p < .001$, $d_z = 0.54$, *CI 95%* = [0.23, 0.84] (Figure 6b).

To summarize, the results of Experiment 3 revealed stronger automatic imitation when both hands made an identical movement compared with when a single hand made a movement even though attention was cued to one hand that moved on each trial. This is consistent with the simultaneous representation account but not with the random representation account because only the former assumes that the movements of multiple agents can be represented together in the motor system (Cracco et al., 2015, 2016). According to the simultaneous representation account, the movements of both hands activated the same motor representation and therefore produced a stronger imitative response (Cracco et al., 2015, 2016). Nevertheless, it remains possible that a random sampling mechanism can explain part of the effects obtained in Experiments 1 and 2. This hypothesis predicts that the additive imitation effect should have been smaller in Experiment 3 than in Experiments 1 and 2.

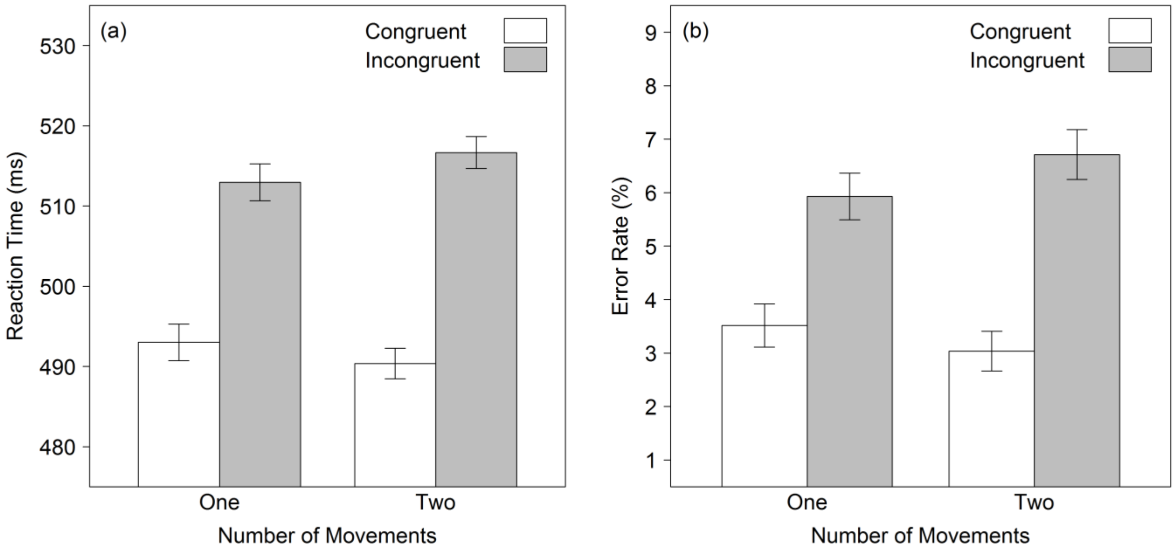

Figure 6. Results of the number x congruency analysis of Experiment 3 for (a) reaction times and (b) error rates. Error bars are SEMs corrected for within-subject designs (Morey, 2008).

In contrast, visual inspection suggested that the number x congruency effect size did not differ between Experiments 1-2 (RT: 0.33; ER: 0.33) and Experiment 3 (RT: 0.35; ER: 0.32). This was confirmed by an experiment x number x congruency repeated measures MANOVA on RTs in which experiment was a between-subject factor that distinguished between Experiments 1-2 and Experiment 3. That is, we found an experiment x congruency interaction, $F(1, 143) = 10.12$, $p = .002$, $d_s = 0.56$, *CI 95%* = [0.21, 0.91], but no experiment x number x congruency interaction, $F(1, 143) = 0.23$, $p = .634$, $d_s = 0.08$, *CI 95%* = [-0.26, 0.43], which indicates that directing attention to the movements of one particular hand in Experiment 3 increased automatic imitation but did not increase the additive imitation effect with respect to Experiments 1-2. To investigate whether the absence of a significant experiment x number x congruency interaction could be interpreted as evidence against the presence of a three-way interaction, we then performed a Bayesian repeated measures ANOVA that compared a model with and without a three-way interaction (Rouder, Morey, Speckman, & Province, 2012). This revealed a $BF_{01} = 5.21$, which suggests that the data was five times more likely under the model without a three-way interaction than under the model with a three-way interaction. As such, it is unlikely that random sampling could partially explain the additive imitation effect obtained in Experiments 1 and 2.

Finally, in the fourth experiment, we further explored the mechanism of multi-actor imitation by asking participants to imitate one of the two hands. There is converging evidence that not only automatic but also intentional imitation relies on motor simulation (Bertenthal et al., 2006; Bien et al., 2009; Brass et al., 2000; Brass & Heyes, 2005; Caspers et al., 2010; Hamilton, 2015; Heyes, 2011; Iacoboni et al., 1999). For example, responses are known to be faster when the instruction is to imitate than when the instruction is to respond to a symbolic cue (e.g., Bertenthal et al., 2006; Brass et al., 2000), suggesting that imitation has direct access to the relevant motor code (Boyer, Longo, & Bertenthal, 2012; Brass, Bekkering, et al., 2001; Brass et al., 2000; Sauser & Billard, 2006). Furthermore, neuroimaging studies have found that both automatic and intentional imitation activate the shared network for perception and action (Bien et al., 2009; Brass & Heyes, 2005; Caspers et al., 2010; Hamilton, 2015; Iacoboni et al., 1999). Since the random representation account assumes that only one movement can be simulated at a time, this account predicts that intentional imitation of the target hand will preclude automatic imitation of the non-target hand. In contrast, the simultaneous representation account assumes that multiple movements can be simulated together and therefore predicts that automatic imitation of the non-target hand will persist.

Experiment 4

Method

Participants. A new sample of 50 participants was recruited for Experiment 4 (33 female, M_{age} = 19.66, SD_{age} = 3.66). Participants were excluded if their overall RT or ER exceeded the sample mean by more than 3 *SD*. This resulted in the exclusion of one participant with a RT of 580 ms, another participant with an ER of 17.41%, and a final participant with an ER of 19.79%. The final sample therefore consisted of 47 participants (30 female, M_{age} = 19.72, SD_{age} = 3.76). Forty-one participants were right-handed and all participants had self-reported normal or corrected-to-normal vision. Subjects received partial course credit or 5 euro in return for participation.

Stimuli, Task, Apparatus, and Procedure. The method of Experiment 4 was identical to that of Experiment 3 except that participants were now required to imitate the left or right hand (Figure 5). The fixation cross was placed between the index and middle finger of the hand that had to be imitated. In contrast to Experiment 3, the fixation cross was not replaced with a symbolic cue but remained on the screen until the response. The experiment consisted of 384 trials divided into two phases that each contained two blocks of 96 trials. All conditions occurred equally often in each block in a randomized order with the restriction that the target hand was not allowed to lift the same finger more than four times in a row. Participants had to imitate the left hand in one phase and the right hand in the other phase. The order of the two phases was counterbalanced across participants. Both phases were preceded by 12 practice trials in which performance feedback was given. The hand that had to be imitated always made a movement. At the same time, the non-target hand either made no movement (i.e., neutral trial), an identical movement (i.e., congruent trial), or a different movement (i.e., incongruent trial). Participants used their dominant hand to respond. In line with Experiments 1-3, automatic imitation was operationalized as faster and more accurate responses on congruent trials than on incongruent trials.

Data Analysis. The data was analyzed with a one-way repeated measures MANOVA that included congruency (congruent, neutral, or incongruent) as a within-subject factor. Trials without a response (0.06%) and trials with a RT faster than 100 ms (0.14%) were excluded from both the RT and ER analysis. For the RT analysis, we additionally excluded error trials (4.54%) and trials with an RT deviating from the participant's mean by more than 3 *SD* (1.45%).

Results and Discussion

The RT analysis revealed a main effect of congruency, $F(2, 45) = 18.41$, $p < .001$, $\eta_p^2 = 0.45$, *CI 95%* = [0.25, 0.57]. Planned comparisons showed that responses were faster on congruent trials than on incongruent trials, $t(46) = -4.17$, $p < .001$, $d_z = 0.61$, *CI 95%* = [0.29, 0.92]. Moreover, responses on neutral trials were faster than responses on both congruent, $t(46) = -2.03$, $p = .048$, $d_z = 0.30$, *CI 95%* = [0.00, 0.59], and incongruent trials, $t(46) = -5.42$, $p < .001$, $d_z = 0.79$, *CI 95%* = [0.46, 1.12] (Figure 7a). The ER analysis likewise found a main effect of congruency, $F(2, 45) = 3.21$, $p = .050$, $\eta_p^2 = 0.13$, *CI 95%* = [0.00, 0.26]. Planned comparisons indicated that participants made fewer errors on congruent trials than on incongruent trials, $t(46) = -2.04$, $p = .047$, $d_z = 0.30$, *CI 95%* = [0.00, 0.59]. Furthermore, participants made fewer errors on neutral trials than on incongruent trials, $t(46) = -2.25$, $p = .029$, $d_z = 0.33$, *CI 95%* = [0.03, 0.62], but not congruent trials, $t(46) = -0.64$, $p = .527$, $d_z = 0.09$, *CI 95%* = [-0.19, 0.38] (Figure 7b).

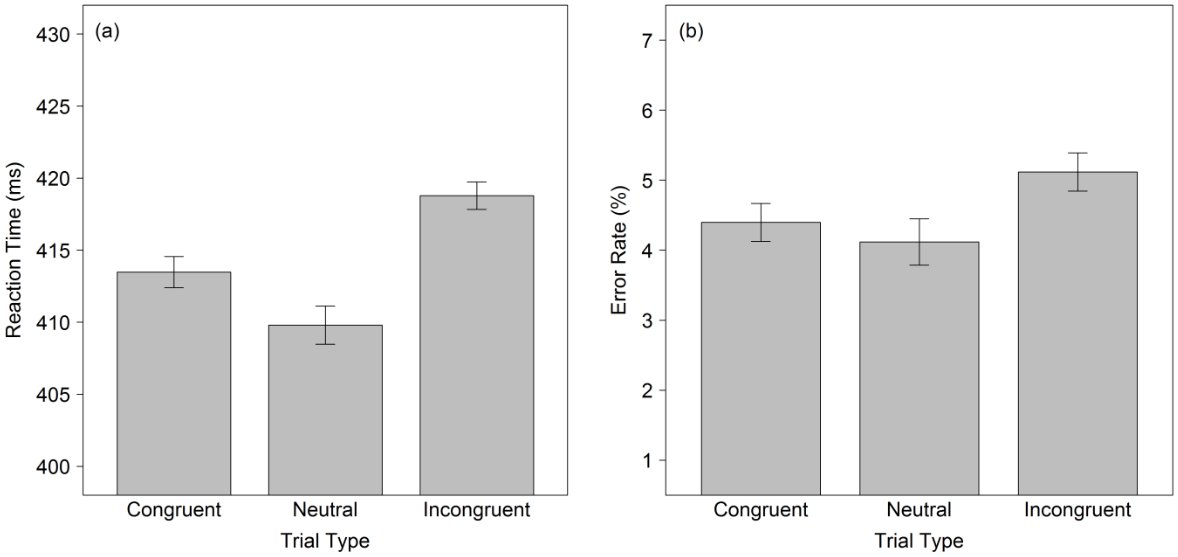

Figure 7. Results of the congruency analysis of Experiment 4 for (a) reaction times and (b) error rates. Error bars are SEMs corrected for within-subject designs (Morey, 2008).

In sum, Experiment 4 found that intentional imitation of the target hand did not preclude automatic imitation of the non-target hand. Welch's *t* test furthermore showed that the average response speed was substantially faster in Experiment 4 than in Experiments 1-3, $t(98.97) = 11.41$, $p < .001$, $d_s = 1.69$, *CI 95%* = [1.32, 2.06]. This is in line with previous work on imitation (Bertenthal et al., 2006; Brass et al., 2000) and indicates that imitation operated via shared representations (Boyer et al., 2012; Brass, Bekkering, et al., 2001; Brass et al., 2000; Sauser & Billard, 2006). As a result, these findings strongly suggest that the movements of both hands were represented together in the motor system and further support the simultaneous representation account of multi-actor imitation. However, it should be noted that we did not expect responses to be faster on neutral trials than on congruent trials. This suggests that participants were distracted by the non-target movements. For example, it could be argued that attention was drawn to the non-target hand when it made a movement. This would have required participants to reorient their attention to the target hand, which would in turn have resulted in slower responses. However, an explanation in terms of attentional reorientation is inconsistent with Experiment 3 where we did not find slower responses when both the cued and non-cued hand made a movement. Therefore, another explanation is that response selection in Experiment 4 was delayed until both stimulus movements were processed. From this perspective, movements from the non-target hand interfered with performance because more information had to be processed before a response could be selected. The reason why a similar pattern was not found in Experiment 3 could then be that the observed movements were task-irrelevant in that experiment and could thus be processed in parallel with response selection.

Finally, a third explanation could be that responses were slower when both hands made a movement because this resulted in the concurrent activation of a relevant and irrelevant motor representation between which participants had to differentiate in order to select the correct response. In other words, participants in Experiment 4 had to solve an other-other distinction problem that could have interfered with response selection. The process of other-other distinction is similar to the process of self-other distinction that has been proposed in the literature on imitative control, but other-other distinction requires participants to make a distinction between two external action plans rather than between one internal and one external action plan (Bardi, Gheza, & Brass, 2017; Brass, Derrfuss, & von Cramon, 2005; Brass, Ruby, & Spengler, 2009; Brass, Zysset, & von Cramon, 2001; Sowden & Catmur, 2013). Participants in Experiment 3 did not have to imitate and therefore did not have to distinguish between two external motor representations to prepare a response. As a result, this could explain why Experiment 3 yielded a different pattern of results than Experiment 4.

However, research has shown that self-other distinction does not usually cause responses on neutral trials to be faster than responses on congruent trials (e.g., Brass et al., 2000; Cracco et al., 2015). An important question is therefore why other-other distinction but not self-other distinction would interfere with congruent responses. A first possibility is that self-other distinction and other-other distinction recruit different processes. For example, it is conceivable that other-other distinction relies more than self-other distinction on attentional processes to facilitate the relevant and inhibit the irrelevant motor plan. From this perspective, attentional reallocation may have interfered solely with other-other distinction and would therefore have only been visible in Experiment 4. A second possibility is that responses were put on hold until self-other distinction or other-other distinction was completed regardless of whether congruent or incongruent movements were observed, but that other-other distinction was more difficult because two external action representations are more similar than one internal and one external action representation. Irrespective of why responses were faster on neutral trials than on congruent trials, the difference between congruent and incongruent trials clearly demonstrates that participants in Experiment 4 co-represented both the target and non-target movements. As a result, this experiment provides strong support for the simultaneous representation account.

General Discussion

Research from various domains has pointed towards the existence of shared representations for perception and action (Brass & Heyes, 2005; Jeannerod, 2001; Keysers & Gazzola, 2006; Knoblich & Sebanz, 2006). These representations can be used to translate observed behavior into planned behavior and for that reason are thought to play an important role in social interaction (Colling et al., 2013; Knoblich & Sebanz, 2006; Rizzolatti & Fabbri-Destro, 2008; Sebanz et al., 2006). However, research on shared processes has mainly focused on interactions between two persons. As a result, little is known about the role of these processes in social exchanges with more than two persons (Cracco et al., 2015, 2016; Ramenzoni et al., 2014; Tsai et al., 2011). In particular, an interesting hypothesis is that shared representations can be extended to include the actions of multiple agents (Cracco et al., 2015, 2016; Ramenzoni et al., 2014; Tsai et al., 2011). In line with this hypothesis, we have shown in recent work that automatic imitation is stronger when participants observe two hands that make an identical movement compared to two hands of which a single hand makes movement (Cracco et al., 2015, 2016). As an explanation, we argued that two identical movements produce a stronger imitative response because both movements activate the same motor representation at the same time (Cracco et al., 2015, 2016). However, an alternative explanation is that participants represented one hand on each trial as a result of a random sampling mechanism. This mechanism assumes that it is more likely that a moving hand is represented when two movements are shown and therefore predicts an additive imitation effect that develops over trials rather than within each trial.

The goal of the current study was to distinguish between the simultaneous and random representation accounts of multi-actor imitation. In Experiments 1 and 2, we first replicated the additive imitation effect reported in Cracco et al. (2015) with a stimulus setup that made a random sampling account implausible. We then investigated whether the same effect was also present when the movements of one hand were cued in Experiment 3 and had to be imitated in Experiment 4. As these manipulations encouraged participants to process the movements of at least one hand, the random representation account no longer predicted automatic imitation of the other hand in these experiments. Nevertheless, the results of Experiment 3 revealed stronger automatic imitation when the cued and non-cued hand both made the same movement. This additive imitation effect was furthermore of similar size as in Experiments 1-2. In the same vein, the results of Experiment 4 indicated that automatic imitation of the non-target hand persisted even when the target hand was being imitated. As a consequence, these experiments are inconsistent with an explanation in terms of random sampling and instead indicate that the actions of multiple persons were represented at the same time in the motor system of the observer (Cracco et al., 2015, 2016).

However, responses on neutral trials in Experiment 4 were not situated between congruent and incongruent trials as was expected based on previous research (e.g., Brass et al., 2000; Cracco et al., 2015). Instead, reaction times were found to be faster on neutral trials than on congruent trials. Albeit speculative, this could indicate that action selection was put on hold until participants were able to separate the target motor plan from the distractor motor plan. That is, if the actions of multiple persons are represented together in the motor system, then imitation of the target hand requires a mechanism that can connect each action representation with its source. In more general terms, concurrent action simulation creates an other-other distinction problem similar to the self-other distinction problem that is experienced when imitation has to be inhibited in favor of an internal action plan (Bardi et al., 2017; Brass et al., 2005, 2009; Brass, Zysset, et al., 2001; Sowden & Catmur, 2013). However, self-other distinction is known to operate on incongruent trials, whereas other-other distinction was visible on congruent trials as well (Bardi et al., 2017; Brass et al., 2009). An interesting question for future work is therefore whether other-other distinction was indeed what caused reaction times to be faster when no movement was observed and, if so, whether it relies on the same mechanisms as self-other distinction.

It is also important to point out that the current study assumed a strong random representation hypothesis in the sense that it predicted motor simulation to be restricted to the actions of one person at a time. In contrast, a weak random representation hypothesis might argue that motor simulation of multiple agents is possible but restricted to a limited number of agents so that people simulate a random subset of the observed agents only when it is not possible to simulate the full set of agents. In line with this hypothesis, research has shown that working memory for observed actions relies on motor processes (Gao, Bentin, & Shen, 2015) and is restricted to two or three actions (Wood, 2007). However, in contrast, research on face perception has demonstrated that observers do not process each individual face when they see a large group of people but instead compute an average of all faces (Haberman & Whitney, 2007, 2009). It is therefore possible that observers do not represent a random subset of observed agents but instead compute the mean across all observed actions when there are too many agents to simulate in parallel. In any case, a weak random representation account agrees that people can represent the actions of multiple persons at the same time in their motor system and is for that reason compatible with the simultaneous representation account.

A potential criticism on the current study could be that participants may have perceived the hands as the left and right hand of the same person. In this sense, a movement of both stimulus hands may have been interpreted as a bimanual movement instead of two individual movements. However, this seems unlikely considering that we used one male and one female hand and disclosed this information to the participants in the instruction phase. In addition, previous research has obtained similar results when the stimulus hands consisted of two left or right hands instead (Cracco et al., 2015, 2016). Finally, it is not clear how bimanual observed movements could produce an additive imitation effect as they should trigger a bimanual and not a unimanual imitative response (Heitger, Mace, Jastorff, Swinnen, & Orban, 2012). In other words, automatic imitation measured from one hand should not depend on whether a uni- or bimanual movement was observed. In support of this view, research has found that bimanual but not unimanual imitation of two tapping hands depended on whether the hands belonged to the same person or to two different persons (Ramenzoni et al., 2014).

Another criticism could be that participants mapped the left stimulus hand onto their left hand and the right stimulus hand onto their right hand (or vice versa) regardless of whether one or two hands made a movement. This hypothesis assumes that participants always imitated one hand and never imitated the other hand. As a result, it predicts an additive imitation effect that developed over trials rather than within trials because the probability that the preferred hand made a movement was 100% when both hands lifted a finger but only 50% when a single hand lifted a finger. However, such a mechanism cannot account for the findings of Experiment 4 where participants had to imitate a hand in order to respond. That is, the finding that irrelevant observed movements still influenced responses even when another movement was being imitated provides strong support for the hypothesis that the movements of multiple persons can be represented at the same time in the motor system of the observer.

To conclude, the current study provides evidence for the hypothesis that individuals are able to simulate the actions of multiple persons at the same time in their motor system (Cracco et al., 2015, 2016). This may have important implications for our understanding of social interaction at the group level. For example, the present research opens up the possibility that motor simulation facilitates coordinated group behavior by allowing individuals to synchronize their movements with multiple persons simultaneously (Colling et al., 2013; Kourtis et al., 2013; Volpe et al., 2016). Furthermore, it could provide insight into the neurocognitive mechanisms behind the finding that synchronized group behavior elicits prosocial behavior (Cohen et al., 2010; Davis et al., 2015; Launay et al., 2013; Reddish et al., 2013; Tarr et al., 2015; Wiltermuth & Heath, 2008; Woolhouse et al., 2016). That is, it is well known that people who are being imitated by their interaction partner experience the interaction to be smoother (Chartrand & Bargh, 1999) and act in a more prosocial manner (van Baaren, Holland, Kawakami, & van Knippenberg, 2004). If individuals mirror the actions of multiple co-actors, then increased motor activation might contribute to the social effects of synchronized group activity.

In addition to performing synchronous behavior, our results also have important implications for studies on seeing synchronous behavior. That is, research in this domain has shown that observing synchronous action is a rewarding experience (Eskenazi, Rueschemeyer, de Lange, Knoblich, & Sebanz, 2015) that increases attributed rapport (Lakens & Stel, 2011), and adds to the aesthetic quality of both music (D'Ausilio et al., 2012) and dance (Hagen & Bryant, 2003; Vicary, Sperling, Zimmermann, Richardson, & Orgs, 2017). However, an important distinction between watching a synchronous performance and producing it is that the production of synchronous behavior can be accomplished through imitation of a randomly selected co-actor, whereas its appreciation requires the simultaneous representation of at least two synchronized performers. In line with the current study, research on the observation of synchronous movements thus favors a simultaneous representation account over a random representation account. From this perspective, the ability to represent the actions of multiple observed agents in the motor system may provide a potential mechanism by which observed synchrony communicates the "coalition quality" of groups (Hagen & Bryant, 2003).

Finally, our research may have implications for the study of social group phenomena such as social contagion and conformity (Cialdini & Goldstein, 2004; Latane, 1981; Raafat, Chater, & Frith, 2009). That is, research has shown that social influence grows stronger when the number of sources increases (Bond, 2005; Gallup et al., 2012; Herrmann, Legare, Harris, & Whitehouse, 2013; Latane, 1981; Milgram, Bickman, & Berkowitz, 1969). Although these findings have mainly been interpreted in terms of interpretive processes, the current study suggests that sensorimotor processes might contribute as well. As a result, the ability to represent the actions of multiple persons together in the motor system may play an important role in social group dynamics.

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Chapter 5

The role of sensorimotor processes in social group contagion[1]

Although it is well known that action observation triggers an imitative response, not much is known about how these responses develop as a function of group size. Research on social contagion suggests that imitative tendencies initially increase but then stabilize as groups become larger. However, these findings have mainly been explained in terms of interpretative processes. Across seven experiments (N = 322), the current study investigated the contribution of sensorimotor processes to social group contagion by looking at the relation between group size and automatic imitation in a task that involved minimal interpretation. The results of Experiments 1-2 revealed that automatic imitation increased with group size according to an asymptotic curve on congruent trials but a linear curve on incongruent trials. The results of Experiments 3-7 showed that the asymptote on congruent trials disappeared when no control was needed, namely in the absence of incongruent trials. This suggests that the asymptote in the relation between group size and automatic imitation can be explained in terms of strategic control mechanisms that aim to prevent unintended imitative responses. The findings of the current study are in close correspondence with previous research in the social domain and as such support the hypothesis that sensorimotor processes contribute to the relation between group size and social contagion.

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Introduction

There is now converging evidence that humans tend to imitate others (Cracco et al., 2018; Heyes, 2011). For example, research on *automatic imitation* has shown that response selection is facilitated by congruent and impeded by incongruent observed actions (Brass et al., 2000; Catmur & Heyes, 2011; Cracco et al., 2018; Stürmer, Aschersleben, & Prinz, 2000). Likewise, research on *social imitation* has revealed that individuals spontaneously imitate the behavior of the persons with whom they interact (Chartrand & Bargh, 1999; Chartrand & van Baaren, 2009). According to ideomotor theory, these imitative tendencies exist because action observation and action execution share a representational format (Greenwald, 1970; Prinz, 1997). More precisely, this theory argues that the visual image of an action is part of its motor representation, and that this causes the motor representation to become activated during action observation (Brass et al., 2000; Brass, Bekkering, & Prinz, 2001; Cracco et al., 2018). Supporting this view, there is now strong evidence from neuroscience that action observation and action execution share activation in the motor system of the brain (Fox et al., 2016; Molenberghs, Cunnington, & Mattingley, 2012; Naish, Houston-Price, Bremner, & Holmes, 2014). This mechanism is thought to translate observed actions into motor programs (Brass & Heyes, 2005), and is therefore often seen as the sensorimotor basis of social cognition (Gallese, Keysers, & Rizzolatti, 2004; Knoblich & Sebanz, 2006; Rizzolatti & Fabbri-Destro, 2008).

However, most research has studied sensorimotor processes in the context of dyadic interactions. As a result, the role of these processes in social exchanges occurring at the group level is not yet known. This is crucial because important social phenomena such as social contagion or conformity emerge from social group dynamics (Cialdini & Goldstein, 2004; Latane, 1981; Raafat, Chater, & Frith, 2009). From this perspective, a deeper understanding of the neurocognitive mechanisms behind group interactions may contribute to our knowledge of how these phenomena unfold (Raafat et al., 2009). A necessary condition for sensorimotor processes to play a role in social group processes is that the actions of multiple persons can be represented together in the motor system. In support of this view, we have shown in recent work that automatic imitation is modulated by the number of observed agents (Cracco & Brass, 2017; Cracco, De Coster, Andres, & Brass, 2015). Specifically, we found that imitative responses were stronger when participants saw two hands performing an identical action compared with one hand performing a single action. Furthermore, a subsequent transcranial magnetic stimulation study showed that this effect was due to an increase in corticospinal excitability (Cracco, De Coster, Andres, & Brass, 2016). Together, this indicates that motor activation during action observation reflects the combined input of the different observed actions. Moreover, related research has shown that imitative responses are not only sensitive the number of observed agents but also to its (mis)match with the number of imitators (Ramenzoni, Sebanz, & Knoblich, 2014; Tsai, Sebanz, & Knoblich, 2011). Collectively, the evidence thus suggests that the actions of multiple individuals can be represented together in the motor system (Cracco & Brass, 2017; Cracco et al., 2015, 2016) in the form of group representations (Ramenzoni et al., 2014; Tsai et al., 2011).

Building on this evidence, an important question is whether sensorimotor processes contribute to social group phenomena. Supporting this view, research has shown that motor synchronization in groups leads to positive social consequences (Cohen, Ejsmond-Frey, Knight, & Dunbar, 2010; Reddish, Fischer, & Bulbulia, 2013; Wiltermuth & Heath, 2008). However, what is the role of sensorimotor processes in social group contagion? Social contagion is the propensity of persons to align their own behavior with the behavior of others (Raafat et al., 2009). Importantly, this propensity depends on the number of observed agents (Darley & Latané, 1968; Fischer et al., 2011; Freedman & Birsky, 1980; Gallup et al., 2012;

Herrmann, Legare, Harris, & Whitehouse, 2013; Knowles & Bassett, 1976; Mann, 1977; Milgram, Bickman, & Berkowitz, 1969). For example, in a seminal study, Milgram et al. (1969) measured how often pedestrians in a busy city street copied groups of one to fifteen confederates looking up at a sixth floor window. The results revealed that passers-by were more likely to look up as the number of confederates increased (see also: Gallup et al., 2012; Knowles & Bassett, 1976). Confirming their hypothesis, the authors argued that this increase in imitation was driven by the fact that a large number of people looking at the same thing are likely to be looking at something of interest.

However, an alternative hypothesis is that large groups were imitated more often simply because they provided a stronger trigger to the motor system (Cracco & Brass, 2017; Cracco et al., 2015, 2016). Although there is some work on gaze processing in the context of groups (Capozzi, Bayliss, Elena, & Becchio, 2015; Capozzi, Becchio, Willemse, & Bayliss, 2016), it is not yet known how sensorimotor processes develop beyond two agents (Cracco & Brass, 2017; Cracco et al., 2015, 2016). Therefore, to understand the role of these processes in social group contagion, the current study investigated the influence of group size on automatic imitation using a task in which shared motor activation was measured in the absence of interpretative processes (Cracco et al., 2018; Heyes, 2011). Specifically, participants had to abduct their right index or little finger in response to a letter while one, two, three, or four hands abducted the congruent or incongruent finger. Automatic imitation in this paradigm is operationalized as slower responses on incongruent trials than on congruent trials (Cracco et al., 2018; Heyes, 2011). This can be seen as a laboratory model of social imitation (Heyes, 2011), and as such is well suited to investigate the sensorimotor mechanisms of social group contagion.

If there is a sensorimotor basis to social group contagion, then automatic imitation should increase as the number of moving hands grows. However, it is also interesting to look at *how* automatic imitation increases with group size. More specifically, research on social contagion has repeatedly demonstrated that the incremental effect of increasing group size diminishes as groups become larger (Darley & Latané, 1968; Gallup et al., 2012; Latane, 1981; Milgram et al., 1969). In previous research, this asymptote has typically been explained in terms of social cognitive processes (Bond, 2005; Latane, 1981; MacCoun, 2012). In contrast, the current study investigated the role of sensorimotor processes. That is, from a sensorimotor perspective, at least three mechanisms can explain why automatic imitation stabilizes as group size increases. A first hypothesis is that motor activation saturates as input to the motor system increases ("input saturation hypothesis"). That is, motor activation may saturate as a result of nonlinear neural response functions (Peirce, 2007) or as a result of limited processing capacity (Gao, Bentin, & Shen, 2015; J. N. Wood, 2007). A second hypothesis argues that it is not motor activation as such but rather its influence on response speed that saturates ("output saturation hypothesis"). Indeed, response speed is restrained by physical bounds. Therefore, responses may become less sensitive to increases in motor activation as they approach their upper or lower bound.

Finally, a third hypothesis proposes that strategic control mechanisms cause automatic imitation to saturate ("strategic control hypothesis"). That is, imitative tendencies have to be inhibited in order to prevent overt imitation (Bien, Roebroeck, Goebel, & Sack, 2009; Brass, Derrfuss, & von Cramon, 2005; Brass, Zysset, & von Cramon, 2001). However, if motor activation increases with group size, more imitative control is needed as groups become larger. As a result, imitative control may be driven by a strategic mechanism that exerts more or less control on each trial depending on the number of observed movements. Importantly, such a mechanism assumes that cognitive control is a fast process. Although this goes against the traditional view that control processes operate between trials (Botvinick, Braver, Barch, Carter, & Cohen, 2001), recent work has shown that they can operate within trials as well

(Janssens, De Loof, Boehler, Pourtois, & Verguts, 2017; Janssens, De Loof, Pourtois, & Verguts, 2016).

Experiment 1

Method

Participants. For all experiments, we will report how we determined our sample size, all data exclusions (if any), all manipulations, and all measures (Simmons, Nelson, & Simonsohn, 2011, 2012). In line with our previous work on automatic imitation (Cracco et al., 2015), we aimed to test 40 participants in Experiment 1. This provided us with good power to detect realistic effect sizes (Brysbaert & Stevens, 2018). Although the eventual sample included 42 participants (33 female, $M_{age} = 22.50$, $SD_{age} = 3.60$), none of the statistical conclusions changed when the last two participants were discarded from the analysis. To remove outliers, we excluded participants whose overall reaction time (RT) or error rate (ER) exceeded the sample mean by more than 3 *SD*. This resulted in the loss of one participant with an ER of 24.22%. As a consequence, the final sample consisted of 41 participants (32 female, $M_{age} = 22.54$, $SD_{age} = 3.63$). All participants were right-handed and had good or corrected vision. A reward of 5 euro was given in return for participation. All experiments were approved by the local ethical committee and all procedures were performed in accordance with the 1964 Helsinki Declaration.

Stimuli, Task, and Apparatus. The experiment was programmed in C with Tscope5 (Stevens, Lammertyn, Verbruggen, & Vandierendonck, 2006). The stimuli showed four identical female hands arranged in a rectangle (Figure 1). The stimuli contained 972 x 996 pixels printed on a black background. An illusion of movement was created by overwriting a picture of the hands in neutral position with a picture of the hands in final position. Each hand could abduct the index finger, abduct the little finger, or not move. The number of hands making a movement varied randomly from one to four hands but the moving hands always made the same movement. Participants responded to a letter that appeared in the center of the screen together with the stimulus movement(s). When W ("wijsvinger") was presented, the right index finger had to be abducted. When P was presented, the right little finger ("pink") had to be abducted. The required response could be congruent (C) or incongruent (IC) with respect to the observed movement. Importantly, all combinations of stimulus movement and response occurred equally often in each block of the experiment. The response box was an optical sensor box with four sensors organized from left to right. Participants were asked to place their right index finger on the second sensor and their right little finger on the fourth sensor. A response was recorded when the participant moved his/her finger from the sensor.

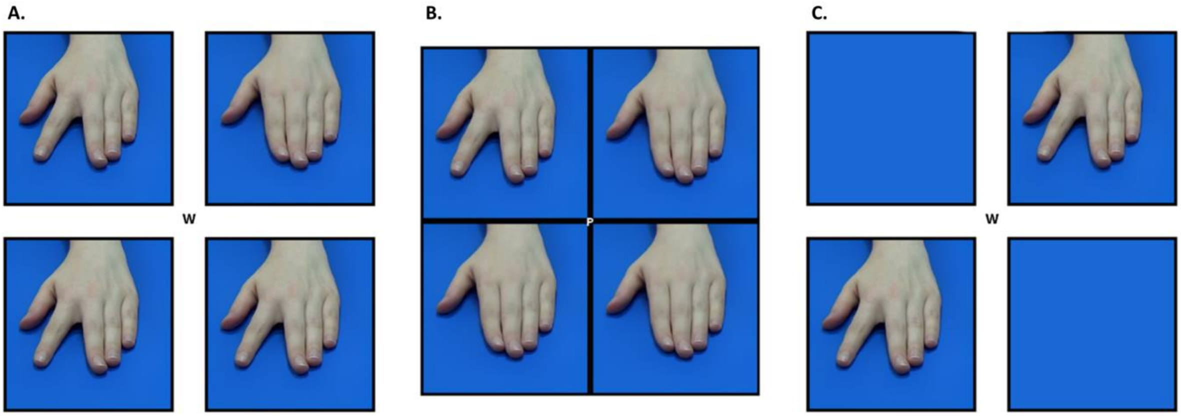

Figure 1. Example of the stimuli used in (a) Experiment 1, 3, 5, and 7, (b) Experiment 2 and 6, (c) Experiment 4. In Experiments 1-6, participants were asked to respond to the letter in the center of the screen. At the same time they saw one, two, three, or four hands performing an identical movement. In Experiment 7, the symbolic cue was replaced by an X and participants were instructed to imitate the stimulus movements to respond.

Procedure. The experiment took about 20 minutes and consisted of 384 trials. Instructions appeared on the screen before the experiment and asked participants to respond as fast as possible without making errors. The experiment started with a practice phase of 16 trials in which accuracy feedback was provided. Participants then completed four blocks of 96 trials each without feedback. All conditions of the number (one, two, three, or four) x congruency (C or IC) design occurred 12 times in each block. All possible hand configurations within each condition occurred equally often every two blocks. After each block, participants had the opportunity to take a self-paced break. Trials were presented randomly with the restriction that the same imperative cue could not appear more than four times in a row. At the end of the experiment, participants were asked to complete the Interpersonal Reactivity Index (Davis, 1983). The questionnaire data was collected for the purpose of a meta-analysis and will not be reported here. However, note that none of the four scales correlated with the congruency effect (IC - C), all $r \leq .23$, all $p \geq .156$. Each trial in the experiment started with a picture of the four hands in their neutral position for 500 ms, and a fixation cross in the center of the screen. This picture was then overwritten by a picture of the hands in their final position, together with the imperative cue replacing the fixation cross for a maximum of 2,000 ms or until the response. This was followed by a black screen for 1,000 ms to indicate the end of the trial.

Data Analysis. To explore whether automatic imitation increased with the number of observed movements, we fitted a linear mixed effects model with a continuous predictor for number and a factor for congruency (Bates, Machler, Bolker, & Walker, 2014). The random effects structure was determined with a backward selection procedure (Matuschek, Kliegl, Vasishth, Baayen, & Bates, 2017), resulting in a random intercept and a random congruency slope. *P*-values were calculated on the basis of Satterthwaite approximated degrees of freedom.

Next, to find the curve of the relation between the number of observed movements and automatic imitation, we used a curve fitting procedure. That is, we fitted an additive model with a parametric term for congruency and a smooth term for number that interacted with congruency (S. N. Wood, 2006). Smooth terms are nonparametric functions that have to be estimated from the data. In the current study, smooth terms were estimated using an iterative procedure that repeatedly varied the model's smoothing parameter to minimize the generalized cross-validation score (GCV) of the model. The GCV is a fit index measuring how well the model can predict non-fitted data points, with lower values indicating better model fit (S. N. Wood, 2006). Since model fit is based on prediction, this procedure offers protection against overfitting (S. N. Wood, 2006). Moreover, because cross-validation performance is maximized during estimation, the estimated model will outperform both less complex models (i.e., less curved) and more complex models (i.e., more curved). In other words, the estimation of additive models can be thought of as an implicit model selection procedure that compares a wide range of models to find the model that optimizes prediction. Smooth functions in the current study were constructed from a thin plate regression spline basis (S. N. Wood, 2006). The use of a repeated-measures design was taken into account by including a random intercept in the additive model (S. N. Wood, 2006).

All analyses were performed in R with the lme4 (Bates et al., 2014) and mgcv packages (S. N. Wood, 2006). Trials were excluded if no response was recorded (0.04%), if the RT was faster than 100 ms (0.05%), if the response was incorrect (4.14%), or if the RT deviated from the participant's mean RT by more than 3 *SD* (1.31%)[2]. The second criterion was used to remove action slips from the data. The fourth criterion was used to reduce the influence of outliers. Errors were not analyzed because there were insufficient incorrect responses to accurately model the curve of the relation between the number of observed movements and automatic imitation. Figures that describe the ER data are provided in

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[2] Due to a technical error in the generation of the output files, the data of the last 50 trials (13%) of 12 participants was not saved. However, note that excluding these participants from the analyses did not change the data pattern or statistical conclusions.

Supplementary Material (Figure S1). Importantly, there was no indication of a speed-accuracy trade-off in the data.

Beta coefficients β and their 95% confidence interval (CI) will be provided as effect size measures. Unstandardized coefficients are reported because these coefficients can be readily interpreted as the estimated change in RT. For example, the congruency beta coefficient shows the estimated difference from the marginal mean. Likewise, the number beta coefficient shows the expected change in RT when number is increased. The data, analyses, stimuli, and experimental programs of all experiments are available at the Open Science Framework: https://osf.io/5yvnb.

Results and Discussion

The hypothesis that automatic imitation increases with group size was investigated with a linear mixed effects model. This revealed a significant main effect of congruency, *t*(259) = -3.03, β = -5.61, *CI 95%* = [-9.24, -1.98], *p* = .003, no main effect of number, *t*(14232) = -0.36, β = -0.21, *CI 95%* = [-1.34, 0.93], *p* = .721, and a significant number x congruency interaction, *t*(14232) = -3.21, β = -1.86, *CI 95%* = [-3.00, -0.73], *p* = .001. The main effect of congruency showed that responses were faster on congruent trials than on incongruent trials. Furthermore, the number x congruency interaction indicated that response speed decreased on congruent trials, *t*(14237) = -2.55, β = -2.07, *CI 95%* = [-3.66, -0.48], *p* = .011, and increased on incongruent trials, *t*(14237) = 2.00, β = 1.66, *CI 95%* = [0.03, 3.28], *p* = .046, as the number of observed movements grew. To explore the curve of the relation between number and congruency, an additive model was estimated. As shown in Figure 2, this revealed that the influence of number on RT was best described by an asymptotic decrease on congruent trials and a linear increase on incongruent trials.

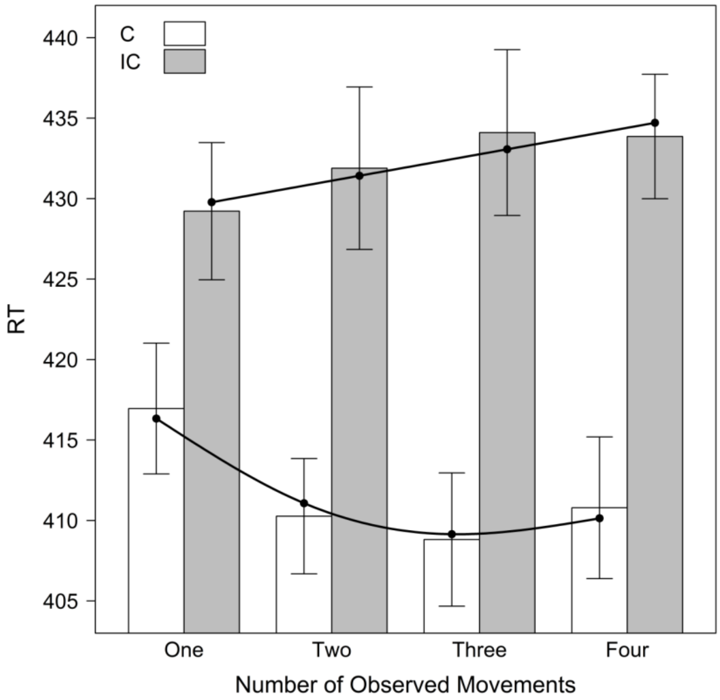

Figure 2. RT results (ms) of Experiment 1. The fit line shows the model fit of the additive model. The error bars depict 95% confidence intervals corrected for within-subject designs according to Morey (2008). C: congruent; IC: incongruent.

Before discussing the implications of these results, we first attempted to replicate them in Experiment 2. Experiment 2 was identical to Experiment 1, except that the white border between the four stimulus hands was removed. This adjustment was based on research showing that automatic imitation is stronger when spatial attention is directed to the stimulus movements (Bach, Peatfield, & Tipper, 2007; Cracco et al., 2018). In particular, it was reasoned that the adjusted setup would result in more automatic imitation because it places the stimulus hands closer to the imperative cue, and that this would in turn make it more likely that the results of Experiment 1 could be replicated.

Experiment 2

Method

Participants. The sampling goal was adjusted from 40 to 50 participants to maximize statistical power[3]. This sampling goal was also used in all following experiments, but the planned sample size could not always be obtained due to participant cancellations. The sample of Experiment 2 consisted of 50 participants (42 female, $M_{\text{age}} = 22.40$, $SD_{\text{age}} = 4.24$). Participants were excluded if their overall RT or ER exceeded the sample mean by more than 3 *SD*. This resulted in the exclusion of one participant with a RT of 644 ms and another participant with an ER of 16.93%. The final sample therefore consisted of 48 participants (40 female, $M_{\text{age}} = 22.48$, $SD_{\text{age}} = 4.28$). All participants were right-handed and had good or corrected vision. A reward of 5 euro was given in return for participation.

Stimuli, Task, Apparatus, and Procedure. The method of Experiment 2 was identical to the method of Experiment 1, except that we removed the white border between the four stimulus hands (Figure 1b).

Data Analysis. The data analysis of Experiment 2 was conducted following the procedure outlined in Experiment 1. The random effects structure of the linear mixed effects model consisted of a random intercept and a random slope for congruency. Prior to analysis, we removed trials without a response (0.03%), trials with a RT faster than 100 ms (0.02%),

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[3] The actual order in which the experiments were conducted was Experiment 1, Experiment 3, Experiment 5, Experiment 2, Experiment 6, Experiment 7, and Experiment 4. The experiments are described in a different order for logical consistency. This means that the sampling goal was first adjusted in Experiment 3 to ensure that we had sufficient statistical power to detect a potential asymptotic curve when we only included congruent trials. The adjusted sampling goal was then also used for all experiments that followed.

error trials (4.88%), and trials where the RT deviated from the participant's mean by more than 3 *SD* (1.35%). The error data was not analyzed but is displayed in Supplementary Material (Figure S1). There was no sign of a speed-accuracy trade-off.

Results and Discussion

The linear mixed effects model revealed a significant main effect of congruency, *t*(178) = -2.73, β = -5.44, *CI 95%* = [-9.34, -1.54], *p* = .007, no main effect of number, *t*(17186) = 1.53, β = 0.85, *CI 95%* = [-0.24, 1.95], *p* = .126, and a significant number x congruency interaction, *t*(17186) = -6.03, β = -3.37, *CI 95%* = [-4.46, -2.71], *p* < .001. The main effect of congruency showed that RTs were faster on congruent trials than on incongruent trials. The interaction effect further indicated that response speed decreased on congruent trials, *t*(17190) = -3.23, β = -2.51, *CI 95%* = [-4.04, -0.99], *p* = .001, but increased on incongruent trials, *t*(17191) = 5.27, β = 4.22, *CI 95%* = [2.65, 5.79], *p* < .001, as the number of observed movements grew. Similar to Experiment 1, the additive model revealed that the number x congruency interaction was best described by an asymptotic decrease on congruent trials and a linear increase on incongruent trials (Figure 3).

In summary, Experiments 1 and 2 both showed that automatic imitation increased with group size according to an asymptotic curve on congruent trials and a linear curve on incongruent trials. Since interpretative processes were minimized, this supports the hypothesis that sensorimotor processes contribute to social group contagion. In line with this view, similar asymptotic relations have also been reported in social imitation research (Bond, 2005; Gallup et al., 2012; MacCoun, 2012; Milgram et al., 1969). Interestingly, however, only congruent trials reached an asymptote. Relating back to our three process hypotheses, this speaks against the input saturation hypothesis because the saturation of motor activation should be visible on incongruent trials as well. Instead, it is more consistent with the two other hypotheses. First, in terms of output saturation, the selective asymptote on congruent trials can be explained by a response speed boundary that prevents participants from speeding up. Second, in terms of strategic control, it can be explained by a mechanism that regulates the response threshold on each trial based on the number of moving hands. That is, if automatic imitation increases with group size, then responses should become faster on congruent trials and slower on incongruent trials as the number of observed movements increases. However, if the response threshold increases with group size as well, then this will counteract the response speed decrease on congruent trials and strengthen the response speed increase on incongruent trials because a heightened response threshold equals slower responses. This, in turn, can explain why RTs reached an asymptote on congruent trials but not on incongruent trials.

To distinguish between these two alternative hypotheses, we conducted a third experiment in which all trials were congruent. If the asymptote on congruent trials was caused by a response speed boundary, then the same pattern should be observed regardless of whether incongruent trials were included in the experiment or not. In contrast, a proportional RT decrease should be observed if the saturating response was caused by a strategic control mechanism because it is not only unnecessary but also counterproductive to exert imitative control when the observed movements always match the required response.

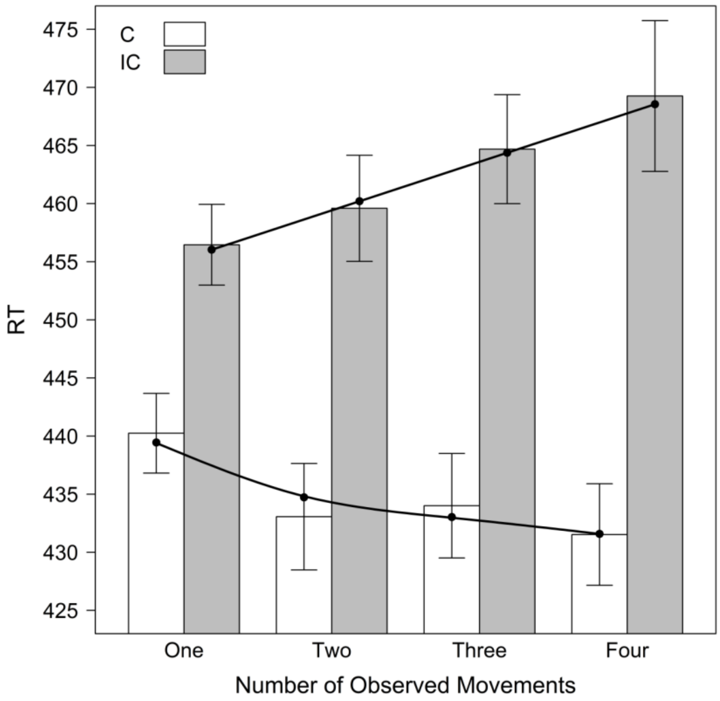

Figure 3. RT results (ms) of Experiment 2. The fit line shows the model fit of the additive model. The error bars depict confidence intervals corrected for within-subject designs according to Morey (2008). C: congruent; IC: incongruent.

Experiment 3

Method

Participants. The sample of Experiment 3 consisted of 48 participants (38 female, M_{age} = 23.58, SD_{age} = 5.04). There were no participants with an RT or ER that exceeded the sample mean by more than 3 *SD*. All participants were right-handed and had good or corrected vision. A reward of 5 euro was given in return for participation.

Stimuli, Task, Apparatus, and Procedure. The method of Experiment 3 was identical to the method of Experiment 1, except that only congruent trials were included. The experiment took about 10 minutes and contained 192 trials. The practice phase consisted of 8 trials.

Data Analysis. The data analysis of Experiment 3 followed the procedure described in Experiment 1. However, the models no longer contained a factor for congruency. Instead, the linear mixed effects model now consisted of a single predictor for number and the additive model of a single smooth term for number. The random effects structure of the linear mixed effects model consisted of a random intercept together with a random number slope. Trials without a response (0.02%), trials with a RT faster than 100 ms (0.05%), error trials (3.80%), and trials with a RT exceeding the participant's mean by more than 3 *SD* (1.40%) were excluded from the analyses. The error data was not analyzed but is presented in Supplementary Material (Figure S2). There was no evidence for a speed-accuracy trade-off.

Results and Discussion

The linear mixed effects model revealed a significant main effect of number, *t*(46.91) = -4.96, β = -4.06, *CI 95%* = [-5.66, -2.45], *p* < .001, indicating that RTs decreased as the number of congruent observed movements increased. Furthermore, in contrast to Experiments 1-2, the additive model showed that the influence of number on RTs was characterized by a linear curve (Figure 4). As response speed in Experiment 3 was also significantly faster than congruent response speed in Experiment 1, *t*(85.76) = 4.10, *p* < .001, *d* = 0.86, this suggests that a response speed boundary cannot explain why congruent responses reached an asymptote in Experiments 1-2. Instead, the data of Experiment 3 are more consistent with the hypothesis that congruent RTs saturated because strategic control mechanisms modulated the response threshold on each trial depending on the number of moving hands. From this perspective, the linear RT decrease in Experiment 3 can be explained by the fact that no imitative control is needed when the observed movements always match the required response. A strategic control mechanism should adapt to this situation and should thus no longer exert imitative control, which should in turn lead to a proportional increase of automatic imitation as a function of the number of observed movements.

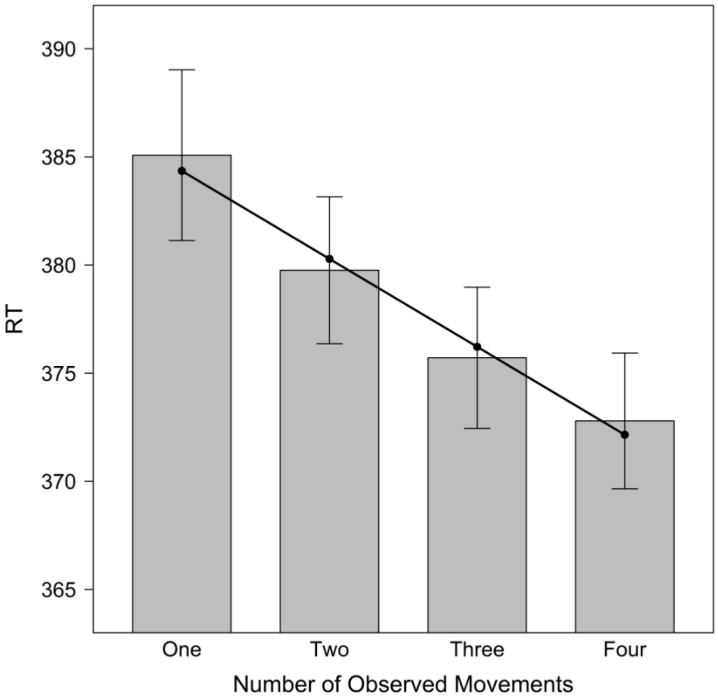

Figure 4. RT results (ms) of Experiment 3. The fit line shows the model fit of the additive model. The error bars depict 95% confidence intervals corrected for within-subject designs according to Morey (2008).

Nevertheless, an alternative explanation could be that participants in Experiment 3 used a different response strategy than participants in Experiments 1-2. For example, participants in Experiment 3 may have allocated attention to a random stimulus hand on each trial in order to maximize performance. While random attentional allocation would have impaired performance in Experiments 1-2 due to the presence of both congruent and incongruent trials, the absence of incongruent trials in Experiment 3 removed this constraint.

If only the attended hand was processed, a random attentional allocation strategy would have caused participants to sometimes process a moving hand and sometimes a non-moving hand. As the probability to sample a moving hand from the combined pool of stimulus hands increased linearly with the number observed movements, this account can explain why the RT curve on congruent trials was linear in Experiment 3 but asymptotic in Experiments 1-2. To rule out this explanation, we conducted a fourth experiment that replicated Experiment 3 with the exception that only those stimulus hands that would also make a movement appeared on the screen. This setup made it clear to participants which location should be attended to optimize performance. As a result, it was no longer possible that participants who used an attentional allocation strategy sometimes represented a non-moving hand. If participants only represented the attended hand, the number of observed movements should therefore no longer have an influence on RTs. However, if participants did not use this strategy or processed all stimulus movements in spite of using this strategy, then the number of observed movements should again have a proportional influence on RTs.

Experiment 4

Method

Participants. The sample of Experiment 4 consisted of 50 participants (34 female, $M_{\text{age}} = 20.36$, $SD_{\text{age}} = 2.59$). There were no participants with a RT or ER that exceeded the sample mean by more than 3 *SD*. All participants were right-handed and had good or corrected vision. A reward of 5 euro or partial course credit was given in return for participation.

Stimuli, Task, Apparatus, and Procedure. The method of Experiment 4 was identical to Experiment 3, except that only the stimulus hands that were about to make a movement were presented. For example, on a trial where one hand would make a movement, we first presented a neutral hand at one location and no hands at the other three locations. We then replaced the picture of the neutral hand with a picture of the moving hand together with the presentation of the imperative cue (Figure 1c).

Data Analysis. The data analysis of Experiment 4 was identical to the data analysis of Experiment 3. The random structure of the linear mixed effects model consisted of a random intercept. Trials without a response (0.01%), trials with a RT faster than 100 ms (0.03%), error trials (2.98%), and trials where the RT deviated from the participant's mean by more than 3 *SD* (1.34%) were excluded from analysis. The error data was not analyzed but is provided in Supplementary Material (Figure S2). There was no indication of a speed-accuracy trade-off.

Results and Discussion

The linear mixed effects model revealed a significant effect of number, $t(9126) = -7.00$, $\beta = -5.45$, *95% CI* = [-6.98, -3.93], $p < .001$, indicating that RTs decreased as the number of congruent observed movements increased. The additive model further indicated that response speed decreased consistently with the number of observed movements (Figure 5). In other words, the results of Experiment 4 replicated the results of Experiment 3 even though participants in Experiment 4 could see which stimulus hands were about to make a movement. This suggests that the proportional decrease in RT as a function of group size observed in Experiment 3 cannot be explained by a random attentional allocation strategy. Instead, it is better explained by a strategic mechanism that no longer exerts control when the observed movements always match the required response.

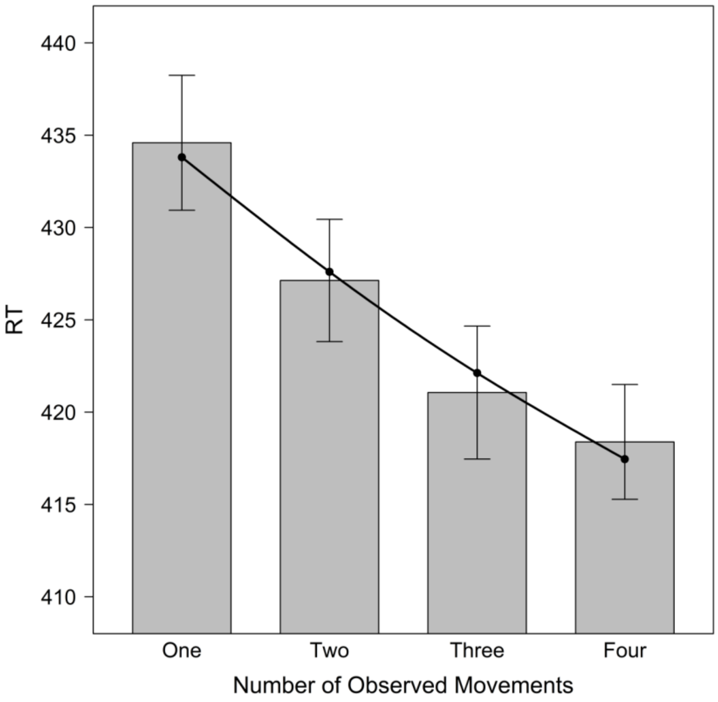

Figure 5. RT results (ms) of Experiment 4. The fit line shows the model fit of the additive model. The error bars depict 95% confidence intervals corrected for within-subject designs according to Morey (2008).

Nevertheless, another alternative explanation could be that participants in Experiments 1-2 responded to the imperative cue, whereas participants in Experiments 3-4 instead responded by imitating the stimulus hands. That is, previous work has shown that responses are faster when the task is to imitate than when the task is to respond to a symbolic cue (Bertenthal, Longo, & Kosobud, 2006; Brass et al., 2000; Cracco & Brass, 2017). As a result, it is possible that participants in Experiments 3-4 used an imitation strategy to maximize performance. Importantly, the same strategy could not be implemented in Experiments 1-2 because it would result in erroneous responses on incongruent trials. The use of an imitation strategy in Experiments 3-4 but not in Experiments 1-2 could therefore explain why the relation between group size and automatic imitation followed a different curve in these two sets of experiments. To address this issue, we conducted a fifth experiment in which participants were encouraged to respond to the cue by adding catch trials in which no movements were presented. Since the observed movements could no longer be used as a reliable response cue in this experiment, a proportional RT decrease would support the notion that group size has a consistent influence on automatic imitation when no imitative control is required.

Experiment 5

Method

Participants. A new sample of 47 participants was recruited for Experiment 5 (40 female, M_{age} = 21.17, SD_{age} = 2.03). Participants were discarded if their overall RT or ER exceeded the sample mean by more than 3 *SD*. As a result, one participant with an ER of 23.11% was excluded. The final sample therefore consisted of 46 participants (39 female, M_{age} = 21.20, SD_{age} = 2.04). All participants were right-handed and had good or corrected vision. A reward of 5 euro was given in return for participation.

Stimuli, Task, Apparatus, and Procedure. The method of Experiment 5 was identical to that of Experiment 3 except that catch trials were included in which none of the hands made a movement. The experiment took about 12 minutes and contained 240 trials of which 48 were catch trials. The practice phase consisted of 10 trials.

Data Analysis. The analysis of Experiment 5 was identical to the analysis of Experiment 3. The random effect structure of the linear mixed effects model consisted of a random intercept. We did not include catch trials in the analysis (M_{RT} = 424, SD_{RT} = 38.63,

M_{ERR} = 5.53%). Furthermore, we excluded trials without a response (0.01%), trials with a RT faster than 100 ms (0.05%), error trials (3.90%), and trials with a RT that deviated from the participant's mean by more than 3 *SD* (1.41%). The error data was not analyzed but is presented in Supplementary Material (Figure S2). There was no indication of a speed-accuracy trade-off in the data.

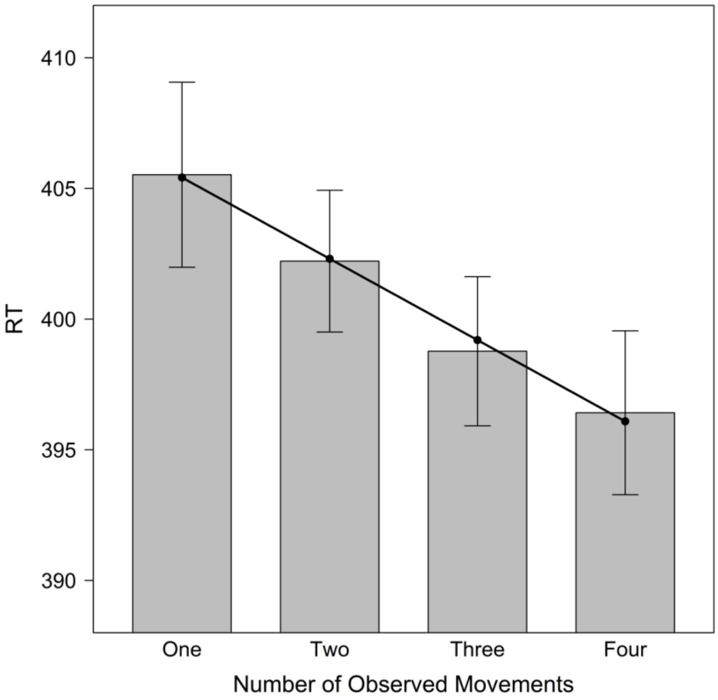

Figure 6. RT results (ms) of Experiment 5. The fit line shows the model fit of the additive model. The error bars depict 95% confidence intervals corrected for within-subject designs according to Morey (2008).

Results and Discussion

The linear mixed effects model revealed a significant main effect of number, *t*(8385) = -4.69, β = -3.11, *95% CI* = [-4.41, -1.81], *p* < .001, indicating that RTs decreased as the number of congruent movements increased. In line with Experiment 3, the additive model further showed that group size had a linear influence on RTs (Figure 6). This supports the hypothesis that participants in Experiments 3 and 4 did not use the observed hand movements as a response cue but instead responded to the symbolic cue. That is, there were no stimulus movements to respond to in 20% of the trials. Furthermore, even in the other trials, it could not be predicted which hand would make a movement. These factors made the hand movements an unreliable response cue and therefore made it unlikely that participants used an imitation strategy. In Experiment 6, we aimed to replicate Experiment 5 using the same stimulus setup as Experiment 2. That is, we replicated Experiment 5 with a setup in which the white border between the four hands was removed.

Experiment 6

Method

Participants. The sample of Experiment 6 consisted of 50 participants (38 female, M_{age} = 20.78, SD_{age} = 4.10). Participants were discarded if their RT or ER exceeded the sample mean by more than 3 *SD*. As a consequence, one participant with an ER of 30.38% and another participant with an ER of 21.55% were excluded from the analyses. This resulted in a final sample of 48 participants (36 female, M_{age} = 20.83, SD_{age} = 4.16). All participants were right-handed and had good or corrected vision. A reward of 5 euro or partial course credit was given in return for participation.

Stimuli, Task, Apparatus, and Procedure. The method of Experiment 6 was identical to the method of Experiment 4, except that we removed the white border between the four stimulus hands as in Experiment 2 (Figure 1b).

Data Analysis. The analysis of Experiment 6 was identical to Experiment 3. As in Experiment 5, catch trials were not included in the analysis (M_{RT} = 420, SD_{RT} = 39.49, M_{ERR}

= 7.58%). Furthermore, we excluded trials without a response (0.25%), trials with a RT faster than 100 ms (0.15%), error trials (4.38%), and trials with a RT that deviated from the participant's mean by more than 3 *SD* (1.37%). The error data was not analyzed but is displayed in Supplementary Material (Figure S2). There was no indication of a speed-accuracy trade-off.

Results and Discussion

The linear mixed effects model yielded a significant main effect of number, $t(8695) = -6.28$, $\beta = -4.56$, *95% CI* = [-5.98, -3.14], $p < .001$, indicating that RTs decreased as the number of congruent observed movements increased. The additive model furthermore revealed a consistent decrease in RTs as a function of group size (Figure 7). In line with Experiment 5, Experiment 6 thus suggests that the linear RT curve obtained in Experiments 3 and 4 was not attributable to an imitation strategy because Experiments 5 and 6 found a similar curve when this strategy was discouraged with the inclusion of catch trials. Nevertheless, it remains possible that catch trials did not suffice to discourage the adoption of an imitation strategy. Importantly, this hypothesis assumes that the use of an imitation strategy should result in a data pattern that is similar to the pattern observed in Experiment 3. To address this possibility, we conducted a seventh experiment in which participants responded by imitating the moving hands. If this experiment yields a different pattern of results, this would provide strong evidence against the hypothesis that participants used an imitation strategy when no incongruent trials were included.

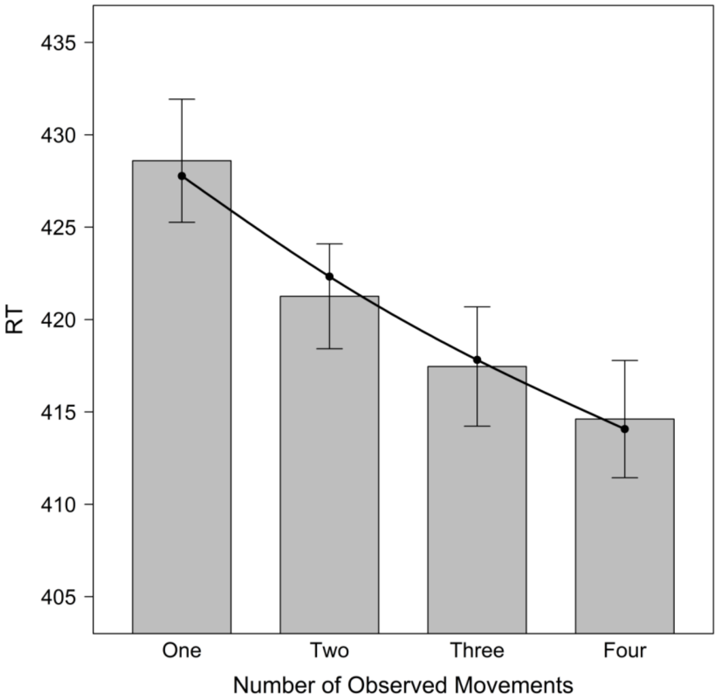

Figure 7. RT results (ms) of Experiment 6. The fit line shows the model fit of the additive model. The error bars depict 95% confidence intervals corrected for within-subject designs according to Morey (2008).

Experiment 7

Method

Participants. A sample of 49 participants was recruited for Experiment 7 (34 female, M_{age} = 18.78, SD_{age} = 1.26). Participants were excluded if their RT or ER exceeded the sample mean by more than 3 *SD*. One participant with a RT of 681 ms and another participant with an ER of 19.64% were excluded from the analyses. As a result, the final sample consisted of 47 participants (34 female, M_{age} = 18.75, SD_{age} = 1.28). All participants were right-handed and had good or corrected vision. Partial course credit was given in return for participation.

Stimuli, Task, Apparatus, and Procedure. The method of Experiment 7 was identical to the method of Experiment 3, except that the letter X was presented on each trial instead of the letter W or P. Participants were instructed to ignore the X and to imitate the observed hand movements instead.

Data Analysis. The analysis of Experiment 7 was identical to the analysis of Experiment 3. The random effects structure of the linear mixed effects model consisted of a random intercept and a random number slope. To compare Experiments 3 and 7, we fitted a linear mixed effects model with a predictor for number and a between-subject factor for experiment. The random structure of this model consisted of a random intercept and a random number slope. Note that we compared Experiment 7 with Experiment 3 because these two experiments used the same stimuli. Trials without a response (0.06%), trials with a RT faster than 100 ms (0.22%), error trials (3.91%), and trials with a RT that deviated from the participant's mean by more than 3 *SD* (1.60%) were excluded. The error data was not analyzed but is presented in Supplementary Material (Figure S3). There was no indication of a speed-accuracy trade-off.

Results and Discussion

Similar to Experiment 3, the linear mixed effects model revealed a significant effect of number, $t(45.72) = -18.65$, $\beta = -21.34$, *CI 95%* = [-23.58, -19.09], $p < .001$, indicating that RTs decreased as the number of observed movements increased. However, the number slope of Experiment 7 was much stronger than the number slope of Experiment 3. This was confirmed by adding experiment as a between-subject factor to the linear mixed effects model. More specifically, this model revealed a highly significant number x experiment interaction, $t(92.45) = 12.34$, $\beta = 8.65$, *CI 95%* = [7.27, 10.02], $p < .001$, indicating that the number slope was stronger in Experiment 7, $t(92.78) = -21.41$, $\beta = -21.35$, *CI 95%* = [-23.30, -19.39], $p < .001$, than in Experiment 3, $t(92.12) = -4.12$, $\beta = -4.05$, *CI 95%* = [-5.98, -2.12], $p <$

.001. We then fitted an additive model, which revealed that RTs decreased according to an asymptotic curve as number increased (Figure 8). Taken together, the results of Experiment 7 thus indicate that intentional imitation of the stimulus movements resulted in a RT curve that was not only stronger but also qualitatively different than the curve produced in Experiments 3-6. As a result, it is highly unlikely that participants in Experiments 3-6 used an imitation strategy.

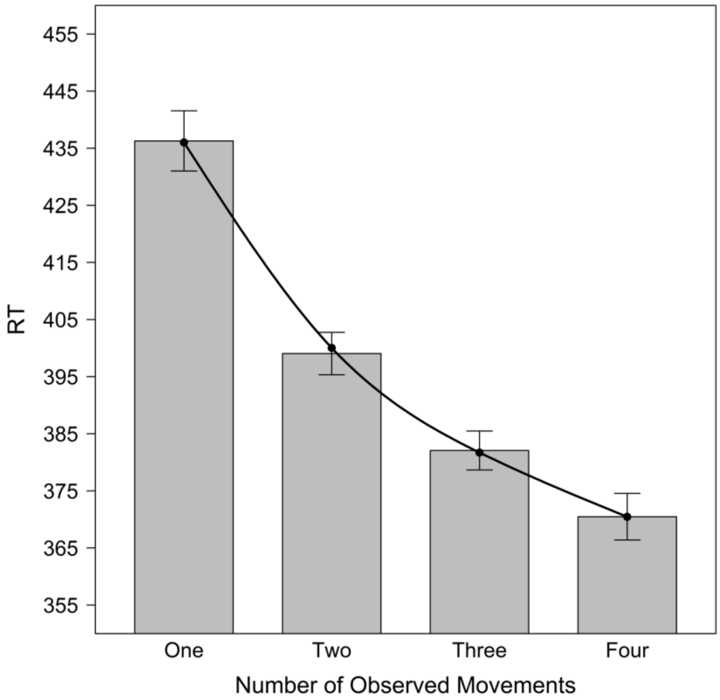

Figure 8. RT results (ms) of Experiment 7. The fit line shows the model fit of the additive model. The error bars depict 95% confidence intervals corrected for within-subject designs according to Morey (2008).

However, it is also important to consider why group size had an asymptotic influence when participants were instructed to imitate the observed movements. It seems unlikely that a strategic regulation of the response threshold was responsible for this pattern because there is no reason to regulate imitation when the task requires an imitative response. However, saturating response functions are often found in visual search paradigms when the number of distractors (Motter & Simoni, 2007; Palmer, 1995; Palmer, Ames, & Lindsey, 1993) or the number of targets (Becker, Anderson, Mortensen, Neufeld, & Neel, 2011) is manipulated. From this perspective, the asymptotic curve reported here could be explained by a visual search strategy in which participants sample one hand after the other in a series until a moving hand is detected (Treisman & Gelade, 1980). For instance, assume that 100 ms is needed to sample one hand. In this case, a serial search strategy would result in an asymptotic response function with an average search time of 250 ms when one movement is shown and an average search time of respectively 167, 125, and 100 ms when two to four movements are shown[4]. To conclude, a steeper and saturating RT curve was obtained when participants had to imitate the observed movements. This is consistent with previous work on visual search and indicates that participants did not use an imitation strategy in Experiments 3-6 when all hands were congruent.

Aggregated Results

Finally, to make optimal use of the large number of experiments presented here, we also analyzed the aggregated results of Experiments 1-2 (N = 89) and Experiments 3-6 (N = 192). To analyze the results of Experiments 1-2, we first fitted a linear mixed effects model with a continuous predictor for number, a within-subjects factor for congruency, and a between-subject factor for experiment. The random effects structure consisted of a random intercept, a random number slope, a random congruency slope, and a random number x

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[4] When two hands make a movement, there is a $\frac{1}{2}$ probability to detect a target after sampling one hand, a $\frac{1}{2} \times \frac{2}{3} = \frac{1}{3}$ probability to detect a target after sampling two hands, and a $\frac{1}{2} \times \frac{1}{3} \times 1 = \frac{1}{6}$ to detect a target after sampling three hands. As a result, the expected search time in this condition is $100 \times \frac{1}{2} + 200 \times \frac{1}{3} + 300 \times \frac{1}{6} = 167$. The same reasoning can be applied to calculate the expected search time in the other conditions.

congruency slope. The results revealed a significant main effect of congruency, *t*(125.46) = -4.53, β = -5.48, *CI 95%* = [-7.85, -3.11], *p* < .001, with slower responses on incongruent trials than on congruent trials, but no main effect of number, *t*(189.97) = 0.91, β = 0.39, *CI 95%* = [-0.45, 1.23], *p* = .363. The number x congruency interaction was also significant, *t*(113.32) = -5.67, β = -2.69, *CI 95%* = [-3.63, -1.76], *p* < .001, showing that RTs on congruent trials decreased, *t*(223.45) = -7.38, β = -3.59, *CI 95%* = [-4.54, -2.63], *p* < .001, and RTs on incongruent trials increased, *t*(97.80) = 7.70, β = 4.70, *CI 95%* = [3.51, 5.90], *p* < .001, as the number of observed movements increased. To explore the shape of the relation between group size and automatic imitation, we then fitted an additive model with a parametric term for congruency, a parametric term for experiment, and a smooth term for number that interacted with congruency. This revealed that RTs followed an asymptotic curve on congruent trials but a linear curve on incongruent trials (Figure 9).

To analyze the results of Experiments 3-6, we first fitted a linear mixed effects model with a continuous predictor for number and a between-subject factor for experiment. The random effects structure consisted of a random intercept and a random number slope. The linear mixed effects model produced a significant effect of number, *t*(191.46) = -11.09, β = -4.32, *CI 95%* = [-5.08, -3.55], *p* < .001, which indicated that RTs decreased as the number of congruent observed movements increased. To investigate how RT decreased with group size, we then fitted an additive model with a parametric term for experiment and a smooth term for number. This model revealed a consistent decrease in RT as a function of group size (Figure 10).

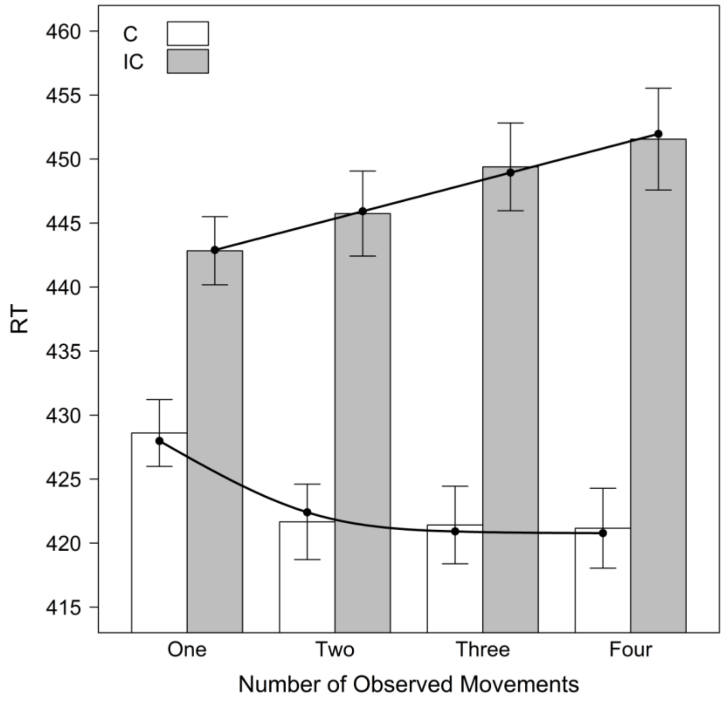

Figure 9. RT results (ms) of Experiment 1 and 2 combined. The fit line shows the model fit of the additive model. The error bars depict 95% confidence intervals corrected for within-subject designs according to Morey (2008). C: congruent; IC: incongruent.

However, to convincingly demonstrate that the congruent RT curve differed between Experiments 1-2 and Experiments 3-6, it has to be shown that these two curves can be distinguished from each other. To this end, we fitted two additive models including only the congruent trials. More specifically, we first fitted an additive model that distinguished between Experiments 1–2 and Experiments 3–6 ("design"), and then compared this model to an additive model that did not distinguish between these two sets of experiments. In other words, we compared a number × design additive model with a number + design additive model. Model fit was quantified with the GCV and the Aikake Information Criterion (AIC). The GCV measures cross-validation performance. The AIC evaluates model likelihood while penalizing model complexity (S. N. Wood, 2006). Similar to the GCV, the AIC protects against overfitting complex models to the data. For both statistics, the model with the lowest score is preferred over the other model (S. N. Wood, 2006). For completeness, we will also report *p*-values. However, these *p*-values are rough approximations and should be interpreted with caution (S. N. Wood, 2006). The comparison of the two additive models revealed that the number × design model provided a better fit than the number + design model (Δ_{GCV} = 1.59, Δ_{AIC} = 14.35, $p < .001$). This shows that there was a qualitative difference between the congruent RT curves of Experiments 1-2 and Experiments 3-6. Moreover, a subsequent response speed comparison confirmed that responses on congruent trials were significantly faster in Experiments 3-6 than in Experiments 1-2, t(184.42) = 3.21, p = .002, d = 0.41. Taken together, this strongly suggests that the asymptote observed in Experiments 1-2 is better explained in terms of strategic control than in terms of a response speed boundary.

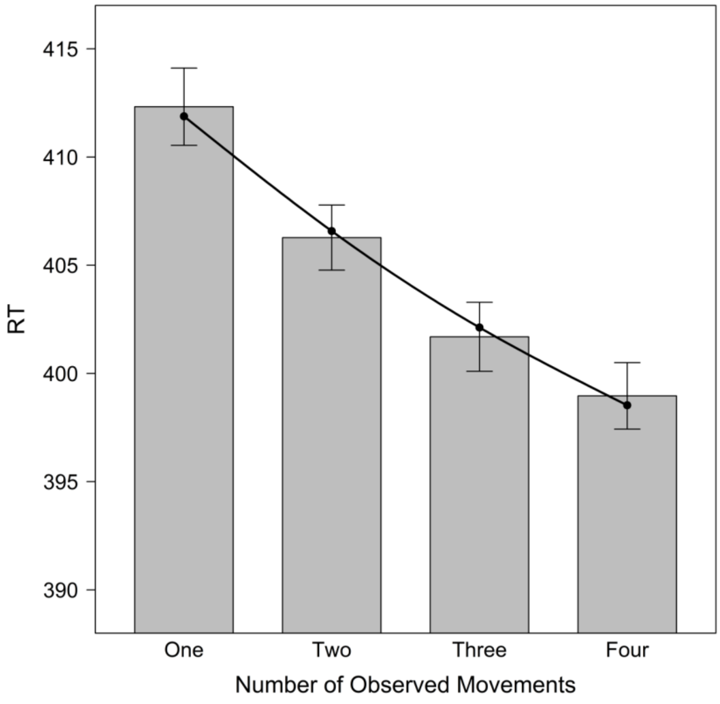

Figure 10. RT results (ms) of Experiment 3 to 6 combined. The fit line shows the model fit of the additive model. The error bars depict confidence intervals corrected for within-subject designs according to Morey (2008).

Spatial Compatiblity

Finally, an important question is whether our results can be explained in terms of spatial processing. Specifically, it could be argued that the index finger movements primed index finger responses because both were leftward movements and that the little finger movements primed little finger responses because both were rightward movements (Catmur & Heyes, 2011; Cracco et al., 2018; Jansson, Wilson, Williams, & Mon-Williams, 2007). To address this question, we made use of the Simon task embedded in our paradigm (Hommel, 2011). That is, our stimulus display included two hands on the left side of the screen and two hands on the right side of the screen (Figure 1). As in the Simon task, this introduces a spatial component, and this component is independent from the imitation component. For example, consider a trial in which participants have to abduct their index finger while the upper left hand abducts its little finger. Such a trial would be spatially congruent (i.e., see left hand, move left finger) but imitatively incongruent (i.e., see little finger, move index finger). By comparing trials in which two hands on the same side of the screen made a movement with trials in which a single hand made a movement, our paradigm can be used to investigate whether spatial compatibility depended on the number of unilateral stimuli.

To test this hypothesis, we conducted an experiment (1, 2, 3, 4, 5, or 6) x spatial congruency (C or IC) x number (1 or 2) repeated measures MANOVA. Experiment 7 was not included because this experiment used a different task. The results revealed a strong main effect of spatial congruency, $F(1, 275) = 204.05$, $p < .001$, $d_z = 0.84$, but no interaction between spatial congruency and number, $F(1, 275) = 1.96$, $p = .163$, $d_z = 0.09$, or between experiment, spatial congruency, and number, $F(5, 275) = 1.79$, $p = .115$, $\eta_p^2 = 0.03$ (Figure 11). This indicates that the spatial effect did not increase when two hands on the same side made a movement compared to when one hand made a movement. This was confirmed by a

Bayesian analysis showing that the data was 4.75 times more likely under the model without the spatial congruency x number interaction than under the model with the spatial congruency x number interaction. Together, this provides strong evidence against the hypothesis that spatial processes can explain the relation between group size and automatic imitation.

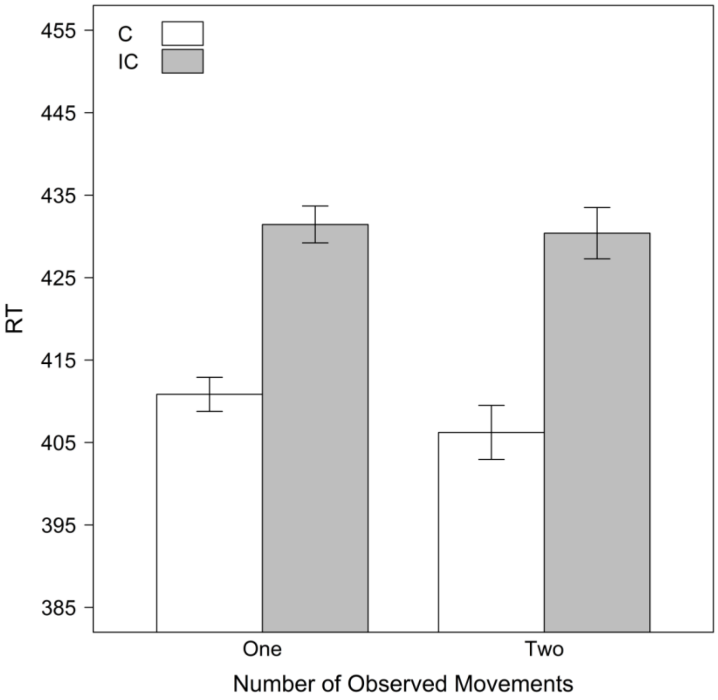

Figure 11. RT results (ms) of the spatial congruency x number analysis across Experiments 3-6. The error bars depict confidence intervals corrected for within-subject designs according to Morey (2008). C: spatially congruent; IC: spatially incongruent.

General Discussion

It is well known from social psychology that larger groups are more contagious (Darley & Latané, 1968; Fischer et al., 2011; Freedman & Birsky, 1980; Gallup et al., 2012; Herrmann et al., 2013; Knowles & Bassett, 1976; Mann, 1977; Milgram et al., 1969) and that the influence of group size on social contagion follows an asymptotic curve (Darley & Latané, 1968; Gallup et al., 2012; Latane, 1981; Milgram et al., 1969). However, the relation between group size and social contagion has so far mainly been approached from a social cognitive perspective (Bond, 2005; MacCoun, 2012). In contrast, the aim of the current study was to investigate the role of sensorimotor processes in social group contagion. In particular, we explored the hypothesis that groups are more contagious simply because their actions provide a stronger trigger to the corresponding motor representation (Cracco & Brass, 2017; Cracco et al., 2015, 2016). To this end, we used a well-established lab-based automatic imitation task that is known to measure shared motor activation with minimal interference from interpretative processes (Cracco et al., 2018; Heyes, 2011). If social contagion has a sensorimotor basis, then automatic imitation should increase with the number of observed agents. Moreover, if sensorimotor processes contribute to the emergence of an asymptote, then automatic imitation should reach an asymptote as well.

Experiments 1 and 2 showed that the relation between group size and automatic imitation was asymptotic on congruent trials but linear on incongruent trials. In contrast, automatic imitation on congruent trials increased proportionally with group size in the absence of incongruent trials (Experiments 3-6), and this could not be explained in terms of different response strategies (Experiments 4-7). In line with social contagion research, these results show that automatic imitation saturated as the number of observed agents increased. Furthermore, the finding that automatic imitation no longer saturated when imitative responses facilitated task performance suggests that the asymptote could not be explained by saturating motor activation ("input saturation hypothesis") or by a response speed boundary ("output saturation hypothesis"). Instead, our results point towards a strategic control mechanism that regulates automatic imitation by lowering or raising the response threshold on each trial depending on the number of observed movements.

More specifically, if motor activation increases with group size, then the response threshold has to be adjusted accordingly to prevent premature imitative responses. Because a heightened response threshold leads to slower responses, such a mechanism masks decreases in response speed on congruent trials but strengthens increases in response speed on incongruent trials. This, then, explains why congruent but not incongruent responses reached an asymptote. Moreover, since it is counterproductive to regulate imitative responses when imitation improves task performance, this mechanism can also explain why the relation between group size and automatic imitation no longer saturated when only congruent trials were included. In sum, the combined evidence across seven experiments indicates that automatic imitation increased with group size and that a strategic control mechanism caused imitative responses to saturate when imitation occasionally impaired task performance (Experiments 1 and 2) but not when it always facilitated task performance (Experiments 3 to 7).

Mechanisms of Group Imitation

The finding that automatic imitation increases with group size is consistent with ideomotor theory, which argues that observed movements are represented in the same format as planned movements and for that reason have direct access to the relevant motor programs (Brass et al., 2000; Brass, Bekkering, et al., 2001; Cracco et al., 2018; Prinz, 1997). In particular, it suggests that individuals are able to simultaneously represent the actions of multiple agents in their motor system and that identical actions are mapped onto the same motor representation, leading to stronger motor responses (Cracco & Brass, 2017; Cracco et al., 2015, 2016). Importantly, this mechanism implies that the relation between group size and automatic imitation should depend on whether multiple identical or multiple different movements were observed. In particular, it assumes that each separate movement activates a distinct motor representation. This means that, in contrast to multiple identical movements, multiple different movements should not cause an increase in automatic imitation. In line with this hypothesis, we have shown in previous work that seeing two different movements does not produce a discernable imitation effect (Cracco et al., 2015). Given that the condition with two different movements was a condition in which participants observed one congruent and one incongruent movement, this suggests that motor simulation of both movements caused a concurrent facilitation and interference effect that cancelled out each other.

Nevertheless, a potential alternative explanation could be that the influence of group size was established over the course of many trials rather than within the context of a single trial. That is, if participants randomly represented one moving or one non-moving hand on each trial, then automatic imitation is expected to increase with the number stimulus movements because the likelihood to sample a moving hand from the combined pool of moving and non-moving hands also increases with the number of stimulus movements. However, we recently addressed this hypothesis in a study where we measured automatic imitation of two hands while participants attended to, in one experiment, or imitated, in a second experiment, the actions of one of the two hands (Cracco & Brass, 2017). The results showed that responses were influenced by the actions of the non-attended or non-imitated hand even though the motor system was already occupied with processing the actions of the target hand. This indicates, in other words, that multiple observed actions can be represented at the same time in the motor system.

Furthermore, the random sampling account is inconsistent with the pattern of results obtained throughout the different experiments. For example, it cannot explain why group size in Experiments 1 and 2 had a saturating influence on congruent trials but a linear influence on incongruent trials. Although it could be argued that the asymptote on congruent trials was caused by a response speed boundary, this cannot explain why the asymptote disappeared when only congruent trials were included. Indeed, there is no need for a strategic control mechanism if participants are unable to process multiple movements at the same time. Moreover, it is difficult to see from a random sampling perspective why automatic imitation also increased with group size in Experiment 4 when the hands were always congruent and participants could predict which hand would make a movement. That is, it seems unlikely that participants also sampled locations where no movement could occur in this situation. Thus, taken together, a likelihood mechanism is inconsistent with both previous research and with the results of the current study. Instead, the data support the hypothesis that participants simulated multiple observed actions at the same time in their motor system.

Another concern could be that all hands were oriented in the same direction. In contrast, in naturalistic situations, different agents tend to be oriented in different directions. However, recent meta-analytic work has revealed that orientation does not modulate automatic imitation (Cracco et al., 2018), which is presumably caused by extensive exposure to the actions of others from various viewpoints (Cracco et al., 2018), and is consistent with evidence that object representations are orientation invariant as well (Harris & Dux, 2005). The notion that orientation does not influence the relation between group size and automatic imitation is further supported by previous work in which two identical observed actions were found to produce a stronger motor trigger than a single observed action regardless of whether the actions were presented in a third- (Cracco et al., 2015) or first-person perspective (Cracco et al., 2016).

Finally, it is interesting to discuss how automatic imitation might develop when the group grows beyond four individuals. Although there was no sign of a floor or ceiling effect in the current study, response speed inevitably has to reach an asymptote also when no imitative control is required. As a result, automatic imitation can be expected to saturate on both congruent and incongruent trials when the number of agents is increased further. However, it is also possible that automatic imitation of large groups involves different processes than automatic imitation of small groups. For example, research on face perception has shown that observers do not process each individual face when they see a group of faces but instead compute the average face across all faces (Haberman & Whitney, 2007, 2009). In the same vein, it was recently demonstrated that observers can rapidly extract the ratio of males to females from a set of faces (Alt, Goodale, Lick, & Johnson, 2017). Albeit speculative, similar sampling mechanisms might also be involved in action perception when the number of observed actions exceeds the processing capacity of the system. From this perspective, automatic imitation of small groups could be stronger than automatic imitation of large groups because observers no longer represent each individual action but instead represent the average action.

Mechanisms of Strategic Response Threshold Regulation

Apart from the mechanisms involved in the imitation of multiple agents, an important question is also what mechanisms caused automatic imitation to saturate on congruent trials but not on incongruent trials. As stated above, our data suggests that strategic regulation of the response threshold was responsible for this pattern. The ability to lower and raise the response threshold is considered a hallmark of cognitive control because it allows individuals to delay action selection so that premature responses can be overruled by more deliberate responses (Bogacz, Wagenmakers, Forstmann, & Nieuwenhuis, 2010; Frank, 2006; Munakata et al., 2011; Wiecki & Frank, 2013). Furthermore, it is well known that cognitive control is sensitive to contextual demands such as time pressure (Forstmann et al., 2008; van Veen, Krug, & Carter, 2008) and the proportion of congruent relative to incongruent trials (Bugg & Crump, 2012; Ridderinkhof, 2002). As such, a strategic control mechanism can explain not only why responses reached an asymptote on congruent trials but also why this asymptote disappeared in the absence of incongruent trials.

Nevertheless, it should be noted that a trial-by-trial strategic regulation mechanism rests on two important assumptions. A first assumption is that cognitive control can modulate responses within the context of a single trial. While this goes against traditional “slow” accounts of cognitive control (Botvinick et al., 2001), recent studies indicate that control is implemented not only between but also within trials (Janssens et al., 2017, 2016). For example, one study found that reward cues presented together with the target stimulus can modulate responses to that stimulus by increasing cognitive control (Janssens et al., 2016). A second assumption is that the number of stimulus movements can quickly be extracted before a response is initiated. This is supported by evidence that individuals immediately get a sense of numerosity when looking at visual displays (Anobile, Cicchini, & Burr, 2016; Burr & Ross, 2008; Harvey & Dumoulin, 2017; Harvey, Klein, Petridou, & Dumoulin, 2013; Piazza, Izard, Pinel, Le Bihan, & Dehaene, 2004). Therefore, based on this, we propose that participants in the current experiments rapidly estimated the number of stimulus movements and then used this information to regulate their response threshold before a response was initiated.

Implications for Social Group Contagion

The results of the current study show that automatic imitation increases with group size, and that this relation follows an asymptotic curve on congruent trials. This pattern closely matches previous research on social imitation (Darley & Latané, 1968; Gallup et al., 2012; Latane, 1981; Milgram et al., 1969), thus supporting the hypothesis that not only social cognitive but also sensorimotor processes contribute to social group contagion (Cracco & Brass, 2017; Cracco et al., 2015, 2016; Raafat et al., 2009). For example, the current study suggests that pedestrians in the study of Milgram et al. (1969) might have been more likely to imitate larger groups of confederates because larger groups provided a stronger motor trigger than smaller groups. Likewise, but more speculative, the asymptote in the relation between group size and social contagion could be explained by strategic regulation of the response threshold. Interestingly, this interpretation fits well with the notion that interpretative processes may serve a role in social imitation at later stages of processing (Cracco et al., 2015, 2016). In particular, a heightened response threshold stops premature responses and therefore allows cognitive processes to influence whether or not to act on external triggers (Bogacz et al., 2010; Frank, 2006; Munakata et al., 2011; Wiecki & Frank, 2013). From this view, social group contagion is best explained as an interaction between sensorimotor and interpretative processes that determine whether or not we align our behavior with others.

Finally, it is important to note that not all social group processes can be explained in terms of shared motor activation. For example, research on bystander apathy has shown that individuals are less likely to help a person in distress when the number of passive bystanders increases (Darley & Latané, 1968; Fischer et al., 2011). Likewise, research on emotional contagion suggests that emotional states spread more widely in large groups than in small groups (Du, Fan, & Feng, 2014). Since there is often not much to imitate in these situations, it is not clear how shared motor activation could explain these effects. However, it is important to note in this respect that shared representations have also been reported outside of the sensorimotor domain (Keysers & Gazzola, 2006). In particular, it has been argued that the brain uses these representations to mirror the behavior and feelings of others as a first step to understand their mental state (Gallese, 2007; Gallese et al., 2004; Keysers & Gazzola, 2006). If shared mental representations are more strongly activated when multiple persons behave similarly, then mental state contagion could explain why individuals are less inclined to help when the number of passive bystanders increases. In support, recent neuroimaging work on the bystander effect found that motor cortex activity decreased as the number of passive bystanders increased even though participants were not able to intervene themselves (Hortensius & De Gelder, 2014). This suggests that participants automatically embodied the bystanders' mental state, causing them to inhibit motor responses.

Conclusion

To conclude, the present study investigated the role of sensorimotor processes in social group contagion with an automatic imitation task that minimized the involvement of interpretative processes. Experiments 1 and 2 showed that group size had an asymptotic influence on congruent trials but a linear influence on incongruent trials. Experiments 3 to 7 then showed that the effect of group size on congruent trials no longer reached an asymptote when no imitative control was needed, namely in the absence of incongruent trials. This suggests that the congruent asymptote was caused by strategic control mechanisms that regulated the response threshold on each trial based on the number of observed movements. Furthermore, the presence of an asymptotic relation between group size and automatic imitation closely matches previous research on social imitation (Darley & Latané, 1968; Gallup et al., 2012; Latane, 1981; Milgram et al., 1969). Together, this indicates that sensorimotor processes contribute to the relation between group size and social contagion.

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Supplementary Material

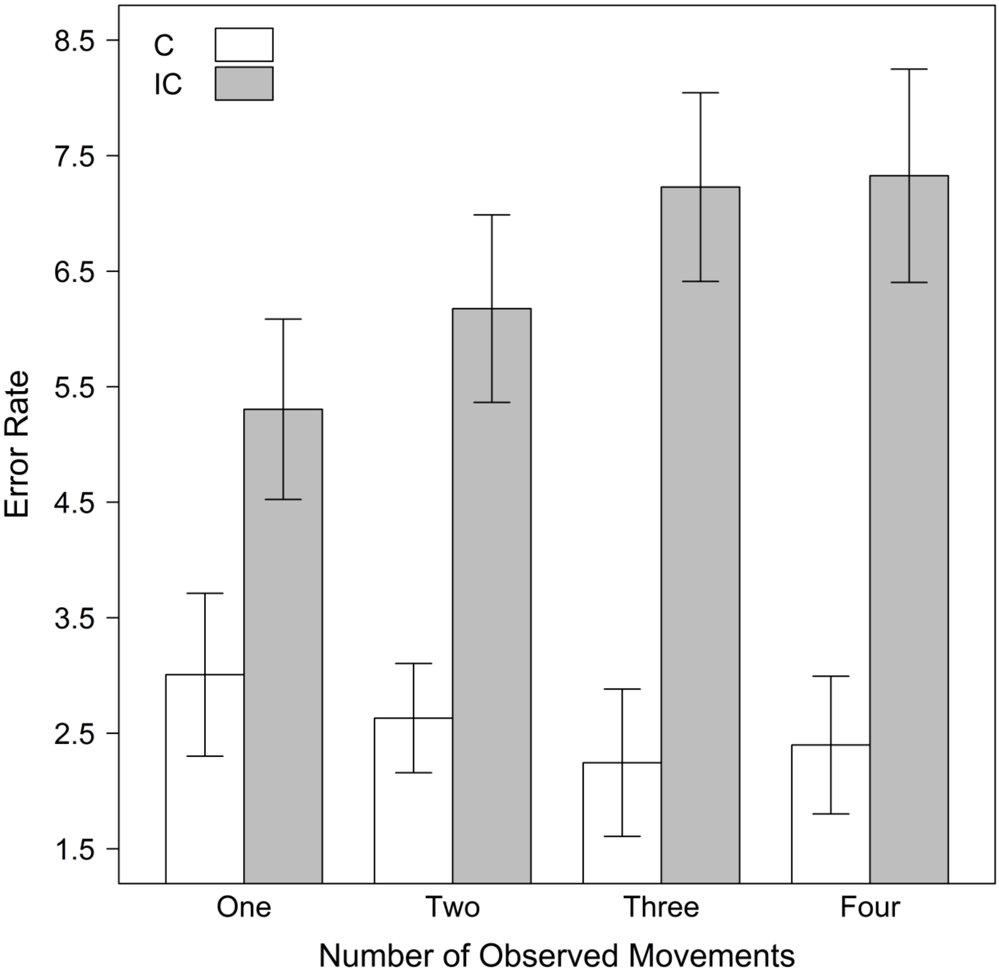

Figure S1. Error rate results (%) of Experiments 1 and 2. The error bars depict 95% confidence intervals corrected for within-subject designs according to Morey (2008). C: congruent; IC: incongruent.

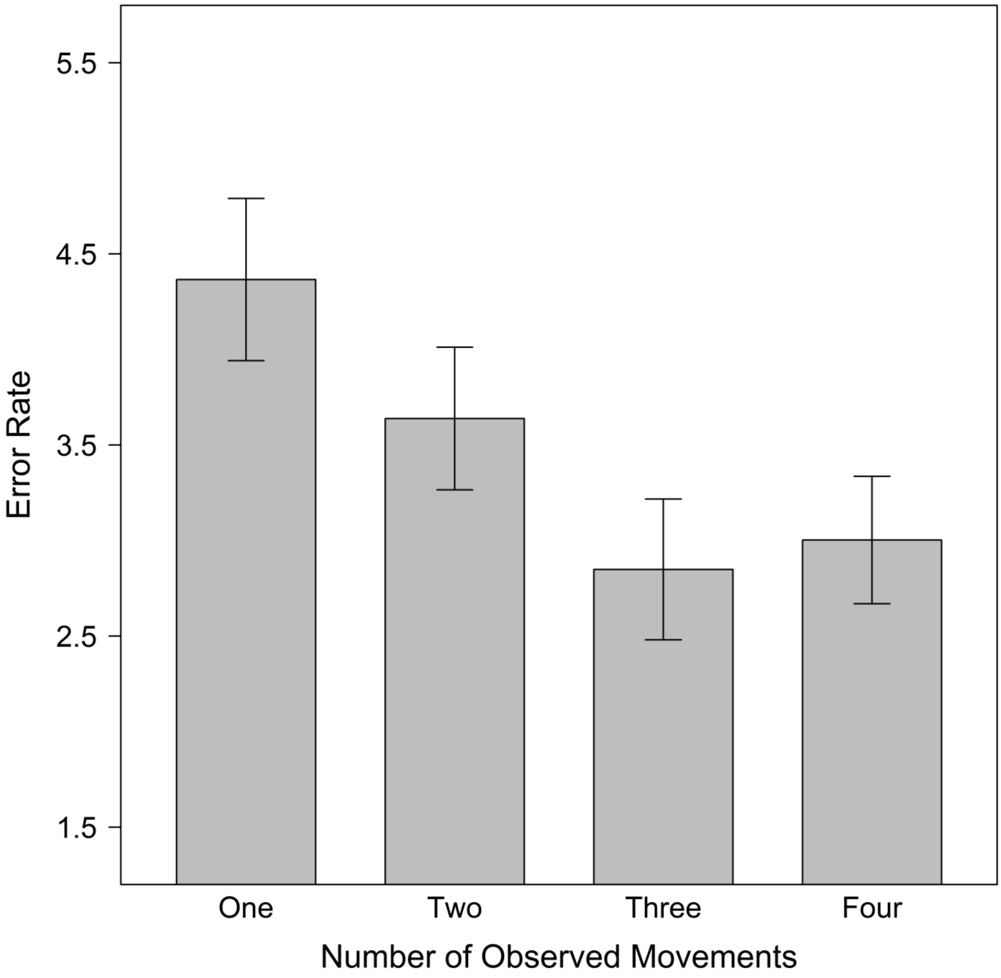

Figure S2. Error rate results (%) of Experiments 3 to 6. The error bars depict 95% confidence intervals corrected for within-subject designs according to Morey (2008).

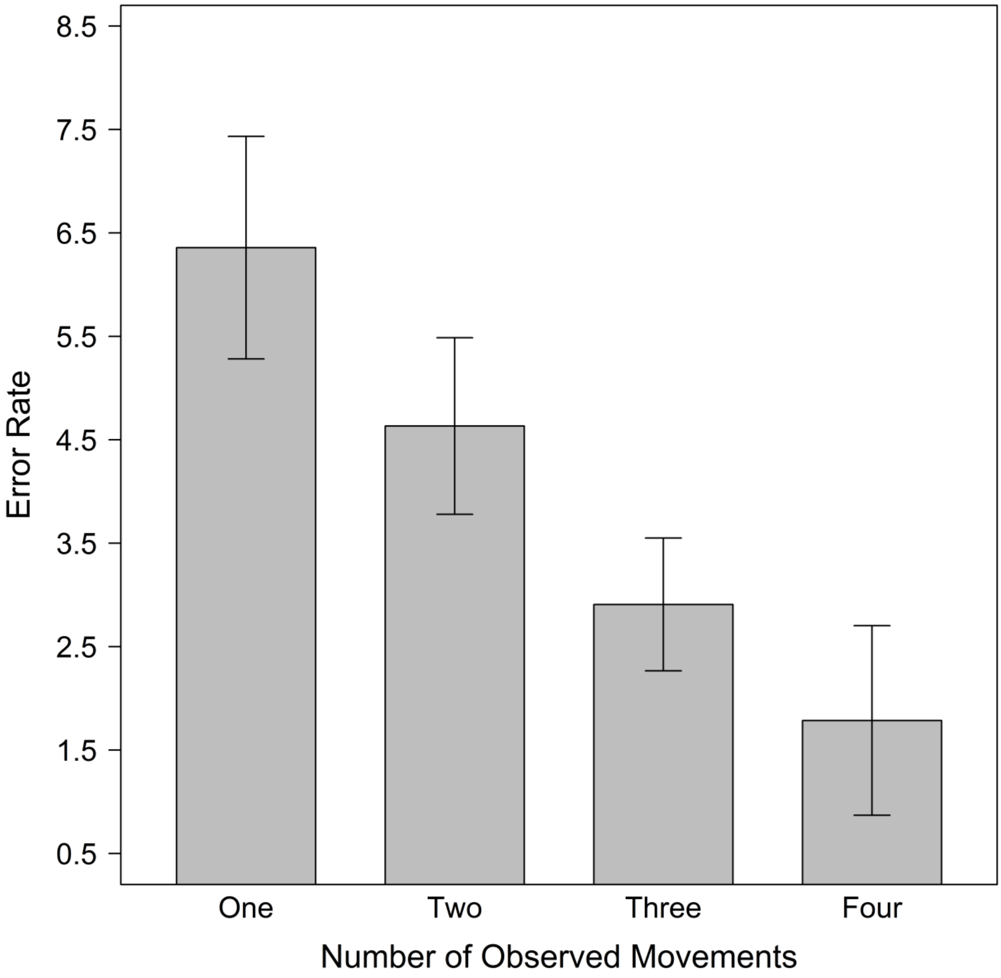

Figure S3. Error rate results (%) of Experiment 7. The error bars depict 95% confidence intervals corrected for within-subject designs according to Morey (2008).

Chapter 6

Motor Simulation of Multiple Observed Actions[1]

Research has shown that observed actions are represented in the motor system, leading to automatic imitative responses. However, in social life, we often see multiple persons acting together. Here, we explore whether these interactions can be represented in the motor system. In particular, to represent interactions, the motor system has to simultaneously represent multiple observed actions. The current study investigated this possibility using an automatic imitation paradigm with four hands. Experiments 1 and 2 revealed weaker automatic imitation when one hand performed a different action than the other three hands, compared with when three or four hands all performed the same action. Experiment 3 replicated this effect with mutually exclusive actions. These results show that multiple observed actions can be represented simultaneously in the motor system, even when they cannot be executed together. This suggests that motor simulation contributes to the representation of social interaction.

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[1] Cracco, E., & Brass, M. (submitted). Motor Simulation of Multiple Observed Actions.

Introduction

Social cognition crucially requires us to interpret and respond to the actions of others. However, it is often difficult to predict from visual input alone how an action will unfold (Brass & Heyes, 2005). Therefore, it has been proposed that we represent observed actions by simulating them in our own motor system (Prinz, 1997), and that this allows us to predict the course and outcome of those actions (Wilson & Knoblich, 2005). Supporting motor simulation, there is now strong evidence that people tend to imitate each other (Chartrand & Lakin, 2013; Cracco et al., 2018). For example, research on automatic imitation has demonstrated that responses to symbolic stimuli are facilitated by congruent and impeded by incongruent observed actions (Brass et al., 2000; Stürmer, Aschersleben, & Prinz, 2000). Similarly, neuroscientific research has shown that action observation and action execution share activation in the motor system of the brain (Gazzola & Keysers, 2009; Molenberghs, Cunnington, & Mattingley, 2012).

However, social cognition requires us not only to represent isolated actions but also to represent social interactions between two or more persons. Recently, it was proposed that social interactions might be represented by simultaneously simulating multiple observed actions in the motor system (Quadflieg & Koldewyn, 2017; Quadflieg & Penton-Voak, 2017). Yet, this hypothesis is currently speculative because previous research has largely focused on situations involving a single agent. Therefore, to address this issue, recent work has started to explore motor simulation in multi-agent settings (Cracco & Brass, 2017, 2018, Cracco, De Coster, Andres, & Brass, 2015, 2016; Ramenzoni, Sebanz, & Knoblich, 2014; Tsai, Sebanz, & Knoblich, 2011). In particular, this work has shown that two hands performing the same action produce stronger automatic imitation (Cracco & Brass, 2017, 2018; Cracco et al., 2015) and corticospinal excitability (Cracco et al., 2016) than one hand performing a single action, indicating that both actions were represented at the same time in the motor system.

Nevertheless, two identical observed actions might still be represented as a single action. Therefore, a fundamental question is whether the motor system can also represent two different observed actions. Indeed, interacting individuals tend to perform different actions, and these actions might even be mutually exclusive in terms of motor execution. As a result, interaction simulation crucially requires observers to simultaneously represent multiple different actions in their motor system (Quadflieg & Koldewyn, 2017; Quadflieg & Penton-Voak, 2017). To date, only one study has looked at motor simulation of different actions (Cracco et al., 2015). The results revealed that two hands performing two different actions did not produce any automatic imitation. Because this corresponded to a condition with one congruent and one incongruent observed action, it was argued that both observed actions were represented simultaneously, and that this led to a concurrent facilitation and interference effect that canceled out each other. However, a likely alternative interpretation could also be that neither action was represented when the hands performed two different actions.

Therefore, to better understand the role of motor simulation in interaction representation, the current study aimed to investigate whether two different observed actions can be simulated at the same time in the motor system, and whether this depends on the extent to which these actions violate motor constraints. To this end, three experiments measured automatic imitation while participants observed three hands performing one action ("THREE"), four hands performing one action ("FOUR"), or three hands performing one action and one hand performing a different action ("THREE-ONE"). Previous research has revealed that up to four identical actions can be represented using this paradigm (Cracco & Brass, 2018). If two different actions can be represented as well, automatic imitation should be reduced in the THREE-ONE condition compared with the THREE and FOUR conditions because the fourth hand then counteracts the other three hands. To explore the role of motor constraints, Experiments 1 and 2 used two actions that could be executed at the same time (“mutually compatible”), whereas Experiment 3 used two actions that could not be executed at the same time (“mutually exclusive”). If motor simulation of different actions is restricted by motor constraints, the same pattern should not be observed when the hands perform mutually exclusive actions.

Experiment 1

Participants

Experiments 1 and 2 aimed to test 50 participants, based on our previous research (Cracco & Brass, 2017, 2018). A sample of 50 participants provides us with 93% power to detect medium-sized effects of $d_z = 0.50$. However, due to cancellations, Experiment 1 contained 48 individuals who were paid 5 euro in exchange for participation. Three participants with a reaction time (RT) or error rate (ER) exceeding the sample mean by more than 3 SD were excluded. The final sample thus consisted of 45 participants (36 female, $M_{\text{age}} = 23.67$, $SD_{\text{age}} = 5.16$). Participants in all experiments were right-handed, had normal or corrected-to-normal vision, and signed an informed consent before the start of the experiment.

Method

The experiment started with a practice phase of 12 trials, followed by an experimental phase of 240 trials divided into four blocks. Stimuli consisted of four hands abducting the index finger, abducting the little finger, or not moving (Figure 1a). In the “THREE” condition, three hands moved the same finger and one hand did not move. In the “FOUR” condition, all four hands moved the same finger. Finally, in the “THREE-ONE” condition, three hands moved one finger and the fourth hand moved the other finger.

An illusion of movement was created by presenting a sequence of two pictures. That is, each trial started with a picture of the hands in their neutral position together with a fixation cross in the center of the screen. After 500 ms, this picture was replaced by a picture of the hands in their final position and a letter indicating the expected response. Participants had to abduct their right index finger when W was presented and their right little finger when P was presented. The observed movements could be congruent or incongruent with respect to the instructed response. Automatic imitation in this paradigm is operationalized as a congruency effect with slower responses on incongruent trials than on congruent trials. In the THREE-ONE condition, a trial was coded as congruent when the majority of the hands were congruent and as incongruent when the majority of the hands were incongruent. Participants had 2,000 ms to respond following the presentation of the imperative cue. Responses were registered with an optical sensor box and were followed by a black screen for 1,000 ms.

All trials of the number (THREE, FOUR, or THREE-FOUR) x congruency (congruent or incongruent) design were presented randomly with the restriction that the same cue could not appear more than four times in a row. The RT data was analyzed with a repeated measures MANOVA. Prior to analysis, we removed trials without a response (0.10%), trials with an RT faster than 100 ms (0.02%), error trials (3.98%), and trials with an RT deviating more than 3 *SD* from the participant’s mean (1.35%). The ER data will not be reported, but there was no sign of a speed-accuracy trade-off. This is supported by the presence of a positive correlation between the RT and ER congruency effect, $r = .37$, $p = .012$. The stimuli, code, data, and analyses from all experiments are available at the Open Science Framework: https://osf.io/8xpc2/?view_only=bcdda96a9b4f4165a572c9867fbb26df.

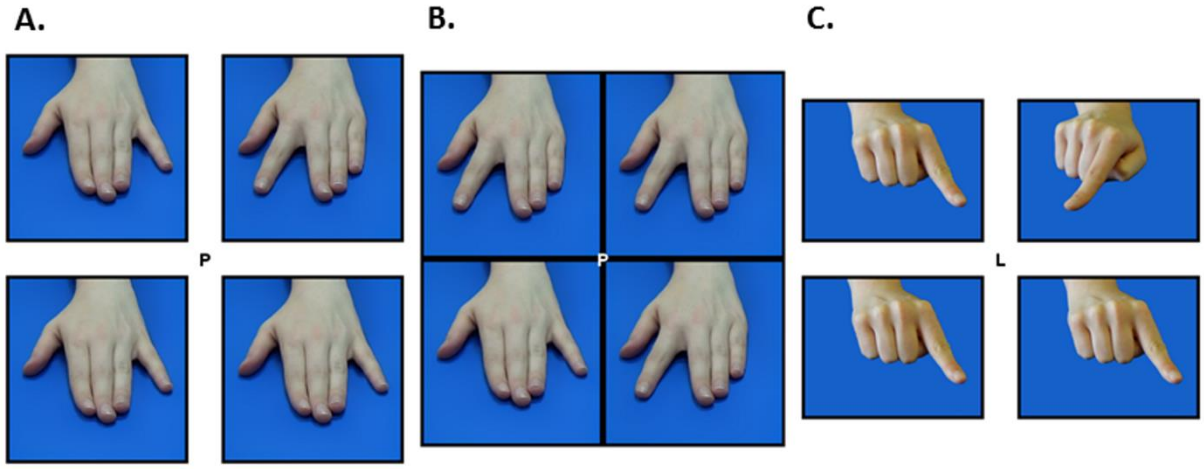

Figure 1. Examples of the stimuli used in (a) Experiment 1, (b) Experiment 2, and (c) Experiment 3.

Results and Discussion

The results revealed a main effect of congruency, $F(1, 44) = 56.07$, $p < .001$, $d_z = 1.12$, with faster RTs on congruent trials than on incongruent trials, but no main effect of number, $F(2, 43) = 0.30$, $p = .741$, $\eta_p^2 = .01$. As predicted, there was a number x congruency interaction, $F(2, 43) = 3.47$, $p = .042$, $\eta_p^2 = .14$. Planned comparisons showed that the congruency effect was smaller in the THREE-ONE condition than in the THREE, $t(44) = -2.10$, $p = .041$, $d_z = 0.31$, and FOUR, $t(44) = -2.56$, $p = .014$, $d_z = 0.38$, conditions. However, there was no significant difference between the THREE and FOUR condition, $t(44) = -0.65$, $p = .520$, $d_z = 0.10$ (Figure 2).

In sum, Experiment 1 found reduced automatic imitation in the THREE-ONE condition compared with the THREE or FOUR condition. This indicates that at least two different observed actions can be represented at the same time in the motor system. However, because the number x congruency interaction was only just significant, we decided to replicate Experiment 1. Experiment 2 was identical to Experiment 1 with the exception that we removed the white border between the four stimulus hands. Previous research has shown that automatic imitation is stronger when the imperative cue is located close to the stimulus movements (Bach, Peatfield, & Tipper, 2007; Cracco et al., 2018; Cracco & Brass, 2017). Therefore, we reasoned that the adjusted setup would lead to stronger automatic imitation, and that this would increase the likelihood to replicate Experiment 1 (see also Cracco & Brass, 2018).

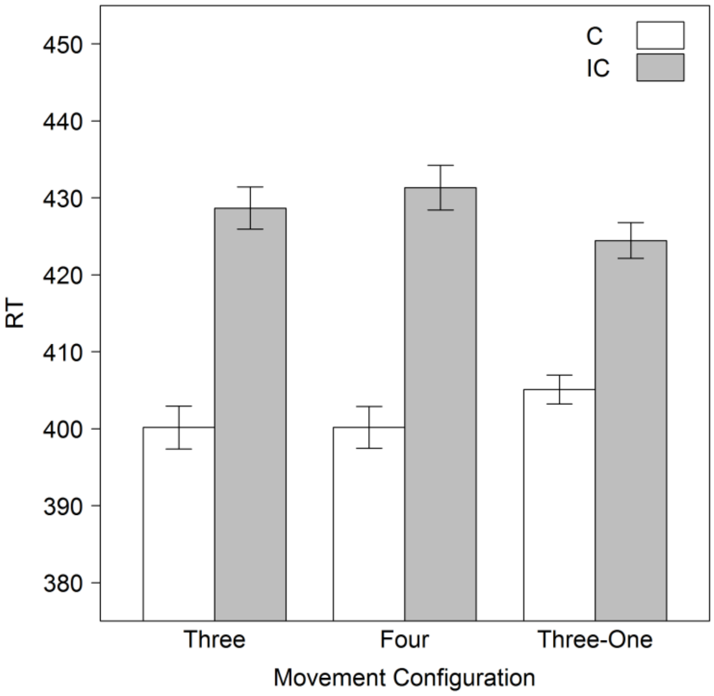

Figure 2. Results of the number x congruency analysis of Experiment 1. Error bars are standard errors of the mean (SEMs) corrected for within-subject designs (Morey, 2008). C: congruent trials; IC: incongruent trials.

Experiment 2

Participants

Similar to Experiment 1, 50 subjects participated in Experiment 2. However, we removed three participants with an RT or ER exceeding the sample mean by more than 3 *SD*.

As a result, the final sample consisted of 47 participants (36 female, $M_{\text{age}} = 20.77$, $SD_{\text{age}} = 4.10$).

Method

The method of Experiment 2 was identical to Experiment 1, except that there was no longer a white border between the four hands (Figure 1b). Prior to analysis, we removed trials without a response (0.04%), trials with an RT faster than 100 ms (0.05%), error trials (4.44%), and trials with an RT deviating more than 3 *SD* from the participant's mean (1.28%). The ER data will not be reported, but there was no sign of a speed-accuracy trade-off. Instead, there was a positive correlation between the RT and ER congruency effect, $r = .33$, $p = .024$.

Results and Discussion

In line with Experiment 1, the results revealed a main effect of congruency, $F(1, 46) = 67.37$, $p < .001$, $d_z = 1.20$, with faster responses on congruent trials than on incongruent trials, but no main effect of number, $F(2, 45) = 0.58$, $p = .562$, $\eta_p^2 = .03$. Importantly, the number x congruency interaction was again significant, $F(2, 45) = 5.76$, $p = .006$, $\eta_p^2 = .20$. Planned comparisons showed that the congruency effect was smaller in the THREE-ONE condition than in the THREE, $t(46) = -2.97$, $p = .005$, $d_z = 0.43$, and FOUR, $t(46) = -3.32$, $p = .002$, $d_z = 0.48$, conditions. However, there was no difference between the congruency effect of the THREE and FOUR conditions, $t(46) = 0.37$, $p = .711$, $d_z = 0.05$ (Figure 3).

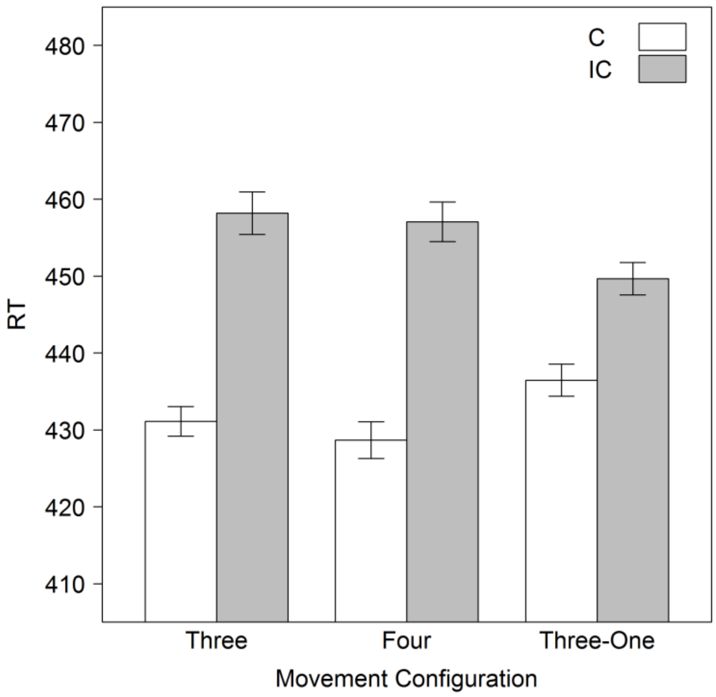

Figure 3. Results of the number x congruency analysis of Experiment 2. Error bars are SEMs corrected for within-subject designs (Morey, 2008). C: congruent trials; IC: incongruent trials.

In sum, Experiment 2 thus replicated Experiment 1. This further strengthens the hypothesis that individuals can simulate multiple different observed actions in parallel. However, is this still true when the observed actions cannot be executed together? That is, it could be that the motor system can only represent two observed actions when they can be combined into a single action. For instance, one hand abducting the index finger and one hand abducting the little finger could be represented as a single hand abducting both the index and little finger. To explore this hypothesis, Experiment 3 used mutually exclusive actions. That is, four hands moved their index finger either to the left or to the right. Because it is impossible to move the same finger in two directions at the same time, this allows us to investigate the degree to which motor simulation of multiple different actions is bound by motor constraints.

Experiment 3

Participants

Experiment 3 tested 70 participants. The sample size was increased because we expected the effects to be smaller for mutually exclusive actions. To determine the sample size, we conducted an a-priori power analysis. This indicated that 70 participants were needed to detect small effects (i.e., $d_z = 0.30$) at $\alpha = 0.05$ with reasonable statistical power (i.e., 70%). However, we removed one participant with an ER exceeding the sample mean by more than 3 *SD*. The final sample thus consisted of 69 participants (58 female, $M_{\text{age}} = 22.12$, $SD_{\text{age}} = 4.38$).

Method

The stimuli in Experiment 3 consisted of four hands moving their index finger either to the left or to the right (Figure 1c). Because it is impossible to move the same finger in two directions at the same time, these movements are mutually exclusive. The visual display[2] and experimental procedure were identical to Experiment 1, except that responses were now recorded using a Mac keyboard. More specifically, participants held down the down arrow key until a response cue (L or R) instructed them to release this key and to press either the left (L) or right (R) arrow key. The RT was the time needed to press the correct key. Prior to analysis, we removed trials without a response (0.00%), trials with an RT faster than 100 ms (0.08%), error trials (4.15%), and trials with an RT deviating more than 3 *SD* from the participant's mean (0.83%). The ER data will not be reported, but there was no sign of a

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[2] The reason why we used the display of Experiment 1 and not Experiment 2 is that, in reality, Experiment 3 was conducted before Experiment 2. The order of the experiments was changed for logical consistency. However, it is notable that removing the white border in Experiment 2 did not increase automatic imitation, suggesting that it did not have an effect.

speed-accuracy trade-off. Instead, there was a positive correlation between the RT and ER congruency effect, $r = .22$, $p = .072$.

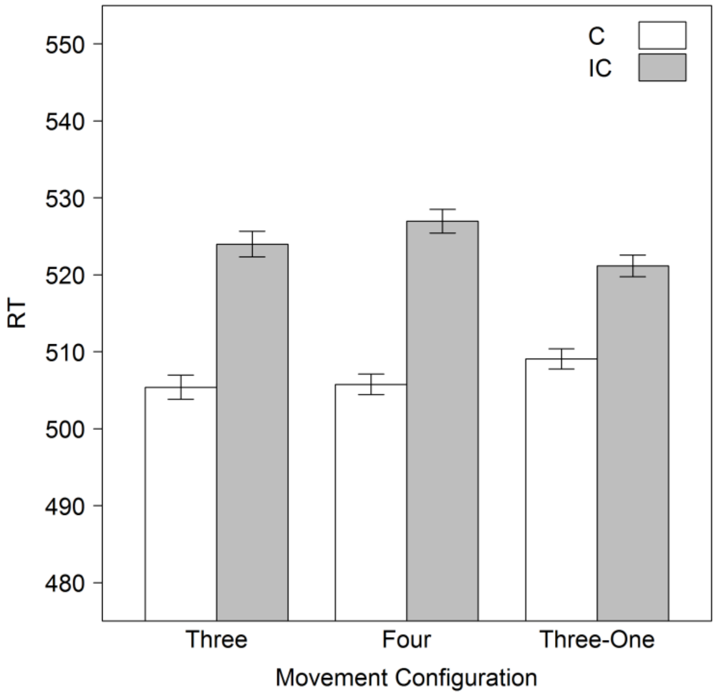

Figure 4. Results of the number x congruency analysis of Experiment 3. Error bars are SEMs corrected for within-subject designs (Morey, 2008). C: congruent trials; IC: incongruent trials.

Results and Discussion

The results revealed a main effect of congruency, $F(1, 68) = 126.47$, $p < .001$, $d_z = 1.35$, with faster RTs on congruent trials than on incongruent trials, but no main effect of number, $F(2, 67) = 1.09$, $p = .340$, $\eta_p^2 = .03$. In line with Experiments 1-2, the interaction between number and congruency was significant as well, $F(2, 67) = 6.95$, $p = .002$, $\eta_p^2 = .17$. Planned comparisons showed that the congruency effect was smaller in the THREE-ONE condition than in the THREE, $t(68) = -2.12$, $p = .037$, $d_z = 0.26$, and FOUR, $t(68) = -3.70$, $p < .001$, $d_z = 0.45$, conditions. However, the congruency effect did not differ between the

THREE and FOUR conditions, *t*(68) = -0.86, *p* = .394, d_z = 0.10 (Figure 4). In sum, Experiment 3 replicated the results of Experiments 1-2 even though the observed actions were mutually exclusive in terms of motor execution. This indicates that motor simulation of multiple observed actions is not restricted by motor constraints.

General Discussion

Motor simulation allows individuals to represent others' actions in their motor system (Wilson & Knoblich, 2005). However, in social life, we have to represent not only the actions but also the interactions of others. Recently, it was argued that observers might represent interactions between two persons by simulating the actions of both persons in their motor system (Quadflieg & Koldewyn, 2017; Quadflieg & Penton-Voak, 2017). Supporting this hypothesis, previous research has shown that multiple identical observed actions can be simulated at the same time (Cracco & Brass, 2017, 2018, Cracco et al., 2015, 2016). However, identical actions might still be represented as a single action. Therefore, the current study investigated whether two different actions could be simulated as well, and whether this was bound by motor constraints. Using automatic imitation, Experiments 1-2 showed that four hands performing two different actions were simulated simultaneously. Experiment 3 replicated this finding when the two actions were mutually exclusive in terms of motor execution. This indicates that multiple observed actions can be simulated together, even when they cannot be executed together.

Nevertheless, it could also be argued that participants randomly represented one moving or non-moving hand on each trial. In the THREE-ONE condition, this would cause them to imitate the majority of the hands in 75% of the trials and the minority of the hands in 25% of the trials. This, in turn, would likewise result in weaker automatic imitation than in the

THREE or FOUR condition. However, we have recently ruled out random sampling in the context of two agents. More specifically, in a paradigm where we measured automatic imitation of two hands, it was found that directing participants' attention to the movements of a target hand or instructing participants to imitate that hand did not preclude automatic imitation of the non-target hand, showing that automatic imitation was modulated by the number of agents even when at least one action was processed on each trial (Cracco & Brass, 2017). Likewise, using the same stimuli as in the current study, we have shown that automatic imitation increased with the number of identical observed movements even when we only presented the hands making a movement (Cracco & Brass, 2018). Because the random sampling account rests on the assumption that only one action can be represented at a time (Cracco & Brass, 2017), these results provide strong evidence against random sampling and instead point towards simultaneous representation.

Furthermore, it is interesting to note that automatic imitation in the FOUR condition was not stronger than automatic imitation in the THREE condition. This is consistent with recent work in which we investigated how automatic imitation developed as the number of observed actions increased (Cracco & Brass, 2018). In particular, this study showed that automatic imitation initially increased but then reached an asymptote when there were more than two observed actions. Interestingly, further experiments revealed that this pattern was the result of a strategic control mechanism regulating response inhibition based on the number of observed actions in order to prevent overt imitation.

Finally, the current study crucially extends motor simulation research from action representation to interaction representation. In particular, it suggests that motor simulation is involved not only in decoding actions (Wilson & Knoblich, 2005) but also in decoding interactions (Quadflieg & Koldewyn, 2017; Quadflieg & Penton-Voak, 2017). The fact that motor simulation was not bound by bodily constraints furthermore indicates that this mechanism can be used across a wide range of social situations. However, it also raises the question how two actions can be simulated together when they cannot even be executed together. One possibility is that individuals extend their body schema with supernumerary limbs when having to simulate two or more mutually exclusive actions. Supporting this hypothesis, research has shown that people can be made to experience the illusion of owning an additional limb (e.g., Ehrsson, 2009). Lastly, the present study has important implications for joint action (Sebanz, Bekkering, & Knoblich, 2006). Indeed, it is well-known that motor simulation facilitates interpersonal coordination in joint action tasks with two agents (Colling, Knoblich, & Sebanz, 2013; Kourtis, Sebanz, & Knoblich, 2013). In extension, our results suggest that individuals might also use this mechanism to coordinate their actions with multiple co-actors at once, such as when ensemble musicians have to tune their performance to one another (Volpe, D'Ausilio, Badino, Camurri, & Fadiga, 2016).

To conclude, the current study shows that multiple observed actions can be represented at the same time in the motor system, even when this violates bodily constraints. These results suggest that motor simulation might contribute to the representation of social interaction, and provides novel insight into the mechanisms underlying interpersonal coordination in joint action tasks that extend beyond the dyad.

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Chapter 7

Representing Multiple Observed Actions in the Motor System[1]

There is now converging evidence that others' actions are represented in the motor system. However, social cognition requires us not only to represent the actions but also the interactions of others. Therefore, a fundamental question is whether social interactions can be represented in the motor system. To represent interactions, the motor system has to process multiple observed actions at the same time. The current fMRI study investigated this possibility by measuring brain activity from 29 participants while they observed two right hands performing sign language gestures. Three key results were obtained. First, activation in premotor and parietal motor regions was stronger when two hands performed two different gestures than when a single hand performed one gesture. Second, the two individual observed gestures could be decoded simultaneously from activation in both motor regions. Third, observing two different gestures compared with two identical gestures activated brain areas associated with motor conflict, and this activation was correlated with activation in the parietal motor region. Together, these results show that multiple observed actions can be represented at the same time in the motor system. This suggests that mirror processes might contribute to the representation of social interaction.

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[1] Cracco, E., Keysers, C, Clauwaert, A., & Brass, M. (submitted). Representing Multiple Observed Actions in the Motor System.

Introduction

There is accumulating evidence that action observation triggers a corresponding motor representation in the observer (Cracco et al., 2018; Rizzolatti & Sinigaglia, 2010, 2016). For example, animal research has uncovered a subset of motor neurons in the premotor and parietal cortex that fire both when an action is executed and when the same action is observed (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Kilner & Lemon, 2013; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996). This is supported by human research, in which the contribution of motor processes to action observation has been demonstrated across a wide range of methods, including fMRI (Gazzola & Keysers, 2009; Molenberghs, Cunnington, & Mattingley, 2012), TMS (Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995; Naish, Houston-Price, Bremner, & Holmes, 2014), M/EEG (Arnstein, Cui, Keysers, Maurits, & Gazzola, 2011; Fox et al., 2016), and intracranial recording (Babiloni et al., 2016; Mukamel, Ekstrom, Kaplan, Iacoboni, & Fried, 2010). Moreover, this research has revealed that mirror activation is not restricted to seeing actions, but also occurs when hearing action-related sounds (Gazzola, Aziz-Zadeh, & Keysers, 2006; Kohler et al., 2002), or when seeing someone being touched (Keysers et al., 2004), someone in pain (Singer et al., 2004), or someone expressing an emotion (Wicker et al., 2003).

Together, these findings indicate that observers represent the actions, sensations, and emotions of others through simulation in shared neural circuits (Keysers & Gazzola, 2006). Motor simulation, in turn, has been argued to facilitate action perception (Rizzolatti & Sinigaglia, 2010, 2016). In support, neuromodulation and lesion studies have revealed that disrupting sensorimotor brain areas causes subtle yet significant impairments in recognizing and predicting observed actions (Avenanti, Candidi, & Urgesi, 2013; Urgesi, Candidi, & Avenanti, 2014). However, in social life, it is not only important to represent the actions but also the interactions of others (Quadflieg & Koldewyn, 2017; Quadflieg & Penton-Voak, 2017). This raises the fundamental question whether social interactions can be represented in the motor system. Critically, to represent interactions, the motor system has to simultaneously represent multiple observed actions (Quadflieg & Koldewyn, 2017; Quadflieg & Penton-Voak, 2017). Yet, whether this is possible is currently unknown since research has focused almost exclusively on situations in which a single agent is observed.

Preliminary evidence indicates that motor activation is stronger when observing an interaction between two persons than when observing a single person (Aihara, Yamamoto, Mori, Kushiro, & Uehara, 2015; Bucchioni, Cavallo, Ippolito, Marton, & Castiello, 2013; Iacoboni et al., 2004) or two independently acting persons (Centelles, Assaiante, Nazarian, Anton, & Schmitz, 2011; Georgescu et al., 2014). However, it does not necessarily follow from a non-specific increase in motor activation that observers simulated multiple actions. Instead, it has to be shown that the corresponding motor representations were simultaneously activated. To this end, in previous work, we have measured automatic imitation (Cracco & Brass, 2017, 2018; Cracco, De Coster, Andres, & Brass, 2015) and corticospinal excitability (Cracco, De Coster, Andres, & Brass, 2016) while participants observed either a single action or two identical actions. The results revealed action-specific increases in both measures when two identical actions were observed, indicating that both actions concurrently activated the same motor representation. Nevertheless, two identical actions might still be represented as a single action in the motor system. Therefore, a crucial question is whether the motor system can also represent two different actions. Indeed, when watching two interacting individuals, it is rarely the case that their actions can be represented as a single action.

To investigate this, the current study recorded brain activity from 29 participants with fMRI while they performed an action observation task, followed by an action execution task. In the action observation task, participants watched short videos of (5 s) of two right hands repeatedly (4 times) performing one out of three sign language gestures (see Figure 1a and Supplementary Videos). There were four conditions. In the Neutral Condition (N), both hands remained still for the entire duration of the video. In the One Hand Condition (1H), one hand performed a gesture while the other hand remained still. In the Two Hands Identical Condition (2H ID), both hands performed the same gesture. Finally, in the Two Hands Different Condition (2H DIFF), the two hands performed different gestures. To maintain attention, participants had to detect a glitch in the video appearing randomly in one out of seven trials on the left hand, on the right hand, or on both hands. The action observation task was followed by the action execution task. In this task, participants had to squeeze or not squeeze a ball with their left or right hand depending on the color and location of a circle presented on the screen (Figure 1b). The action execution task was included to localize shared voxels (sVx). Shared voxels are voxels that become activated both during action observation and during action execution, and will be used as a proxy for the human mirror neuron system in the current study (Arnstein et al., 2011; Gazzola & Keysers, 2009).

The hypothesis that multiple observed actions can be mirrored in parallel was tested in three ways. First, we compare sVx activation in the 1H condition with sVx activation in the 2H DIFF condition. If two different actions are mirrored simultaneously, this should be visible as stronger sVx activation in the 2H DIFF condition than in the 1H condition (Cracco & Brass, 2017, 2018, Cracco et al., 2015, 2016). Second, we test with multivariate analyses whether both gestures in the 2H DIFF condition can be decoded at the same time from activation in sVx. Finally, we explore the consequences of mirroring multiple different gestures. Specifically, representing two different gestures in the motor system should produce motor conflict because it is impossible to execute two gestures at the same time with a single hand. Importantly, while previous work has established that motor conflict can occur during motor preparation (Botvinick, Braver, Barch, Carter, & Cohen, 2001), the current study is the first to test whether passive action observation of conflicting actions is sufficient to generate motor conflict. That is, we predict stronger activation in brain areas associated with motor conflict when observing two mutually exclusive actions (2H DIFF) compared with observing two mutually compatible actions (2H ID). More precisely, we expect that this contrast will activate the anterior cingulate cortex (ACC), which is at the core of the conflict monitoring network (Botvinick et al., 2001; Botvinick, Cohen, & Carter, 2004; Braver, Barch, Gray, Molfese, & Snyder, 2001; Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004).

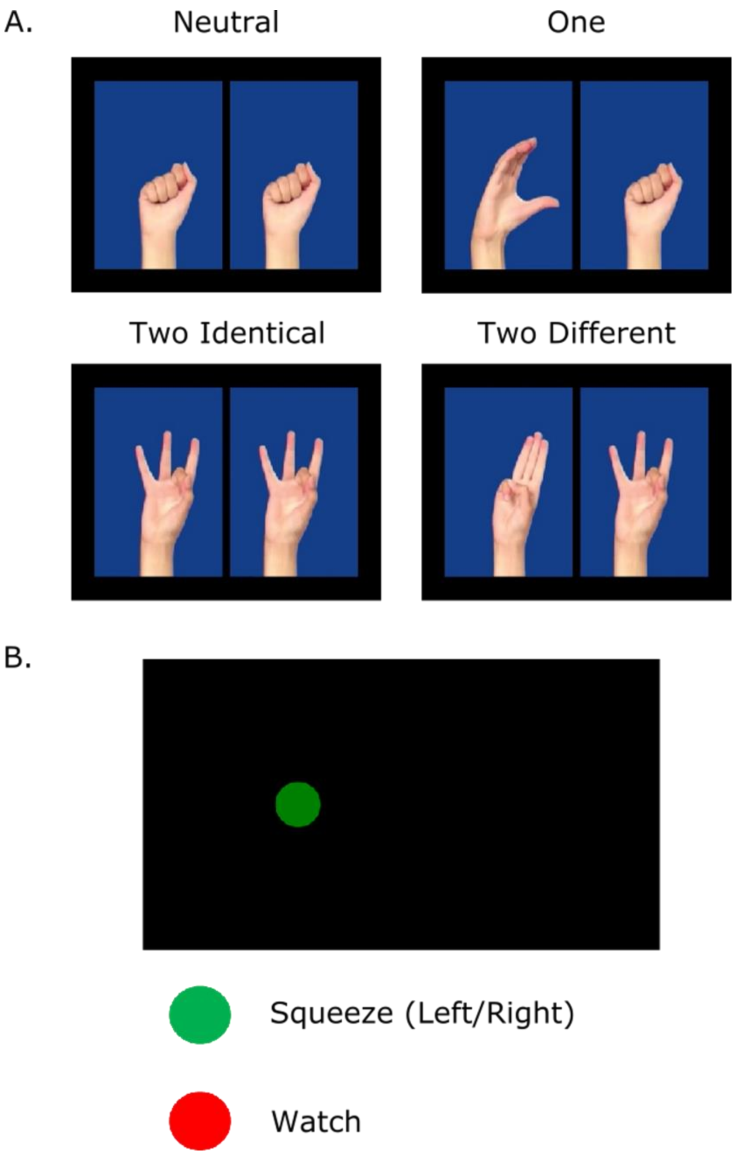

Figure 1. Examples of the stimuli used (a) in the action observation task and (b) in the action execution task. In the action observation task, participants watched short videos of two hands repeatedly performing one out of three possible gestures. The task of participants was to detect a glitch in the video appearing randomly in one out of seven trials. In the action execution task, participants had to either squeeze a bubble wrap ball or look at the screen depending on whether the color of the circle was, respectively, green or red. In case of a green circle, participants had to squeeze the ball each time the circle decreased in size with the hand that corresponded to the location of the circle on the screen.

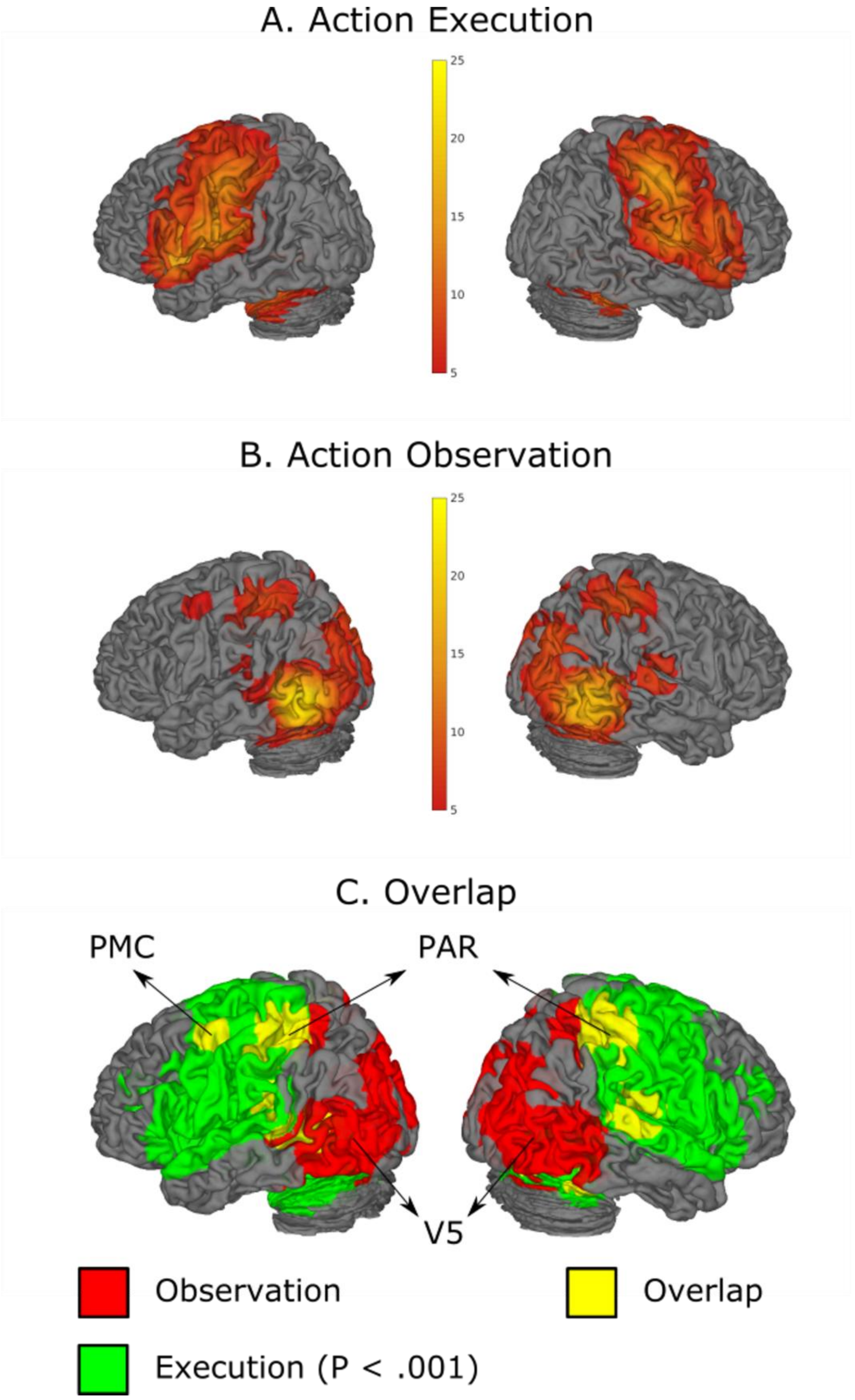

Figure 2. The top panel shows the activation in the action observation task (Observation > Neutral). The middle panel shows the activation in the action execution task (Squeeze > No Squeeze). The bottom panel shows the activation overlap between both tasks. Unless otherwise specified, images were thresholded using a $p < .05$ FWE-corrected threshold. In line with previous work, action execution data was thresholded at $p < .001$ to determine shared voxels (Arnstein et al., 2011).

Results

Shared Voxel Localization

Shared voxel activation was determined by measuring the overlap in brain activation between action observation and action execution. First, to find action execution activation, we calculated the contrast Squeeze > No Squeeze. As can be seen in Figure 2a, this revealed widespread activation in the sensorimotor system, which is similar to what has been found in previous research using this task (Arnstein et al., 2011). Next, to find action observation activation, we compared activation in the N condition with activation in the 1H, 2H ID, and 2H DIFF conditions using the contrast Observation > Neutral (i.e. 0.33 x [1H + 2H ID + 2H DIFF] > N). As expected, action observation produced bilateral activation in the visual cortex around V5, as well as bilateral activation in the inferior parietal cortex, the superior parietal cortex, the postcentral gyrus, and the superior temporal gyrus, and lateralized activation in the left dorsal premotor cortex (Fig 2b). Finally, to localize sVx, we determined the overlap between both tasks. In line with meta-analyses on action observation (Caspers, Zilles, Laird, & Eickhoff, 2010; Molenberghs et al., 2012), this revealed sVx activation in the inferior parietal cortex, the superior parietal cortex, the postcentral gyrus, the superior temporal gyrus, and the dorsal premotor cortex, but not in the visual cortex.

Representing Two Observed Actions Simultaneously

Is There More Activation? To investigate whether two different gestures could be represented at the same time in both the visual and motor system, we analyzed activation in three core regions of the action observation network, namely the visual cortex (V5), the parietal cortex (PAR), and the premotor cortex (PMC). To prevent biasing the analysis toward the 2H conditions, we constructed 5 mm bilateral spheres around the peak coordinate of the conjunction [1H > N] ∩ [2H ID > N] ∩ [2H DIFF > N] in each region and each participant. Furthermore, to secure statistical independence, we used a leave-one-out cross-validation procedure in which the regions-of-interest (ROIs) for each participant were calculated using the data of all participants except that one participant (Esterman, Tamber-Rosenau, Chiu, & Yantis, 2010). Importantly, in this process, we used the action execution activation (Squeeze > No Squeeze) as an exclusive mask to localize the V5 peak and as an inclusive mask to localize the PAR and PMC peaks. The ROI analyses were conducted by extracting the beta values for each ROI (Brett, Anton, Valabregue, & Poline, 2002), and then using these values to calculate the percent signal change relative to the N condition.

To examine whether two observed actions could be represented in the three ROIs, we compared the relative signal change in the 1H condition with the relative signal change in the 2H DIFF condition after averaging across the right and left hemisphere (but see Figures S1 and S2 for the results of both hemispheres separately). That is, we conducted a region x condition repeated measures MANOVA. As predicted, this revealed a main effect of condition, $F(1, 28) = 79.15$, $p < .001$, indicating stronger activation in the 2H DIFF condition than in the 1H condition. However, the region x condition interaction was significant as well, $F(2, 27) = 86.06$, $p < .001$ (Fig 3). This showed that the effect of condition was stronger in V5 than in both PAR, $t(28) = 11.35$, $p < .001$, and PMC, $t(28) = 13.34$, $p < .001$. Nevertheless, in addition to V5, $F(1, 28) = 155.60$, $p < .001$, the condition effect was also significant in PAR, $F(1, 28) = 16.40$, $p < .001$, and in PMC, $F(1, 28) = 5.56$, $p = .026$. In other words, these results indicate that activation in visual as well as motor areas was stronger when two different gestures were observed relative to when a single gesture was observed. This, in turn, indicates that both 2H DIFF gestures were simultaneously represented in the sVx serving as a proxy for the mirror neuron system.

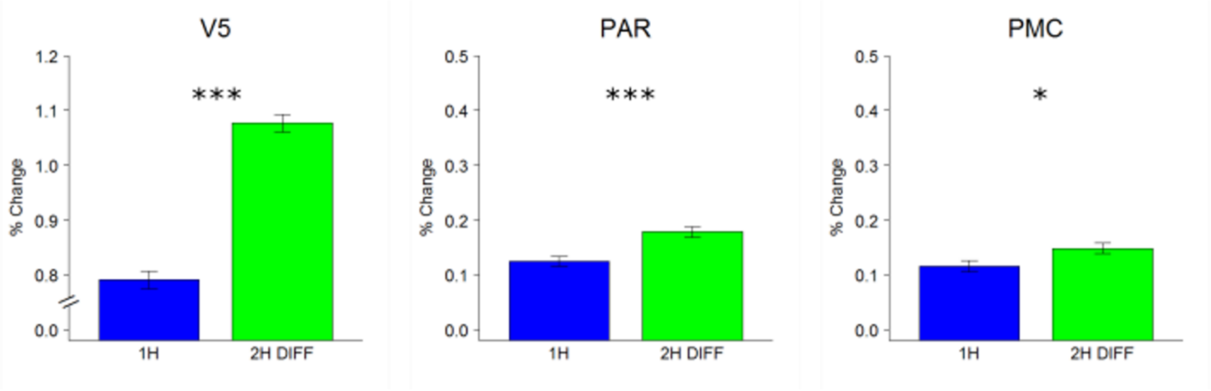

Figure 3. Results of the ROI analyses testing whether activation is stronger in the 2H DIFF condition than in the 1H condition. The y-axis shows the % signal change with respect to the N condition. Details on the % signal change calculation are provided in the methods. Post-hoc two-tailed *t* tests comparing 1H with 2H DIFF are displayed. * p < .05; ** p < .01; *** p < .001.

Can We Decode Both Individual Actions? Next, to investigate whether both individual actions could be decoded from sVx activation, we performed a representational similarity analysis (RSA). RSA is a multivariate analysis technique that measures the similarity between the representations of two stimuli by calculating the spatial correlation between their activation patterns (Kriegeskorte, Mur, & Bandettini, 2008). Applied to the current study, we calculated the spatial correlation between the unsmoothed activation pattern in the 2H DIFF condition and the unsmoothed activation pattern in the 1H condition because this allowed us to compare three correlations, namely two correlations with gesture overlap and one correlation without gesture overlap. More precisely, as illustrated in Figure 4a, we can compare the activation pattern when seeing both gesture A and B with the activation pattern when seeing only gesture A (Overlap A), only gesture B (Overlap B), or only gesture C (No Overlap).

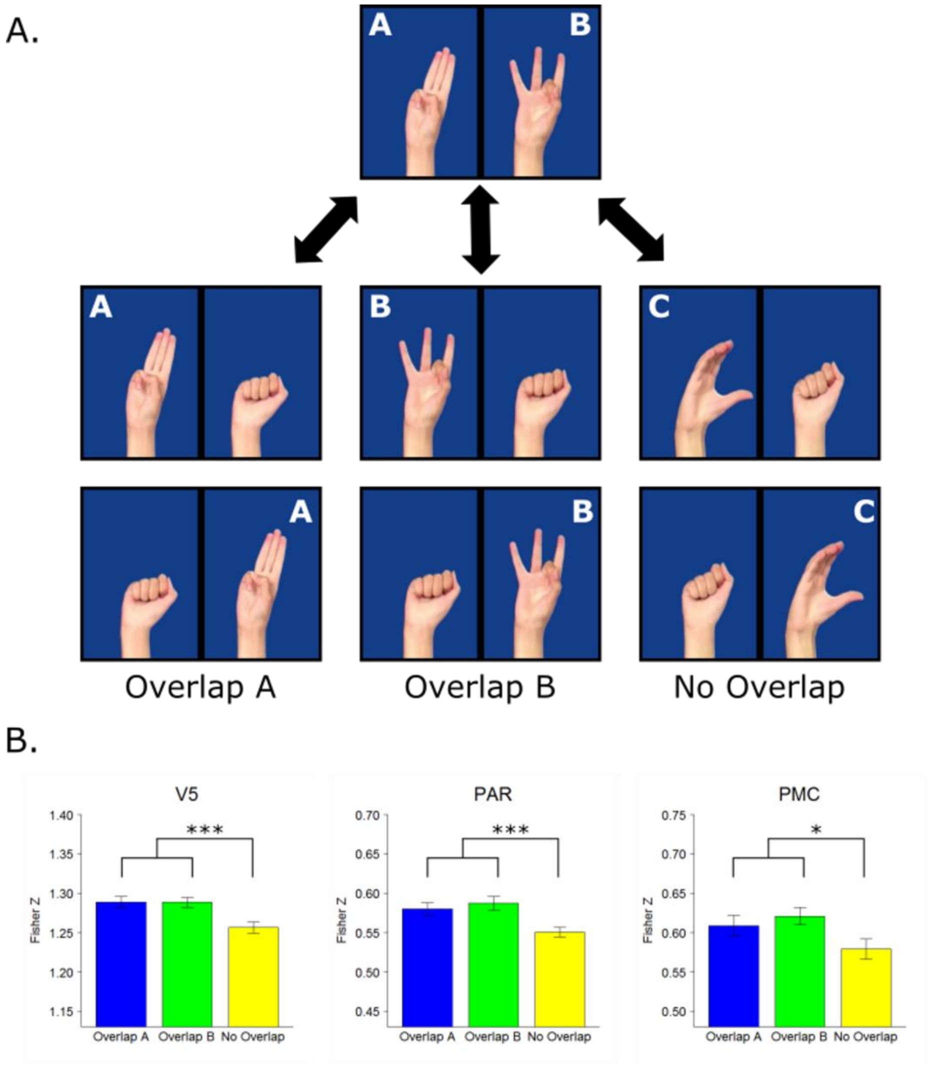

Figure 4. Results of the representational similarity analyses testing whether the two gestures observed in the 2H DIFF condition can be simultaneously decoded from brain activation in the three ROIs. Panel A is a visual representation of the analysis. In the Overlap A condition, gesture A overlaps. In the Overlap B condition, gesture B overlaps. In the No Overlap condition, neither of the two gestures overlaps. The analysis disregards the location of the gestures on the screen. Panel B shows the Fisher *Z*-transformed correlation coefficients in each of the three conditions separately for each ROI. Post-hoc two-tailed *t* tests comparing the average of Overlap A and B with No Overlap are displayed. The difference between Overlap A and Overlap B was never significant. * p < .05; ** p < .01; *** p < .001.

If the two gestures observed in the 2H DIFF condition were represented simultaneously, spatial correlations should be stronger when there is gesture overlap than when there is no gesture overlap. To evaluate this hypothesis, we conducted a region x overlap repeated measures MANOVA on the Fisher *Z*-transformed spatial correlations in the three ROIs (Fig. 4b). As predicted, this produced a main effect of overlap, *F*(2, 27) = 10.11, *p* < .001, revealing stronger spatial correlations in the Overlap A condition than in the No Overlap condition, *t*(28) = 3.21, *p* = .003, stronger correlations in the Overlap B condition than in the No Overlap condition, *t*(28) = 4.41, *p* < .001, but no difference between the Overlap A and Overlap B conditions, *t*(28) = -0.70, *p* = .491 (Fig 4b). There was no region x overlap interaction, *F*(4, 25) = 0.14, *p* = .966. Taken together, these results thus indicate that both 2H DIFF gestures could be decoded at the same time from activation in all three ROIs when the hands performed different gestures.

Does Representing Multiple Observed Actions Produce Motor Conflict?

Finally, if both 2H DIFF gestures were represented at the same time in the motor system, then this should have perceivable consequences in the brain. That is, the simultaneous representation of two mutually exclusive actions in the motor system should lead to motor conflict (Botvinick et al., 2001, 2004), which is known to activate the ACC (Botvinick et al., 2001, 2004; Braver et al., 2001; Ridderinkhof et al., 2004). The motor conflict hypothesis was tested by comparing whole brain activation in the 2H DIFF condition with whole brain activation in the 2H ID condition using the contrast 2H DIFF > 2H ID (Fig 5). Apart from activation in the action observation network, this revealed robust activation in the ACC, together with activation in the right AI (Table 1), which is known to co-activate with the ACC (Ullsperger, Danielmeier, & Jocham, 2014). Next, to further inform whether this activation pattern was consistent with motor conflict, we ran a Neurosynth meta-analysis using the search string “(Response* | Motor) & (Conflict* | Compet*)”. That is, we calculated reverse inference maps to identify brain regions that were associated selectively with motor conflict by comparing studies using the term motor conflict with studies not using the term motor conflict (Yarkoni, Poldrack, Nichols, Van Essen, & Wager, 2011). As shown in Fig 5, this confirmed that both the ACC and AI were associated relatively selectively with motor conflict, and an overlap analysis revealed substantial overlap with the activation obtained in the current study.

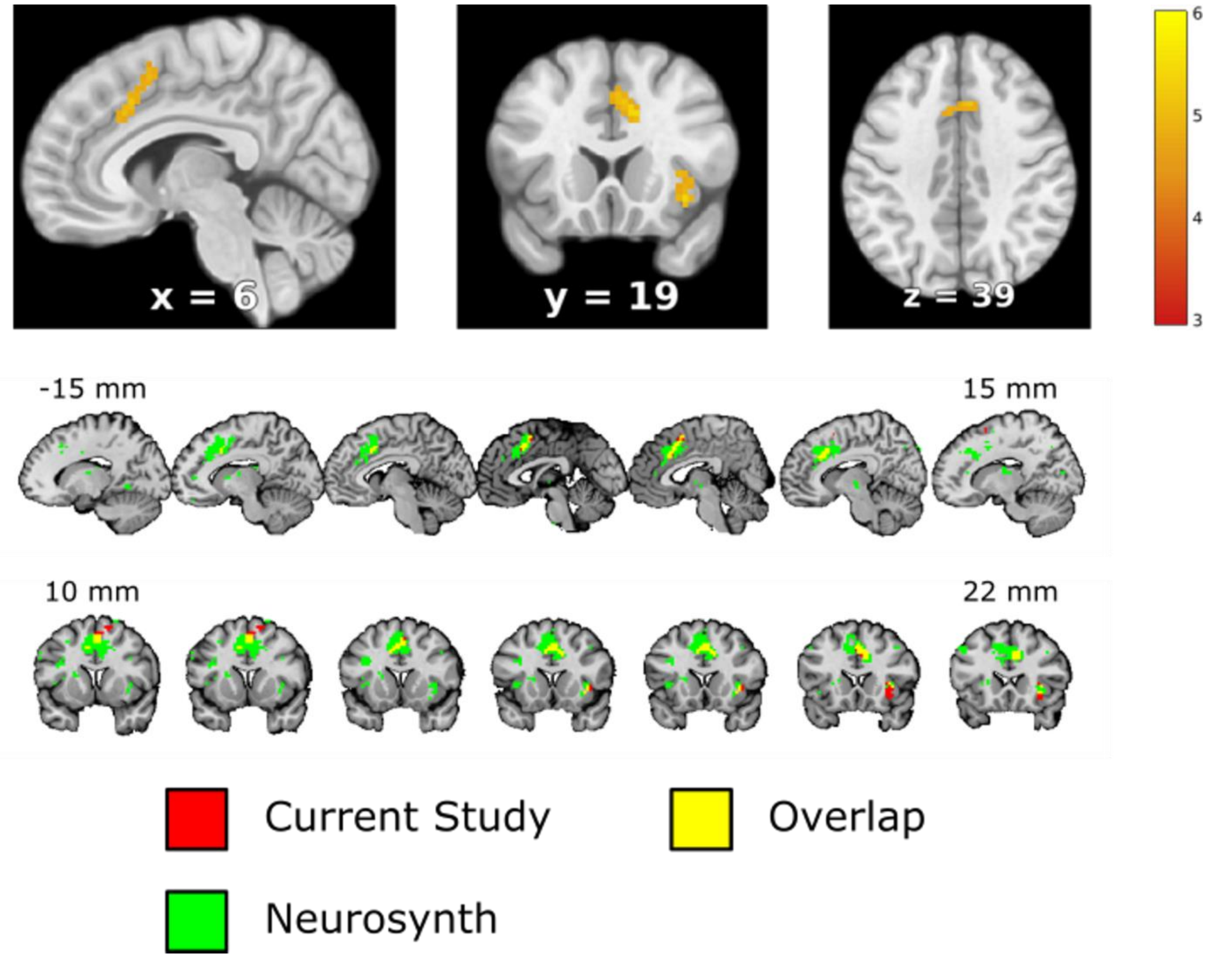

Figure 5. The top panel shows the univariate results of the 2H DIFF > 2H ID contrast in the action observation task. The bottom panel shows the overlap between the results of the current study and the results of a Neurosynth meta-analysis on motor conflict. Brain activation from the current study is thresholded at $p < .05$ using FWE correction. Brain activation from Neurosynth is thresholded at $p < .01$ using FDR correction.

Table 1

Peak MNI Coordinates of the 2H DIFF > 2H ID contrast.

Brain area	Peak coordinates	T-score	Cluster size
ACC, Pre-SMA	12, 20, 34	5.42	85
	3, 11, 52	5.07	
	3, 17, 43	5.05	
Right AI	36, 20, -8	5.37	28
	42, 17, -2	5.01	
	33, 23, 4	4.95	
Right IPG	30, -49, 46	5.07	7
Left dPMC	-33, -4, 52	5.06	8
Right MTG	45, -70, 13	5.00	6
Right SFG	12, 11, 64	4.89	4
Right dPMC	36, -4, 55	4.82	8
	42, 2, 58	4.77	

Note. ACC = Anterior Cingulate Cortex, pre-SMA = Pre-supplementary Motor Area, AI = Anterior Insula, IPG = Inferior Parietal Gyrus, dPMC = dorsal premotor cortex, MTG = middle temporal gyrus, SFG = superior frontal gyrus. All results are FWE-corrected at $p < .05$.

Finally, if the ACC activation was indeed caused by motor conflict, then it should depend on the degree to which sVx were activated. That is, according to the response conflict model of cognitive control, the function of the ACC is to detect and signal the presence of motor conflict (Botvinick et al., 2001, 2004). In particular, this model argues that response conflict can be seen as the product of activation in two simultaneously active response nodes. As a result, if only one response is active, then there is no response conflict. In contrast, if two responses are active, then response conflict depends on the activation in the two response nodes. In the current study, two identical observed gestures should trigger the same “response”, whereas two different observed gestures should trigger two different “responses”. Therefore, response conflict is expected in the 2H DIFF but not in the 2H ID condition, and response conflict in the 2H DIFF condition should depend on the strength of activation in the motor system.

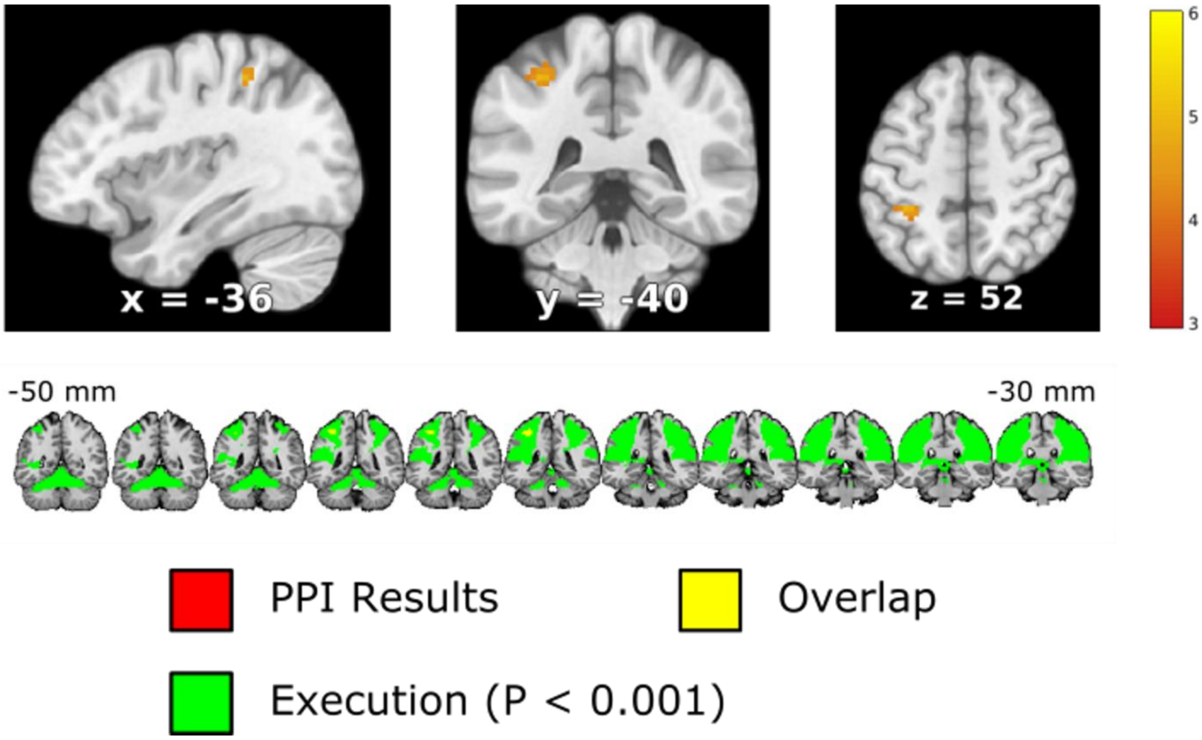

Figure 6. The top panel shows the PPI results of the 2H DIFF > 2H ID contrast in the action observation task. The displayed coordinates are the peak coordinates of the PPI analysis (t = 4.99, k = 20). Note that the PPI results are masked with the activation obtained in the action observation task (Observation > Neutral). The bottom panel shows the overlap between the activation obtained in the PPI analysis and the activation obtained in the action execution task (Squeeze > No Squeeze). There was no PPI activation that was not captured by the action execution activation. Unless otherwise specified, brain activation is thresholded with a small-volume FWE-corrected $p < .05$ threshold. In line with previous work, action execution data was thresholded at $p < .001$ to determine activation overlap (Arnstein et al., 2011).

To test this hypothesis, we calculated the psychophysiological interaction (PPI) of the 2H DIFF > 2H ID contrast using the ACC as seed region and the action observation activation

(Observation > Neutral) as a small-volume corrected inclusive mask (Fig 6). In other words, PPI was used to identify voxels that were more strongly correlated with the ACC seed region in the 2H DIFF condition than in the 2H ID condition (McLaren, Ries, Xu, & Johnson, 2012; O'Reilly, Woolrich, Behrens, Smith, & Johansen-Berg, 2012). In line with the motor conflict hypothesis, the PPI analysis revealed activation in the inferior parietal cortex, and this activation completely overlapped with the activation observed in the action execution task (Squeeze > No Squeeze). In other words, the PPI analysis showed that activation in parietal sVx was more strongly associated with ACC activation in the 2H DIFF condition than in the 2H ID condition. Consistent with the motor conflict hypothesis, this suggests that ACC activation reflected motor conflict produced by representing two mutually exclusive observed gestures in the motor system.

Discussion

The mirror mechanism is a fundamental neural mechanism that translates observed actions into motor programs (Rizzolatti & Sinigaglia, 2010, 2016). It has been argued that this mechanism supports action representation through motor simulation (Avenanti et al., 2013; Urgesi et al., 2014). However, in contrast to representing actions, little is known about the role of mirror processes in representing interactions. To represent interactions, the motor system has to process multiple observed actions at the same time (Quadflieg & Koldewyn, 2017; Quadflieg & Penton-Voak, 2017). In the current study, we investigated whether this is possible by asking participants to watch short videos of two right hands performing sign language gestures. Three key results were obtained. First, the motor system was activated more strongly when two different gestures were observed compared with when a single gesture was observed. Second, both individual gestures could be decoded simultaneously from activation in the motor system. Third, observing two different gestures relative to observing two identical gestures produced motor conflict related activation in the ACC, and this activation was correlated more strongly with parietal sVx in the former condition than in the latter condition. Together, these results indicate that multiple observed actions can be represented at the same time in the motor system, even when it is not possible to simultaneously execute them. Instead, when the mirrored actions violate motor constraints, this is signaled in the form of motor conflict.

Nevertheless, an alternative explanation could be that participants did not represent both gestures simultaneously but instead randomly represented one gesture on each trial. In particular, this assumes that the left gesture was represented in one half of the trials and that the right gesture was represented in the other half of the trials. In this case, the activation pattern over trials should combine the activation pattern of the two individual gestures, which would likewise make it possible to decode both gestures from the average brain activation. However, a random sampling mechanism seems unlikely considering that the attentional task required participants to simultaneously monitor both hands. Indeed, performance on this task (i.e., 85%) was well above chance (i.e., 50%). Moreover, a random sampling mechanism is difficult to reconcile with the other two main results, namely that observing two different gestures produced stronger motor responses and led to motor conflict. That is, if only one gesture was represented on each trial, then motor activation should not be stronger when two gestures were observed, nor should there be any motor conflict. Finally, a random sampling account is inconsistent with evidence that non-attended observed actions modulate automatic imitation even when another observed action is being attended or imitated (Cracco & Brass, 2017).

Yet, in addition to the above, one might also object to our interpretation of ACC activation as motor conflict. For example, an alternative explanation could be that this activation was driven by stimulus conflict rather than motor conflict. Stimulus conflict is similar to motor conflict but occurs already at the visual level (Verbruggen, Notebaert, Liefooghe, & Vandierendonck, 2006). As such, it does not require both observed gestures to be represented simultaneously in the motor system. Importantly, however, an explanation in terms of stimulus conflict is inconsistent with previous research on the neural substrates of conflict processing. In particular, this work has demonstrated that the ACC is sensitive to motor conflict but not to stimulus conflict (Liston, Matalon, Hare, Davidson, & Casey, 2006; Liu, Banich, Jacobson, & Tanabe, 2004; Mayer et al., 2012; Milham et al., 2001; van Veen, Cohen, Botvinick, Stenger, & Carter, 2001; Wendelken, Ditterich, Bunge, & Carter, 2009). Furthermore, stimulus conflict cannot easily explain why ACC activation was correlated with parietal motor activation but not with purely visual activation. That is, if the ACC coded stimulus conflict, it should co-activate with the visual cortex (Botvinick et al., 2001). More generally, alternative explanations are not credible unless they are able to explain why ACC activation was correlated with motor activation, and why this correlation was stronger when the hands performed different gestures than when they performed identical gestures. Since this pattern was derived directly from conflict monitoring theories (Botvinick et al., 2001, 2004), it strongly favors the motor conflict hypothesis.

Thus, taken together, the current study indicates that at least two observed actions can be represented at the same time in the motor system. These results critically extend the literature on mirror processes from action representation (Rizzolatti & Sinigaglia, 2010, 2016) to interaction representation (Quadflieg & Koldewyn, 2017; Quadflieg & Penton-Voak, 2017). That is, in contrast to what might be expected, our results show that motor simulation does not break down when observing multiple actions. Instead, in that case, multiple actions are simulated in parallel. This, in turn, implies that motor simulation might not only be involved in decoding observed actions (Avenanti et al., 2013; Urgesi et al., 2014) but also in decoding observed interactions (Quadflieg & Koldewyn, 2017; Quadflieg & Penton-Voak, 2017). From this view, a key challenge for future research will be to determine how exactly how motor simulation contributes to interaction representation.

Moreover, in addition to interaction representation, the current study also has important implications for joint action. That is, previous research has shown that motor simulation facilitates interpersonal coordination in tasks where two persons have to cooperate (Colling, Knoblich, & Sebanz, 2013; Kourtis, Sebanz, & Knoblich, 2013). For example, a recent study found that musicians' ability to tune their own actions to those of another musician in a musical duet was impaired when the dorsal premotor cortex was disturbed (Hadley, Novembre, Keller, & Pickering, 2015). However, some social tasks extend beyond the dyad (Tsai, Sebanz, & Knoblich, 2011). For instance, musicians in a musical ensemble have to coordinate their actions not with one but with multiple co-musicians (Volpe, D'Ausilio, Badino, Camurri, & Fadiga, 2016). The results of the present study suggest that this may likewise rely on motor simulation. In particular, it suggests that mirror processes can be used to simultaneously predict the action outcomes of several co-actors (Aglioti, Cesari, Romani, & Urgesi, 2008; Hamilton & Grafton, 2008) to achieve interpersonal coordination in multi-agent settings (Colling et al., 2013; Kourtis et al., 2013).

Finally, to the best of our knowledge, the current study is the first demonstration that motor conflict is not restricted to action planning (Botvinick et al., 2001, 2004), but can also occur during action observation. This has important implications for theories of cognitive control. For instance, a prominent view is that motor conflict signals the need to increase attentional control (Botvinick et al., 2001, 2004). From this view, when observers experience motor conflict, this might trigger compensatory mechanisms that increase attention toward the observed actions, and this might then facilitate social processes such as interaction understanding (Quadflieg & Koldewyn, 2017; Quadflieg & Penton-Voak, 2017) or interpersonal coordination (Colling et al., 2013; Kourtis et al., 2013). To conclude, the present work shows that multiple observed actions can be represented simultaneously in the motor system. This has important implications for interaction representation as well as joint action, and opens up new hypotheses on the role of motor conflict in action observation.

Methods

Participants

Thirty volunteers participated in the experiment in exchange for 30 euro (17 female, M_{age} = 22.67, SD_{age} = 2.48, $range_{\text{age}}$ = 18 - 28), but one participant was excluded due to excessive head motion. This resulted in a sample of twenty-nine participants (17 female, M_{age} = 22.76, SD_{age} = 2.47, $range_{\text{age}}$ = 18 - 28). However, the action execution data of three participants could not be used. That is, for one participant, a technical error prevented the randomization from being saved. Furthermore, for two participants, there was excessive head motion between the action observation and action execution phase, which led to missing data in the occipital lobe as a consequence of realignment. In other words, the action observation analyses were conducted on 29 participants and the action execution analyses on 26 participants. All participants were right-handed according to the Edinburgh Handedness Inventory (Oldfield, 1971), could not speak sign language, had no history of neurological or psychiatric disorder, and gave written informed consent. The study was approved by the Medical Ethic Review Board of the Ghent University Hospital.

Method

Experimental Design. The experiment was structured in three phases. The first phase took place outside of the scanner. In this phase, participants were familiarized with the two experimental tasks, namely the action observation task and the action execution task. Moreover, to ensure that participants were able to execute the three gestures presented in the action observation task, the familiarization phase included an imitation task in which each gesture was presented 10 times. Participants had to imitate the gesture with their right hand and then press the space bar to continue. Performance on this task was monitored by the experimenter and mistakes were corrected. Following the familiarization phase, participants were put into the scanner for the second and third phase of the experiment. In the second phase, participants performed the action observation task. In the third phase, they performed the action execution task.

Action Observation Task. In the action observation task, participants watched short videos (5 s) of two right hands repeatedly (4 times) performing one out of three sign language gestures (Fig 1). The gestures were chosen on the basis of a pilot study in which 40 participants used a 5-point Likert scale to rate eight sign language gestures on whether the gesture was familiar, whether they had seen the gesture before, whether the gesture was clearly visible, whether the gesture was difficult to execute, and whether the gesture had a meaning. For each gesture, participants were furthermore asked to guess its meaning. Based on the results of the pilot study, we chose three gestures that were clearly visible, not difficult to execute, and with unknown meaning. The videos were presented as a sequence of 28 frames (see Supplementary Videos). The first frame depicted the hands in rest position and was presented for 300 ms. Next, all 28 frames were presented for 33 ms each. Finally, the last frame remained on the screen for another 300 ms before the 28 frames were presented again for 33 ms each. This was repeated for four cycles so that each video had a total duration of 5196 ms (300 ms + 4 x 28 x 33 ms + 4 x 300 ms).

To ensure that attention was maintained throughout the experiment, participants had to detect glitches in the videos. A glitch was presented randomly in one out of seven trials at a random point during the video on the left hand, on the right hand, or on both hands. To implement the glitch, we replaced 1 of the 28 frames with a blue frame. This resulted in a brief flicker (33 ms) that was easily missed unless attention was divided between the two hands. In other words, the detection task required participants to allocate attention to both hands at the same time. After each glitch trial, two questions were presented on the screen. The first question required participants to indicate the gesture(s) on which the glitch had appeared. More specifically, a series of four pictures was presented showing the neutral hand followed by the three gestures. Participants had to indicate for each picture whether a glitch had appeared on the presented gesture or not. The second question asked participants whether the glitch had appeared on one hand or on both hands. Accuracy was 75% on the first question and 85% on the second question, indicating that the task was challenging but not too difficult. All participants scored above chance level on both questions. Trials with a glitch were not included in the analyses.

The action observation task comprised two runs consisting of 126 trials each. Trials were presented randomly with the restriction that all 18 gesture combinations occurred equally often in both runs. The following gesture combinations were included in the experiment: nG1/nG1, nG2/nG2, nG3/nG3, nG1/G1, G1/nG1, nG2/G2, G2/nG2, nG3/G3, G3/nG3, G1/G1, G2/G2, G3/G3, G1/G2, G2/G1, G1/G3, G3/G1, G2/G3, G3/G2, with G1, G2, and G3 representing the three gestures and nG1, nG2, and nG3 representing the corresponding neutral hand. For example, G2/G3 means that gesture 2 was presented left and that gesture 3 was presented right. The 18 gesture combinations were combined to form four conditions. In the Neutral condition (N), neither hand performed a gesture. In the One Hand condition (1H), one hand performed a gesture. In the Two Hand Identical condition (2H ID), both hands performed the same gesture. Finally, in the Two Hand Different condition (2H DIFF), the two hands each performed a different gesture. All trials were separated by a black screen that was presented for a jittered duration drawn from a pseudo-logarithmic distribution with 50% short durations (200, 800, 1400, or 2000 ms), 33.3% intermediate durations (2600, 3200, 3800, or 4400 ms), and 16.7% long durations (5000, 5600, 6200, or 6800 ms).

Action Execution Task. Immediately after the action observation task, participants performed the action execution task. In this task, a green or red circle was presented on the left or right side of the screen. The circle then decreased in size every second until it disappeared after four seconds. During the action execution task, participants wore gloves with a ball made of bubble wrap attached to the palm. When a green circle was presented, participants had to squeeze the ball each time the circle decreased in size using the hand that corresponded to the location of the circle on the screen. For example, when a green circle appeared on the left side, participants had to squeeze the ball using their left hand. In contrast, when a red circle was presented, participants simply had to watch the screen. The action execution task consisted of 60 trials that were randomly subdivided into 20 squeeze left trials, 20 squeeze right trials, and 20 watch trials. Trials were separated by a black screen that was presented for a jittered duration of 4000, 5000, 6000, 7000, or 8000 ms. The action execution task was based on the task used by Arnstein et al. (2011). In particular, these authors found that a simple squeeze task like the one used in the current study activated a network very similar to the network activated by a more complex object manipulation task.

fMRI Parameters. MRI images were acquired with a 3T Siemens Trio scanner using a 32-channel radiofrequency head coil. Participants entered the scanner head first and supine. The scanning procedure started with an anatomical scan in which 176 high-resolution anatomical images were acquired using a T1-weighted 3D MPRAGE sequence [repetition time (TR) = 2250 ms, echo time (TE) = 4.18 ms, image matrix = 256 x 256, field of view (FOV) = 256 x 256 mm, flip angle = 9°, voxel size = 1.00 x 1.00 x 1.00 mm]. This was followed by two action observation runs and one action execution run in which whole-brain functional images were obtained. These functional images were acquired using a T2*-weighted echo planar imaging (EPI) sequence, sensitive to BOLD contrast (TR = 2000 ms, TE = 28 ms, image matrix = 64 x 64, FOV = 224 mm, flip angle = 80°, distance factor = 17%, voxel size 3.5 x 3.5 x 3.0 mm, 34 axial slices).

fMRI Preprocessing. All fMRI data was processed with SPM8 (Wellcome Department of Imaging Neuroscience, UCL, London, U.K.; www.fil.ion.ucl.ac.uk/spm). To account for T1 relaxation effects, the first four scans of all runs were dummy scans. The data of all three runs were preprocessed together. First, the functional images were spatially realigned using a rigid body transformation. Second, the realigned images were slice-time corrected with respect to the middle acquired slice. Third, the structural image of each subject was co-registered with its mean functional image. Fourth, the anatomical images were segmented according to the SPM8 tissue probability maps and the resulting parameters were used to normalize the functional images to standard MNI space. Finally, the images were resampled into 3 mm^3 voxels and spatially smoothed with an 8 mm Gaussian kernel (full-width at half maximum). Importantly, the representational similarity analyses were performed on the unsmoothed data.

Analyses

Univariate Analyses. The data was filtered using a high-pass filter of 128 Hz. First level analyses were conducted by fitting a general linear model in SPM8. The action observation model consisted of 10 regressors per run, namely one regressor for each condition (N, 1H, 2H ID, and 2H DIFF) and six regressors representing the realignment parameters. The signal was modeled over the entire duration of the videos and was convolved with the canonical hemodynamic response function (HRF). The action execution model also consisted of 10 regressors, with one regressor for each condition (Watch Left, Watch Right, Squeeze Left, Squeeze Right) and six regressors representing the realignment parameters. The entire duration of the trial, from the moment the circle appeared until the moment it disappeared, was modeled and convolved with the canonical HRF. The second level analyses of both tasks were performed using a within-subject one-way ANOVA with equal variances. Unless otherwise specified, all results are thresholded at the peak level using a $p < .05$ FWE-corrected threshold. The Observation > Neutral contrast used to find action observation activation was calculated as 0.33 x [1H + 2H ID + 2H DIFF] > N. The Squeeze > No Squeeze contrast used to find action execution activation was calculated as [Squeeze Left + Squeeze Right] > [Watch Left + Watch Right].

Region of Interest Analyses. The regions of interest (ROIs) were constructed from brain activation in action observation task. To ensure that the ROIs were not biased towards the 2H conditions, we calculated the conjunction [1H > N] ∩ [2H ID > N] ∩ [2H DIFF > N] (Figure S1). Furthermore, to secure statistical independence, we used a leave-one-out cross-validation procedure in which the ROIs for each participant were calculated using the data of all participants except that one participant (Esterman et al., 2010). That is, for each participant, we performed the specified conjunction analysis on the data of all the other participants. We then defined the ROIs by constructing 5 mm spheres around the peak coordinates in the left and right visual cortex (V5), the left and right parietal cortex (PAR), and the left premotor cortex (PMC). The right PMC was not consistently activated. Therefore, to obtain a bilateral PMC ROI, we mirrored the left PMC sphere onto the right hemisphere.

Importantly, the activation pattern was highly similar in the left and right PMC (Figures S2-S3).

The V5 peak coordinates were determined using the Squeeze > No Squeeze action execution activation as an exclusive mask ($p < .001$, uncorrected). Conversely, the PAR and PMC peak coordinates were determined using the Squeeze > No Squeeze action execution activation as an inclusive mask ($p < .001$, uncorrected). The use of an uncorrected $p < .001$ thresholds for the masks was based on previous work (Arnstein et al., 2011). Finally, we intersected the obtained spheres with a grey matter mask to ensure that the ROIs were within the boundaries of the brain. The peak coordinates used to construct the ROIs are reported separately for each participant in Table S1. To perform the ROI analyses, we extracted the beta values using the MARSBAR package in SPM8 (Brett et al., 2002), and then used these values to calculate the percent signal change with respect to the N condition. More specifically, we first added the intercept to each beta value before calculating the relative signal change in the 1H and 2H DIFF conditions as $100 \times \frac{(1H-N)}{N}$ and $100 \times \frac{(2H\ DIFF-N)}{N}$.

Representational Similarity Analysis. The representational similarity analyses were performed on the unsmoothed data. First level analyses were conducted by fitting a general linear model in SPM8. The action observation model consisted of 24 regressors per run, namely one regressor for each of the 18 gesture combinations and six regressors for the realignment parameters. The signal was modeled over the entire duration of the videos and was convolved with the canonical HRF. Next, for every voxel in each of the three ROIs, we extracted the beta values corresponding to the 18 gesture combinations and computed pairwise correlations between the different gesture combinations across voxels so that we obtained an 18 x 18 correlation matrix per run per ROI. We then applied Fisher's *z*-transformation to the correlation coefficients to make them normally distributed, and these *z*-scores were used in the analyses.

To investigate whether the two gestures in the 2H DIFF condition could be decoded simultaneously from brain activation, we calculated the spatial correlation between the activation patterns in the 2H DIFF and 1H conditions separately for each ROI because this allowed us to compare three correlations, namely two correlations with gesture overlap and one correlation without gesture overlap. For example, the activation pattern when seeing both gesture A and B can be compared with the activation pattern when seeing only gesture A (Overlap A), only gesture B (Overlap B), or only gesture C (No Overlap) (Fig 4a). Importantly, this analysis was conducted without considering the location of the gestures on the screen. For example, in A/B trials, Overlap A was the mean of r(A/B, nA/A) and r(A/B, A/nA), Overlap B was the mean of r(A/B, nB/B) and r(A/B, A/nB), and No Overlap was the mean of r(A/B, nC/C) and r(A/B, C/nC). These correlations were calculated separately for the six possible gesture combinations in the 2H DIFF condition, and were then averaged per condition over these gesture combinations.

Psychophysiological Interaction Analysis. The psychophysiological interaction (PPI) analysis was performed using the gPPI toolbox in SPM8 (McLaren et al., 2012). The ACC seed region was the cluster identified with the 2H DIFF > 2H ID contrast in the action observation task. PPI regressors were calculated at the first level for all four conditions (N, 1H, 2H ID, and 2H DIFF) and were then analyzed with a within-subject one-way ANOVA with equal variances at the second level. Because we were only interested in connections with the action observation network, the PPI analysis was restricted to voxels that were significant in the action observation task (Observation > Neutral) at an uncorrected $p < .001$ threshold. Within this volume, the PPI results were thresholded at FWE-corrected $p < .05$ peak threshold.

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Supplementary Information

Table S1

Center MNI coordinates for the three ROIs per participant.

	Left V5	Right V5	Left PAR	Right PAR	Left PMC	Right PMC
Subject 1	-51, -76, -2	51, -70, -2	-30, -43, 52	30, -40, 46	-42, -4, 58	42, -4, 58
Subject 2	-51, -73, 1	51, -70, -2	-33, -43, 55	30, -40, 49	-42, -7, 58	42, -7, 58
Subject 3	-51, -76, -2	51, -70, -2	-30, -43, 52	30, -40, 46	-42, -4, 58	42, -4, 58
Subject 4	-51, -76, -2	51, -67, -2	-30, -43, 52	30, -40, 46	-42, -4, 58	42, -4, 58
Subject 5	-51, -76, -2	51, -70, 2	-33, -43, 55	30, -43, 52	-42, -4, 58	42, -4, 58
Subject 6	-51, -76, -2	51, -70, -2	-30, -46, 52	30, -40, 46	-42, -4, 58	42, -4, 58
Subject 7	-51, -76, -2	51, -67, -2	-30, -43, 52	30, -37, 46	-42, -4, 58	42, -4, 58
Subject 8	-51, -76, -2	51, -70, -2	-30, -46, 52	30, -43, 49	-42, -4, 58	42, -4, 58
Subject 9	-51, -76, -2	51, -70, -2	-33, -43, 55	30, -43, 49	-42, -4, 58	42, -4, 58
Subject 10	-51, -76, -2	51, -70, -2	-33, -43, 55	30, -43, 49	-42, -4, 58	42, -4, 58
Subject 11	-51, -76, -2	51, -70, -2	-30, -46, 52	30, -43, 49	-42, -4, 58	42, -4, 58
Subject 12	-51, -76, -2	51, -70, -2	-30, -43, 52	30, -43, 52	-42, -4, 58	42, -4, 58
Subject 13	-51, -76, -2	51, -72, -2	-30, -46, 52	30, -40, 49	-42, -4, 58	42, -4, 58
Subject 14	-48, -67, 4	51, -70, -2	-30, -43, 52	30, -43, 52	-42, -4, 58	42, -4, 58
Subject 15	-51, -76, -2	51, -70, -2	-30, -43, 52	30, -40, 46	-42, -4, 58	42, -4, 58
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Subject 17	-51, -76, -2	51, -70, -2	-30, -43, 52	30, -40, 46	-42, -7, 58	42, -7, 58
Subject 18	-51, -76, -2	51, -70, -2	-30, -43, 52	30, -43, 49	-42, -4, 58	42, -4, 58
Subject 20	-51, -73, -2	51, -70, -2	-30, -43, 52	30, -40, 49	-42, -4, 58	42, -4, 58
Subject 21	-51, -76, -2	51, -70, -2	-30, -43, 52	30, -43, 49	-42, -4, 58	42, -4, 58
Subject 22	-51, -76, -2	51, -70, -2	-30, -43, 52	30, -43, 52	-42, -4, 58	42, -4, 58
Subject 23	-51, -76, -2	51, -70, -2	-30, -43, 52	30, -43, 49	-42, -4, 58	42, -4, 58
Subject 24	-48, -73, -2	51, -70, -2	-30, -43, 52	30, -43, 52	-42, -4, 58	42, -4, 58

	Left V5	Right V5	Left PAR	Right PAR	Left PMC	Right PMC
Subject 25	-51, -76, -2	51, -70, -2	-30, -43, 52	30, -43, 49	-42, -4, 58	42, -4, 58
Subject 26	-51, -76, -2	51, -70, -2	-30, -43, 52	30, -40, 46	-42, -4, 58	42, -4, 58
Subject 27	-51, -76, -2	51, -70, -2	-30, -46, 52	30, -43, 52	-42, -4, 58	42, -4, 58
Subject 28	-51, -76, -2	51, -70, -2	-30, -43, 52	30, -43, 52	-42, -4, 58	42, -4, 58
Subject 29	-51, -76, -2	51, -70, -2	-30, -46, 52	30, -43, 49	-42, -4, 58	42, -4, 58
Subject 30	-51, -76, -2	51, -70, -2	-30, -43, 52	30, -43, 52	-42, -4, 58	42, -4, 58

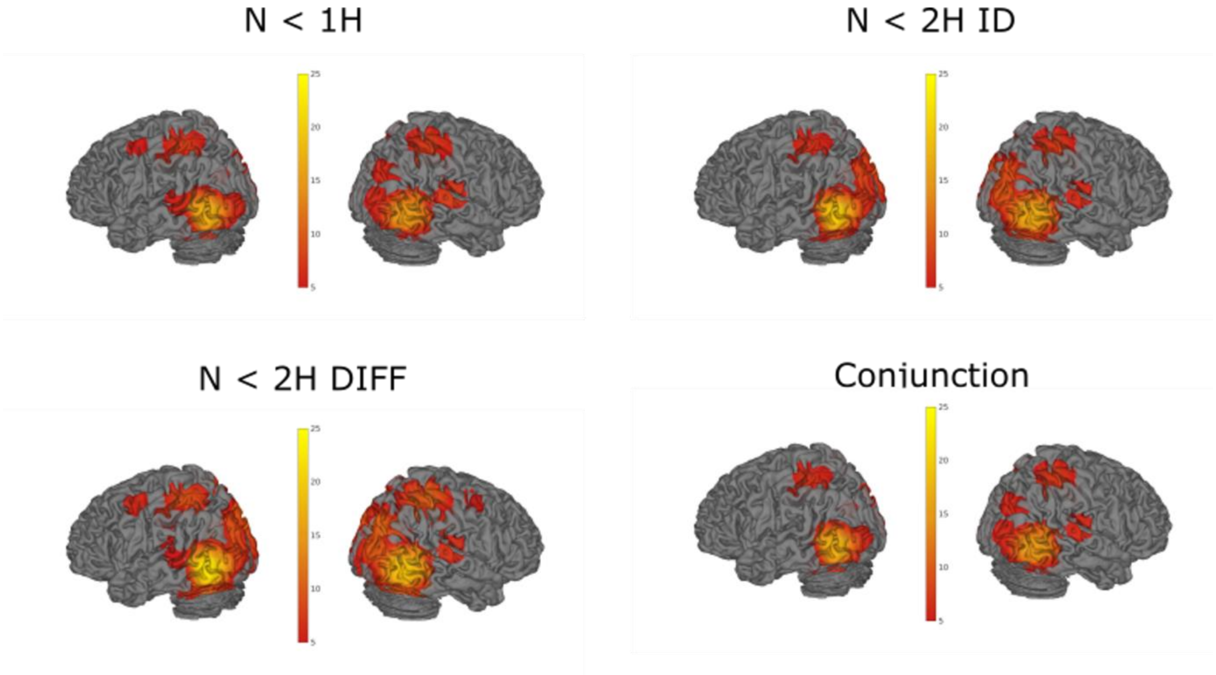

Figure S1. Brain activation in each of the action observation conditions compared with the neutral condition. The bottom right figure shows the conjunction of the other three contrasts. Images were thresholded using a $p < .05$ FWE-corrected threshold. Left premotor activation was also present in the conjunction analysis at an uncorrected threshold of $p < .001$.

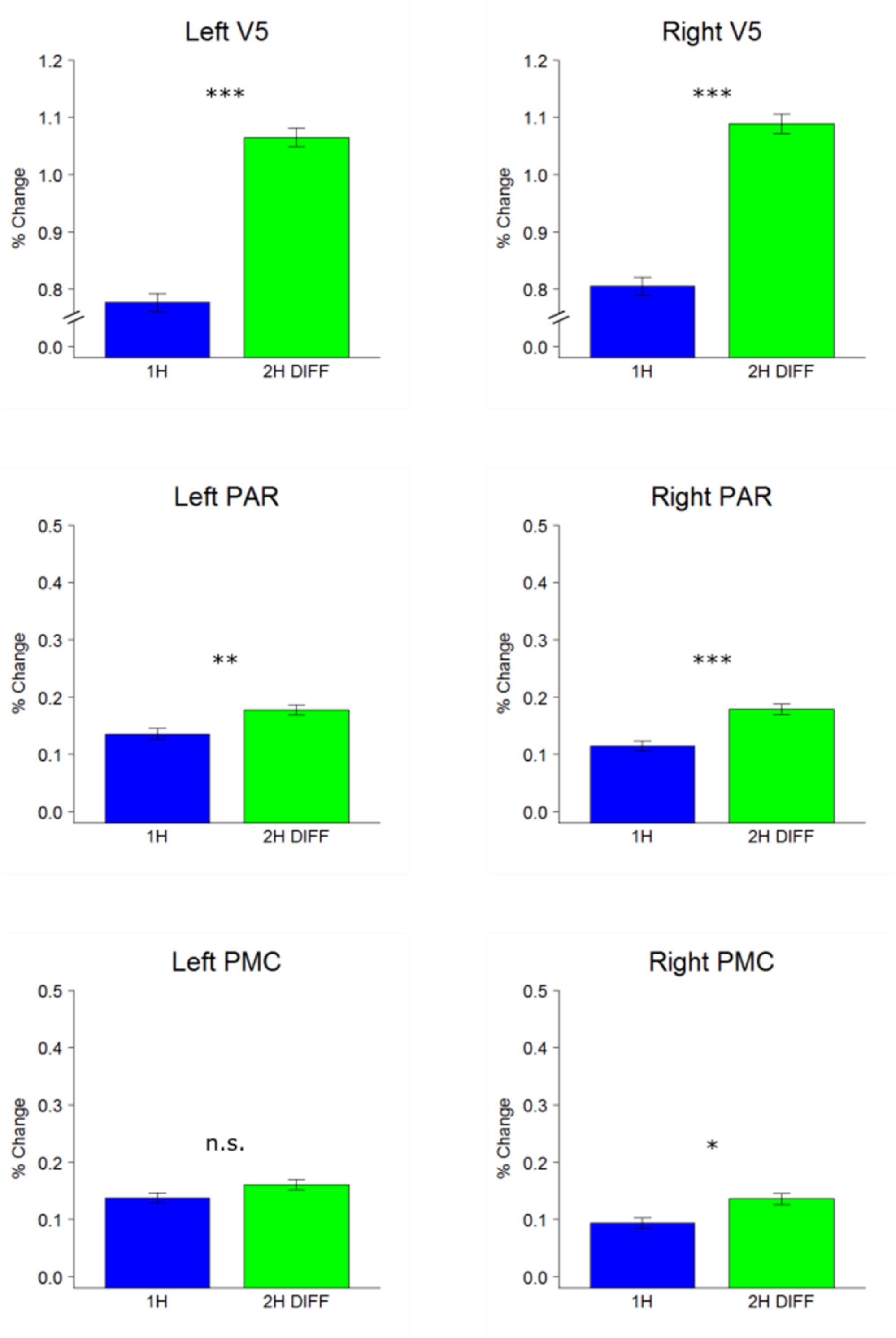

Figure S2. Results of the ROI analyses testing whether activation is stronger in the 2H DIFF condition than in the 1H condition separately for the left and right hemisphere. The y-axis shows the % signal change with respect to the N condition. Details on the % signal change calculation are provided in the methods. Post-hoc two-tailed *t* tests comparing 1H with 2H DIFF are displayed. * p < .05; ** p < .01; *** p < .001.

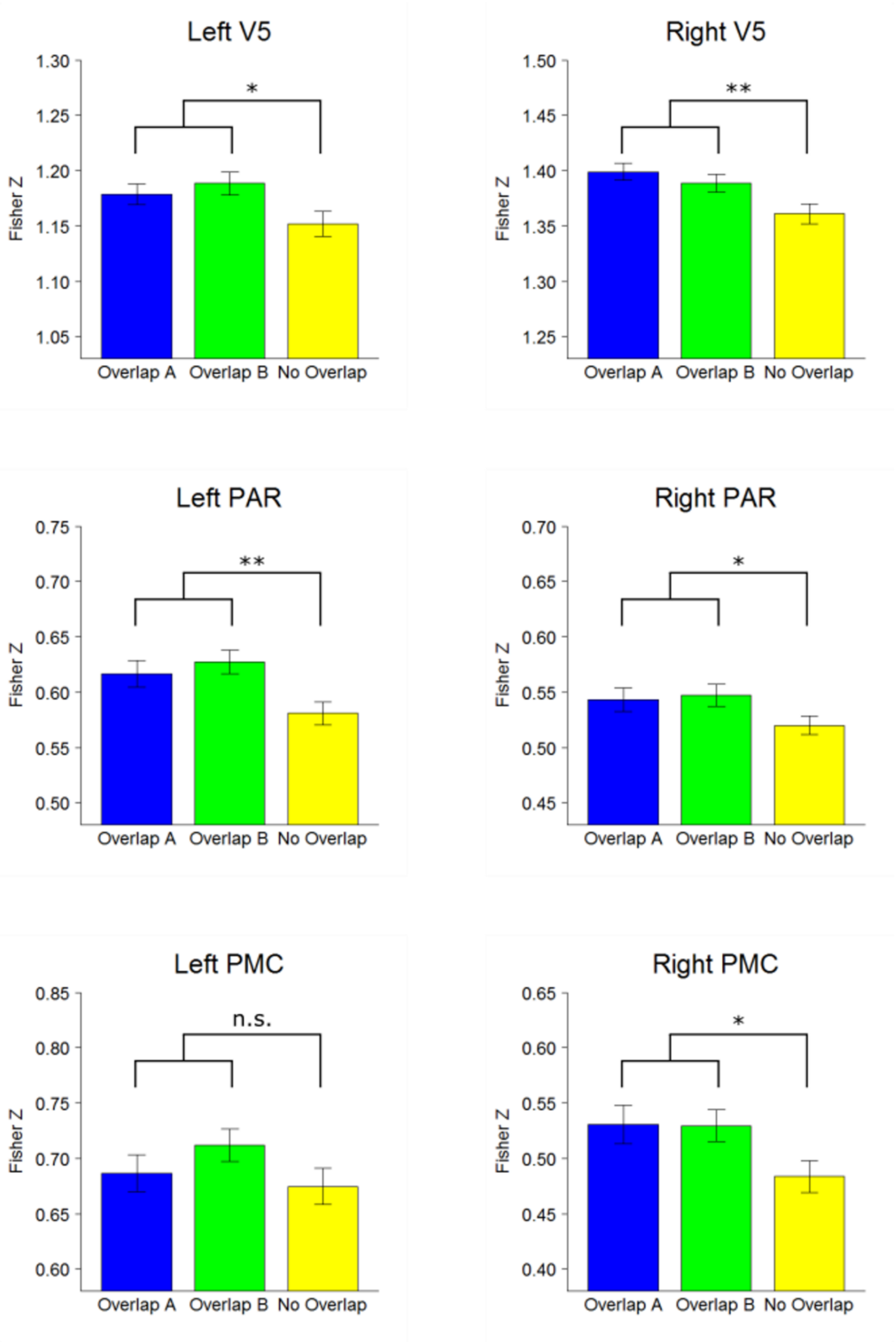

Figure S3. Results of the representational similarity analyses testing whether the two observed gestures in the 2H DIFF condition can be decoded from brain activation in the three ROIs separately for the left and right hemisphere. Post-hoc two-tailed *t* tests comparing the average of Overlap A and B with No Overlap are displayed. The difference between Overlap A and Overlap B was never significant. * p < .05; ** p < .01; *** p < .001.

Chapter 8

General Discussion

In the current dissertation, I set out to investigate whether it is possible to simultaneously represent the actions of multiple observed agents in the motor system. To this end, I studied both identical and different observed actions, and did so using behavioral as well as neuroscientific methods. In Chapters 2, 4, 5, and 6, I used automatic imitation, which is the finding that action execution is facilitated by compatible and impeded by incompatible observed actions (Cracco, Bardi, et al., 2018; Heyes, 2011). In Chapters 3 and 7, I then measured motor activation during passive action observation. More specifically, Chapter 3 measured corticospinal excitability by stimulating the primary motor cortex with TMS (Naish, Houston-Price, Bremner, & Holmes, 2014) and Chapter 7 measured BOLD activation in the motor system of the brain using fMRI (Molenberghs, Cunnington, & Mattingley, 2012). The results across these six chapters provided converging evidence for the hypothesis that observers can simultaneously represent the actions of multiple agents in their motor system. The current discussion will summarize these results, explain them in a computational model, and discuss their theoretical impact, implications, and limitations.

Overview of the Results

Representing Multiple Identical Observed Actions

The question whether multiple identical observed actions can be represented in the motor system was investigated with automatic imitation and TMS. In **Chapter 2**, I measured automatic imitation while participants observed two hands of which either one hand performed an action or both hands performed the same action. The results revealed stronger automatic imitation when two identical actions were observed, indicating that both actions were represented in the motor system. Interestingly, the same additive effect could not be observed for non-human agents, which rules out that it was driven by differences in attentional processing. Instead, for non-human agents, there was an additive effect on slow but not on fast responses. Together, these results suggest the presence of an initial attentional boost in early processing stages that disappeared in later stages. Next, in **Chapter 3**, I used TMS to obtain a more direct measure of motor activation. That is, I measured corticospinal excitability in a passive observation task with similar stimuli as the ones used in Chapter 2. The results confirmed the results of Chapter 2, with stronger MEPs when two identical actions were observed compared with when a single action was observed. Importantly, this was true even though MEPs were measured at longer delays where attentional processes were unlikely to still contribute (Cracco, De Coster, Andres, & Brass, 2015; Klein, 2000; Samuel & Kat, 2003).

Chapter 4 addressed an alternative explanation for the results of the previous two chapters. That is, it investigated whether participants, instead of representing two hands, randomly represented one hand on each trial. This would cause the probability to represent a moving hand to be 100% when both hands made a movement but only 50% when one hand made a movement. In other words, random sampling would result in an additive effect across trials rather than within trials. To rule out this account, Chapter 4 ensured that the actions of at least one hand were represented on every trial. More specifically, it used a stimulus setup that positioned the two hands close together (Experiments 1-4), and requested participants to either attend to (Experiment 3) or imitate (Experiment 4) the actions performed by one of the two hands. The results revealed an additive imitation effect even though task requirements made it highly unlikely that participants sometimes represented only the non-moving hand. This speaks against a random sampling mechanism and instead suggests that participants simultaneously represented multiple observed actions in their motor system.

Finally, **Chapter 5** extended the number of hands from two to four. In Experiments 1-2, reaction times were found to decrease with group size according to an asymptotic curve on congruent trials and to increase with group size according to a linear curve on incongruent trials. Importantly, however, the asymptotic relation on congruent trials became linear when no imitative control was needed, namely in the absence of incongruent trials (Experiments 3-7). This indicates that strategic control processes caused congruent responses to saturate. Indeed, if larger groups provide a stronger motor trigger, then imitative control has to be adjusted accordingly to prevent unwanted imitative responses. The selective asymptote on congruent trials indicates that this was achieved by regulating the response threshold based on the number of observed movements. That is, because a heightened response threshold leads to slower responses, such a mechanism masks decreases in response speed on congruent trials while strengthening increases in response speed on incongruent trials. Interestingly, the finding of an asymptotic relation between group size and automatic imitation closely corresponds to the literature on social contagion in social psychology (e.g., Gallup et al., 2012; Knowles & Bassett, 1976; Milgram, Bickman, & Berkowitz, 1969). However, this literature has mainly explained social contagion in terms of interpretative processes. In contrast, Chapter 5 used a task that minimized the role of interpretation. As a consequence, it supports the hypothesis that social contagion has a sensorimotor basis.

Representing Multiple Different Observed Actions

The second question, whether the motor system can also represent multiple different observed actions, was investigated with automatic imitation and fMRI. First, **Chapter 2** used automatic imitation to compare responses in a condition where two stimulus hands performed different actions with responses in a condition where neither stimulus hand performed an action. The results revealed that performance in these two conditions could not be distinguished. Given that seeing two different actions in this paradigm corresponds to seeing one congruent action and one incongruent action, these results indicate that both actions were represented at the same time in the motor system, and that this produced a concurrent facilitation and interference effect that cancelled out each other. However, another explanation could also be that participants represented neither action in this condition. Therefore, to address this issue, **Chapter 6** extended the number of stimulus hands from two to four. This, then, allowed me to compare two conditions in which three or four hands performed the same action with a condition in which three hands performed one action and a fourth hand performed a different action. The results revealed weaker automatic imitation in the third condition than in the other two conditions, indicating that the actions of the four hands were represented together in the motor system even when they performed different actions.

Finally, in **Chapter 7** I directly measured motor activation during passive observation using fMRI. In this study, participants observed two right hands performing sign language gestures. Three key results were obtained. First, the motor system was activated more strongly when two different gestures were observed compared with when a single gesture was observed. Second, both individual gestures could be decoded simultaneously from activation in the motor system using multivariate analysis techniques. Third, observing two different compared with two identical gestures activated brain areas associated with motor conflict, and this activation was correlated with activation in the motor system. Together, these results show that two different observed actions can be represented at the same time in the motor system.

A Formal Theory of Representing Multiple Observed Actions[1]

To understand the relation between perception and action in multi-agent settings, it is important not only to show that the actions of multiple persons can be represented simultaneously in the motor system, but also to provide a formal account of *how* this can be achieved. Therefore, the current section will describe a computational model of the automatic imitation studies conducted in Chapters 2, 5, and 6. Figure 1 shows the model representing the Chapter 2 task. That is, it shows a dual-route model (Cooper, Catmur, & Heyes, 2013) based on the associative sequence learning theory of automatic imitation (Heyes, 2011). The main assumption of the model is that the imperative cue and stimulus movement influence the motor system via separate routes. In particular, it assumes that the imperative cue activates a response via short-term intentional stimulus-response associations established solely for the purpose of the task, while the stimulus movement activates a response via long-term automatic stimulus-response associations established as a consequence of genetic disposition or learning experience (Heyes, 2011). When both routes converge on the correct response, there is an increase in motor activation, and this causes response facilitation. In contrast, when the automatic route activates the incorrect response, response inhibition is required, and this causes response interference instead.

The current model extends an existing model by Cooper et al. (2013). In this model, it was shown that automatic imitation – also known as imitative compatibility – and spatial compatibility can be modeled using the same dual-route mechanism, and that differences in the time course of these two effects (Catmur & Heyes, 2011) can be explained as variations in the processing time of finger location (spatial compatibility) and finger identity (imitative compatibility). The model shown in Figure 1 follows the architecture of the Cooper et al.

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[1] The computational model presented here is based on Cracco, E. & Cooper, R.P. (in prep). Automatic Imitation of Multiple Agents: A Computational Model.

(2013) model but includes an additional stimulus hand to mimic the experimental setup of Chapter 2, in which participants responded to an imperative cue (W or P) while one or two hands moved either the index finger or little finger.

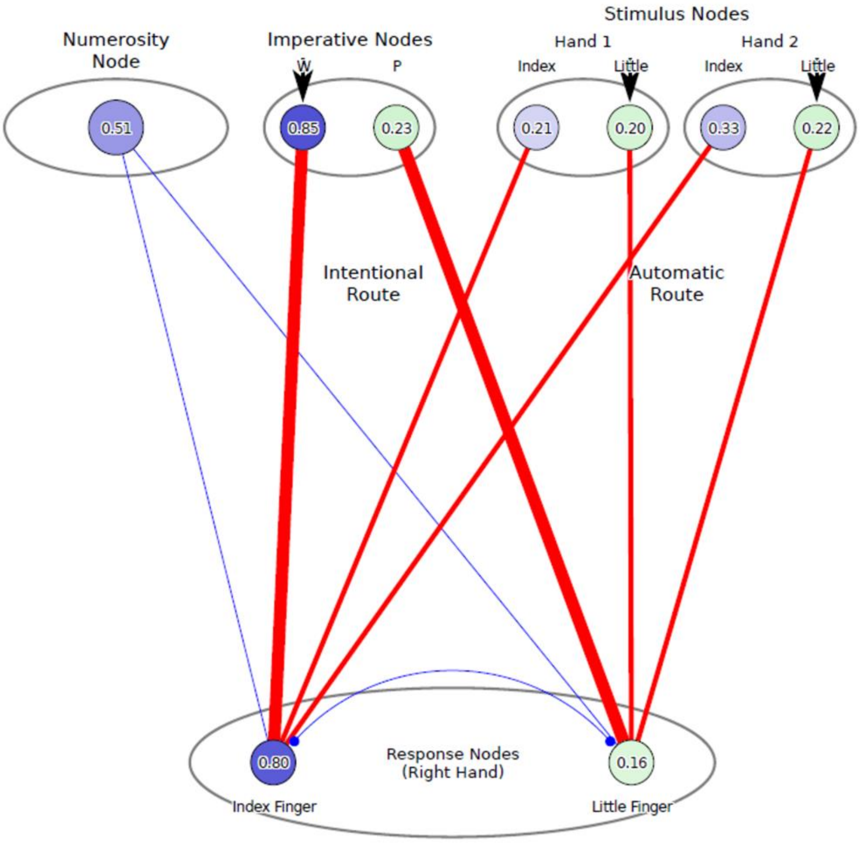

Figure 1. Model architecture used to simulate Chapter 2. The stimulus nodes encode the actions performed by the two stimulus hands. The imperative node encodes the imperative cue. The numerosity node encodes the number of hands performing an action. The stimulus nodes and imperative nodes are connected to the response nodes via excitatory connections (red). The numerosity node is connected to the response nodes via inhibitory connections (blue). Lateral inhibition is implemented at the motor level. The line thickness indicates the strength of the connection.

The stimulus, imperative, and numerosity nodes are visual nodes processing respectively the stimulus movements, the imperative cue, and the number of hands making a movement. Stimulus and imperative node activation is propagated to the motor system via excitatory connections. Imperative-to-motor connections are assumed to be stronger than stimulus-to-motor connections because this is necessary to select the correct response on incongruent trials. Activation in the numerosity node is propagated to the motor system via inhibitory connections. In particular, the numerosity node receives input for each hand making a movement, and then inhibits both motor nodes proportional to the amount of input. This node thus implements the strategic control mechanism proposed in Chapter 5. That is, if motor activation increases with the number of observed movements, imitative control should increase accordingly to prevent overt imitation. In the current model, imitative control was implemented by inhibiting both responses. This is equivalent to increasing the response threshold in the sense that it delays action selection so that premature responses can be be overruled by more deliberate responses (Bogacz, Wagenmakers, Forstmann, & Nieuwenhuis, 2010; Frank, 2006; Munakata et al., 2011; Wiecki & Frank, 2013).

Figure 2 shows the activation profile of the different nodes in a typical two hands incompatible trial. The model first settles for 500 cycles without input to obtain a stable activation level in all nodes. Next, the relevant imperative node is excited. This causes activation in this node to gradually increase until a response is provided after 295 cycles. The numerosity and stimulus nodes are excited respectively 20 cycles before and 80 cycles after the imperative node. The early excitation of the numerosity node was based on evidence that the brain can rapidly estimate the number of items in a visual display (Harvey, Klein, Petridou, & Dumoulin, 2013; Piazza, Izard, Pinel, Le Bihan, & Dehaene, 2004). The late excitation of the stimulus nodes was taken from the Cooper et al. (2013) model. Similar to the imperative nodes, numerosity node activation increases gradually. In contrast, activation in the stimulus nodes is transitory, which corresponds to the transitory nature of the stimulus movements. The activation profile of the response nodes is displayed in the bottom right panel. Activation in the correct response node increases together with activation in the imperative node, whereas activation in the incorrect response node increases together with activation in the stimulus nodes. After initially increasing, activation in the incorrect response node decreases due to a combination of lateral inhibition and activation decay in the stimulus nodes. The model registers a response when activation in one of the two response nodes exceeds the response threshold.

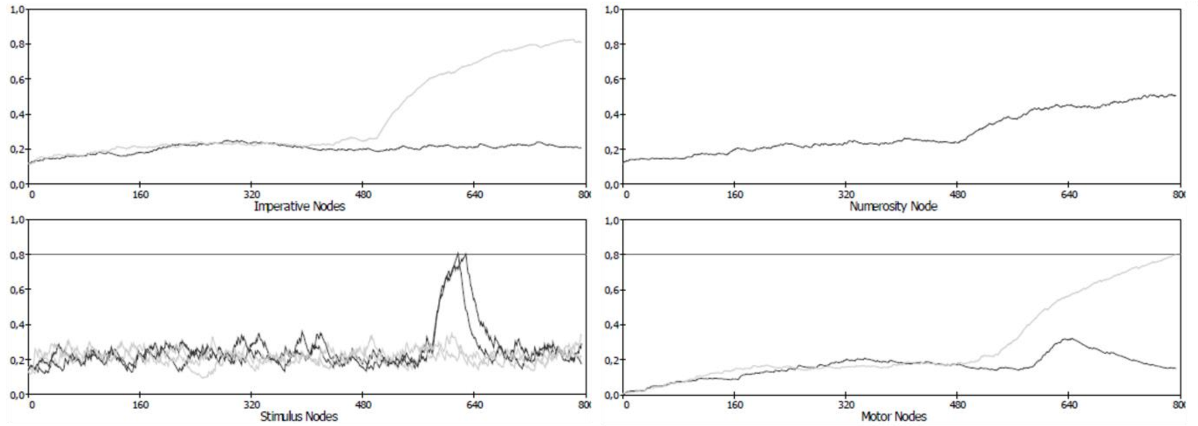

Figure 2. Activation profiles of the different nodes in a typical two hands incompatible trial. The x-axis shows the time course (in cycles) and the y-axis shows the activation level. The activation functions and model parameters were taken from the Cooper et al. (2013) model, with exception of the stimulus node decay parameters and the numerosity node parameters. The stimulus node decay parameters were set so that an effect of 1 cycle roughly corresponded to an effect of 1 ms (see also Cooper et al., 2013). The numerosity node parameters were set so that the facilitation and interference effects were approximately the same size (Genschow et al., 2017).

Figure 3 shows the empirical and simulation results of Chapter 2 Experiment 1. The top panel shows the analysis comparing the condition in which two identical movements were observed (“Two”) with the condition in which a single movement was observed (“One”). The bottom panel shows the analysis comparing the condition in which two different movements were observed (“C/IC”) with the condition in which no movements were observed (“N/N”). As can be seen, the simulation results closely captured the empirical results, indicating that the dual-route model presented in Figure 1 can explain why automatic imitation increased when two identical movements were observed as well as why it disappeared when two different movements were observed.

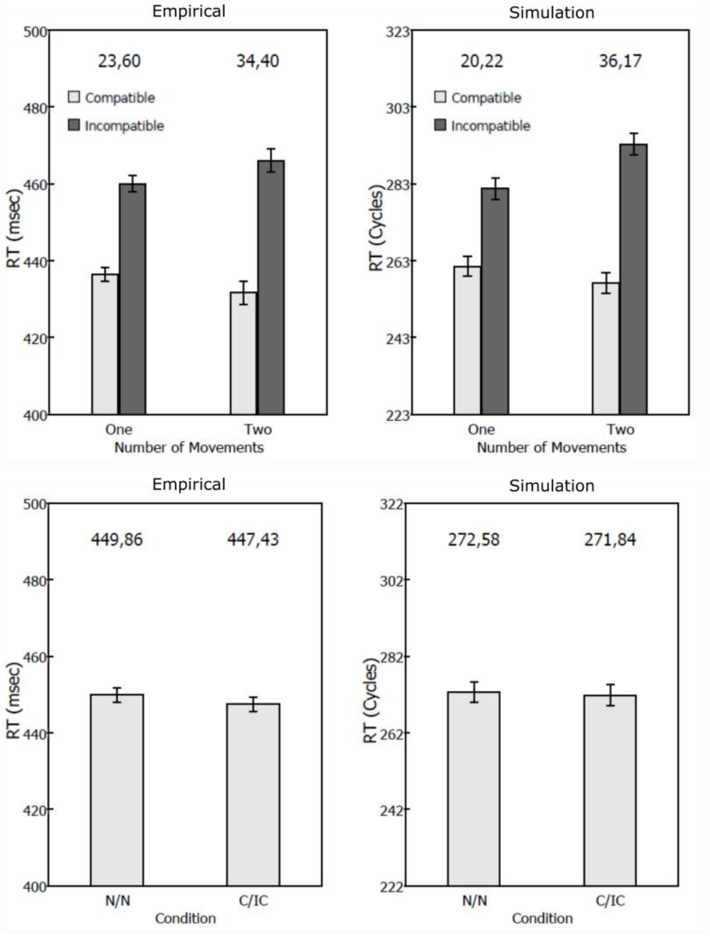

Figure 3. Empirical and simulation results of Chapter 2 Experiment 1. The top panel shows the analysis comparing the condition in which two identical movements were observed (“Two”) with the condition in which a single movement was observed (“One”). The bottom panel shows the analysis comparing the condition in which two different movements were observed (“C/IC”) with the condition in which no movements were observed (“N/N”).

However, can it also explain why reaction times in Chapter 5 decreased with group size according to an asymptotic curve on congruent trials but increased with group size according to a linear curve on incongruent trials? To address this question, two more stimulus hands were added to the model (Figure 4). Figure 5 shows the empirical and simulation results. The top panel describes the experiments in which compatible trials were mixed with incompatible trials (“mixed experiments”). As can be seen, the simulation results accurately described the empirical results. The reason for this is that motor inhibition from the numerosity node increased when more hands made a movement. This then led to an increase in response speed that worked against automatic imitation on congruent trials but together with automatic imitation on incongruent trials, explaining why congruent but not incongruent responses saturated.

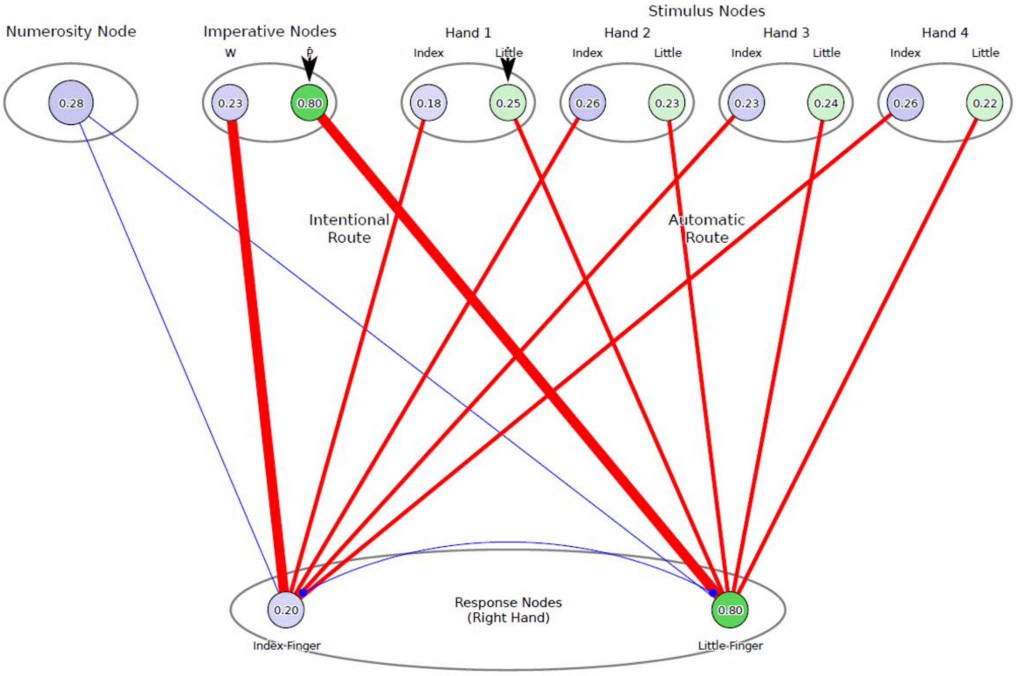

Figure 4. Model architecture used to simulate Chapter 5 and 6. The model is identical to the model presented in Figure 1, but contains four sets of stimulus nodes instead of two sets of stimulus nodes.

The bottom panel shows the experiments in which only compatible trials were included (“non-mixed experiments”). In line with the assumption that imitation should no longer be inhibited when it facilitates task performance, the numerosity-to-motor connections were set to zero for these simulations. Similar to the empirical results, removing the strategic regulation mechanism caused the asymptote to disappear. Thus, taken together, the simulation results support the hypothesis that the asymptote on congruent trials was caused by a strategic regulation mechanism that increased motor inhibition depending on the number of observed movements in order to prevent overt imitation.

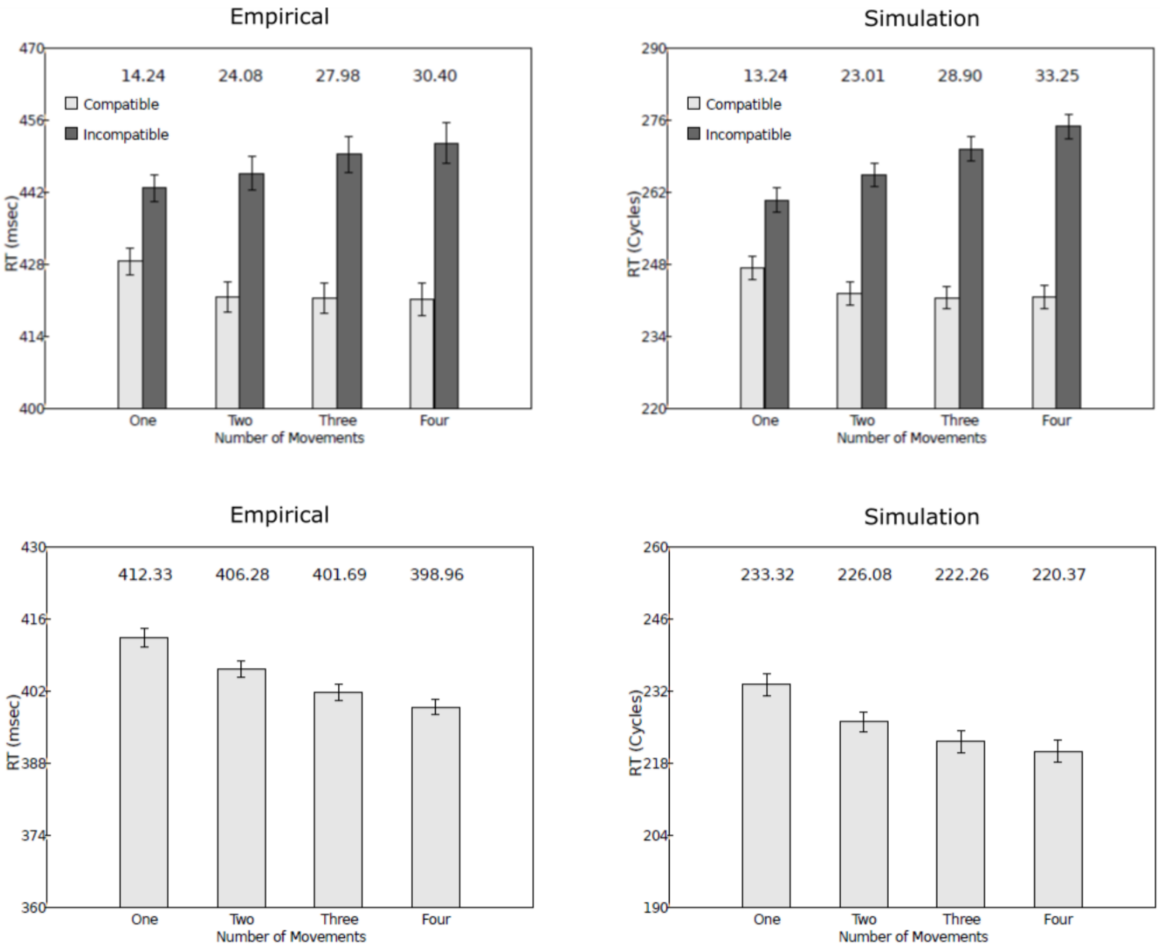

Figure 5. Simulation and empirical results of Chapter 5 using the model presented in Figure 4. The top panel shows the mixed experiments (Experiments 1-2). The bottom panel shows the non-mixed experiments (Experiments 3-6).

Nevertheless, it could be argued that manually setting the numerosity-to-motor weights is reminiscent of a homunculus. Instead, a more mechanistic approach would be to make the model learn how to adjust the weights based on previous experience. Figure 6 presents a model that continuously adjusts the numerosity-to-motor weights on the basis of response conflict. More specifically, the model is identical to the previous model, except for two changes. First, the connections between the numerosity and response nodes now run via a control node. This implements the assumption that motor inhibition is implemented not by visual regions but by executive control regions (Bogacz et al., 2010; Wiecki & Frank, 2013). Second, similar to existing cognitive control models, the connections between the control and motor nodes are learned throughout the experiment on the basis of response conflict (Botvinick, Braver, Barch, Carter, & Cohen, 2001).

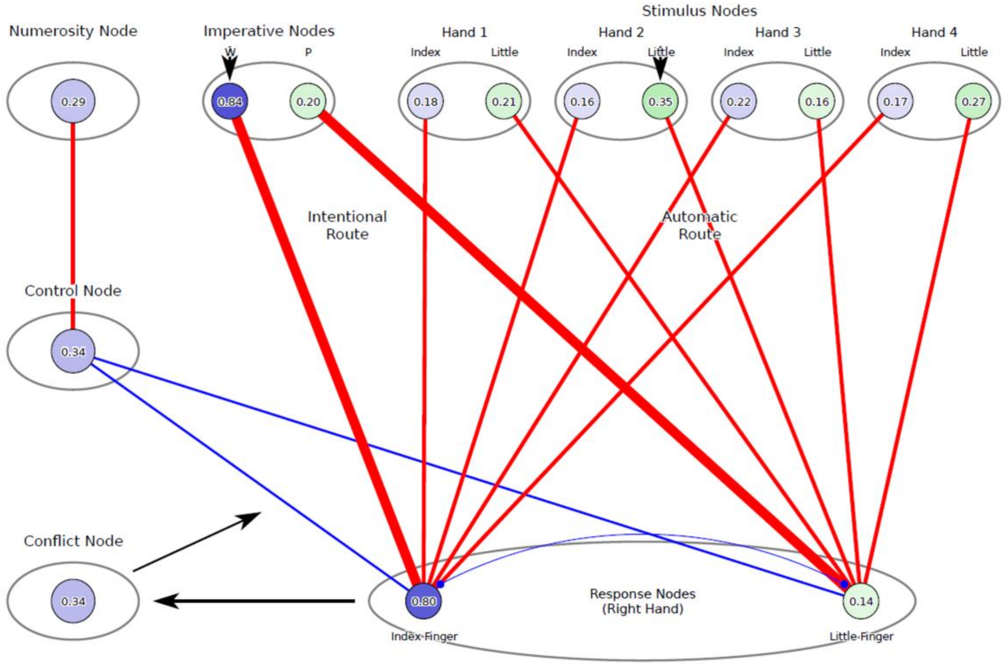

Figure 6. Model architecture used to simulate Chapter 5. The model is identical to the model presented in Figure 4, but the numerosity node now inhibits the response nodes via a control node and the connections from the control node to the response nodes are learned on the basis of response conflict.

In line with previous work, response conflict was modeled as the product of activation in the two response nodes (Botvinick et al., 2001). This means that response conflict is high on incompatible trials, when both response nodes are activated, but low on compatible trials, when only one response node is activated. The control-to-response weights are initially set to zero but are updated on each trial based on the amount of response conflict experienced in the previous trial. That is, when response conflict is high, the weights become more negative. Instead, when response conflict is low, a decay parameter makes the weights tend towards zero (see also Botvinick et al., 2001). Therefore, in the mixed experiments, the control-to-response weights become gradually more negative until they reach a state of equilibrium. In contrast, in the non-mixed experiments, the weights fluctuate around zero.

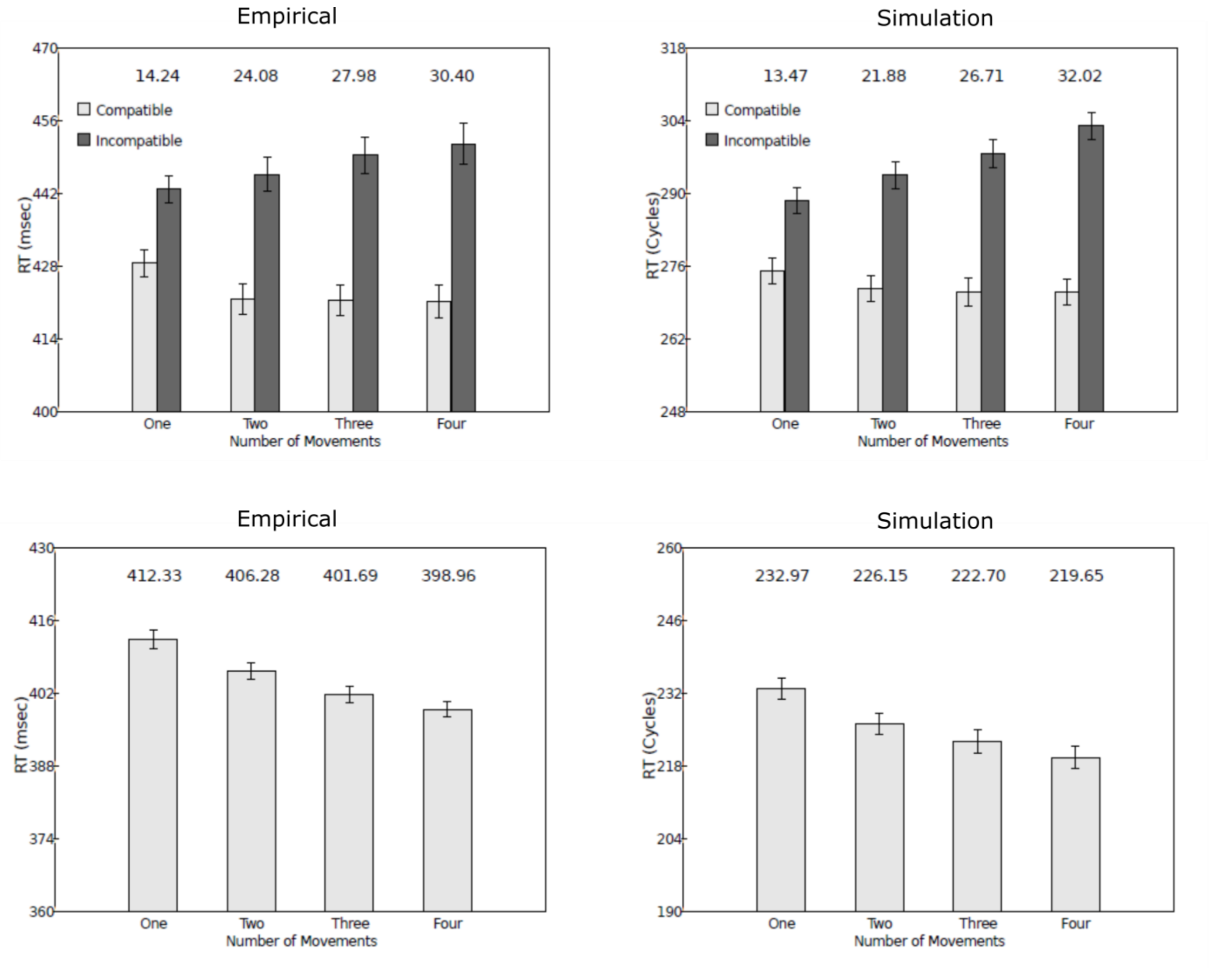

Figure 7. Simulation and empirical results of Chapter 5 using the model presented in Figure 6. The top panel shows the mixed experiments (Experiments 1-2). The bottom panel shows the non-mixed experiments (Experiments 3-6).

Figure 7 shows the results obtained with the response conflict model. As can be seen, the simulation results closely match not only the empirical results but also the simulation results shown in Figure 5. This indicates that the strategic regulation mechanism proposed in Chapter 5 could have been implemented on the basis of response conflict. In other words, the response conflict model provides a mechanistic account of why congruent responses reached an asymptote in the mixed experiments but not in the non-mixed experiments. That is, in the mixed experiments, participants experienced response conflict, which caused them to inhibit motor activation based on the number of observed movements. In contrast, in the non-mixed experiments, participants did not experience response conflict, and no inhibitory control was exerted.

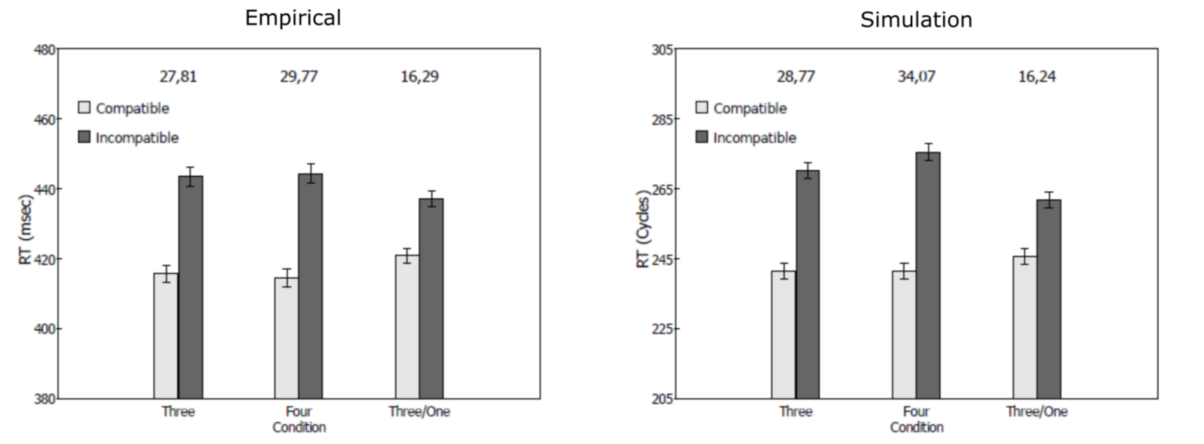

Figure 8. Empirical and simulation results of Experiments 1-2 from Chapter 6. The graphs compare responses in the condition where three hands ("Three") or four hands ("Four") all make the same movement with the condition where three hands make the same movement while the fourth hand performs the other movement ("Three/One").

Finally, the Figure 4 model was used to simulate the results of Chapter 6, in which participants observed four hands of which three hands made the same movement ("Three"), four hands made the same movement ("Four"), or three hands made one movement while the fourth hand made a different movement ("Three/One"). Again, the model accurately captured the behavioral pattern (Figure 8). That is, similar to the empirical results, the model predicted a smaller congruency effect in the Three/One condition than in both the Three condition and in the Four condition.

To conclude, the simulations presented here show that the automatic imitation results of the current dissertation can be explained with a dual-route model that simultaneously codes the different stimulus hands and inhibits motor activation based on the number of observed movements. As such, this model successfully extends perception-action theories from single-agent to multi-agent settings. However, the dual-route architecture is based on the associative sequence learning theory of automatic imitation (Cooper et al., 2013; Heyes, 2011). Therefore, an important question is whether the same results can also be modeled within the ideomotor framework (Brass et al., 2000; Brass, Bekkering, & Prinz, 2001; Brass & Heyes, 2005). On first sight, there is no reason to assume that an ideomotor model would make different predictions. Indeed, it is likely that existing ideomotor models can be extended in a similar way as shown here to explain the results obtained in this dissertation (Haazebroek, Raffone, & Hommel, 2016).

Representing Multiple Agents or Multiple Actions?

While the results indicate that individuals can represent two actions performed by two or more agents in their motor system, it remains an open question whether this differs from representing two actions performed by a single agent. That is, in the present dissertation, there was always one agent for each action. As a consequence, it is not clear whether observers mirrored multiple actions or multiple agents. To address this question, it is interesting to compare the current results with research on bimanual action observation (Heitger, Mace, Jastorff, Swinnen, & Orban, 2012; Möttönen, Farmer, & Watkins, 2010). For example, Heitger et al. (2012) measured brain activation while participants observed one person manipulating an object either with one hand or with both hands. The results revealed that bimanual observed actions did not produce stronger visual or motor activation than unimanual observed actions. Instead, brain activation in the bimanual condition was more bilateral than brain activation in the unimanual condition, which is similar to TMS research showing weak bilateral MEPs during the observation of bimanual gestures relative to a no-movement baseline (Möttönen et al., 2010).

Taken together, it thus appears that seeing two agents performing one action modulates the strength of the motor response, whereas seeing one agent performing two actions modulates its laterality. This, in turn, indicates that individuals represent the same two actions differently depending on whether they are performed by one agent or by two agents. In the same vein, Chapters 6 and 7 revealed that not only mutually compatible but also mutually exclusive actions were represented in the motor system. This illustrates that the motor system can represent two observed actions even when those actions cannot be executed at the same time by a single person, and therefore that this system is sensitive to the number of agents performing the observed actions. From this perspective, an interesting question is what happens when the number of actions is increased further. That is, whereas some studies in the current dissertation presented more than two agents, they never presented more than two actions. Since it is not possible to execute more than two hand actions at the same time, this could provide further insights into how the actions of multiple agents are represented in the brain.

In any case, to fully establish that two actions performed by two agents are represented differently than two actions performed by one agent, future work should compare these two conditions directly. When doing so, an important question is how the brain connects actions to agents. That is, social cognition not only requires us to represent others' actions but also to link each represented action to its corresponding agent. This, in turn, requires individuals to distinguish between multiple external representations ("other-other distinction"). A first hypothesis is that other-other distinction relies on the temporo-parietal junction, which is considered to be a core region in distinguishing between internal ("self) and external ("other") representations (Brass, Derrfuss, & von Cramon, 2005; Brass, Ruby, & Spengler, 2009; Sowden & Catmur, 2013). However, other-other distinction might also rely on visual areas that process person identity. Supporting this view, previous work has shown that the identity of someone grasping an object is encoded in the fusiform gyrus (Ramsey & Hamilton, 2010), a key region in face (Kanwisher, McDermott, & Chun, 1997) and body perception (Downing, 2001).

The Limitations of Representing Multiple Observed Actions

Another interesting question concerns the limitations of representing multiple observed actions. Chapter 5 revealed that automatic imitation increased consistently with group size up to four agents. However, what happens when the number of agents increases beyond this point? To address this question, we have to consider the boundaries of both the motor system and the visual system. Regarding the motor system, research has shown that working memory for observed actions relies on motor processes and is restricted to a maximum of three to four actions (Gao, Bentin, & Shen, 2015; Wood, 2007). This suggests, in other words, that capacity restrictions may prevent the motor system from representing more than four observed actions at a time.

Similar restrictions also apply to the visual system. Indeed, a well-known finding from the numerical cognition literature is that individuals can process up to four items in parallel, but have to use serial counting processes when there are more than four items (Kaufman, Lord, Reese, & Vokmann, 1949; Trick & Pylyshyn, 1994). This suggests that the visual system – like the motor system – is unable represent more than four actions. When this number is exceeded, encoding could instead rely on ensemble processing. In line with this view, it has been shown that individuals often do not represent individual faces but rather represent the average face across all faces (Haberman & Whitney, 2007, 2009). For instance, in one study, participants had to indicate if a test face was happier or sadder than a previously viewed set of four to sixteen faces (Haberman & Whitney, 2007). It was found that participants performed well on this task, but were unable to indicate whether or not they had seen the test face in the probe set. This suggests that the mean emotion across all probe faces was represented even though none of the individual faces were represented. Furthermore, recent work has shown that similar effects can be obtained when estimating the ratio of males to females (Alt, Goodale, Lick, & Johnson, 2017), and that ensemble processing requires only limited attention (Ji, Rossi, & Pourtois, 2018).

Moving to action observation, ensemble processing could be implemented by forming “composite actions” (Cracco, Bardi, et al., 2018). For example, one hand lifting the index finger and another hand lifting the middle finger could be represented as a single hand lifting both the index and middle finger. In line with this hypothesis, meta-analytic evidence indicates that effector compatibility paradigms produce stronger automatic imitation than movement compatibility paradigms (Cracco, Bardi, et al., 2018). That is, an important distinction between these two paradigms is that effector incompatible trials trigger two actions that can be executed at the same time (e.g., lift index and middle finger), whereas movement incompatible trials trigger two actions that cannot be executed at the same time (e.g., lift and tap index finger). Therefore, on effector incompatible trials, the stimulus action (e.g., lift index finger) could be integrated with the response action (e.g., lift middle finger) into a composite action (e.g., lift both index and middle finger). This, in turn, would lead to stronger automatic imitation because it requires participants to inhibit not only the stimulus action but also the composite action. Nevertheless, because direct evidence is currently lacking, further research will be needed to evaluate whether observed actions can be integrated into composite actions.

Moreover, it is also important to consider that not all actions can be integrated into composite actions. For example, when one hand lifts its index finger and another hand taps its index finger, it is not possible to combine both actions into a composite action because they are mutually exclusive in terms of motor execution. Chapter 7 indicated that observing mutually exclusive actions produced motor conflict. However, because this was based on activation in the anterior cingulate cortex (Botvinick et al., 2001; Botvinick, Cohen, & Carter, 2004), additional research is needed to circumvent the reverse inference problem (Poldrack, 2006). A promising approach in this respect could be to look at the consequences of motor conflict. That is, research has shown that response speed is slower (Verguts, Notebaert, Kunde, & Wühr, 2011) and congruency effects smaller (Gratton, Coles, & Donchin, 1992) following incongruent trials than following congruent trials. According to a prominent theory, this is caused by compensatory mechanisms that modulate cognitive processing to optimize task performance following response conflict (Botvinick et al., 2001, 2004). In particular, it is argued that response conflict causes individuals to become more cautious, which increases response speed, and more focused, which decreases congruency effects, in order to prevent future errors.

Implications

Although previous work has shown that perception-action links play a crucial role in social cognition (Gallese, Keysers, & Rizzolatti, 2004; Rizzolatti & Fabbri-Destro, 2008;

Sebanz, Knoblich, Prinz, & Wascher, 2006), little is known about its role in social situations involving more than one agent (Cracco & Brass, 2017, 2018; Cracco et al., 2015; Cracco, De Coster, Andres, & Brass, 2016). By showing that multiple observed actions can be represented simultaneously in the motor system, the current dissertation has important implications for our understanding of social interaction beyond the dyad. In particular, it provides insights into how individuals represent social interactions between two or more persons (Quadflieg & Koldewyn, 2017; Quadflieg & Penton-Voak, 2017) and provides a sensorimotor perspective on the relation between group size and social contagion (Gallup et al., 2012; Knowles & Bassett, 1976; Milgram et al., 1969).

Interaction Representation

To accurately represent our social environment, we not only have to represent others' actions but also their interactions. However, in contrast to action representation, interaction representation has remained largely unexplored (Quadflieg & Koldewyn, 2017; Quadflieg & Penton-Voak, 2017). In a recent theoretical framework, it was argued that interaction representation is supported by three interdependent brain networks, namely the person-perception network, the mentalizing network, and the action observation network (Quadflieg & Koldewyn, 2017). First, the person-perception network consists of visual brain areas in the occipitotemporal cortex involved in recognizing faces (Kanwisher et al., 1997) and bodies (Downing, 2001). Second, the mentalizing network revolves around the medial prefrontal cortex and the temporoparietal junction, and is reliably activated when reasoning about the mental state of others (Schurz, Radua, Aichhorn, Richlan, & Perner, 2014; Van Overwalle & Baetens, 2009). Finally, the action observation network is a network of high-level visual regions, like the superior temporal sulcus, and high-level motor regions, like the inferior parietal lobe and the premotor cortex, that are activated when observing others' actions (Caspers, Zilles, Laird, & Eickhoff, 2010; Molenberghs et al., 2012). While the results of the current dissertation have little to say about the person-perception and mentalizing networks, they have significant implications for the role of the action observation network in interaction representation. In particular, they suggest that individuals may represent observed interactions by simulating the actions of the involved agents in their own motor system (Quadflieg & Koldewyn, 2017; Quadflieg & Penton-Voak, 2017).

Importantly, however, a motor simulation account of interaction representation relies on two crucial assumptions, namely that observers can simulate the actions of multiple agents at the same time and that this allows them to simulate not only their actions but also their interactions (Quadflieg & Koldewyn, 2017; Quadflieg & Penton-Voak, 2017). While the current thesis supports the first assumption, the second assumption remains to be investigated. That is, it is not because individuals can represent multiple observed actions that they can also represent social interactions. To further explore the role of motor processes in interaction representation, future research will have to investigate how motor simulation of multiple actions can lead to motor simulation of interactions. In particular, an interesting hypothesis is that the "composite actions" described earlier contribute to interaction representation because this would enable individuals to represent, for instance, a handshake not as two separate actions but as a single action in the motor system.

Social Contagion

In addition to interaction representation, the current study has important implications for social contagion. Social contagion is the propensity of persons to align their own behavior with the behavior of others (Raafat, Chater, & Frith, 2009). Previous work has shown that social contagion increases with group size (e.g., Fischer et al., 2011; Freedman & Birsky, 1980; Gallup et al., 2012; Milgram et al., 1969) according to an asymptotic curve (Bond, 2005; Gallup et al., 2012; Latane, 1981; Milgram et al., 1969). However, the relation between group size and social contagion has mainly been explained in terms of interpretative processes. In Chapter 5, it was shown that automatic imitation increased with group size according to an asymptotic curve even when the role of interpretative processes was minimized. This supports the hypothesis that not only social cognitive but also sensorimotor processes contribute to social contagion (Raafat et al., 2009). In particular, it suggests that individuals are more likely to copy the behavior of larger groups because larger groups provide a stronger trigger to the motor system.

The sensorimotor account of social contagion is consistent with evidence that motor inhibition increases with the number of bystanders ignoring a person in need even when participants are unable to intervene themselves (Hortensius & De Gelder, 2014). However, it is unlikely that only sensorimotor processes contribute to social contagion. Instead, social contagion is presumably best explained as an interaction between sensorimotor and interpretative processes. For example, when mirror processes trigger the urge to imitate, interpretative processes could be recruited to evaluate whether imitation is reasonable in the present context. From this view, interpretation might function as a gating mechanism that can decide to either inhibit or act on imitative triggers depending on whether or not they are deemed appropriate. In support of this view, neuroimaging has revealed that the conscious decision to imitate is associated with the gating of mirror activation (Bien, Roebroeck, Goebel, & Sack, 2009). Similarly, it has been shown that automatic imitation is inhibited when it would result in the execution of a taboo gesture, and this effect depended on the degree to which the gesture fitted the social context (Cracco, Genschow, Radkova, & Brass, 2018).

Taken together, the current dissertation thus provides an important first step towards a sensorimotor theory of social contagion. Nevertheless, further development of this theory will require a better balance between ecological validity and experimental control. That is, while experimental control is needed to rule out interpretative processes, ecological validity is needed to compare the results to social psychological research on social contagion. A promising approach to balance both sides is to use virtual reality (Maister, Slater, Sanchez-Vives, & Tsakiris, 2015; Sanchez-Vives & Slater, 2005; Slater, Spanlang, Sanchez-Vives, & Blanke, 2010). For example, virtual reality could be used to systematically manipulate the trade-off between experimental control and ecological validity to understand the complex interplay between low-level sensorimotor processes and high-level interpretative processes in social contagion.

Beyond Actions

Finally, while the current thesis shows that multiple observed actions can be represented at the same time in the motor system, social cognition not only requires us to represent the actions of others but also to share their tasks (Sebanz, Bekkering, & Knoblich, 2006) and to represent their perspective (Frischen, Bayliss, & Tipper, 2007; Samson, Apperly, Braithwaite, Andrews, & Bodley Scott, 2010), mental states (Frith & Frith, 2006; Saxe & Kanwisher, 2003), and emotions (Bird & Viding, 2014; Singer et al., 2004). In other words, an important question is the extent to which the results obtained here can be extended to different domains.

Joint Action

When interacting with others, we have to represent not only their actions but also their tasks (Sebanz, Bekkering, et al., 2006). In line with action representation, research indicates that individuals automatically represent their co-actors’ tasks (Atmaca, Sebanz, & Knoblich, 2011; Eskenazi, Doerrfeld, Logan, Knoblich, & Sebanz, 2013; Schmitz, Vesper, Sebanz, & Knoblich, 2017; Sebanz, Knoblich, & Prinz, 2003). For example, Sebanz et al. (2003) investigated whether the Simon effect could still be observed when two participants were each responsible for one response. More specifically, participants saw a hand on the screen pointing either to the left or to the right, but were instructed to ignore this event and to respond to the color of a ring around the hand’s index finger instead. Importantly, rather than responding to both colors, each participant responded to just one color so that one participant responded when the ring was green and the other participant when the ring was red.

The results revealed that responses were faster when the hand pointed to the responding participant than when it pointed to the non-responding participant. However, the same spatial compatibility effect could not be observed when the task was performed alone, indicating that participants automatically represented each other’s task in the joint condition. Although this paradigm has been criticized because similar results can be obtained with non-human co-actors such as pendulums (Dolk, Hommel, Prinz, & Liepelt, 2013), there is now converging evidence from various paradigms that individuals do indeed represent the task of their co-actors (e.g., Eskenazi et al., 2013; Schmitz et al., 2017). Therefore, an interesting question is whether task sharing – like action sharing – can be extended beyond the dyad, and whether this facilitates interpersonal coordination in multi-agent joint action tasks (Cracco & Brass, 2017; Cracco et al., 2015).

Perspective Taking and Mentalizing

Moving even further away from actions, we sometimes also have to represent the perspective of multiple agents. An often-used paradigm to measure perspective taking is the task developed by Samson and colleagues (2010). In this task, participants see a room with an avatar looking at red discs on the walls. The participant always sees all discs. In the consistent condition, the avatar also sees all discs. In contrast, in the inconsistent condition, the avatar sees only a subset of the discs. When having to indicate the number of discs in the room, responses are typically slower in the inconsistent condition than in the consistent condition, indicating that participants automatically represented the perspective of the avatar (“altercentric intrusion effect”).

In recent work, this task was extended to multiple avatars (Capozzi, Cavallo, Furlanetto, & Becchio, 2014). That is, participants observed two avatars looking either at the same discs or at different discs. Relative to a single avatar, altercentric intrusion did not increase when two avatars looked at the same disks and disappeared when two avatars looked at different disks. These results thus indicate that participants do not automatically track the perspective of multiple persons. However, related research suggests that a more nuanced conclusion might be in order (Capozzi, Bayliss, Elena, & Becchio, 2015). In this study, one or seven faces looked to the left or to the right before an object appeared on the cued side or on the non-cued side. When participants had to categorize the object as “kitchen tool” or “garage tool”, they were faster in the cued condition than in the non-cued condition, and this cuing effect did not depend on the number of faces. In contrast, when participants had to provide an affective evaluation of the presented object, they liked the cued objects more than the non-cued objects, but only when the object was looked at by multiple faces. Together, the evidence thus indicates that support for tracking multiple perspectives depends on the dependent measure under investigation.

Importantly, perspective taking is often seen as an initial step towards understanding others’ mental states (Samson et al., 2010). However, whether individuals can represent multiple beliefs in parallel is currently unknown. An interesting study in this respect is the aforementioned study by Hortensius et al. (2014), in which motor inhibition was found to increase with the number of passive bystanders. That is, a plausible explanation for this finding is that participants embodied the bystanders’ mental state, causing them to inhibit motor responses more strongly as the bystanders increased in number (Cracco & Brass, 2018). Nevertheless, more research is needed to better understand multi-belief tracking, and this research should investigate not only identical but also different beliefs.

Conclusion

To conclude, the present dissertation demonstrated across six studies comprising eighteen experiments (N = 816) that observers can simultaneously represent the actions of multiple agents in their motor system, not only when these agents perform identical actions but also when they perform different actions. This provides important insights into the neurocognitive mechanisms supporting social interaction in multi-agent settings, and as such has important implications for research on interaction representation, joint action, and social contagion. However, additional research will be needed to investigate whether individuals represent multiple actions or multiple agents in their motor system, and to establish the limits of representing multiple observed actions. Finally, to obtain a more comprehensive understanding of social interaction beyond the dyad, future research will have to extend the research presented in the current dissertation from actions to tasks, perspectives, and mental states.

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English Summary

The Perception-Action Link

To understand social interaction, a fundamental question is how the actions of others are processed in the brain. While traditional views have emphasized the dissociable nature of perception and action (Hurley, 2001), it has become clear in the past two decades that both processes may be more closely connected than originally thought (Chartrand & Lakin, 2013; Chartrand & van Baaren, 2009; Cracco et al., 2018; Heyes, 2011; Rizzolatti & Sinigaglia, 2010, 2016). More specifically, there are currently three research lines supporting a relation between perception and action, namely research on motor mimicry (Chartrand & Lakin, 2013; Chartrand & van Baaren, 2009), research on automatic imitation (Cracco et al., 2018; Heyes, 2011), and research on the mirror neuron system (Rizzolatti & Sinigaglia, 2010, 2016).

Motor mimicry is the observation that individuals tend to imitate each other during social encounters (Chartrand & Lakin, 2013; Chartrand & van Baaren, 2009). In one of the first studies, participants were asked to take turns in describing photographs with a confederate who was, unbeknownst to the participant, instructed to either rub his face or shake his foot and to either smile or not smile throughout the interaction (Chartrand & Bargh, 1999). The results revealed that participants imitated the confederate without being aware of it. This has important social consequences because people who are being imitated experience social interactions to be smoother (Chartrand & Bargh, 1999; Lakin & Chartrand, 2003; Stel & Vonk, 2010) and behave in a more prosocial manner (van Baaren, Holland, Kawakami, & van Knippenberg, 2004; van Baaren, Holland, Steenaert, & van Knippenberg, 2003).

However, the fact that imitation can occur without awareness does not necessarily imply that it is an involuntary process (Moors & De Houwer, 2006). For example, social reward theories have argued that people use imitation – be it consciously or unconsciously – as a means to obtain positive social consequences (Lakin, Jefferis, Cheng, & Chartrand, 2003;

Stel, van Dijk, & van Baaren, 2016; Wang & Hamilton, 2012). Instead, a process is involuntary if it is beyond voluntary control (Moors & De Houwer, 2006). Evidence for the involuntary nature of imitation comes from research on automatic imitation. In particular, this research has shown that imitation occurs even when it impairs task performance (Cracco et al., 2018; Heyes, 2011). For instance, Brass et al. (2000) instructed participants to lift their index finger in response to the number “1” and their middle finger in response to the number “2”. At the same time, a hand on the screen also lifted its index finger, also lifted its middle finger, or did not move. The results showed that, compared to when the hand did not move (neutral trial), responses were faster and more accurate when the observed action matched the instructed response (congruent trial), but slower and less accurate when the observed action did not match the instructed response (incongruent trial). This finding has now been replicated across a multitude of studies, as was recently demonstrated in a meta-analysis of 226 experiments conducted between 2000 and 2016 (Cracco et al., 2018).

Finally, there is also evidence from neuroscience that perception and action are intimately connected. That is, research on the mirror neuron system has shown across fMRI (Gazzola & Keysers, 2009; Molenberghs, Cunnington, & Mattingley, 2012), TMS (Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995; Naish, Houston-Price, Bremner, & Holmes, 2014), and EEG (Fox et al., 2016; Muthukumaraswamy, Johnson, & McNair, 2004) studies that observed actions are processed not only in the visual but also in the motor areas of the brain (Rizzolatti & Sinigaglia, 2010, 2016). This is consistent with animal studies showing that a subset of neurons in the ventral premotor cortex (Rizzolatti, Fadiga, Gallese, & Fogassi, 1996), the inferior parietal lobe (Rozzi, Ferrari, Bonini, Rizzolatti, & Fogassi, 2008), and the intraparietal sulcus (Fujii, Hihara, & Iriki, 2007) fire both when an action is executed and when the same action is observed (Kilner & Lemon, 2013).

Perception-Action Theories

In sum, the above research demonstrates that there is an intrinsic connection between perception and action. Theories regarding this perception-action link can be divided into specialist and generalist theories (Brass & Heyes, 2005). Specialist theories assume the presence of a special purpose mechanism that is uniquely dedicated to matching observed actions to motor representations (Gallese & Goldman, 1998; Simpson, Murray, Paukner, & Ferrari, 2014). Importantly, this mechanism is often held to be inborn (e.g., Meltzoff & Moore, 1983, 1989), consistent with evidence that imitation occurs already at birth (e.g., Meltzoff & Moore, 1983, 1989). However, recent work has called the evidence supporting neonatal imitation into question (Oostenbroek et al., 2016). Together with evidence that both mirror activation (Catmur, Walsh, & Heyes, 2007; Heyes, 2010) and automatic imitation (Cracco et al., 2018; Heyes, Bird, Johnson, & Haggard, 2005) are sensitive to sensorimotor learning, this supports the view that connections between perception and action might be acquired rather than inborn (Cook, Bird, Catmur, Press, & Heyes, 2014; Heyes, 2010, 2016; Keysers & Perrett, 2004).

The idea that perception-action links are learned is at the core of two related yet distinct generalist theories (Brass & Heyes, 2005). The first theory is the associative sequence learning (ASL) theory (Brass & Heyes, 2005; Cook et al., 2014; Heyes, 2010; Ray & Heyes, 2011). This theory argues that the visual representation of an action is initially unconnected to its motor representations. Instead, it assumes that motor commands gradually become connected to their sensory consequences as a result of contingent co-activation. For example, when we grasp an object, we typically see how our hand grasps the object. Likewise, when we express an emotion, we tend to see the same emotion expressed on the face of others. These experiences lead to bidirectional connections between action perception and action execution.

This, in turn, causes mirror activation (Cook et al., 2014; Heyes, 2010) and therefore also imitation (Cracco et al., 2018; Heyes, 2011).

The second theory, ideomotor theory (IM), extends ASL by assuming an additional mechanism (Brass & Heyes, 2005; Greenwald, 1970; Prinz, 1997; Shin, Proctor, & Capaldi, 2010). Like ASL, IM posits that associative learning leads to connections between visual and motor representations. However, IM also predicts that this learning process culminates in the development of ideomotor representations that code actions in terms of their anticipated sensory consequences (Greenwald, 1970). Given that the visual image of an action is part of its sensory consequences, seeing an action primes the ideomotor representation controlling that action. Thus, according to IM, mirror neurons are the neurophysiological manifestations of ideomotor representations (Brass & Muhle-Karbe, 2014), and priming these representations leads to imitation (Brass et al., 2000; Cracco et al., 2018). In other words, IM and ASL differ in whether or not they assume ideomotor representations, but agree in their emphasis on the role of motor learning (Brass & Heyes, 2005).

The Current Dissertation

While there is already an extensive literature on the perception-action link in situations where a single person watches a single agent, virtually nothing is known about the perception-action link in multi-agent settings. This is surprising because social interaction regularly exceeds a dyadic structure. Therefore, to understand social interaction, it is imperative to study action observation not only in the context of single agents but also in the context of multiple agents. Given the social function of the perception-action link, this could provide important insights into currently understudied social processes such as interaction representation (Quadflieg & Koldewyn, 2017; Quadflieg & Penton-Voak, 2017), group interactions (Ramenzoni, Sebanz, & Knoblich, 2014; Tsai, Sebanz, & Knoblich, 2011), and social contagion (Gallup et al., 2012; Hortensius & De Gelder, 2014; Latane, 1981; Milgram, Bickman, & Berkowitz, 1969).

To this end, the goal of the current dissertation was to investigate whether individuals are able to simultaneously represent the actions of multiple agents in their motor system. When two or more persons perform an action at the same time, they can perform either identical or different actions. The present dissertation looked at both situations, and did so using behavioral as well as neuroscientific methods. In Chapters 2, 4, 5, and 6, automatic imitation was used to measure motor co-representation (Cracco et al., 2018; Heyes, 2011). In Chapters 3 and 7, motor activation was measured during passive observation. In particular, Chapter 3 measured corticospinal excitability with TMS (Naish et al., 2014) and Chapter 7 measured motor brain activation with fMRI (Molenberghs et al., 2012).

Representing Multiple Identical Observed Actions

The question whether multiple identical observed actions can be represented in the motor system was investigated with automatic imitation and TMS. In **Chapter 2**, I measured automatic imitation while participants observed two hands of which either one hand performed an action or both hands performed the same action. The results revealed stronger automatic imitation when two identical actions were observed, indicating that both actions were represented in the motor system. Interestingly, the same additive effect could not be observed for non-human agents, which rules out that it was driven by differences in attentional processing. Instead, for non-human agents, there was an additive effect on slow but not on fast responses. Together, these results thus suggest that attentional processes influenced the effect in early but not in late processing stages. Next, in **Chapter 3**, I used

TMS to obtain a more direct measure of motor activation. That is, I measured corticospinal excitability in a passive observation task with similar stimuli as the ones used in Chapter 2. The results confirmed the results of Chapter 2, with stronger motor responses when two identical actions were observed compared with when a single action was observed. Importantly, this was true even when corticospinal excitability was measured at longer delays where attentional processes no longer contributed (Cracco, De Coster, Andres, & Brass, 2015; Klein, 2000; Samuel & Kat, 2003).

Chapter 4 addressed an alternative explanation for the results of the previous two chapters. That is, it investigated whether participants, instead of representing two hands, randomly represented one hand on each trial. This would cause the probability to represent a moving hand to be 100% when both hands made a movement but only 50% when one hand made a movement. In other words, random sampling would result in an additive effect across trials rather than within trials. To rule out this account, Chapter 4 ensured that the actions of at least one hand were represented on every trial. More specifically, it used a stimulus setup that positioned the two hands close together (Experiments 1-4), and requested participants to either attend to (Experiment 3) or imitate (Experiment 4) the actions performed by one of the two hands. The results revealed an additive imitation effect even though task requirements made it highly unlikely that participants sometimes represented only the non-moving hand. This speaks against a random sampling mechanism and instead suggests that participants simultaneously represented multiple observed actions in their motor system.

Finally, **Chapter 5** extended the number of hands from two to four. Experiments 1-2 showed that the influence of group size on reaction times was characterized by an asymptotic decrease on congruent trials but by a linear increase on incongruent trials. Importantly, however, the asymptotic relation on congruent trials became linear when imitative control was no longer needed, namely in the absence of incongruent trials (Experiments 3-7). This indicates that strategic control processes caused congruent responses to saturate. Indeed, if larger groups provide a stronger motor trigger, then imitative control has to be adjusted accordingly to prevent unwanted imitative responses. The selective asymptote on congruent trials indicates that this was achieved by regulating the response threshold based on the number of observed movements. That is, because a heightened response threshold leads to slower responses, such a mechanism masks decreases in response speed on congruent trials but strengthens increases in response speed on incongruent trials. Interestingly, the finding of an asymptotic relation between group size and automatic imitation closely corresponds to the literature on social contagion in social psychology (e.g., Gallup et al., 2012; Knowles & Bassett, 1976; Milgram, Bickman, & Berkowitz, 1969). This literature has mainly explained social contagion in terms of interpretative processes. In contrast, Chapter 5 used a task that minimized the role of interpretation. As a consequence, it supports the hypothesis that social contagion has a sensorimotor basis.

Representing Multiple Different Observed Actions

The second question, whether the motor system can also represent multiple different observed actions, was investigated with automatic imitation and fMRI. First, **Chapter 2** used an automatic imitation paradigm comparing responses in a condition where two stimulus hands performed different actions with responses in a condition where neither stimulus hand performed an action. The results revealed that performance in these two conditions could not be distinguished. Given that seeing two different actions corresponded to seeing one congruent action and one incongruent action, this indicates that both actions were represented at the same time in the motor system, producing a concurrent facilitation and interference effect that cancelled out each other. However, another explanation could be that participants represented neither action. Therefore, to address this issue, **Chapter 6** extended the number of stimulus hands from two to four. This, then, allowed me to compare two conditions in which three or four hands performed the same action with a condition in which three hands performed one action and the fourth hand performed a different action. The results revealed weaker automatic imitation in the third condition than in the other two conditions, indicating that the actions of all four hands were represented together in the motor system even when they performed different actions.

Finally, **Chapter 7** directly measured motor activation during passive observation using fMRI. In this study, participants observed two right hands performing sign language gestures. Three key results were obtained. First, the motor system was activated more strongly when two different gestures were observed compared with when a single gesture was observed. Second, both individual gestures could be decoded simultaneously from activation in the motor system using multivariate analysis techniques. Third, observing two different compared with two identical gestures activated brain areas associated with motor conflict, and this activation was correlated with activation in the motor system. Together, these results show that two different observed actions can be represented at the same time in the motor system.

Conclusion

To conclude, the present dissertation showed across six studies comprising eighteen experiments (N = 816) that observers can simultaneously represent the actions of multiple agents in their motor system, not only when these agents perform identical actions but also when they perform different actions. This provides important insights into the neurocognitive mechanisms supporting social interaction in multi-agent settings, and as such has important implications for research on interaction representation, joint action, and social contagion. However, additional research will be needed to investigate whether individuals represent multiple actions or multiple agents in their motor system, and to establish the limits of representing multiple observed actions. Finally, to obtain a more comprehensive understanding of social interaction beyond the dyad, future research will have to extend the research presented in the current dissertation from actions to tasks, perspectives, and mental states.

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Nederlandstalige Samenvatting

De Perceptie-Actie Link

Om sociale interactie te begrijpen, is het essentieel om te weten hoe de acties van anderen verwerkt worden in onze hersenen. Hoewel perceptuele en motorische processen traditioneel als twee dissocieerbare processen werden gezien (Hurley, 2001), lijkt het er na twee decennia onderzoek steeds meer op dat ze in realiteit sterk met elkaar verweven zijn (Chartrand & van Baaren, 2009; Cracco et al., 2018; Heyes, 2011; Rizzolatti & Sinigaglia, 2010). Meer specifiek zijn er momenteel drie belangrijke onderzoekslijnen die een relatie tussen perceptie en actie ondersteunen, namelijk onderzoek naar motorische mimicry (Chartrand & Lakin, 2013; Chartrand & van Baaren, 2009), onderzoek naar automatische imitatie (Cracco et al., 2018; Heyes, 2011), en onderzoek naar het spiegelneuronsysteem (Rizzolatti & Sinigaglia, 2010, 2016).

Motorische mimicry is de neiging om elkaar te imiteren tijdens sociale interacties (Chartrand & Lakin, 2013; Chartrand & van Baaren, 2009). In één van de eerste studies naar mimicry werd aan participanten gevraagd om foto’s te beschrijven aan een medewerker die zonder medeweten van de participant geïnstrueerd was om op regelmatige tijdstippen ofwel aan zijn gezicht te krabben ofwel zijn voet te schudden en om daarnaast ook al dan niet te glimlachen doorheen het experiment (Chartrand & Bargh, 1999). De resultaten toonden aan dat participanten de medewerker imiteerden zonder dat ze zich hiervan bewust waren. Dit heeft belangrijke sociale gevolgen, aangezien mensen die geïmiteerd worden sociale interacties als aangenamer ervaren (Chartrand & Bargh, 1999; Lakin & Chartrand, 2003; Stel & Vonk, 2010) en zich prosocialer gaan gedragen (van Baaren, Holland, Kawakami, & van Knippenberg, 2004; van Baaren, Holland, Steenaert, & van Knippenberg, 2003).

Het feit dat imitatie zonder bewustzijn kan plaatsvinden betekent echter nog niet dat het ook onvrijwillig is (Moors & De Houwer, 2006). Zo wordt in sociale beloningstheorieën beweerd dat we imitatie – zij het bewust of onbewust – als middel gebruiken om sociale voordelen te verkrijgen (Lakin, Jefferis, Cheng, & Chartrand, 2003; Stel, van Dijk, & van Baaren, 2016; Wang & Hamilton, 2012). Om uit te maken of een proces onvrijwillig is, moet onderzocht worden of het gecontroleerd kan worden (Moors & De Houwer, 2006). Evidentie voor het onvrijwillige karakter van imitatie komt voornamelijk uit onderzoek naar automatische imitatie (Cracco et al., 2018; Heyes, 2011). De hoofdbevinding van dit onderzoek is dat mensen elkaar imiteren zelfs wanneer dit taakprestaties belemmert. Zo moesten deelnemers in een studie van Brass en collega's (2000) reageren op het nummer "1" door hun wijsvinger op te heffen en op het nummer "2" door hun middelvinger op te heffen. Tegelijkertijd hief ook een hand op het scherm de wijsvinger, de middelvinger, of geen enkele vinger op. De resultaten toonden aan dat deelnemers sneller en accurater reageerden wanneer de geobserveerde actie overeenkwam met de vereiste actie (congruente trial), maar trager en minder accuraat wanneer dit niet zo was (incongruente trial), vergeleken met wanneer de hand niet bewoog (neutrale trial). Bovendien is deze bevinding ondertussen reeds veelvuldig gerepliceerd, zoals recent werd aangetoond in een meta-analyse van 226 experimenten uitgevoerd tussen 2000 en 2016 (Cracco et al., 2018).

Tot slot is er ook vanuit de neurowetenschappen evidentie dat perceptie en actie nauw met elkaar verbonden zijn. Meer specifiek heeft onderzoek naar het spiegelneuronsysteem aan de hand van fMRI (Gazzola & Keysers, 2009; Molenberghs, Cunnington, & Mattingley, 2012), TMS (Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995; Naish, Houston-Price, Bremner, & Holmes, 2014), en EEG (Fox et al., 2016; Muthukumaraswamy, Johnson, & McNair, 2004) studies aangetoond dat geobserveerde acties niet enkel in visuele maar ook in motorische hersengebieden verwerkt worden (Rizzolatti & Sinigaglia, 2010, 2016). Dit komt overeen met onderzoek bij dieren waarin werd gevonden dat bepaalde neuronen in de ventrale premotor cortex (Rizzolatti, Fadiga, Gallese, & Fogassi, 1996), inferieur pariëtale cortex (Rozzi, Ferrari, Bonini, Rizzolatti, & Fogassi, 2008), en intrapariëtale sulcus (Fujii, Hihara, & Iriki, 2007) zowel vuren tijdens het uitvoeren van een actie als tijdens het observeren van diezelfde actie (Kilner & Lemon, 2013).

Perceptie-Actie Theorieën

Samengevat toont bovenstaand onderzoek dus aan dat er een intrinsieke connectie is tussen perceptie en actie. Theorieën hieromtrent kunnen ruwweg opgedeeld worden in “specialist” en “generalist” theorieën (Brass & Heyes, 2005). De eerste categorie, met name de specialist theorieën, veronderstelt een gespecialiseerd mechanisme dat geobserveerde acties linkt aan hun motor representatie (Gallese & Goldman, 1998; Simpson, Murray, Paukner, & Ferrari, 2014). Een belangrijke assumptie hierbij is bovendien dat dit een aangeboren mechanisme betreft (Meltzoff & Moore, 1983, 1989), in overeenstemming met evidentie dat imitatie reeds voorkomt bij pasgeboren baby’s (Meltzoff & Moore, 1983, 1989). Dit laatste is echter in twijfel getrokken door recenter onderzoek (Oostenbroek et al., 2016). Daarnaast hebben verscheidene studies aangetoond dat zowel spiegelneuronactivatie (Catmur, Walsh, & Heyes, 2007; Heyes, 2010) als automatische imitatie (Cracco et al., 2018; Heyes, Bird, Johnson, & Haggard, 2005) gevoelig zijn aan sensorimotorische training. Samengenomen lijkt het er dus steeds meer op dat het verband tussen perceptie en actie niet aangeboren is, maar zich in plaats daarvan ontwikkelt doorheen de levensloop (Cook, Bird, Catmur, Press, & Heyes, 2014; Heyes, 2010, 2016; Keysers & Perrett, 2004).

De idee dat perceptie-actie connecties ontstaan ten gevolge van algemene leermechanismes ligt aan het hart van de generalist theorieën (Brass & Heyes, 2005). Een eerste belangrijke generalist theorie is de zogenaamde associatief sequentieleren (ASL) theorie (Brass & Heyes, 2005; Cook et al., 2014; Heyes, 2010; Ray & Heyes, 2011). Deze theorie stelt dat visuele en motorische actierepresentaties initieel onafhankelijk zijn, maar vervolgens gradueel met elkaar verbonden raken als gevolg van contingente co-activatie. Bijvoorbeeld, wanneer we een object vastnemen, dan zien we meestal hoe onze hand dit object grijpt. Deze ervaringen leiden tot bidirectionele connecties tussen actie observatie en actie executie die spiegelneuronactiviteit (Cook et al., 2014; Heyes, 2010) en dus ook imitatie teweegbrengen (Cracco et al., 2018; Heyes, 2011).

De tweede generalist theorie is de ideomotor (IM) theorie (Brass & Heyes, 2005; Greenwald, 1970; Shin, Proctor, & Capaldi, 2010). Net zoals ASL stelt IM dat associatief leren leidt tot bidirectionele connecties tussen visuele en motorische actierepresentaties. Daarnaast voorspelt IM echter ook dat dit leerproces uitmondt in het ontstaan van ideomotor representaties die acties coderen aan de hand van hun geanticipeerde sensorische uitkomsten (Greenwald, 1970). Aangezien actie observatie een gevolg is van actie executie, activeert volgens deze theorie het zien van een actie de ideomotor representatie die de geobserveerde actie controleert. Dit betekent dat spiegelneuronen binnen dit kader gezien kunnen worden als de neurofysiologische manifestaties van ideomotor representaties (Brass & Muhle-Karbe, 2014) en dat het activeren van deze representaties leidt tot imitatie (Brass et al., 2000; Cracco et al., 2018). Samengevat zijn ASL en IM het dus eens over de rol van leren bij het ontwikkelen van perceptie-actie connecties, maar verschillen ze over de noodzaak van ideomotor representaties (Brass & Heyes, 2005).

Het Huidige Proefschrift

Hoewel er reeds een uitgebreide literatuur bestaat over de perceptie-actie link in situaties waarin één persoon een andere persoon observeert, is er tot dusver heel weinig geweten over de perceptie-actie link in multi-actor settings. Dit is verrassend, aangezien sociale interactie regelmatig de samenwerking van meerdere personen vereist. Om sociale interactie te begrijpen is het daarom van essentieel belang om actie observatie niet alleen te bestuderen in de context van één enkele actor, maar ook in de context van meerdere actoren. Gezien de sociale functie van de perceptie-actie link kan dit immers belangrijke inzichten opleveren over voorlopig weinig begrepen sociale processen zoals interactie representatie (Quadflieg & Koldewyn, 2017; Quadflieg & Penton-Voak, 2017), groepsinteractie (Ramenzoni, Sebanz, & Knoblich, 2014; Tsai, Sebanz, & Knoblich, 2011), en sociale besmetting (Gallup et al., 2012; Hortensius & De Gelder, 2014; Latane, 1981; Milgram, Bickman, & Berkowitz, 1969).

Het doel van het huidige proefschrift was om hieraan bij te dragen door te onderzoeken of individuen in staat zijn om meerdere geobserveerde acties tegelijk te representeren in hun motorisch systeem. Wanneer twee of meer personen tegelijk een actie uitvoeren, kunnen deze acties ofwel identiek ofwel verschillend zijn. In dit proefschrift werden beide situaties bestudeerd, en dit niet alleen met gedragsmatige, maar ook met neurowetenschappelijke methoden. In Hoofdstukken 2, 4, 5, en 6 werd motorische co-representatie gemeten door middel van automatische imitatie (Cracco et al., 2018; Heyes, 2011). In Hoofdstukken 3 en 7 werd vervolgens motorische activiteit gemeten tijdens passieve observatie. Meer specifiek werd in Hoofdstuk 3 de corticospinale exciteerbaarheid gemeten met TMS (Naish et al., 2014) en werd in Hoofdstuk 7 de motorische hersenactiviteit gemeten met fMRI (Molenberghs et al., 2012).

Meerdere Identieke Geobserveerde Acties Representeren

De vraag of meerdere identieke geobserveerde acties in het motorisch systeem kunnen gerepresenteerd worden, werd onderzocht aan de hand van automatische imitatie en TMS.

Hoofdstuk 2 keek naar automatische imitatie van twee handen waarvan ofwel één hand een actie uitvoerde ofwel beide handen dezelfde actie uitvoerden. De resultaten toonden aan dat twee identieke geobserveerde acties sterkere automatische imitatie teweegbrachten dan een enkele geobserveerde actie, wat erop wijst dat beide acties tegelijk in het motorisch systeem werden gerepresenteerd. Hetzelfde additief effect was echter niet aanwezig wanneer houten handen in plaats van menselijke handen werden gebruikt. Meer specifiek werd in deze conditie enkel een additief effect gevonden bij snelle, maar niet bij trage reacties. Dit wijst erop dat aandachtsprocessen het effect beïnvloedden in vroege verwerkingsstadia, maar daarna uitdoofden in latere stadia. Het bekomen additief effect werd vervolgens verder onderzocht in **Hoofdstuk 3** door corticospinale exciteerbaarheid te meten met TMS tijdens een passieve observatietaak met gelijkaardige stimuli als in Hoofdstuk 2. De resultaten bevestigden de bevindingen van Hoofdstuk 2 in de zin dat twee identieke geobserveerde acties sterkere motorische resonantie uitlokten dan een enkele geobserveerde actie. Dit effect werd bovendien gevonden ondanks het feit dat TMS werd toegediend op latere tijdstippen waar aandachtsprocessen geen invloed meer kunnen uitoefenen (Cracco, De Coster, Andres, & Brass, 2015; Klein, 2000; Samuel & Kat, 2003).

In **Hoofdstuk 4** werd een alternatieve verklaring onderzocht voor de resultaten van de vorige twee hoofdstukken. Meer precies werd nagegaan of deelnemers, in plaats van beide handen tegelijk te representeren, mogelijk telkens één hand at random representeerden. Dit zou er immers voor zorgen dat de kans om een bewegende hand te representeren 100% was wanneer beide handen een actie uitvoerden, maar slechts 50% wanneer één hand een actie uitvoerde. Met andere woorden, deze theorie stelt dat het bovengenoemde additief effect niet binnen trials maar over trials tot stand kwam. Om dit uit te sluiten, werd er in Hoofdstuk 4 voor gezorgd dat minstens één hand gerepresenteerd werd op elke trial. Dit gebeurde door een stimulusopzet te gebruiken waarbij de twee handen dicht bij elkaar gepositioneerd stonden

(Experimenten 1-4) en door aan participanten te vragen om hun aandacht te richten op de acties van één van de twee handen (Experiment 3) of om deze acties te imiteren (Experiment 4). Er werd opnieuw een additief effect gevonden hoewel het nu niet langer waarschijnlijk was dat participanten soms enkel de niet-bewegende hand representeerden. Deze bevinding druist dus in tegen de random representatie theorie en wijst in plaats daarvan richting de simultane representatie theorie.

Tot slot werd in **Hoofdstuk 5** het aantal handen uitgebreid van twee naar vier. Experimenten 1-2 toonden aan dat de invloed van het aantal handen op reactietijden gekenmerkt werd door een asymptotische daling op congruente trials en door een lineaire stijging op incongruente trials. Wanneer geen imitatieve controle meer nodig was, met name in de afwezigheid van incongruente trials, werd echter gevonden dat de asymptotische daling op congruent trials veranderde in een min of meer lineaire daling (Experimenten 3-7). Dit doet vermoeden dat strategische controleprocessen ervoor zorgden dat congruente reactietijden een asymptoot bereikten. Als motorische activiteit stijgt naargelang het aantal geobserveerde acties, dan moet de uitgeoefende controle immers meestijgen om te voorkomen dat de handen ongewenst worden geïmiteerd. De selectieve asymptoot op congruente trials wijst erop dat dit gebeurde door de responsgrens te reguleren op basis van het aantal geobserveerde acties. Een verhoogde responsgrens zorgt namelijk voor tragere reactietijden en werkt dus tegen de reactietijddaling op congruente trials, maar samen met de reactietijdstijging op incongruente trials. Interessant hierbij is ook dat de geobserveerde asymptotische relatie sterke gelijkenissen vertoont met de literatuur omtrent sociale besmetting binnen de sociale psychologie (Gallup et al., 2012; Knowles & Bassett, 1976; Milgram et al., 1969). Deze literatuur heeft sociale besmetting echter voornamelijk verklaard aan de hand van interpretatieve processen. De bevindingen van Hoofdstuk 5 suggereren daarentegen dat sociale besmetting ook een sensorimotorische basis heeft, aangezien de gebruikte taak weinig interpretatie toeliet.

Meerdere Verschillende Geobserveerde Acties Representeren

De tweede vraag, of het motorisch systeem ook meerdere verschillende geobserveerde acties kan representeren werd onderzocht aan de hand van automatische imitatie en fMRI. In **Hoofdstuk 2** werd eerst een automatische imitatietaak gebruikt waarin reacties in een conditie waar twee handen verschillende acties uitvoerden werden vergeleken met reacties in een conditie waar twee handen geen enkele actie uitvoerden. De resultaten wezen uit dat er geen verschil was in reactietijden tussen deze twee condities. Aangezien de conditie met twee verschillende acties in deze taak overeenkomt met het zien van één congruente en één incongruente actie, is een mogelijke verklaring dat beide acties gerepresenteerd werden in het motorisch systeem en dat dit twee tegenstrijdige effecten teweegbracht die elkaar vervolgens teniet deden. Een tweede mogelijke verklaring is echter dat geen van beide acties verwerkt werd. Om deze verklaring uit te sluiten werd in **Hoofdstuk 6** het aantal handen uitgebreid van twee naar vier. Dit maakte het mogelijk om twee condities waarin drie of vier handen dezelfde actie uitvoerden te vergelijken met een conditie waarin drie handen één actie uitvoerden en de vierde hand een andere actie uitvoerde. De resultaten toonden aan dat automatische imitatie minder sterk was in de derde conditie dan in de twee andere condities, wat erop wijst dat alle vier de handen tegelijk in het motorisch systeem gerepresenteerd werden zelfs wanneer ze verschillende acties uitvoerden.

Tot slot gebruikte **Hoofdstuk 7** fMRI om hersenactiviteit te meten tijdens een passieve observatietaak. In deze studie zagen de deelnemers twee rechterhanden die gelijktijdig gebaren uitvoerden uit de gebarentaal. Drie belangrijke resultaten werden bekomen. Het eerste resultaat is dat het motorisch systeem sterker geactiveerd was wanneer twee verschillende gebaren geobserveerd werden dan wanneer een enkel gebaar geobserveerd werd. Het tweede resultaat is dat beide individuele gebaren tegelijk gedecodeerd konden worden uit de motorische hersenactivatie door middel van multivariate analysetechnieken. Tot slot is het derde resultaat dat het zien van twee verschillende gebaren ten opzichte van twee identieke gebaren zorgde voor activatie in hersengebieden die geassocieerd zijn met het verwerken van motorisch conflict. Samengevat betekent dit dus dat het motorische systeem niet alleen twee identieke, maar ook twee verschillende geobserveerde acties tegelijk kan verwerken.

Conclusie

Het huidige proefschrift toonde doorheen zes studies met in totaal achttien experimenten (N = 816) aan dat de acties van verschillende actoren tegelijk in het motorisch systeem kunnen gerepresenteerd worden, zowel wanneer de actoren identieke acties uitvoeren als wanneer ze verschillende acties uitvoeren. Dit biedt meer inzicht in de neurocognitieve mechanismen die sociale interactie ondersteunen in multi-actor settings en heeft daarom belangrijke implicaties voor onderzoek naar interactie representatie, groepsinteracties, en sociale besmetting. Er blijven echter ook een aantal belangrijke vragen over. Zo is het voorlopig niet duidelijk of het motorisch systeem meerdere actoren dan wel meerdere acties representeert, en is meer onderzoek nodig om de limieten van het representeren van meerdere acties na te gaan. Tot slot wordt een belangrijke taak voor verder onderzoek om niet alleen het representeren van meerdere acties, maar ook het representeren van meerdere taken, perspectieven, en gedachten te bestuderen.

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Data Storage Fact Sheets

% Chapter 2 (Motor Simulation Beyond the Dyad: Automatic Imitation of Multiple Actors)
% Author: Emiel Cracco
% Date: 19-02-2018

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2. Information about the datasets to which this sheet applies

* Reference of the publication in which the datasets are reported: Cracco, E., De Coster, L., Andres, M., & Brass, M. (2015). Motor simulation beyond the dyad: Automatic imitation of multiple actors. Journal of Experimental Psychology: Human Perception and Performance, 41(6), 1488-501.

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% Chapter 3 (Mirroring multiple agents: Motor resonance during action observation is modulated by the number of agents)
% Author: Emiel Cracco
% Date: 19-02-2018

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% Chapter 4 (Automatic Imitation of Multiple Agents: Simultaneous or Random Representation?)
% Author: Emiel Cracco
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% Chapter 5 (The role of sensorimotor processes in social group contagion)
% Author: Emiel Cracco
% Date: 19-02-2018

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* Reference of the publication in which the datasets are reported: Cracco, E., & Brass, M. (in press). The role of sensorimotor processes in social group contagion. Cognitive Psychology.

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3a. Raw data
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3b. Other files
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  - [ ] files(s) containing information about informed consent
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% Chapter 6 (Motor Simulation of Multiple Observed Actions)
% Author: Emiel Cracco
% Date: 19-02-2018

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3b. Other files

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  - [ ] file(s) containing processed data. Specify: ...
  - [X] file(s) containing analyses. Specify: R analysis file
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% Chapter 7 (Representing Multiple Observed Actions in the Motor System)
% Author: Emiel Cracco
% Date: 19-02-2018

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3a. Raw data
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