



Special issue: Research report

Distinct neural processes are engaged in the modulation of mimicry by social group-membership and emotional expressions



Birgit Rauchbauer ^{a,b}, Jasminka Majdandžić ^{a,b}, Allan Hummer ^{c,d},
Christian Windischberger ^{c,d} and Claus Lamm ^{a,b,*}

^a Social, Cognitive and Affective Neuroscience Unit, Department of Basic Psychological Research and Research Methods, Faculty of Psychology, University of Vienna, Vienna, Austria

^b Cognitive Science Research Platform, University of Vienna, Vienna, Austria

^c MR Center of Excellence, Medical University of Vienna, Vienna, Austria

^d Center for Medical Physics and Biomedical Engineering, Medical University of Vienna, Vienna, Austria

ARTICLE INFO

Article history:

Received 30 September 2014

Reviewed 18 November 2014

Revised 22 January 2015

Accepted 4 March 2015

Published online 20 March 2015

Keywords:

Imitation

Mimicry

Chameleon effect

Emotional expressions

Affiliation

ABSTRACT

People often spontaneously engage in copying each other's postures and mannerisms, a phenomenon referred to as behavioral mimicry. Social psychology experiments indicate that mimicry denotes an implicit affiliative signal flexibly regulated in response to social requirements. Yet, the mediating processes and neural underpinnings of such regulation are largely unexplored. The present functional magnetic resonance imaging (fMRI) study examined mimicry regulation by combining an automatic imitation task with facial stimuli, varied on two social-affective dimensions: emotional expression (angry vs happy) and ethnic group membership (in- vs out-group). Behavioral data revealed increased mimicry when happy and when out-group faces were shown. Imaging results revealed that mimicry regulation in response to happy faces was associated with increased activation in the right temporo-parietal junction (TPJ), right dorsal premotor cortex (dPMC), and right superior parietal lobule (SPL). Mimicry regulation in response to out-group faces was related to increased activation in the left ventral premotor cortex (vPMC) and inferior parietal lobule (IPL), bilateral anterior insula, and mid-cingulate cortex (MCC). We suggest that mimicry in response to happy and to out-group faces is driven by distinct affiliative goals, and that mimicry regulation to attain these goals is mediated by distinct neuro-cognitive processes. Higher mimicry in response to happy faces seems to denote reciprocation of an affiliative signal. Higher mimicry in response to out-group faces, reflects an appeasement attempt towards an interaction partner perceived as threatening (an interpretation supported by implicit measures showing that out-group members are more strongly associated with threat). Our findings show that subtle social cues can result in the implicit regulation of mimicry. This regulation serves to achieve distinct affiliative goals, is

* Corresponding author. Social, Cognitive and Affective Neuroscience Unit, Department of Basic Psychological Research and Research Methods, Liebiggasse 5, 1010 Vienna, Austria.

E-mail address: claus.lamm@univie.ac.at (C. Lamm).

<http://dx.doi.org/10.1016/j.cortex.2015.03.007>

0010-9452/© 2015 Elsevier Ltd. All rights reserved.

mediated by different regulatory processes, and relies on distinct parts of an overarching network of task-related brain areas. Our findings shed new light on the neural mechanisms underlying the interplay between implicit action control and social cognition.

© 2015 Elsevier Ltd. All rights reserved.

1. Introduction

Imagine yourself in a conversation with a friend, or even somebody you have just met. You laugh and have a good time and then you might come to notice that you're sitting in the same position: you both have your legs crossed and lean forward in your chair. In many social interactions, individuals unconsciously align their body postures or mannerisms to each other. This engagement in behavioral mimicry has been termed the Chameleon effect (Chartrand & Bargh, 1999), referring to the chameleon-like way in which interaction partners “merge” with their social surroundings (Chartrand & Bargh, 1999; Chartrand & Lakin, 2013; Heyes, 2011; Lakin & Chartrand, 2003). The Chameleon effect has been ascribed multiple socially beneficial functions, such as affiliating and bonding with others (Lakin & Chartrand, 2003; Lakin, Jefferis, Cheng, & Chartrand, 2003; Stel & Vonk, 2010), stabilizing group cohesiveness (Lakin, et al., 2003), and enhancing prosocial behavior (Van Baaren, Holland, Kawakami, & Knippenberg, 2004; Van Baaren, Janssen, Chartrand, & Dijksterhuis, 2009). Moreover, contextual factors such as liking of the interaction partner (Stel et al., 2010), or the goal to affiliate with him or her (Lakin & Chartrand, 2003), have been shown to enhance behavioral mimicry. Conversely, decreased mimicry has been observed in situations in which it is advantageous to inhibit mimicry (Brass, Zysset, & von Cramon, 2001; Spengler, von Cramon, & Brass, 2009), such as disliking an interaction partner (Stel, et al., 2010) or not wanting to affiliate with him or her (Johnston, 2002).

Mimicry thus seems to be regulated in a versatile fashion to different affiliative motives. The present study aimed to identify the (neural) processes engaged in such a flexible regulation of mimicry, in order to gain a better understanding of the role of mimicry in the implicit regulation of social interaction. To this end, we investigated whether and how mimicry of arbitrary finger lifting movements is modulated by salient social signals, i.e., the emotional expressions (happy vs angry) and group-membership (in- vs out-group) of putative interaction partners.

However, behavioral mimicry has thus far mostly been studied by social psychologist, using naturalistic paradigms, which usually manipulated or measured the frequency of mimicking acts in interactions between a participant and a confederate (Chartrand & Bargh, 1999; Lakin, Chartrand, & Arkin, 2008; Stel, et al., 2010; Stel & Vonk, 2010; Van Baaren, et al., 2004; Van Baaren, et al., 2009). While such naturalistic paradigms have high ecological validity, they suffer from a number of limitations. For one, they are limited in their ability to experimentally control social cues relevant for social interactions, such as emotion displays or eye contact. Secondly, measuring the frequency of mimicry provides only a crude quantification of the extent of behavioral mimicry. Also, behavioral measures alone are limited in identifying the

underlying processes regulating mimicry. While neural measures would be more informative in this respect, naturalistic paradigms are hardly suitable for use in neuroimaging experiments, which usually require repeated trials, and whose measurement constraints mostly preclude the investigation of naturalistic social interaction.

Automatic imitation paradigms have therefore been proposed as laboratory models of mimicry (Heyes, 2011), providing an intriguing possibility to study the neural bases of chameleon-like mimicry effects to varying social cues (Heyes, 2011; Klapper, Ramsey, Wigboldus, & Cross, 2014; Wang & Hamilton, 2012, 2014, 2015; Wang, Newport, & Hamilton, 2011; Wang, Ramsey, & Hamilton, 2011). Central to automatic imitation paradigms is the notion that the mere observation of a movement triggers motor resonance processes that facilitate the execution of this very movement (Brass, Bekkering, Wohlschläger, & Prinz, 2000). The label “automatic”, in this context, refers to the fact that the perception-action link operates independently of the explicit intentions of the individual exerting it, as participants are instructed to respond to a number cue (e.g., with a finger-lifting movement (Brass et al., 2000)), but are “automatically” influenced by a simultaneously displayed movement (e.g., a congruent or incongruent finger-lifting movement) acting as a distractor irrelevant to the task at hand (Heyes, 2011).

Notably, there is consistent evidence that situational and contextual variables implicitly modify automatic imitation (Grecucci, Koch, & Rumiati, 2011; Klapper et al., 2014; Leighton, Bird, Orsini, & Heyes, 2010; Wang & Hamilton, 2012, 2014, 2015; Wang, Newport, et al., 2011; Wang, Ramsey, et al., 2011). For instance, automatic imitation has been shown to be modulated by pro-versus antisocial primes (Leighton, et al., 2010; Wang & Hamilton, 2015), the social status of the interaction partner (Wang & Hamilton, 2012), or the occurrence of direct eye-contact (Wang, Newport, et al., 2011; Wang, Ramsey, et al., 2011). Studies by Losin, Iacoboni, Martin, Cross, and Dapretto (2012) & Losin, Cross, Iacoboni, and Dapretto (2014) have investigated the modulation of conscious imitation (i.e., instructed imitation of gestures) by group-membership. Importantly, the results suggest that it is the implicit perception of the out-group's social status and not ethnic¹ similarity per se which modulates conscious imitation and underlying

¹ Note that although the term “racial” has been mostly used in previous work, this term and its use has some problematic connotations in its public use (for instance motivating measures against certain racial groups based on their presumed “biologically determined” inferiority). We therefore prefer to use the term “ethnicity” as a more neutral description of what we are dealing with – i.e., differences between individuals in socio-cultural and physical, but not in biological-genetic terms (AAPA, 1996; see also Lamm & Majdandžić, 2015; Riečanský, Paul, Kölble, Stieger, & Lamm, 2014).

neural processes (Losin et al., 2012; Losin et al., 2014). This is vital to notice, as it suggests that it might be first and foremost implicit perceptions and the relevance of the stimuli for one's own current social interest that are crucial for guiding mimicry in a goal-directed fashion. Overall, the stark analogy with the malleability of mimicry in the Chameleon effect renders automatic imitation paradigms a promising tool to investigate mimicry's versatility in implicitly supporting and improving social interaction. As we are using automatic imitation as a laboratory model of mimicry, we will furthermore refer to automatic imitation assessed with this paradigm as *mimicry*. The term *mimicry effect* will henceforth be used to refer specifically to the difference in reaction times from incongruent versus congruent trials in such automatic imitation paradigms.

Due to their high experimental control and the repeated measurement over multiple trials automatic imitation paradigms also enable studies of mimicry with neuroimaging methods. This allows assessments of the neuro-cognitive mechanisms underpinning the regulation of mimicry in different social contexts and in response to different social signals. In this way some central questions on how the modulation of mimicry is implemented functionally can be addressed. For instance, as proposed by Heyes (2011), the mimicry response could be altered on the one hand by enhanced attention to the task-irrelevant hand stimuli, thus modulating mimicry via input modulation. On the other hand, social-cognitive variables might alter mimicry via modulating its overt behavioral output (i.e., output modulation) (Heyes, 2011). Conducting a functional neuroimaging study might thus allow us to also shed more light on the involvement of in- and output modulation in the course of tailoring mimicry to affiliative goals.

Neuroimaging studies on this topic have thus far mainly focused on understanding the phenomenon of automatic imitation itself (Brass, Derrfuss, & von Cramon, 2005; Catmur & Heyes, 2011, 2013; Catmur, Mars, Rushworth, & Heyes, 2011; Cooper, Catmur, & Heyes, 2013; Sowden & Catmur, 2015; Spengler, et al., 2009). In these studies, the processes underlying mimicry regulation are typically assessed by contrasting incongruent with congruent trials. In this way it has been shown that mimicry regulation using the imitation inhibition task mentioned above has repeatedly revealed increased activation of the medial prefrontal cortex (mPFC) and the temporo-parietal junction (TPJ) (Brass & Heyes, 2005; Brass, Ruby, & Spengler, 2009; Spengler, Brass, Kuhn, & Schutz-Bosbach, 2010; Spengler, et al., 2009). Only few studies have investigated the neural processes associated with the regulation of mimicry when presented with different social signals (e.g., Klapper et al., 2014; Wang & Hamilton, 2014, 2015; Wang, Ramsey, et al., 2011). For instance, the modulation of mimicry when priming participants with pro- and anti-social words has been associated with activation changes in the anterior medial prefrontal cortex (amPFC) (Wang & Hamilton, 2015). Moreover, modulation of mimicry while an "interaction partner" was presented who was either engaging in direct or averted eye-contact was associated with a network comprising the mPFC, the inferior frontal gyrus (IFG) and the superior temporal sulcus (STS) – which all showed higher activation in the direct-gaze condition (Wang & Hamilton, 2012; Wang, Ramsey, et al., 2011). These studies provide

important first insights into the psychological and neural mechanisms of the regulation of mimicry. Nevertheless, given the remarkable flexibility of mimicry, different behavioral goals evoked through relevant information in the social environment may engage different social-cognitive and behavior (mimicry) regulation processes. This should be reflected in distinct neural pathways.

Direct eye-gaze in a social interaction represents an important social signal, as it may express affiliative intent (Wang, Newport, et al., 2011; Wang, Ramsey, et al., 2011). Beside eye contact, emotional expressions likewise are highly salient social cues which might enhance or temper mimicry, respectively. A smile, for example, inherently signals affiliative intention, whereas an angry facial expression rather indicates dominance motives (Bourgeois & Hess, 2008; Van Kleef, De Dreu, & Manstead, 2004, 2010). Hence mimicry should be enhanced in response to smiling others, and decreased when confronted with an angry interaction partner. Another powerful factor in human social life is belonging to a cohesive and functional social group (Dunbar, 2012; Dunbar & Shultz, 2010; Machin & Dunbar, 2011). To signal and to reciprocate affiliation, in order to stabilize social bonds, mimicry might therefore be enhanced more towards in-group members, while out-group members might be imitated less. This has indeed been demonstrated previously (Van der Schalk et al., 2011; Yabar, Johnston, Miles, & Peace, 2006).

On the other hand, some studies have shown opposite effects, suggesting that negative social signals may enhance mimicry. For instance, Grecucci et al. (2011) have shown enhanced mimicry to stimuli with non-social negative valence. Lakin et al. (2008) demonstrated enhanced mimicry after experiencing social rejection, which was interpreted as an attempt to achieve the affiliative goal of regaining social inclusion. As mentioned above, Losin et al. (2012) & Losin et al. (2014) have demonstrated that implicit perceptions of an out-group of low social status modulates conscious imitation and associate neural activations. Thus, implicit social perceptions of an out-group and their relevance for current affiliative goals might also guide mimicry (i.e., unconscious imitation). More specifically, mimicry as an affiliative signal might be up-regulated in response to negative social cues to soothe potentially harmful conflicts (de Waal, 1986, 2003; Keltner, Young, & Buswell, 1997). It has been reported for other primates that, depending on the context, affiliative signals, such as embracing or kissing, may reflect attempts to soothe a potential conflict. Primates seem to display these affiliative behaviors to reduce aggression or prevent a potentially harmful encounter, as an alternative to engaging in withdrawal or fighting behavior (Keltner et al., 1997; de Waal, 1986, 2003). In many western countries, Black out-group members are implicitly perceived as posing enhanced (physical) threat (Amodio, 2004, 2008; Amodio, Devine, & Harmon-Jones, 2008; Amodio et al., 2004; Neuberg & Cottrell, 2008). This might in particular be the case if they display anger. This notion seems to be confirmed by previous behavioral results from our group (Rauchbauer, Majdandžić, Stieger, & Lamm, 2014, 2015). In a series of experiments with more than 180 participants, we revealed enhanced mimicry towards angry Black out-group members, as compared to angry in-group members. Based on these considerations, we suggest that the implicit

perception of angry Black out-group members as threatening might lead to an up-regulation of mimicry for the affiliative goal of appeasement (Rauchbauer et al., 2014, 2015). That is, rather than eliciting reduced mimicry, reflecting a withdrawal or fight signal, angry out-group members might evoke an up-regulation of mimicry which serves to appease the interaction partner and to de-escalate a potential conflict.

These observations suggest that the fine-tuning of mimicry (as an affiliative response) might be even more delicate than previously shown. Moreover, the question emerges how such adaptively tailored modulation of mimicry to distinct affiliative goals, that is, reciprocation of affiliative intent on the one, and appeasement of a potentially threatening encounter on the other hand, is achieved on a process level, and how this is implemented and reflected on the neural level.

The aim of the present study was, therefore, to investigate whether and how mimicry (in this case mimicry of arbitrary finger-lifting movements) is modulated by social-affective variables such as emotion displays and group membership of a putative “interaction partner”. To investigate the behavioral and neuro-cognitive processes associated with this modulation, we used an automatic imitation paradigm while participants underwent functional magnetic resonance imaging (fMRI). We extended the imitation inhibition task developed by Brass et al. (2000), which we, in the context of our design, will refer to as *mimicry task*, by adding social-affective stimuli (social-affective mimicry task (SAMT)). To this end, we presented finger-lifting movements simultaneously with face stimuli differing in ethnic group membership (White/European Caucasian and Black/African-American) and emotional expression (happy and angry). Thus it is important to point out, that we did not measure facial mimicry itself, but were interested in how mimicry of arbitrary finger-lifting movements (carrying no inherent affective or social information) were modulated by task-irrelevant social-affective stimuli. In line with the notion that mimicry might be used as an affiliative signal which is flexibly regulated to varying social requirements, we expected mimicry of the task-irrelevant finger lifting movements to be higher in response to happy facial expressions (signaling affiliative intent) than to angry ones (signaling non-affiliative intent). As for the effects of group-membership previous evidence (reviewed above) suggested an open hypothesis: mimicry might either be enhanced towards in-group members, reflecting affirmation of group bonds, or towards out-group members, in an attempt to appease a potentially threatening interaction partner. Moreover, as our design enabled us to explore interactions between emotion displays and group membership, we predicted based on previous findings (Rauchbauer et al., 2014, 2015) that mimicry should be strongest in response to happy in-group faces, in line with its function to reciprocate affiliative intent, and speculated that it would be stronger in response to angry out-group faces as compared to angry in-group faces, in serving an implicit appeasement function. In the SAMT enhanced mimicry to different social-affective cues is reflected in a uniform measure, which is the magnitude of the mimicry effect. This, however, might not reflect the distinct underlying processes involved in goal-directed regulation of mimicry. Specifically, reciprocation of affiliation and appeasement serve distinct

affiliative goals. The former might aim to ensure continuative positive social interaction with the other (Bourgeois & Hess, 2008; Hess & Fischer, 2013; Van Kleef et al., 2010), whereas the latter might aim to soothe a potentially negative social exchange (Keltner et al., 1997). Thus, such distinct types of goal-directed mimicry regulation might potentially be underpinned by distinct processes and neural mechanisms. This could include attentional and sensorimotor, as well as behavior regulation processes. Moreover, social-cognitive processes involved in representing and actively discerning the representation of others' internal states from one's own current state, as self-other distinction, might be engaged in the regulation of mimicry. These processes may operate at different stages, involving both the modification of sensory input and of behavioral output (see Heyes, 2011). We predicted that these processes should be reflected in the engagement of distinct neural networks.

First, the right TPJ has been assigned a crucial role in self-other distinction, which in the present context is the active distinction of one's own motor representations or intentions from those related to observed actions (Brass et al., 2001; Brass et al., 2005; Brass et al., 2009; Santiesteban, Banissy, Catmur, & Bird, 2012; Spengler et al., 2009; Spengler et al., 2010). Causal evidence from a tDCS-study reports that excitatory tDCS stimulation of the TPJ enhances self-other distinction in the imitation inhibition task (Santiesteban et al., 2012). The TPJ has further been shown to be engaged in the distinction of self-generated movements from those of a human, as opposed to a non-human agent (Klapper et al., 2014). Thus, the TPJ might be of particular importance in an experimental manipulation where salient social signals, as in our case, interfere with one's task requirements, requiring a higher effort to disambiguate one's own actions from those of others, in order to better comply with task demands. The mPFC is another area that might play a role in mimicry regulation, as overlapping neural activation in social-cognition tasks (investigating mentalizing and self-referential judgments) and in the imitation inhibition task have been shown (Spengler et al., 2009). Moreover, the mPFC has been linked to the modulation of mimicry behavior by gaze processing and social context (Wang & Hamilton, 2012, 2015; Wang, Ramsey, et al., 2011), and in tasks that require integrating one's own actions with those of out-group members (specifically African-American) (Amodio, 2008; Amodio, Kubota, Harmon-Jones, & Devine, 2006). In the context of controlling mimicry by eye contact (gaze processing), it is interesting to note that the mPFC has been reported (by means of dynamic causal modeling) to modulate sensory input to the STS and the IFG.

Second, taking into account contextual information in order to regulate mimicry in a goal-directed fashion suggests the involvement of behavior regulation processes sensitive to social needs. Behavioral and homeostatic regulation, in particular in the social domain, have been repeatedly linked to a network including the anterior insula (AI) and the mid-cingulate cortex (MCC; e.g., Lamm & Singer, 2010; Medford & Critchley, 2010; Shackman et al., 2011). In the present context, these areas might constitute an in- and output module aimed at the regulation of mimicry. The AI, the input-module, codes sensory multi-modal information of the social environment and signals the need for behavioral regulation to

the output-module, the MCC. Moreover, recent evidence specifically reports involvement of the (AI) and anterior parts of the MCC in the control of mimicry (Cross, Torrisi, Losin, & Iacoboni, 2013).

Third, modulation of sensorimotor processes might allow us to clarify how modifications of mimicry are accompanied by changes in attentional processing of the primary task (the number cue) versus the (task-irrelevant) hand stimulus. Since evidence on the malleability of mimicry by salient social cues is scarce (with the exception of e.g., Wang & Hamilton, 2012, 2014, 2015; Wang, Ramsey, et al., 2011), hypotheses about the specific roles of these processes in modifying mimicry in response to our social-affective context manipulation were open. More in general, in line with the different presumed functions of mimicry in either reciprocating affiliative intent, or in appeasing a threatening interaction partner, we predicted that there is no unitary process engaged in all kinds of mimicry regulation, but that distinct processes, engaging different neural networks, underlie mimicry's flexibility.

2. Material and methods

2.1. Participants

Overall we tested 50 white European-Caucasian (predominantly Austrian and German), healthy right-handed participants with the SAMT in the MR scanner. The paradigm reported in this paper was the last task for all subjects, after completing other tasks and scanning runs (tapping into empathy and prosocial behavior) which are outside the scope of this paper. Data from 9 participants had to be discarded from further analyses (i.e., 3 were excluded due to excessive head-movement, 3 for failure to complete scanning, and 3 for lack of compliance with the task instructions). Thus, 41 participants remained as the final sample for the fMRI analyses (23 males; age $M = 22.63$, $SD = 2.86$). Behavioral data from the first 14 participants unfortunately had to be discarded from behavioral analyses since due to a logging error, button presses instead of button releases were recorded in this sub-sample (adding a constant of, on average, about 320 msec to reaction times (RTs)). Crucially, these participants showed a modulation of mimicry across conditions that was similar to the rest of the sample. Moreover, inclusion of these participants into the main sample did not essentially alter the overall pattern of behavioral effects, apart from a general shift towards longer RTs across all conditions. Likewise, exclusion of the sub-sample from our imaging analysis did not alter the results of the group analyses, apart from minor differences that we ascribe to a reduced power of analyses with 27 versus 41 participants. Thus, for the sake of higher analytical power, we included data from all 41 participants in the fMRI analyses, while restricting our behavioral analyses to the 27 participants for whom responses had been correctly recorded (15 males; age: $M = 22.61$, $SD = 3.25$).

Participants received detailed information regarding the scanning procedure and gave their written informed consent prior to MRI scanning. Participants were paid a flat fee of 35 Euro for participation. All participants had normal or corrected-to-normal eye-vision and no history of psychiatric

or neurological conditions. The study was approved by the local ethics committee of the Medical University of Vienna and performed in accordance with the Declaration of Helsinki.

2.2. Experimental design, materials and procedure

2.2.1. Social-affective mimicry task (SAMT)

During the fMRI scanning procedure participants performed the social-affective mimicry task (SAMT). This task is a modification of the imitation inhibition task (Brass et al., 2000) in which participants are instructed to lift their right index or middle finger in response to a number cue which is presented on an image of a hand that mirrors the participant's hand. Index finger movements are cued by the number "1", and middle finger movements by the number "2". Simultaneously to presentation of the number cue the hand stimulus shows a finger lifting movement. This finger movement is irrelevant to the task and shows either a movement of the same finger as the one required to lift by the participant (congruent trials), or movement of the other finger (incongruent trials) (see Fig. 1A). Although participants are not instructed to consider the task-irrelevant hand movements in any way, response times are faster on congruent trials and slowed down on incongruent trials, due to motor resonance effects either facilitating or interfering with movement execution. The difference between the mean response times (in milliseconds (msec)) of incongruent and congruent trials is therefore taken as an index of the extent of the mimicry effect (Brass et al., 2000).

We extended this task to investigate modification of the mimicry response (i.e., mimicry of arbitrary movements) by social-affective variables. To this end we presented pictures of female faces who differed in ethnic group membership (European-Caucasian and African-American), and displayed either happy or angry emotional expressions above the hand stimulus and the number cues (see Fig. 1B). The face stimuli were taken from the NimStim Set of Facial Expressions (Tottenham et al., 2009), and depicted a Caucasian and an African American female expressing happiness and anger. This yielded a $2 \times 2 \times 2$ full-factorial within-subjects design with the factors GROUP (In-group, Out-group), EMOTION (Happy, Angry) and CONGRUENCY (Congruent, Incongruent finger movements).

The face stimulus was presented above the hand stimulus, which was shown from a frontal perspective, mirroring the participant's right hand. Stimuli were presented on a blue background. In contrast to the original version of the task, hand stimuli matched the ethnicity of the displayed face. As a pilot behavioral study (data not shown) had indicated that low-level perceptual effects of skin color might confound task effects, due to the differing visual contrast of the execution cue against a white versus black surrounding stimulus, the white and the black hands were wearing a beige cotton glove in our experiment. Skin color (white or black), indicating ethnic group-membership, however, was visible at the wrist and matched that of the face stimulus. Participants were wearing an identical glove as shown on the screen. The number cue consisted of a "1" (lift index finger) or "2" (lift middle finger) in black on a grey square, which was shown between index and middle finger of the hand stimulus (position matched for all conditions) (see Fig. 1A).

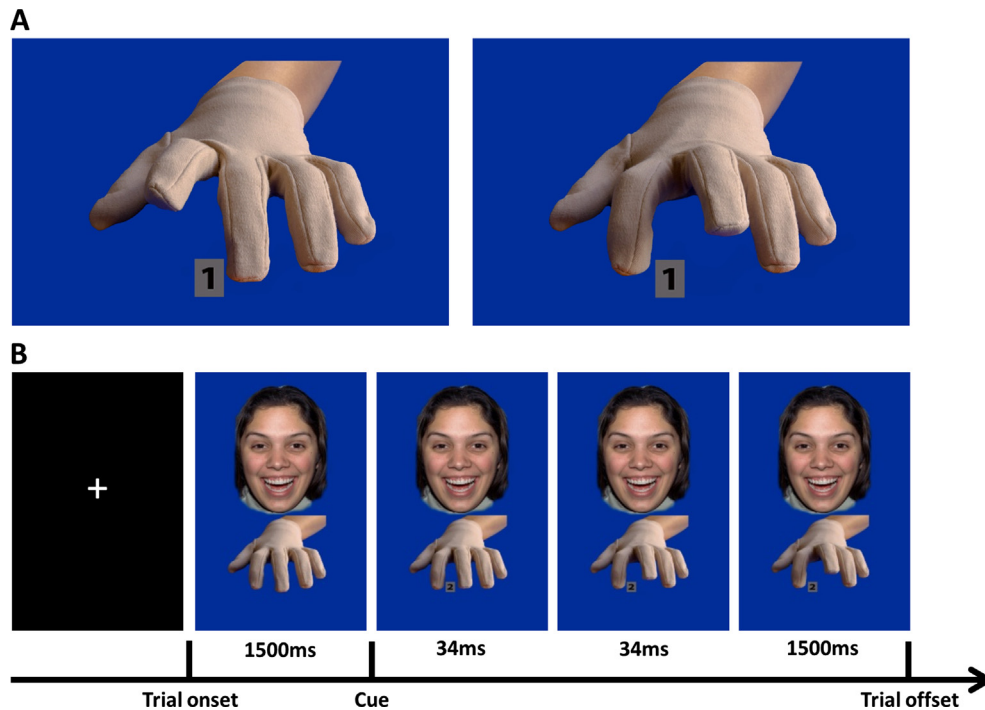


Fig. 1 – The social-affective mimicry task (SAMT). (A) Congruent and incongruent trials. Illustration of congruent and incongruent trials. Target cues (numbers ‘1’ or ‘2’) indicated a finger-lifting movement. The hand on the screen (white or black hand in a beige glove) simultaneously performed a task-congruent or incongruent movement. **(B) Trial timecourse.** Illustration of the timeline of one trial. Simultaneous display of social-affective stimuli of happy and angry Caucasian and African American faces (NimStim set of facial expressions (Tottenham et al., 2009)) and the imitation inhibition task by Brass et al., (2000).

Each trial consisted of four frames (see Fig. 1B). The first frame simultaneously displayed the hand in resting position and the static face stimuli and was presented for 1500 msec. Subsequently on the second frame the number cue appeared; concurrently a finger lifting movement was depicted by showing two consecutive frames of 34 msec duration. This produced the respective congruent (i.e., cued and presented movements were the same), or incongruent trials (i.e., cued movement and presented movement were different, for example: the number cue indicated lifting of middle finger, while an index finger movement was shown). The fourth and last frame, with the finger shown in fully lifted position, was presented for 1500 msec, resulting in a trial length of 3068 msec. Inter-trial interval was jittered at 3000–6300 msec. Presentation of stimuli was carried out with Cogent (<http://www.vislab.ucl.ac.uk/cogent.php>). The experiment consisted of 12 congruent and incongruent trials for each of the 8 conditions, presented in randomized order. This resulted in a total of 96 trials and a total scanning duration of approximately 12 min. In addition, as mentioned above, participants performed other tasks and scanning runs before the SAMT (tapping into empathy and prosocial behavior), which are outside the scope of the present paper. The SAMT was the last task presented for all subjects.

Participants performed the task while lying in the scanner. The stimuli were shown via a back projection system and a

mirror that was attached to the head coil. Before starting with the task, participants were presented with written instructions on the screen, and performed 8 practice trials. Responses were recorded with an optical response box. Participants had to keep the two buttons belonging to their right index and middle finger pressed down throughout the experiment. They were instructed to lift, as fast as possible, their index finger whenever a “1” and their middle finger whenever a “2” appeared on the screen and informed that the other depicted stimuli were irrelevant to their task. Response times to individual trials were obtained by recording button release times.

Only behavioral data from correct trials were included in the analysis. To account for potential outliers in the behavioral data we performed a winsorising procedure on the mean response times (RT; in msec) of every participant for each of the 16 combinations of condition and target cue (Wilcox, 2011). This procedure replaced all mean RTs higher than the value corresponding to the 75th percentile plus 1.5 times the interquartile range with the maximum RT within this range in the corresponding condition. Accordingly mean RTs lower than 25th percentiles minus 1.5 times the interquartile range were replaced with the minimal RT within this range in the correspondent condition. Furthermore we conducted a three way repeated measures ANOVA on the factors GROUP (In-Group, Out-Group), EMOTION (Happy, Angry) and CONGRUENCY

(Congruent, Incongruent). To specifically assess the mimicry effect we carried out two-way repeated measures ANOVA with factors GROUP (In-Group, Out-Group) and EMOTION (Happy, Angry) on the difference between reaction times in incongruent and congruent trials for each condition. In addition, we explored possible effects of sex/gender by incorporating sex/gender as an additional variable in these analyses. This was motivated by the fact that all face stimuli showed females, hence making it possible that male and female participants responded differently to them.

2.3. Post-scanning ethnic attitude measures

2.3.1. Threat implicit association task (Threat-IAT)

To substantiate the interpretation of our findings, participants completed a Threat/Security implicit association task (IAT; Greenwald, McGhee, & Schwartz, 1998) after the scanning procedure. The IAT is a frequently used measure to assess implicit ethnic bias (for meta-analytic review see Greenwald, Poehlman, Uhlmann, & Banaji, 2009). We specifically hypothesized that Black people would be associated with threat rather than with security, as compared to White people. Thus we designed an IAT that specifically tested for the strength of implicit associations between the target concepts of “Blacks” (ethnic out-group) and “Whites” (in-group) with attributes describing “Threat” and “Security”. The attributes describing “Threat” were: threat, fear, violence, danger and attack. The matched nouns describing “Security” were: security, peace, shelter, protection and calmness. All terms were presented in German and matched for word length. The IAT was designed following the approach by Greenwald et al. (1998) and was composed of five tasks with separate instructions.

Participants performed the task on a computer running Adobe Flash Player for stimulus presentation. Across all tasks they were instructed to keep the letters “E” and “I” on the keyboard pressed with their index, or middle fingers, to respond as fast as possible, and to disregard errors, indicated by a red cross. In the first task pictures of the target-concepts of Whites and Blacks had to be sorted to the left and right hand side, respectively, by lifting the corresponding keys. In the second task the instructions were to sort the target concepts of Security to the left, and Threat to the right hand side. The third task required sorting both the attributes describing Security and the target concept of Whites to the left, and those describing Threat and Blacks to the right. The fourth task reversed the mapping of target-concepts Whites and Blacks to right, respectively left with regard to the first task. In the fifth task this reversed mapping of group was combined with the Threat and Security attributes. Instructions were to sort the combination of the target-concept of Blacks and the attributes of Security to the left, respectively Whites and Threat to the right hand side.

The “D-measure” (for details see Greenwald, Nosek, & Banaji, 2003) describes the implicit association of Whites with Security and Blacks with Threat. Firstly the latency standard deviation (SD) from the combined third and fifth task was calculated. The “D-measure” was then furthermore calculated by dividing the difference in reaction times (msec) of the third and fifth task by this SD. In the case of a stronger

association of Blacks with Threat attributes a positive D-value is expected.

2.3.2. Attitudes towards Blacks Scale

After assessing participants' implicit attitudes using the Threat/Security IAT we conducted a German translation of the Attitudes towards Blacks Scale (Brigham, 1993) to assess their explicit ethnicity bias. The Attitudes towards Blacks Scale comprises 20 statements concerning the aim of the questionnaire, which have to be rated from “1” (strongly disagree) to “7” (strongly agree). Thus a high score indicates highly positive, whereas low scores reflect highly negative attitudes towards blacks.

2.4. MRI acquisition

MRI data were acquired using a 3 T Siemens Tim Trio MRI system (Siemens Medical, Erlangen, Germany) using a 32-channel head coil for signal reception. Blood oxygen level-dependent (BOLD) sensitive functional imaging was performed using a multi-band accelerated echoplanar imaging (EPI) sequence with the following parameters: echo time (TE)/repetition time (TR) = 33/1800 msec, flip angle 60°, interleaved acquisition, 54 axial slices co-planar the connecting line between anterior and posterior commissure, FOV 192 mm × 192 mm × 108 mm, matrix size 128 × 128, voxel size 1.5 × 1.5 × 2 mm, no interslice gap). Structural images were acquired after functional scanning using a magnetization-prepared rapid gradient-echo (MPRAGE) sequence (TE/TR = 4.21/2300 msec, 160 sagittal slices, voxel size = 1.0 × 1.0 × 1.1 mm, field of view = 256 mm).

2.5. Analysis of MRI data

MRI data were analyzed using SPM8 (Statistical Parametric Mapping, <http://www.fil.ion.ucl.ac.uk/spm>). The first five volumes of each participant's fMRI data were discarded to allow for T1 equilibration. The time series for each voxel was then realigned temporally to the acquisition of the first slice in time to correct for differences in slice time acquisition. The image time series were spatially realigned using a sinc interpolation algorithm that estimates rigid body transformations (translations, rotations) by minimizing head-movements between each image and the reference image. Subsequently, each participant's functional image was segmented into gray matter (GM), white matter (WM), and cerebral spinal fluid (CSF) using GM, WM, and CSF tissue probability maps provided by SPM8 and then spatially normalized to the International Consortium for Brain Mapping (ICBM) space templates (European brains) using both linear and nonlinear transformations. Finally, the images were spatially smoothed using an isotropic 8 mm full-width-at-half-maximum Gaussian kernel.

The fMRI time series were analyzed using an event-related approach in the context of the General Linear Model (GLM). Single-subject models consisted of multiple regressors describing, for each of the 8 conditions resulting from the 2 × 2 × 2 design, the time period from presentation of the facial stimulus until the time that the stimuli disappeared from the screen. Duration of a trial was fixed at 3.068 s. Trials

on which an incorrect response or no response was given were modeled in a separate error regressor.

Each effect was modeled on a trial-by-trial basis as a concatenation of square-wave functions. Each of these square-wave functions was then convolved with a canonical hemodynamic response function, as implemented in SPM8, in order to generate 9 regressors modeling the main effects described above.

Head movement effects were accounted for by including the six rigid-body motion parameters (translation and rotation) as well as two regressors describing signal intensities in WM and CSF as nuisance covariates.

2.6. Statistical inference

The statistical significance of the estimated evoked hemodynamic responses was assessed using t-statistics in the context of general linear model-based analyses, as implemented in SPM8. We were specifically interested in assessing mimicry regulation (i.e., Incongruent > Congruent) effects related to the enhanced behavioral mimicry responses, that is specifically for the conditions Out-group and Happy on brain activity during the finger lifting trials. Note therefore that since the behavioral data analysis showed no interaction effects between these factors ($\text{GROUP} \times \text{EMOTION}$), we did not test for $\text{GROUP} \times \text{EMOTION}$ effects in the fMRI data. Note that inclusion of the data of the 14 imperfectly logged participants neither changed the basic pattern of behavioral results, in particular of the mimicry effect across conditions; nor did this exclusion essentially alter the results of the imaging analyses. Thus for the sake of enhanced analytical power we included functional imaging data of all 41 participants in the fMRI analyses. For completeness of reporting we also report changes in imaging results in the sub-sample of 27 participants in the results section (see section 3.2).

Contrasts of the parameter estimates with respect to baseline for all trials were calculated, separately for the different levels of GROUP , EMOTION and CONGRUENCY , with the intertrial interval being used as an implicit baseline. The resulting 8 contrasts were entered into a random-effects second-level analysis using a repeated measures ANOVA, in order to enable inferences on a population level (Penny & Holmes, 2004).

In line with the behavioral data analysis, in which we contrasted reaction times to incongruent and congruent trials, and based on previous fMRI studies using the imitation inhibition task (Brass et al., 2000; Brass, et al., 2001; Brass, Derrfuss, Forstmann, et al., 2005; Brass, Derrfuss, & von Cramon, 2005; Spengler, et al., 2009), we also contrasted incongruent with congruent trials in our fMRI analysis in order to assess neural activation related to the regulation of mimicry. To isolate the parts of this activation specifically related to our main conditions of interest (which were mimicry in response to Happy faces, or to Out-group faces, respectively), we confined our analyses to effects that showed stronger activation during these conditions, as compared to their counterpart. This was implemented using an implicit masking procedure which restricted the display of results to those voxels which had shown higher activation in the condition of interest compared to its counterpart. Stated explicitly, we tested our effects of

interest (i.e., [Happy Incongruent > Happy Congruent], or [Out-group Incongruent > Out-group Congruent], and inclusively masked the ensuing effects with the corresponding interaction effects (i.e., [[Happy Incongruent > Happy Congruent] > [Angry Incongruent > Angry Congruent]]; or [[Out-group Incongruent > Out-group Congruent] > [In-group Incongruent > In-group Congruent]]). In this way we isolated differential neural responses to incongruent versus congruent trials that were stronger for happy than angry facial stimuli, or for out-group than in-group stimuli (and vice versa).

Note that this analysis is not circular (as would be the case if one analysis was used to assess the significance of a second, non-independent analysis (Kriegeskorte, Simmons, Bellgowan, & Baker, 2009)): the masking procedure was part of a single analysis in which we confined the effects obtained by our main contrast to effects that were specific for this condition. Thus, this analysis did not reduce the search volume of the main effect, and hence left its significance unaffected (which was corrected for multiple comparisons using cluster-level correction at the whole-brain level). All the masking approach added to the analysis was to selectively display only those voxels which were specifically associated with higher activation in the effect of interest. For completeness and full data reporting, however, we also report the main effects of all conditions without the masking procedure in the supplementary material (see Tables S1–S4 in the supplementary material).

All statistical inference was performed using a threshold of $p = .05$ corrected for multiple comparisons over the whole brain, using the Gaussian random fields approach at cluster-level (Friston, Holmes, Poline, Price, & Frith, 1996) with a voxel-level intensity threshold of $p = .001$; the masking contrast which only served to control for the directionality of effects but not its significance was thresholded at $p = .05$ uncorrected. The SPM Anatomy Toolbox, version v1.8 (Eickhoff et al., 2005), was used to guide anatomical and probabilistic cytoarchitectonic localization of the resulting clusters.

To corroborate the functional interpretation of our fMRI findings, we investigated the relationship between the behavioral and the imaging results by calculating Pearson correlations between the size of the individual mimicry effects and the corresponding individual fMRI activation. To calculate these post-hoc brain-behavior correlations, we used the MarsBaR toolbox v0.43 (<http://www.marsbar.sourceforge.net>) to create 10 mm spherical functional ROIs centered at peak coordinates of activation foci related to our contrasts of interest (see Table 1 for details of maximum activations). ROI selection was based on the maxima of activation clusters yielded by inclusively masking the [Out-group Incongruent > Out-group Congruent] contrast with the interaction contrast [[Out-group Incongruent > Out-group Congruent] > [In-group Incongruent > In-group Congruent]]. For correlation with the mimicry effect in the out-group condition ROIs were created in left and right AI; right and left MCC; and left inferior parietal lobule (IPL) and left IFG. Respectively ROI selection was based on maxima of activation clusters revealed by the [Happy Incongruent > Happy Congruent] contrast inclusively masked with the interaction contrast [[Happy Incongruent > Happy Congruent] > [Angry Incongruent > Angry Congruent]]. ROIs for correlation with the mimicry effect in the happy condition were right superior

Table 1 – Behavioral results of the interaction effect (A) Group \times Congruency and (B) Emotion \times Congruency; mean RT on congruent and incongruent trials in the SAMT, in ms; italic numbers referring to standard error of the mean (SE).

	A.			B.	
	Congruent	Incongruent		Congruent	Incongruent
In-Group	501.87 (7.03)	572.87 (10.34)	Happy	495.60 (7.02)	580.83 (10.90)
Out-group	498.21 (7.77)	584.39 (11.32)	Angry	504.48 (7.67)	576.43 (10.78)

parietal lobule (rSPL), the right TPJ and the right superior frontal gyrus (rSFG). We used the REX (Region-of-interest extraction) Toolbox implemented in Matlab (<http://web.mit.edu/swg/software.htm>) to extract, for each participant, the mean parameter estimates of the contrasts [Out-group Incongruent > Out-group Congruent], respectively [Happy Incongruent > Happy Congruent] from the ROIs. Subsequently, Pearson correlations were calculated between these values and the behavioral mimicry effect of the out-group, as well as the happy condition (mean RTs: Incongruent – Congruent). Note that the correlation analysis has been performed in line with previous recommendations aiming to avoid biased/inflated results (Vul, Harris, Winkelman, & Pashler, 2009). The imaging data used to define the ROIs was based on a contrast exploiting the different levels of the factorial design, and hence a priori independent of the individual differences in the behavioral parameters (reaction times). Moreover, we also calculated only one single correlation value (as opposed to repeated testing within our ROIs). This implies that our correlation analyses were neither circular nor that they could be inflated by repeated testing (Kriegeskorte et al., 2009).

3. Results

3.1. Behavioral results

3.1.1. SAMT

The three-way repeated measures ANOVA on the factors GROUP \times EMOTION \times CONGRUENCY revealed a significant main effect of CONGRUENCY [$F(1,26) = 216.35$, $p < .001$, partial $\eta^2 = .84$] in the expected direction of higher mean RT for incongruent than congruent trials (incongruent: $M = 707.12$ msec, $SE = 38.3$; congruent: $M = 627.99$ ms, $SE = 38.21$). We found a significant GROUP \times CONGRUENCY interaction [$F(1,26) = 9.45$, $p = .005$, partial $\eta^2 = .27$], as well as an EMOTION \times CONGRUENCY interaction [$F(1,26) = 13.01$, $p = .001$, partial $\eta^2 = .33$] (see Table 1). All other effects were not significant (all p -values $\geq .09$, effect size estimates $\leq .11$).

Thus from the significant interaction effect of GROUP \times CONGRUENCY, as well as EMOTION \times CONGRUENCY it follows that also the mimicry effect (i.e., the RT difference between incongruent and congruent trials) exhibits the equivalent significant effects of GROUP and EMOTION. For the factor GROUP a higher mimicry effect was found when out-group than when in-group stimuli were presented (Out-group: $M = 86.17$ ms, $SE = 6.39$; In-Group: $M = 71.01$ msec, $SE = 5.46$). The results also revealed that the mimicry effect was bigger for happy than for angry faces (Happy: $M = 85.22$ msec, $SE = 6.25$; Angry: $M = 71.96$ msec, $SE = 5.12$). The interactions GROUP \times EMOTION were not significant ($p = .29$, partial $\eta^2 = .042$).

Incorporating SEX/GENDER in the two-way repeated measures ANOVA as between-subject factor did not reveal any significant sex/gender differences in the mimicry effect (p -values $\geq .29$, effect size estimates $\leq .045$). In the absence of behavioral effects, we also did not analyze the imaging data with respect to sex/gender.

3.1.2. Threat IAT

From the 41 participants included in fMRI analyses, data of five participants were incomplete, due to technical errors, and had to be excluded from analysis. In the remaining 36 participants (20 males) a D-value of medium effect size ($M = .43$, $SE = .05$) was observed. This indicates that Black people are implicitly more associated with threat, whereas White people are more associated with security. Correlation analyses (Pearson correlation) did not reveal significant correlations between the results of the IAT and the behavioral measures of the mimicry effect.

3.1.3. Attitudes towards Black Scale

Data of 40 participants entered analysis; data of one participant was missing. Participants exhibited a neutral explicit attitude towards blacks ($M = 4.27$, $SE = .06$).

3.2. fMRI results

3.2.1. Mimicry regulation: incongruent versus congruent trials

Testing for main effects of mimicry regulation (contrast: mean/Incongruent > mean/Congruent, i.e., mean of all regressors from conditions showing incongruent movements versus mean of all conditions showing congruent movements) revealed activation clusters in a large number of brain areas. Frontal activation was found in the right and left superior frontal gyrus (SFG), as well as the left precentral gyrus (PCG) and the middle frontal gyrus (MFG). Moreover activation in bilateral AI was found, with the cluster on the right side extending into the right IFG. In addition a cluster in MCC extending into the supplementary motor area (SMA) and rostral cingulate zone (RCZ) was activated, and another cluster in a slightly more anterior portion of cingulate cortex was only slightly above the chosen significant threshold ($p = .051$). Parietal activation was found in the left posterior parietal cortex (comprising the left IPL and left superior parietal lobule (SPL)) extending into the postcentral sulcus on the left side and into the precuneus on the right side. In the right hemisphere activation in the rTPJ was identified. For a detailed list of all activated areas see Table 2. Confining analyses to the sub-sample of 27 participants with correctly logged behavioral data did not reveal any further activated brain areas. Besides, in this sub-sample all the mentioned areas, except for

Table 2 – Local maxima of activation clusters (MNI stereotactic coordinates) resulting from the contrast between Incongruent versus Congruent trials. IPL = inferior parietal lobule, PCG = postcentral gyrus, SPL = superior parietal lobule, IFG = inferior frontal gyrus, SFG = superior frontal gyrus, SMA = supplementary motor area, MTG = middle temporal gyrus, IOG = inferior occipital gyrus, MCC = mid-cingulate cortex, MFG = middle frontal gyrus, x = Subpeaks of a cluster. Threshold $p = .05$, cluster level multiple comparison correction (selection threshold $p = .001$).

Area	Hemisphere	Peak MNI-coordinates			Cluster size(voxels)	T-value	p-value (corrected)
		x	y	z			
Incongruent > Congruent							
IPL/PCG/SPL	Left	−32	−46	44	2448	7.74	<.001
Precuneus/SPL/IPL	Right	12	−64	52	1915	5.81	<.001
xTPJ	Right	58	−40	32		5.02	
Anterior insula/IFG (pars triangularis)	Right	40	18	−6	852	5.60	<.001
SFG/SMA	Right	26	−10	54	526	5.94	<.001
PCG/SMA/SFG	Left	−30	−8	−62	354	5.12	<.001
Anterior insula/IFG (pars orbitalis)	Left	−34	14	−10	331	4.85	<.001
MTG/IOG	Left	−56	−64	2	252	4.68	<.001
SMA/MCC	Right	2	8	46	232	4.32	<.001
Cerebellum	Right	−12	2	68	138	5.03	.001
MFG	Right	28	34	24	98	4.20	.010
Cerebellar vermis		4	−48	−12	96	4.46	.012
Cerebellum	Left	−24	−58	−20	74	4.18	.045
MCC	Right	6	28	26	72	4.01	.051

activation in the precuneus, also survived whole-brain multiple comparison.

3.2.2. Mimicry regulation: effects of happy facial expressions
The behavioral results had indicated enhanced mimicry when happy compared to angry faces were shown. The contrast targeting regulation of mimicry in response to arbitrary movements when happy faces were displayed revealed activation in the left SMA, bilateral SFG, on the right side corresponding to right dorsal premotor cortex (dPMC), and right SPL. Furthermore right TPJ was activated, notably in a location overlapping with meta-analytic activations related to the imitation inhibition task (Silani, Lamm, Ruff, & Singer, 2013). For a detailed list of all activated areas see Table 3. Restricting functional analyses to the sub-sample of 27 participants revealed additional activation of a cluster comprising the right SMA and right MCC, as well as cerebellum and cerebellar vermis, and confined activation in the SFG to the right side.

We also explored the reverse comparison, masking the Incongruent versus Congruent main effect for angry trials inclusively with the interaction to test for (lower) mimicry effects specific to angry facial stimuli. This only revealed activation in the left inferior occipital lobe (see Table 3). Confining the analyses to the sub-sample (i.e., 27 participants) did not reveal any activations surviving multiple comparison in this condition.

3.2.3. Mimicry regulation: effects of out-group membership
The behavioral results had revealed enhanced mimicry in response to out-group stimuli. Assessing activation associated with mimicry regulation of this effect, we found significant activation in the left IFG, corresponding to ventral premotor cortex (vPMC) and located in cytoarchitectonically defined Area 44 of the Anatomy toolbox, in left IPL, the right SMA and bilateral MCC, as well as in dorsal bilateral AI. For details see Table 4. Analyses of the sub-sample (i.e., 27 participants) confined the results to the right SMA and MCC, as well as

bilateral insula. Activation in the vPMC as well as the left IPL was however also visible, but did not survive the strict whole-brain multiple comparison corrected statistical threshold.

We also investigated the reverse effect of regulation of mimicry in the in-group condition. This only revealed significant activation in the cerebellar vermis (see Table 4 for details). Testing for this contrast in the sub-sample only revealed activation in the right SPL.

3.3. Correlation analysis of fMRI and behavioral data

Bonferroni corrected Pearson correlations ($p \leq .0125$) between the mimicry effect of the sub-sample of 27 participants (mean RT of Incongruent – Congruent trials) to out-group stimuli and the mean contrast estimates received by inclusively masking the [Out-group Incongruent > Out-group Congruent] contrast with the interaction contrast [[Out-group Incongruent > Out-group Congruent] > [In-group Incongruent > In-group Congruent]] revealed a trend significant positive Pearson correlation in left IFG ($r = .41$, $p = .032$). No significant other correlation was found for the MCC, AI, and left IPL ($p \geq .1$). When testing for Pearson correlations between the mimicry effect for happy faces and the mean contrast estimates of the contrast [Happy Incongruent > Happy Congruent] inclusively masked with the interaction contrast [[Happy Incongruent > Happy Congruent] > [Angry Incongruent > Angry Congruent]] we found a trend significant negative Pearson correlation in the right SFG ($r = -.37$, $p = .058$) and right TPJ ($r = -.36$, $p = .064$). No significant correlation was found for the right SPL ($p = .39$).

4. Discussion

The objective of the present study was to investigate the malleability of mimicry by affiliation-relevant social signals, with automatic imitation serving as a laboratory model of

Table 3 – Local maxima of activation clusters (MNI stereotactic coordinates) resulting from the contrast between Happy (Incongruent vs Congruent trials) masked inclusively with Happy (Incongruent vs Congruent trials) versus Angry (Incongruent vs Congruent trials), respectively corresponding for the contrast between Angry (Incongruent vs Congruent trials) masked inclusively with Angry (Incongruent vs Congruent trials) versus Happy (Incongruent vs Congruent trials). SPL = superior parietal lobule, TPJ = temporo-parietal junction, SMA = supplementary motor area, SFG = superior frontal gyrus, IOG = inferior occipital gyrus. Threshold $p = .05$, cluster level multiple comparison correction (selection threshold $p = .001$).

Area	Hemisphere	Peak MNI-coordinates			Cluster size(voxels)	T-value	p-value (corrected)
		x	y	z			
Happy (Incongruent > Congruent) masked inclusively with Happy (Incongruent > Congruent) > Angry (Incongruent > Congruent)							
SPL	Right	30	−52	68	347	4.96	<.001
TPJ	Right	64	−46	38	185	4.64	<.001
SFG (dPMC)	Right	22	−8	56	171	4.66	<.001
SMA/SFG	Left	−8	−6	68	111	4.56	.005
Cerebellar vermis/Left cerebellum		4	−52	−8	89	4.83	.018
Angry (Incongruent > Congruent) masked inclusively with Angry (Incongruent > Congruent) > Happy (Incongruent > Congruent)							
IOG	Left	−38	−74	−4	90	4.31	.017

mimicry. While previous evidence has shown that mimicry is modulated by social cues, our main intention was to show how it is regulated in accordance to distinct affiliative goals. On a process level we had hypothesized that distinct social-cognitive and behavior regulation processes, as well as shifts in sensorimotor processing would be involved in the adaptive regulation of mimicry to achieve these distinct goals, and that this should be reflected in the engagement of distinct neural networks. The behavioral results show that mimicry was increased in the presence of happy facial expressions, and that the same effect was observed in the presence of out-group members. These similar behavioral effects were accompanied by differential modulations of the neural networks involved in task processing. Increases in mimicry when happy facial expressions were presented were accompanied by activation of the rTPJ, as well as of the dPMC-SPL circuit. On the other hand, higher mimicry when out-group members were presented was associated with activation increases in a network including aMCC/RCZ and AI, as well as the vPMC-IPL. In the following sections, we will

interpret these findings in detail and discuss their relevance and putative functional role for the implicit regulation of mimicry.

4.1. Effects of social cues on mimicry behavior

We found three main behavioral effects, which directed the analyses of the functional imaging data. First, we replicated the congruency effect previously found in automatic imitation paradigms (Brass et al., 2000; Brass, et al., 2001; Brass, Derrfuss, & von Cramon, 2005; Heyes, Bird, Johnson, & Haggard, 2005; Sowden & Catmur, 2015; Spengler, et al., 2009), with higher reaction times on incongruent than on congruent trials. This confirmed that our participants “automatically” mimicked the task-irrelevant hand stimulus. Interestingly, reaction times for both incongruent and congruent trials were on average about 100 msec longer than those found in other imaging studies which had not added social-affective stimuli (for example Brass, Derrfuss, & von Cramon, 2005). Thus, increased attentional processing of the

Table 4 – Local maxima of activation clusters (MNI stereotactic coordinates) resulting from the contrast between Out-group (Incongruent vs Congruent trials) masked inclusively with Out-group (Incongruent vs Congruent trials) versus In-group (Incongruent vs Congruent trials), respectively of the contrast between In-group (Incongruent vs Congruent trials) masked inclusively with In-group (Incongruent vs Congruent trials) versus Out-group (Incongruent vs Congruent trials). IPL = inferior parietal lobule, SFG = superior frontal gyrus, SMA = supplementary motor area, IFG = inferior frontal gyrus, MCC = mid-cingulate cortex, MTG = middle temporal gyrus; Threshold $p = .05$, cluster level multiple comparison correction (selection threshold $p = .001$).

Area	Hemisphere	Peak MNI-coordinates			Cluster size(voxels)	T-value	p-value (corrected)
		x	y	z			
Out-group (Incongruent > Congruent) masked inclusively with Out-group (Incongruent > Congruent) > In-group (Incongruent > Congruent)							
IPL	Left	−34	−42	40	247	5.91	<.001
Anterior insula	Right	32	24	4	231	4.83	<.001
SFG	Right	22	−8	56	171	4.66	<.001
SMA/MCC	Left + Right	2	8	46	173	4.58	<.001
Rolandic operculum/IFG	Left	−52	2	10	103	4.26	.008
Anterior insula	Left	−28	22	12	98	4.29	.010
MTG	Left	−48	−58	−2	72	4.15	.051
In-group (Incongruent > Congruent) masked inclusively with In-group (Incongruent > Congruent) > Out-group (Incongruent > Congruent)							
Cerebellar vermis/Left cerebellum		4	−64	−14	130	4.96	.002

facial stimuli might have led to a general increase in reaction times. Notably, the magnitude of the mimicry effect is comparable to the one found in another fMRI study which had also implied contextual manipulations (Klapper et al. (2014), as well as to behavioral studies using this paradigm with a social stress manipulation (Tomova, von Dawans, Heinrichs, Silani, & Lamm, 2014), and priming with negatively valenced pictures (Grecucci et al., 2011). Thus, it seems that an added social and/or emotional context leads to generally enhanced mimicry effects.

Second, we found higher mimicry of task-irrelevant movements when confronted with happy faces. This is in line with the hypothesis that mimicry reflects the implicit reciprocation of affiliative intent. Similar results have been found in a study by Bourgeois and Hess (2008), showing that implicit facial mimicry was similarly enhanced for happy faces. Notably, this effect was observed for in-group and out-group faces alike, which has been interpreted in the sense that the affiliative intent conveyed by happy facial expressions is reciprocated irrespective of group-membership (Bourgeois & Hess, 2008; Van Kleef, et al., 2004, 2010). Our findings are in line with this interpretation (as we did not observe an interaction of emotion and group membership). They however also crucially extend it to mimicry of movements that carry no intrinsic affective information – as we studied mimicry of arbitrary finger lifting movements, and not of emotion displays via facial mimicry themselves.

Third, we found enhanced mimicry when out-group faces were presented. As suggested by evidence in social psychology, mimicry might represent an affiliative signal (e.g., Chartrand & Bargh, 1999; Chartrand & Lakin, 2013; Lakin et al., 2003). Also, accounts from behavioral biology suggest that affiliative displays (“such as kissing and embracing” (de Waal, 2003)) of non-human primates could represent a flexible and context-dependent behavioral means to de-escalate a socially threatening situation – as an alternative to engage in a fight with an aggressor, or to withdraw from him or her (de Waal, 1986, 2003; Keltner et al., 1997). Affiliation signals might thus have two functions: to strengthen social bonds, and to soothe a potential conflict. Increased mimicry in response to out-group faces might, therefore, reflect a regulative response to avert potential threat. This interpretation is supported by the results of the Threat IAT, which showed that Blacks are implicitly more strongly associated with the concept of threat – a finding that has in a similar fashion also been reported elsewhere (Amodio, 2004, 2008; Amodio et al., 2008; Amodio et al., 2004; Amodio et al., 2006; Neuberg & Cottrell, 2008). Interestingly, the present results suggest that out-group faces might generally elicit an implicit threat response, independently of the emotions they are showing (as, somewhat unexpectedly, we did not find an interaction effect of emotion and group membership – implying that being confronted with angry out-group members did not result in even higher mimicry). We therefore suggest that mimicry, as an affiliative signal, is, in the case of presentation of out-group members, enhanced to reach the goal of appeasement. Grecucci et al. (2011) found enhanced mimicry to negatively valenced pictures, which they interpreted as being related to a fight-or-flight response. Our results extend those of Grecucci et al. (2011), by suggesting that the implicit perception of threat

(which carries negative valence) might, depending on the social context, also lead to approach behavior in the form of appeasement. In a series of three previous behavioral experiments involving more than 180 participants, in which we also used the SAMT, we consistently found enhanced mimicry in response to angry out-group faces (Rauchbauer et al., 2014, 2015). Unexpectedly, as mentioned before, we did not replicate these results with regard to the interaction of emotion and group-membership (i.e., angry out-group members) in the present study. This might be due to the different experimental setting (lying supine in a dark, loud scanner environment), which might have enhanced the focus on the more salient happy and out-group stimuli. Results of the behavioral studies consistently showed that mimicry's malleability by social-affective cues was based on modulation of RTs on congruent trials, as also found by Grecucci et al., 2011. Although it might be argued that the enhanced RTs on negatively valenced congruent trials reflect a general enhanced motor responsiveness due to higher arousal, this interpretation seems implausible. First, enhanced responsiveness to task-irrelevant motor cues due to negatively valenced stimuli (angry out-group faces) should have also been reflected in a speeding of RTs in incongruent trials, which was not the case. Moreover, no increase in RTs in response to baseline trials (trials without movement of the other's hand) was observed in our behavioral study, where such trials had been included. Second, results from a control experiment included in the latter study, in which we had assessed effects of our social-affiliative stimuli on responses in a (non-imitative) Simon task, showed that negatively valenced stimuli did not affect responses on congruent trials in this task in the same way as in the mimicry task. Therefore, the modulation of mimicry behavior by out-group faces on congruent trials most likely reflects a specific effect of social context on mimicry behavior, and we propose that this effect is related to appeasement of a potentially threatening interaction partner.

In sum, the behavioral results confirm that mimicry was affected by our social-affective manipulation. Yet, the reaction time measures alone are non-informative with respect to the processes underlying these modulations of mimicry. Thus, in the next sections we will discuss how different cognitive processes, and their reflection in distinct neural activations, might explain the behavioral effects.

4.2. Imaging effects related to regulation of mimicry

4.2.1. Incongruent versus congruent trials (generalized regulation of mimicry)

By contrasting incongruent and congruent trials we aimed to identify the neural activations specific to the regulation of mimicry, that is, the activation underlying the increased need to regulate mimicry if the hand stimulus moved differently versus similarly with respect to the required movement. Contrasting activation during incongruent and congruent trials revealed a broad network of brain areas. We observed activation in the right TPJ, the AI and MCC, as well as in frontoparietal areas involved in sensorimotor control and action observation (see Table 2).

Involvement of right TPJ has repeatedly been found using the imitation inhibition task (Brass, Derrfuss, Forstmann,

et al., 2005; Brass, Derrfuss, & von Cramon, 2005; Santiesteban et al., 2012; Spengler et al., 2009; Spengler et al., 2010). It has been suggested that rTPJ is related to self-other distinction in various domains, ranging from theory of mind and empathy over agency to regulation of mimicry (Brass et al., 2001; Brass et al., 2009; Decety & Lamm, 2007; Klapper et al., 2014; Mar, 2011; Santiesteban et al., 2012; Spengler et al., 2009). More specifically, in the original version of the task we used, the involvement of the rTPJ was ascribed to keeping the distinction between one's own and the other's movement intentions (Brass, et al., 2001; Brass, Derrfuss, & von Cramon, 2005; Brass, et al., 2009; Spengler, et al., 2009).

We also observed activation in the AI and MCC. Recent evidence reports a specific involvement of AI and anterior parts of the MCC in the process of controlling mimicry (Cross et al., 2013). On a broader level, we had also predicted involvement of the AI and MCC, as these areas have been proposed to conjointly operate in the sense of an in- and output system serving behavioral and homeostatic regulation (Medford & Critchley, 2010). Moreover, we have previously argued that this network is specifically associated with the processing and the regulation of socially salient and relevant information (Lamm & Singer, 2010). In this system, the AI is supposed to code interoceptive and multi-modal (e.g., sensory, motoric, affective and cognitive) information about the social environment (see also: Craig, 2009; Lamm & Singer, 2010; Simmons et al., 2013; Singer, Critchley, & Preuschoff, 2009), and signals this information to the output module, the MCC. The latter, together with adjacent rostral cingulate zone (RCZ), is involved in response control, via its strong connections to motor regions of the brain (Medford & Critchley, 2010; Shackman, et al., 2011). Within the context of the current task, which included highly salient social cues, the recruitment of this network might therefore reflect the signaling of salient information in the AI, which in turn may have resulted in a concurrent behavior regulation demand guided by the MCC/RCZ.

We now turn in detail to the distinct activations associated with the regulation of mimicry in response to differing facial expressions and group membership. Of special note, these activations were all situated in different parts of the general (and just described) network engaged in the regulation of mimicry.

4.2.2. Regulation of mimicry in response to happy facial expressions

The higher behavioral mimicry effect in response to happy facial expressions was accompanied by higher activation in the right TPJ, the right SPL, and the right dPMC (see Table 3 and Fig. 2; see also Table S1 for all areas activated in the unmasked contrast of mimicry regulation for the Happy condition).

Since happy faces represent a highly salient affiliative signal which might elicit a tendency to reciprocate this affiliation, self-other distinction might become harder to achieve. We therefore suggest that rTPJ activation is related to the higher demands of maintaining the differentiation between other and self-generated movements in controlling the boundless reciprocation of affiliation via mimicry. This could have served to support participants in better adherence to the task-assignment (which was to focus on the self-related

number cues, while ignoring all other information, including the interfering movements of the other hand). While fMRI only informs us about neural correlates, the causal involvement of rTPJ and adjacent rSMG in self-other distinction has recently been documented (Santiesteban, et al., 2012; Silani et al., 2013). For the present case, these findings suggest that the rTPJ, figuratively speaking, seemingly needs to work harder to avoid unrestraint mimicry in response to the highly affiliative social cue of the happy face. In line with this interpretation, the correlation analyses revealed a trend towards significance for higher activation of the TPJ with lower mimicry.

As suggested, modulation of activation of sensorimotor areas might allow inferences on a shift in processing resources towards solving the rule-based task at hand (i.e., responding to the number cue) or towards processing the task-irrelevant imitative movement (i.e., hand cue). In the case of presenting happy faces, we found significant activation in the dPMC and the SPL. These areas, which are strongly connected anatomically (Matelli, Govoni, Galletti, Kutz, & Luppino, 1998), are essential for controlling motor responses based on arbitrary cues (Hoshi & Tanji, 2007; Majdandžić, Bekkering, van Schie, & Toni, 2009). Their involvement in the present task is thus likely related to generating motor responses based on the number cues. We speculate that their higher involvement in response to happy faces reflects an active attempt to execute the movement indicated by the task-relevant number cue, instead of mimicking the movement of an interaction partner showing highly affiliative signals.

Taken together, we propose that the regulation of mimicry in response to happy faces serves to control for social task interference and to reduce boundless (over-) reciprocation of the affiliative signal. This might be achieved by enhancing self-other distinction and by an increased diversion of sensorimotor processes towards the task-relevant cue, as a means to disengage from the salient but task-irrelevant face and hand stimuli.

4.2.3. Regulation of mimicry in response to out-group faces

Higher mimicry when out-group faces were presented was accompanied with activation in the left IPL and the vPMC, and a network consisting of bilateral AI and bilateral MCC/RCZ (see Table 4 and Fig. 3; and Table S3).

The vPMC and IPL are closely connected (Luppino, Murata, Govoni, & Matelli, 1999) perceptuo-motor areas known to be crucially involved in motor planning based on visuospatial properties rather than arbitrary cues (Hoshi & Tanji, 2006, 2007), and are frequently discussed for their role in action observation, mimicry, and “motor resonance” (Brass & Heyes, 2005; Heyes, 2001, 2011; Hoshi & Tanji, 2006; Iacoboni et al., 1999; Luppino, et al., 1999; Rizzolatti & Craighero, 2004; Rizzolatti, Fogassi, & Gallese, 2001, 2002). This suggests that their engagement in the present context relates to enhanced processing of the hand stimulus rather than the number cue, which in turn might have triggered increased mimicry and higher interference with task performance.

As outlined above, the AI has been associated with integrating interoceptive signals and multi-modal inputs from the (social) environment into an overall affective representation of the organism's state (Lamm & Singer, 2010; Medford &

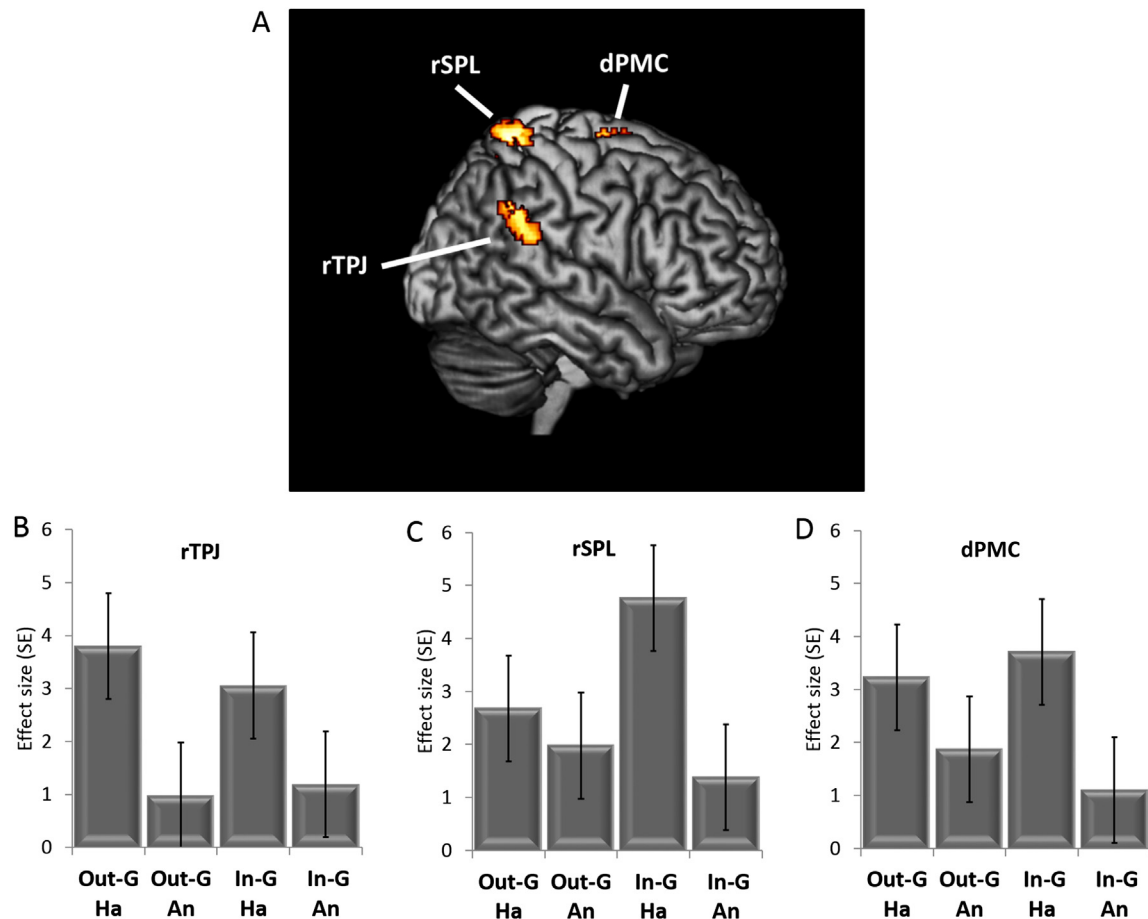


Fig. 2 – Activation related to mimicry regulation in response to seeing happy facial expressions. (A) Shown are significant clusters for the contrast Happy faces (Incongruent > Congruent) masked inclusively with Happy (Incongruent > Congruent) > Angry (Incongruent > Congruent). Clusters show activation in the right superior parietal lobule (rSPL) and the right dorsal premotor cortex (dPMC), as well as in the right temporo-parietal junction (rTPJ). Display in neurological convention on the high-resolution structural MRI template brain in SPM8, threshold $p = .05$, with family-wise error correction at cluster-level (cluster selection threshold $p = .001$). Effect size (beta/SE) within (B) rTPJ (64, –46, 38), (C) rSPL (30, –52, 68) and (D) dPMC (22, –8, 56) for mimicry regulation (Incongruent > Congruent) separate for presentation of out-group happy (Out-G Ha), out-group angry (Out-G An), in-group happy (In-G Ha) and in-group angry (In-G An) facial expressions. Note that the bar plots of effect size represent only a graphical illustration of changes in BOLD activation for mimicry regulation (i.e., incongruent > congruent trials) per condition. The displayed effect sizes per condition are expected to be biased as they are based on the same statistical contrast used to select the areas of activation (Kriegeskorte et al., 2009). No additional inferences should be drawn from these plots.

Critchley, 2010; Simmons, et al., 2013; Singer, et al., 2009). As such, the AI is thought to respond strongly to salient social signals, such as, in our case, out-group faces. Thus, the involvement of the AI might reflect the higher social salience of the implicitly more threatening out-group face (see results of the Threat/Security IAT, as well as previous evidence e.g.: Amodio, 2004, 2008; Amodio & Devine, 2006; Amodio, et al., 2008; Amodio, et al., 2004), which in turn signals an increased need for an immediate regulative response. This behavioral regulation might be implemented by the MCC and adjacent RCZ, which have been associated with regulating behavior during enhanced threat and, generally, highly aversive states (Shackman, et al., 2011).

We therefore suggest that in the case of out-group faces, regulation of mimicry serves a social affiliative function. Here, participants increase mimicry in response to the salient cue of an out-group member implicitly eliciting the perception of threat, reflecting an attempt to appease the threatening other.

4.3. General discussion

Our findings suggest that on a behavioral level mimicry represents reciprocation of affiliation and appeasement, which is reflected in an increased mimicry effect. Yet on a process-level our findings suggest that mimicry is adaptively

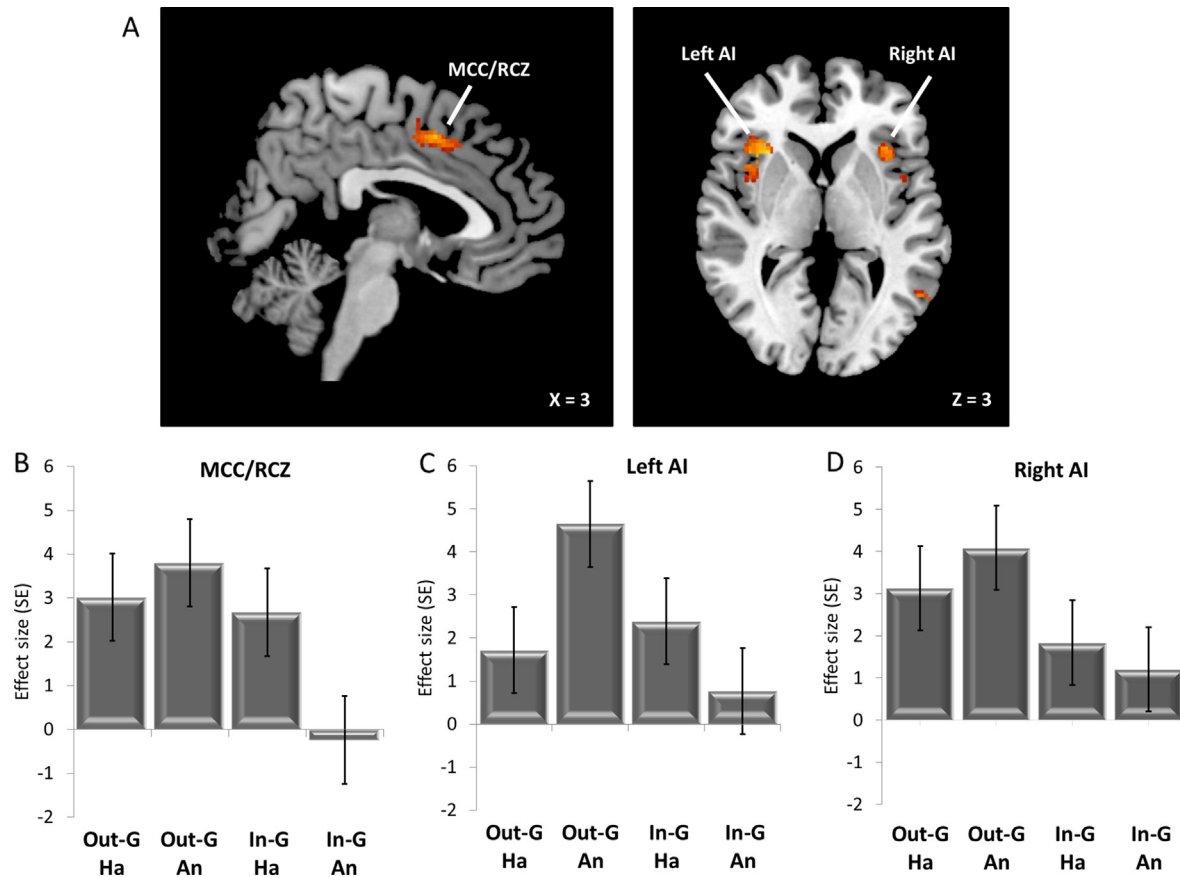


Fig. 3 – Activation related to mimicry regulation in response to seeing out-group members. (A) Shown are significant clusters for the contrast Out-group (Incongruent > Congruent) masked inclusively with Out-group (Incongruent > Congruent) > In-group (Incongruent > Congruent). (Left) Activation in mid-cingulate cortex (MCC) and rostral cingulate zone (RCZ). (Right) Activation in bilateral anterior insula (AI). Display in neurological convention on the high-resolution structural MRI template brain in SPM8, threshold $p = .05$, with family-wise error correction at cluster-level (cluster selection threshold $p = .001$). Effect size (beta/SE) within (B) MCC/RCZ (2, 8, 46), (C) left AI (–28, 22, 12) and (D) right AI (32, 24, 4) for mimicry regulation (Incongruent > Congruent) separate for presentation of out-group happy (Out-G Ha), out-group angry (Out-G An), in-group happy (In-G Ha) and in-group angry (In-G An) facial expressions. Note that the bar plots of effect size represent only a graphical illustration of changes in BOLD activation for mimicry regulation (i.e., incongruent > congruent trials) per condition. The displayed effect sizes per condition are expected to be biased as they are based on the same statistical contrast used to select the areas of activation (Kriegeskorte et al., 2009). No additional inferences should be drawn from these plots.

regulated while pursuing these distinct affiliative goals: either to control the (overly strong) reciprocation of an affiliative signal (mimicry when happy faces are presented), or to increase affiliation as when trying to appease a potentially threatening interaction partner (mimicry when out-group faces are presented). Hence, of all the processes generally involved in mimicry regulation based on social cues, we suggest that specific sub-processes were differentially involved for these distinct instances of mimicry regulation.

As happiness inherently signals affiliative intent, reciprocating affiliation via mimicry might aim at securing future positive exchanges with the other (Bourgeois & Hess, 2008; Hess & Fischer, 2013; Van der Schalk et al., 2011; Van Kleef et al., 2004, 2010). Thus with respect to keeping the focus on specific (task) demands in the affiliative social situation,

unrestraint reciprocation of affiliation might be withheld. More specifically, regulating the unbounded reciprocation of the affiliative cue of a happy face requires heightened self-other distinction and a stronger focus on the target cue, increasing relevance of the self. Appeasement on the other hand is aimed at soothing a possible conflict (Keltner et al., 1997). Thus the encounter of an out-group face seems to increase the focus on the other, resulting in behavior regulation processes enabling stronger mimicry and hence increasing affiliative signaling and appeasement.

The question of whether mimicry's malleability by social cues is based on in- or output modulation (Heyes, 2011) cannot be univocally answered by our data. We observed a shift in low-level sensorimotor processing during mimicry regulation in the presence of happy and out-group faces. Enhanced

mimicry when happy faces were presented resulted in activation in the right SPL and dPMC. This might suggest that in this condition, sensorimotor processing was shifted towards processing the response to the task-relevant number cue for the sake of task-adherence. On the other hand, when out-group faces were presented, sensorimotor contributions in the vPMC/left IPL network were increased. This suggests that regulation of mimicry in this condition was accompanied by a shift of sensorimotor processing towards visuospatial properties of the task-irrelevant hand. These observed shifts in sensorimotor processing might suggest that the regulation of mimicry by social-affective cues is driven by input modulation. On the other hand, we also observed changes in activation of the rTPJ, reflecting self-other distinction processes that have been related to output modulation of the mimicry response (Heyes, 2011). In line with this, the involvement of the AI/MCC network for behavior regulation according to detected saliency (in our case threat) in the environment (Medford & Critchley, 2010; Shackman et al., 2011) could speak for output modulation regulating mimicry behavior goal-directedly. Thus, based on the current data alone, we cannot fully discern the involvement of in- or output modulation in the modulation of mimicry to social-affective cues, and our interpretations remain speculative. Further studies should aim to further clarify the pathways by which mimicry is regulated in response to social context stimuli. A more time-sensitive measure, as event-related brain potential (ERP) studies, might be able to tap into the temporal dynamics of this modulation and thereby possibly capture processes attributable to in- or output modulation.

We suggest that along sensorimotor mechanisms, the processes of self-other distinction and behavioral regulation are involved in the modulation of mimicry to social-affective information in general. Yet, we did not replicate previous findings regarding the involvement of mPFC in the modulation of mimicry by contextual information (Wang & Hamilton, 2012, 2015; Wang, Ramsey, et al., 2011). Note though that the involvement of mPFC in these studies has been attributed to the processing of eye gaze (Wang & Hamilton, 2012; Wang, Ramsey, et al., 2011) or pro- and antisocial priming (Wang & Hamilton, 2015). In our study, gaze was not varied, and we used clearly valenced facial expressions. Hence, the clear social-affective nature of our paradigm could have also resulted in lower mentalizing demands, which could also explain the absence of mPFC activations.

5. Conclusion

Our study demonstrates that automatic imitation paradigms are a valid tool to investigate the influence of social-affective cues on mimicry. Our results show that subtle manipulations of such social-affective cues significantly affect both behavioral and neural measures of mimicry. Crucially, our findings suggest that the regulation of mimicry is not a unitary phenomenon. Depending upon the affiliative goals, it may be supported by distinct social-cognitive, behaviorally regulative, and sensorimotor processes. Thus, the present study confirms the notion that despite its automaticity, mimicry is a highly context-sensitive and implicitly modifiable motor response,

and provides further evidence on how the regulation of this response is supported by distinct neuro-cognitive processes.

Acknowledgments

The study was supported by the Viennese Science and Technology Fund (WWTF, CS11-005, to CL). The authors would like to thank Christina Rauchbauer and Abba Marie-Jose Bedi for lending a helping hand; Doris Lamplmair and Andreas Martin for invaluable support in participant recruitment and data collection; Stefan Stieger for highly appreciated support regarding the IAT; Ludwig Huber (Veterinary University of Vienna, Messerli Research Institute) for valuable discussions of the research design.

Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.cortex.2015.03.007>.

REFERENCES

- Amodio, D. M. (2004). The role of conflict-detection in the regulation of race-biased behavior. *Psychophysiology*, 41, S6–S6.
- Amodio, D. M. (2008). The social neuroscience of intergroup relations. *European Review of Social Psychology*, 19, 1–54. <http://dx.doi.org/10.1080/10463280801927937>.
- Amodio, D. M., & Devine, P. G. (2006). Stereotyping and evaluation in implicit race bias: evidence for independent constructs and unique effects on behavior. *Journal of Personality and Social Psychology*, 91(4), 652–661. <http://dx.doi.org/10.1037/0022-3514.91.4.652>.
- Amodio, D. M., Devine, P. G., & Harmon-Jones, E. (2008). Individual differences in the regulation of intergroup bias: the role of conflict monitoring and neural signals for control. *Journal of Personality and Social Psychology*, 94(1), 60–74. <http://dx.doi.org/10.1037/0022-3514.94.1.60>.
- Amodio, D. M., Harmon-Jones, E., Devine, P. G., Curtin, J. J., Hartley, S. L., & Covert, A. E. (2004). Neural signals for the detection of unintentional race bias. *Psychological Science*, 15(2), 88–93. <http://dx.doi.org/10.1111/j.0963-7214.2004.01502003.x>.
- Amodio, D. M., Kubota, J. T., Harmon-Jones, E., & Devine, P. G. (2006). Alternative mechanisms for regulating racial responses according to internal vs external cues. *Social Cognitive and Affective Neuroscience*, 1(1), 26–36. <http://dx.doi.org/10.1093/scan/nsi002>.
- Bourgeois, P., & Hess, U. (2008). The impact of social context on mimicry. *Biological Psychology*, 77(3), 343–352. <http://dx.doi.org/10.1016/j.biopsycho.2007.11.008>.
- Brass, M., Bekkering, H., Wohlschläger, A., & Prinz, W. (2000). Compatibility between observed and executed finger movements: comparing symbolic, spatial, and imitative cues. *Brain and Cognition*, 44(2), 124–143. <http://dx.doi.org/10.1006/brcg.2000.1225>.
- Brass, M., Derrfuss, J., Forstmann, B., & von Cramon, D. Y. (2005). The role of the inferior frontal junction area in cognitive control. *Trends in Cognitive Sciences*, 9(7), 314–316. <http://dx.doi.org/10.1016/j.tics.2005.05.001>.
- Brass, M., Derrfuss, J., & von Cramon, D. Y. (2005). The inhibition of imitative and overlearned responses: a functional double

- dissociation. *Neuropsychologia*, 43(1), 89–98. <http://dx.doi.org/10.1016/j.neuropsychologia.2004.06.018>.
- Brass, M., & Heyes, C. (2005). Imitation: is cognitive neuroscience solving the correspondence problem? *Trends in Cognitive Sciences*, 9(10), 489–495. <http://dx.doi.org/10.1016/j.tics.2005.08.007>.
- Brass, M., Ruby, P., & Spengler, S. (2009). Inhibition of imitative behaviour and social cognition. *Philosophical Transactions of the Royal Society of London Series B Biological Sciences*, 364(1528), 2359–2367. <http://dx.doi.org/10.1098/rstb.2009.0066>.
- Brass, M., Zysset, S., & von Cramon, D. Y. (2001). The inhibition of imitative response tendencies. *NeuroImage*, 14(6), 1416–1423. <http://dx.doi.org/10.1006/nimg.2001.0944>.
- Brigham, J. C. (1993). College students' racial attitudes. *Journal of Applied Social Psychology*, 23(23), 1933–1967. <http://dx.doi.org/10.1111/j.1559-1816.1993.tb01074.x>.
- Catmur, C., & Heyes, C. (2011). Time course analyses confirm independence of imitative and spatial compatibility. *Journal of Experimental Psychology: Human Perception and Performance*, 37(2), 409–421. <http://dx.doi.org/10.1037/a0019325>.
- Catmur, C., & Heyes, C. (2013). Is it what you do, or when you do it? The roles of contingency and similarity in pro-social effects of imitation. *Cognitive Science*, 37(8), 1541–1552. <http://dx.doi.org/10.1111/cogs.12071>.
- Catmur, C., Mars, R. B., Rushworth, M. F., & Heyes, C. (2011). Making mirrors: premotor cortex stimulation enhances mirror and counter-mirror motor facilitation. *Journal of Cognitive Neuroscience*, 23(9), 2352–2362. <http://dx.doi.org/10.1162/jocn.2010.21590>.
- Chartrand, T. L., & Bargh, J. A. (1999). The Chameleon effect: the perception-behavior link and social interaction. *Journal of Personality and Social Psychology*, 76(6), 893–910. <http://dx.doi.org/10.1037/0022-3514.76.6.893>.
- Chartrand, T. L., & Lakin, J. L. (2013). The antecedents and consequences of human behavioral mimicry. *Annual Review of Psychology*, 64, 285–308. <http://dx.doi.org/10.1146/annurev-psych-113011-143754>, 64.
- Cooper, R. P., Catmur, C., & Heyes, C. (2013). Are automatic imitation and spatial compatibility mediated by different processes? *Cognitive Science*, 37(4), 605–630. <http://dx.doi.org/10.1111/j.1551-6709.2012.01252.x>.
- Craig, A. D. (2009). How do you feel—now? the anterior insula and human awareness. [Research Support, Non-U.S. Gov't]. *Nature Reviews Neuroscience*, 10(1), 59–70. <http://dx.doi.org/10.1038/nrn2555>.
- Cross, K. A., Torrisi, S., Losin, E. A. R., & Iacoboni, M. (2013). Controlling automatic imitative tendencies: Interactions between mirror neuron and cognitive control systems. *NeuroImage*, 83, 493–504. <http://dx.doi.org/10.1016/j.neuroimage.2013.06.060>.
- Decety, J., & Lamm, C. (2007). The role of the right temporoparietal junction in social interaction: how low-level computational processes contribute to meta-cognition. *Neuroscientist*, 13(6), 580–593. <http://dx.doi.org/10.1177/1073858407304654>.
- Dunbar, R. I. (2012). Bridging the bonding gap: the transition from primates to humans. *Philosophical Transactions of the Royal Society of London Series B Biological Sciences*, 367(1597), 1837–1846. <http://dx.doi.org/10.1098/rstb.2011.0217>.
- Dunbar, R. I., & Shultz, S. (2010). Bondedness and sociality. *Behaviour*, 147(7), 775–803. <http://dx.doi.org/10.1163/000579510x501151>.
- Eickhoff, S. B., Stephan, K. E., Mohlberg, H., Grefkes, C., Fink, G. R., Amunts, K., et al. (2005). A new SPM toolbox for combining probabilistic cytoarchitectonic maps and functional imaging data. *NeuroImage*, 25(4), 1325–1335. <http://dx.doi.org/10.1016/j.neuroimage.2004.12.034>.
- Friston, K. J., Holmes, A., Poline, J. B., Price, C. J., & Frith, C. D. (1996). Detecting activations in PET and fMRI: levels of inference and power. *NeuroImage*, 4(3), 223–235. <http://dx.doi.org/10.1006/nimg.1996.0074>.
- Grecucci, A., Koch, I., & Rumiati, R. I. (2011). The role of emotional context in facilitating imitative actions. *Acta Psychologica*, 138(2), 311–315. <http://dx.doi.org/10.1016/j.actpsy.2011.07.005>.
- Greenwald, A. G., McGhee, D. E., & Schwartz, J. L. K. (1998). Measuring individual differences in implicit cognition: the implicit association test. *Journal of Personality and Social Psychology*, 74(6), 1464–1480. <http://dx.doi.org/10.1037/0022-3514.74.6.1464>.
- Greenwald, A. G., Nosek, B. A., & Banaji, M. R. (2003). Understanding and using the implicit association test: I. An improved scoring algorithm. *Journal of Personality and Social Psychology*, 85(2), 197–216. <http://dx.doi.org/10.1037/0022-3514.85.2.197>.
- Greenwald, A. G., Poehlman, T. A., Uhlmann, E. L., & Banaji, M. R. (2009). Understanding and using the implicit association Test: III. Meta-analysis of predictive validity. *Journal of Personality and Social Psychology*, 97(1), 17–41. <http://dx.doi.org/10.1037/a0015575>.
- Hess, U., & Fischer, A. (2013). Emotional mimicry as social regulation. *Personality and Social Psychology Review*, 17(2), 142–157. <http://dx.doi.org/10.1177/1088868312472607>.
- Heyes, C. (2001). Causes and consequences of imitation. *Trends in Cognitive Sciences*, 5(6), 253–261.
- Heyes, C. (2011). Automatic imitation. *Psychological Bulletin*, 137(3), 463–483. <http://dx.doi.org/10.1037/A0022288>.
- Heyes, C., Bird, G., Johnson, H., & Haggard, P. (2005). Experience modulates automatic imitation. *Brain Research Cognitive Brain Research*, 22(2), 233–240. <http://dx.doi.org/10.1016/j.cogbrainres.2004.09.009>.
- Hoshi, E., & Tanji, J. (2006). Differential involvement of neurons in the dorsal and ventral premotor cortex during processing of visual signals for action planning. *Journal of Neurophysiology*, 95(6), 3596–3616. <http://dx.doi.org/10.1152/jn.01126.2005>.
- Hoshi, E., & Tanji, J. (2007). Distinctions between dorsal and ventral premotor areas: anatomical connectivity and functional properties. *Current Opinion in Neurobiology*, 17(2), 234–242. <http://dx.doi.org/10.1016/j.conb.2007.02.003>.
- Iacoboni, M., Woods, R. P., Brass, M., Bekkering, H., Mazziotta, J. C., & Rizzolatti, G. (1999). Cortical mechanisms of human imitation. *Science*, 286(5449), 2526–2528.
- Johnston, L. (2002). Behavioral mimicry and stigmatization. *Social Cognition*, 20(1), 18–35. <http://dx.doi.org/10.1521/soco.20.1.18.20944>.
- Keltner, D., Young, R. C., & Buswell, B. N. (1997). Appeasement in human emotion, social practice, and personality. *Aggressive Behavior*, 23(5), 359–374. [http://dx.doi.org/10.1002/\(Sici\)1098-2337\(1997\)23<359::Aid-Ab5>3.0.Co;2-D](http://dx.doi.org/10.1002/(Sici)1098-2337(1997)23<359::Aid-Ab5>3.0.Co;2-D).
- Klapper, A., Ramsey, R., Wigboldus, D., & Cross, E. S. (2014). The control of automatic imitation based on bottom-up and top-down cues to animacy: insights from brain and behavior. *Journal of Cognitive Neuroscience*, 26(11), 2503–2513. http://dx.doi.org/10.1162/jocn_a_00651.
- Kriegeskorte, N., Simmons, W. K., Bellgowan, P. S., & Baker, C. I. (2009). Circular analysis in systems neuroscience: the dangers of double dipping. [Research Support, N.I.H., Intramural Review]. *Nature Neuroscience*, 12(5), 535–540. <http://dx.doi.org/10.1038/nn.2303>.
- Lakin, J. L., & Chartrand, T. L. (2003). Using nonconscious behavioral mimicry to create affiliation and rapport. *Psychological Science*, 14(4), 334–339. <http://dx.doi.org/10.1111/1467-9280.14481>.
- Lakin, J. L., Chartrand, T. L., & Arkin, R. M. (2008). I am too just like you – nonconscious mimicry as an automatic behavioral response to social exclusion. *Psychological Science*, 19(8), 816–822. <http://dx.doi.org/10.1111/j.1467-9280.2008.02162.x>.
- Lakin, J. L., Jefferis, V. E., Cheng, C. M., & Chartrand, T. L. (2003). The chameleon effect as social glue: evidence for the

- evolutionary significance of nonconscious mimicry. *Journal of Nonverbal Behavior*, 27(3), 145–162. <http://dx.doi.org/10.1023/A:1025389814290>.
- Lamm, C., & Majdandžić, J. (2015). The role of shared neural activations, mirror neurons, and morality in empathy—a critical comment. *Neuroscience Research*, 90, 15–24. <http://dx.doi.org/10.1016/j.neures.2014.10.008>.
- Lamm, C., & Singer, T. (2010). The role of anterior insular cortex in social emotions. *Brain Structure & Function*, 214(5–6), 579–591. <http://dx.doi.org/10.1007/s00429-010-0251-3>.
- Leighton, J., Bird, G., Orsini, C., & Heyes, C. (2010). Social attitudes modulate automatic imitation. *Journal of Experimental Social Psychology*, 46(6), 905–910. <http://dx.doi.org/10.1016/j.jesp.2010.07.001>.
- Losin, E. A. R., Cross, K. A., Iacoboni, M., & Dapretto, M. (2014). Neural processing of race during imitation: self-similarity versus social status. *Human Brain Mapping*, 35(4), 1723–1739. <http://dx.doi.org/10.1002/Hbm.22287>.
- Losin, E. A. R., Iacoboni, M., Martin, A., Cross, K. A., & Dapretto, M. (2012). Race modulates neural activity during imitation. *NeuroImage*, 59(4), 3594–3603. <http://dx.doi.org/10.1016/j.neuroimage.2011.10.074>.
- Luppino, G., Murata, A., Govoni, P., & Matelli, M. (1999). Largely segregated parietofrontal connections linking rostral intraparietal cortex (areas AIP and VIP) and the ventral premotor cortex (areas F5 and F4). *Experimental Brain Research*, 128(1–2), 181–187.
- Machin, A. J., & Dunbar, R. I. (2011). The brain opioid theory of social attachment: a review of the evidence. *Behaviour*, 148(9–10), 985–1025. <http://dx.doi.org/10.1163/000579511x596624>.
- Majdandžić, J., Bekkering, H., van Schie, H. T., & Toni, I. (2009). Movement-specific repetition suppression in ventral and dorsal premotor cortex during action observation. *Cerebral Cortex*, 19(11), 2736–2745. <http://dx.doi.org/10.1093/cercor/bhp049>.
- Mar, R. A. (2011). The neural bases of social cognition and story comprehension. [Review]. *Annual Review of Psychology*, 62, 103–134. <http://dx.doi.org/10.1146/annurev-psych-120709-145406>.
- Matelli, M., Govoni, P., Galletti, C., Kutz, D. F., & Luppino, G. (1998). Superior area 6 afferents from the superior parietal lobule in the macaque monkey. *Journal of Comparative Neurology*, 402(3), 327–352.
- Medford, N., & Critchley, H. D. (2010). Conjoint activity of anterior insular and anterior cingulate cortex: awareness and response. *Brain Structure & Function*, 214(5–6), 535–549. <http://dx.doi.org/10.1007/s00429-010-0265-x>.
- Neuberg, S. L., & Cottrell, C. A. (2008). Managing the threats and opportunities afforded by human sociality. *Group Dynamics—Theory Research and Practice*, 12(1), 63–72. <http://dx.doi.org/10.1037/1089-2699.12.1.63>.
- Penny, W. D., & Holmes, A. (2004). Random-effects analysis. In W. Penny, A. Holmes, & K. J. Friston (Eds.), *Human brain function* (pp. 843–850). San Diego: Elsevier.
- Rauchbauer, B., Majdandžić, J., Stieger, S., & Lamm, C. (2014). The effects on emotional in- and outgroup context on mimicry. UK: University of Surrey. Poster presentation at the workshop on Social Cognition: Origins, Mechanisms and Disorders.
- Rauchbauer, B., Majdandžić, J., Stieger, S., & Lamm, C. (2015). The modulation of mimicry by social group-membership and emotional expressions. Manuscript submitted for publication.
- Riečanský, I., Paul, N., Kölbl, S., Stieger, S., & Lamm, C. (2014). Beta oscillations reveal ethnicity ingroup bias in sensorimotor resonance to pain of others. *Social Cognitive Affective Neuroscience*. <http://dx.doi.org/10.1093/scan/nsu139>. Epub ahead of print.
- Rizzolatti, G., & Craighero, L. (2004). The mirror-neuron system. *Annual Review of Neuroscience*, 27, 169–192. <http://dx.doi.org/10.1146/annurev.neuro.27.070203.144230>.
- Rizzolatti, G., Fogassi, L., & Gallese, V. (2001). Neurophysiological mechanisms underlying the understanding and imitation of action. *Nature Reviews Neuroscience*, 2(9), 661–670. <http://dx.doi.org/10.1038/35090060>.
- Rizzolatti, G., Fogassi, L., & Gallese, V. (2002). Motor and cognitive functions of the ventral premotor cortex. *Current Opinion in Neurobiology*, 12(2), 149–154.
- Santesteban, I., Banissy, M. J., Catmur, C., & Bird, G. (2012). Enhancing social ability by stimulating right temporoparietal junction. *Current Biology: CB*, 22(23), 2274–2277. <http://dx.doi.org/10.1016/j.cub.2012.10.018>.
- Shackman, A. J., Salomons, T. V., Slagter, H. A., Fox, A. S., Winter, J. J., & Davidson, R. J. (2011). The integration of negative affect, pain and cognitive control in the cingulate cortex. *Nature Reviews Neuroscience*, 12(3), 154–167. <http://dx.doi.org/10.1038/nrn2994>.
- Silani, G., Lamm, C., Ruff, C. C., & Singer, T. (2013). Right supramarginal gyrus is crucial to overcome emotional egocentricity bias in social judgments. *Journal of Neuroscience*, 33(39), 15466–15476. <http://dx.doi.org/10.1523/JNEUROSCI.1488-13.2013>.
- Simmons, W. K., Avery, J. A., Barcalow, J. C., Bodurka, J., Drevets, W. C., & Bellgowan, P. (2013). Keeping the body in mind: insula functional organization and functional connectivity integrate interoceptive, exteroceptive, and emotional awareness. *Human Brain Mapping*, 34(11), 2944–2958. <http://dx.doi.org/10.1002/hbm.22113>.
- Singer, T., Critchley, H. D., & Preuschoff, K. (2009). A common role of insula in feelings, empathy and uncertainty. *Trends in Cognitive Sciences*, 13(8), 334–340. <http://dx.doi.org/10.1016/j.tics.2009.05.001>.
- Sowden, S., & Catmur, C. (2015). The role of the right temporoparietal junction in the control of imitation. *Cerebral Cortex*, 25(4), 1107–1113. <http://dx.doi.org/10.1093/cercor/bht306>.
- Spengler, S., Brass, M., Kuhn, S., & Schutz-Bosbach, S. (2010). Minimizing motor mimicry by myself: self-focus enhances online action-control mechanisms during motor contagion. *Consciousness and Cognition*, 19(1), 98–106. <http://dx.doi.org/10.1016/j.concog.2009.12.014>.
- Spengler, S., von Cramon, D. Y., & Brass, M. (2009). Control of shared representations relies on key processes involved in mental state attribution. *Human Brain Mapping*, 30(11), 3704–3718. <http://dx.doi.org/10.1002/hbm.20800>.
- Stel, M., van Baaren, R. B., Blascovich, J., van Dijk, E., McCall, C., Pollmann, M. M. H., et al. (2010). Effects of a priori liking on the elicitation of mimicry. *Experimental Psychology*, 57(6), 412–418. <http://dx.doi.org/10.1027/1618-3169/A000050>.
- Stel, M., & Vonk, R. (2010). Mimicry in social interaction: benefits for mimickers, mimicked, and their interaction. *British Journal of Psychology*, 101, 311–323. <http://dx.doi.org/10.1348/000712609x465424>.
- Tomova, L., von Dawans, B., Heinrichs, M., Silani, G., & Lamm, C. (2014). Is stress affecting our ability to tune into others? Evidence for gender differences in the effects of stress on self-other distinction. *Psychoneuroendocrinology*, 43, 95–104. <http://dx.doi.org/10.1016/j.psyneuen.2014.02.006>.
- Tottenham, N., Tanaka, J. W., Leon, A. C., McCarry, T., Nurse, M., Hare, T. A., et al. (2009). The NimStim set of facial expressions: judgments from untrained research participants. *Psychiatry Research*, 168(3), 242–249. <http://dx.doi.org/10.1016/j.psychres.2008.05.006>.
- Van Baaren, R., Janssen, L., Chartrand, T., & Dijksterhuis, A. (2009). Where is the love? the social aspects of mimicry.

- Philosophical Transactions of the Royal Society B: Biological Sciences, 364(1528), 2381–2389. <http://dx.doi.org/10.1098/rstb.2009.0057>.
- Van Baaren, R. B., Holland, R. W., Kawakami, K., & van Knippenberg, A. (2004). Mimicry and prosocial behavior. *Psychological Science*, 15(1), 71–74. <http://dx.doi.org/10.1111/j.0963-7214.2004.01501012.x>.
- Van Kleef, G., De Dreu, C., & Manstead, A. (2004). The interpersonal effects of anger and happiness in negotiations. *Journal of Personality and Social Psychology*, 86(1), 57.
- Van Kleef, G., De Dreu, C., & Manstead, A. (2010). Chapter 2-An interpersonal approach to emotion in social decision making: the emotions as social information model. In P. Z. Mark (Ed.), *Advances in experimental social psychology* (Vol. 42, pp. 45–96). Academic Press.
- Van der Schalk, J., Fischer, A., Doosje, B., Wigboldus, D., Hawk, S., Rotteveel, M., et al. (2011). Convergent and divergent responses to emotional displays of ingroup and outgroup. *Emotion*, 11(2), 286–298. <http://dx.doi.org/10.1037/A0022582>.
- Vul, E., Harris, C., Winkielman, P., & Pashler, H. (2009). Puzzlingly high correlations in fMRI studies of emotion, personality, and social cognition. *Perspectives on Psychological Science*, 4(3), 274–290. <http://dx.doi.org/10.1111/j.1745-6924.2009.01125.x>.
- de Waal, F. B. (1986). The integration of dominance and social bonding in primates. *The Quarterly Review of Biology*, 61(4), 459–479. <http://dx.doi.org/10.2307/2827744>.
- de Waal, F. B. (2003). Darwin's legacy and the study of primate visual communication. *Annals of the New York Academy of Sciences*, 1000, 7–31.
- Wang, Y., & Hamilton, A. (2012). Social top-down response modulation (STORM): a model of the control of mimicry in social interaction. *Frontiers in Human Neuroscience*, 6. <http://dx.doi.org/10.3389/fnhum.2012.00153>.
- Wang, Y., & Hamilton, A. (2015). Anterior medial prefrontal cortex implements social priming of mimicry. *Social Cognitive and Affective Neuroscience*, 10(4), 486–493. <http://dx.doi.org/10.1093/scan/nsu076>.
- Wang, Y., & Hamilton, A. (2014). Why does gaze enhance mimicry? Placing gaze-mimicry effects in relation to other gaze phenomena. *Quarterly Journal of Experimental Psychology (Hove)*, 67(4), 747–762. <http://dx.doi.org/10.1080/17470218.2013.828316>.
- Wang, Y., Newport, R., & Hamilton, A. (2011). Eye contact enhances mimicry of intransitive hand movements. *Biology Letters*, 7(1), 7–10. <http://dx.doi.org/10.1098/rsbl.2010.0279>.
- Wang, Y., Ramsey, R., & Hamilton, A. (2011). The control of mimicry by eye contact is mediated by medial prefrontal cortex. *Journal of Neuroscience*, 31(33), 12001–12010. <http://dx.doi.org/10.1523/Jneurosci.0845-11.2011>.
- Wilcoxon, R. (2011). *Modern statistics for the social and behavioral sciences: A practical introduction*. CRC Press.
- Yabar, Y., Johnston, L., Miles, L., & Peace, V. (2006). Implicit behavioral mimicry: Investigating the impact of group membership. *Journal of Nonverbal Behavior*, 30(3), 97–113. <http://dx.doi.org/10.1007/s10919-006-0010-6>.