Social Mimicry Enhances Mu-Suppression During Action Observation

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During social interactions, there is a tendency for people to mimic the gestures and mannerisms of others, which increases liking and rapport. Psychologists have extensively studied the antecedents and consequences of mimicry at the social level, but the neural basis of this behavior remains unclear. Many researchers have speculated that mimicry is related to activity in the human mirror system (HMS), a network of parietofrontal regions that are involved in both action execution and observation. However, activity of the HMS during reciprocal social interactions involving mimicry has not been demonstrated. Here, we took an electroencephalographic (EEG) index of a network of parietofrontal regions that are involved in both action that mimicry is related to activity in the human mirror system (HMS), a network of parietofrontal regions that are involved in both action execution and observation. However, activity of the HMS during reciprocal social interactions involving mimicry has not been demonstrated. Here, we took an electroencephalographic (EEG) index of mirror activity—mu-suppression during action observation—in a pretest/post-test design with 1 of 3 intervening treatments: 1) social interaction in which the participant was mimicked, 2) social interaction without mimicry, or 3) an innocuous computer task, not involving another human agent. The change in mu-suppression from pre- to post-test varied as a function of the intervening treatment, with participants who had been mimicked showing an increase in mu-suppression during the post-treatment action observation session. We propose that this specific modulation of HMS activity as a function of mimicry constitutes the first direct evidence for mirror system involvement in real social mimicry.

Keywords: EEG, human mirror system, social mimicry, social neuroscience

Introduction

In social settings, humans routinely mimic the gestures, postures, and other bodily movements of interaction partners (Chartrand and Bargh 1999; Chartrand and Lakin 2013). Such mimicry appears to happen in the absence of conscious intention, and is generally thought to function as a form of “social glue” that increases rapport and liking, among other things. Despite the voluminous research on the phenomenon within the tradition of social psychology, a fundamental question regarding underlying neural mechanisms remains unanswered. One popular suggestion is that the human mirror system (HMS), which is involved in both production and observation of action, underlies mimicry, and this suggestion is often presumed to be a factual explanation. However, despite the intuitive appeal of this suggestion, there is a dearth of empirical evidence connecting mimicry with activity of the HMS. The aim of the experiment reported here was to investigate the proposed link between HMS activity and mimicry in social interactions, thus unifying the cognitive neuroscience and social psychology literatures on human imitation.

The macaque brain contains “mirror neurons” that are engaged during action execution and the passive observation of similar actions (di Pellegrino et al. 1992; Rizzolatti et al. 1996). Evidence for a frontoparietal action observation-execution matching system in the human brain has been strongly suggested via functional magnetic resonance imaging repetition suppression (Chong et al. 2008; Press, Catmur, et al. 2012; Press, Weiskopf, et al. 2012), and this is referred to here as the HMS.

In the social psychological domain, researchers have explored the moderators, downstream consequences, and functional impact of the tendency to mimic others, with many fascinating findings (see Chartrand and Lakin 2013 for a review). The HMS is involved during the observation and imitation of simple actions in tightly controlled laboratory settings (Iacoboni et al. 1999; Catmur et al. 2009; Press, Weiskopf, et al. 2012), and it is this finding that has led researchers to speculate that mimicry in social settings is also implemented by the HMS.

In general conceptual terms, mimicry could be thought about in terms of a dynamic, observation-dependent activation of motor representations in an observer’s brain when exposed to actions of a social partner (a “target”). This type of motor resonance could, when other contingencies are met, lead to the production of a similar action by the observer. This conceptual explanation hinges on the involvement of motor resonant processes, and by extension the HMS, in reciprocal social interactions involving mimicry.

Yet, there is a dearth of empirical data confirming this conceptual explanation, since social mimicry and the HMS come from studies employing predominantly naturalistic social interactions and contrived action observation tasks, respectively. Social interactions contain a whole-body model, are reciprocal, and involve an implicit level of emotional engagement with the other person. In contrast, action observation tasks contain a “disembodied” limb performing a movement on a computer screen, are unidirectional, and involve minimal emotional engagement with the other (cf. Heyes 2011; Schilbach et al. 2013). These differences make it unclear whether the HMS plays the same, or a fundamentally different role during interactions with another person as it does during the observation of an unspecified other. Thus, despite the intuitive connection between social mimicry and the HMS, it is a leap to presume that the HMS underlies mimicry as it occurs in everyday life, and a critical question remains: Is the HMS recruited during social interactions in which mimicry is present?

To test the notion that the HMS is involved in mimicry, the present study hybridized the neuroscientific and social psychological approaches in a sequential fashion. Using a pretest/post-test design, we determined the degree of HMS activity during action observation before and after a “music-rating” task (van Baaren et al. 2005). Participants were assigned to groups that performed the task with 3 different experimental treatments: 1) a social interaction with an experimenter who subtly mimicked the posture, gestures, and mannerisms of the participant (mimicry condition), 2) a social interaction with an experimenter who changed her behavior if the participant began to mimic her movements (antimimicry condition), or 3) a computer program (CPU condition; Fig. 1).
HMS activity was measured indirectly using electroencephalography (EEG). In an EEG environment, rest is associated with high spectral density in the alpha (8–13 Hz) band over central sensors—the mu-rhythm. During action execution, mu-power is reduced, thought to reflect event-related activation of the underlying sensorimotor cortex (Salmelin et al. 1995; Pfurtscheller et al. 1997; Neuper and Pfurtscheller 2001). Crucially, this mu-suppression effect is also found during passive action observation, and has been interpreted as an EEG index of HMS activity (Pineda 2005; Hari 2006).

Of relevance to the present study, mu-suppression is also elicited when experiencing empathic pain (Cheng et al. 2008), and empathic pain is significantly reduced after being imitated by another person (De Coster et al. 2013). Specifically, in De Coster et al.’s (2013) study, participants performed freely chosen finger movements that were either imitated or not imitated by a computerized hand, prior to observing painful stimulation being applied to the hand. Behavioral and physiological markers of affective response to the painful event were increased after imitation relative to nonimitation, an effect that was strongly mediated by participants’ experience of ownership over the observed hand. De Coster et al.’s (2013) data suggest that being imitated facilitated simulation of the painful event in one’s own somatosensory coordinates, and the HMS is likely essential to this affective sharing between self and other (Preston and de Waal 2002). A similar self-other overlap explanation was invoked in a study by Santiesteban et al. where participants were trained to imitate on day 1, and found it significantly harder to inhibit their desire to imitate the observed action on day 2 (Santiesteban, White, et al. 2012). Building from past work, the logic behind the present study was as follows: Given the link between imitation and downstream shared representation in tightly controlled laboratory settings, if the HMS is functional during “naturalistic” social interaction, its activation—as indexed indirectly using mu-suppression—should be enhanced following behavioral mimicry. If such a pattern were observed, the mimicry manipulation would maintain the ecological validity typical of the social psychology literature, while providing the most direct evidence to date of mirror system involvement in mimicry.

**Materials and Methods**

**Participants**

Thirty people (13 females, $M_{age} = 21.93$, $SD_{age} = 4.39$) participated in the present study in exchange for financial remuneration or partial course credit. Of the 30 participants, all had normal or corrected-to-normal vision, and 27 were right-handed. The study conformed to local ethical guidelines, and all participants signed an informed consent statement prior to completing the study. Before their arrival on the day of the study, each participant was randomly assigned to one of the experimental conditions, namely: mimicry ($n = 10$, 5 females, $M_{age} = 22.60$, $SD_{age} = 5.89$), antimimicry ($n = 10$, 4 females, $M_{age} = 21.40$, $SD_{age} = 2.37$), or CPU ($n = 10$, 4 females, $M_{age} = 21.80$, $SD_{age} = 4.59$).

**Stimuli and Apparatus**

The EEG task for measuring mu-suppression during action observation was roughly based on previous work by Oberman et al. (2005), and contained 3 types of stimuli presented to all participants: action observation, action execution, and rest. Action observation stimuli contained a video of a hand squeezing a rubber ball (1231 ms), which was run in a loop for a total duration of 80 s (note: final squeeze of the video was played at

![Figure 1](http://cercor.oxfordjournals.org/ at INSERM on September 7, 2015)
a very slightly accelerated frame rate). In the action execution condition, a fixation cross was presented onscreen, and participants were asked to repeatedly squeeze a similar ball for 80 s. The rest condition contained a visual white noise video, consisting of 30 frames of Gaussian noise created in Adobe Photoshop CS4 (Adobe Systems). All video editing was performed using Adobe Premier CS4 (Adobe Systems). Videos and task instructions were presented on a 20” LCD monitor from a computer running Superlab V.4.0 (Cedrus). Participants who performed the music-rating task on a computer also did so in a Superlab program, albeit this was run on a computer in another laboratory.

A 64-channel hydrogel geodesic sensor net was used to record EEG activity (Electrical Geodesics; EGI). The EEG signal was sampled at 1 kHz, and impedances of <50 kΩ were established prior to beginning the recording. The signal was referenced to vertex (Cz) online, and recorded using Netstation (EGI), run on a powermac G5 computer (Apple) for subsequent offline analysis.

**Experimental Procedures and EEG Analysis**

At the start of the experiment, participants were informed that they would be doing 2 experiments: One EEG experiment and one behavioral experiment. A slight deception was used, whereby participants were informed that the system could only handle roughly 10 min of continuous EEG recording before the data files became unmanageable large, and the behavioral task was a way for participants to stay busy while EEG was prepared for a second recording. Participants’ head circumference was measured to determine the ideal cap size for each participant (54–56, 56–58, or >58 cm). While the appropriately sized cap was being soaked in a conductive electrolytic solution, vertex was measured as the crossing point between the inion-nasion line and the 2 preauricular points, and was marked directly on the participant’s scalp with a red grease pencil. The cap was then applied ensuring that the red mark was aligned to electrode Cz.

Once the cap was on, participants were brought into the sound-attenuated and electrically shielded EEG chamber, and additional solution was added to any electrodes that were not below the impedance threshold. Total setup time for the pretest was ~10–15 min. During the pretest, each event type (action observation, execution, and rest) was repeated twice for a total of 160 s of data per event per session. Order of presentation was pseudo-randomized such that the same condition was never presented twice in a row. During the pretest and the post-test, participants were asked to covertly count either the number of squeezes (action observation, execution), or the number of seconds (rest), on each trial.

At the end of the pretest EEG session, the electrode cap was removed and participants were brought to another laboratory, located almost immediately below the EEG laboratory, by a second experimenter to complete an ostensibly unrelated “music-rating” task (van Baaren et al. 2003). Specifically, participants listened to and rated the pleasantness of a series of 4 music fragments. In the mimicry condition, participants were played these fragments by an experimenter seated opposite them, and the experimenter mimicked the participant’s motor behaviors, such as hair and face touching, foot shaking, and shifts in posture. The experimenter was asked to perform a very similar movement on the same side of space and staggered by a second or two to the participant’s movement, as we reasoned that too strong of a temporal contiguity between movements (e.g., bringing the mimicry into conscious awareness. In the antimimicry condition, participants performed the exact same task, but instead of mimicking the participant, the experimenter was instructed to change her behavior if the participant began to mimic her (Ashton–James et al. 2007). Again, the experimenter ended any participant-initiated mimicry after a second or two, to increase the subtlety of the manipulation. Lastly, to control for any general effects of interacting with another person, rather than mimicry per se, a third group of participants performed the same music-rating task on a computer program.

After the music-rating task was completed, participants were brought back to the EEG laboratory, and the post-test action observation session was performed. The caps had been soaked in electrolytic solution during the music-rating task, and the vertex location was still marked, so the setup time for the post-test was roughly 5 min. The post-test session was then run identically to the pretest session. After the post-test, the electrode caps were removed, participants answered a computerized questionnaire, and participants were debriefed about the purpose of the experiment. The questionnaire contained 2 questions about how the participants felt about the second experimenter. Specifically, they were asked “how likeable was the other experimenter during the music-rating task?” and “how smoothly would you say your interaction went with the other experimenter during the music-rating task?” Responses were rated on a 5-point Likert scale, and answers to the 2 questions were summed to provide a composite liking/rapport measure for each participant. Participants also completed the Prosocial Personality Battery (PSB; Penner et al. 1995) and the Inclusion of Others in the Self scale (IOS; Aron et al. 1992), and were asked a series of questions about their intuitions regarding the study. Importantly, none of the participants were aware of the presence or absence of mimicry. Several participants were suspicious that the 2 tasks were related in some way, but when probed further, all of the suspicious parties believed the study was interested in how the music fragments might have impacted the counting task they performed during the EEG sessions.

The first stages of the offline EEG analysis process were performed using Netstation (EGI). Here, the data were re-referenced to the common average and band-pass filtered from 1 to 60 Hz. The recordings were initially segmented by total event length (80 s epochs) to separate the experimental conditions, and then the conditions were broken into 1251 ms segments, corresponding to the length of the squeeze in the observed action stimulus. Next, the data were exported to an EGIS file format, and the rest of the analysis routine was performed in a MATLAB (Mathworks) environment.

The data were processed using the Fieldtrip toolbox (Oostenveld et al. 2011; http://fieldtrip.fcdonders.nl), and customized MATLAB routines in concert. First, the data were opened using the Fieldtrip preprocessing routine, and each 1251 ms segment was analyzed using an automated ocular artifact rejection criteria (z-score > 4). Further, the first and last 8 segments of each trial were trimmed to reduce the influence of attentional shifts on our data (Oberman et al. 2005). Next, power spectra were extracted using Fieldtrip’s multitaper FFT function, from 1 to 100 Hz with 1 Hz spectral smoothing. Given the contralateral dominance of mu-suppression during action execution (Pfurtscheller et al. 1997), data in the alpha band (8–13 Hz) from a cluster of 4 left-hemisphere electrodes surrounding the standard C3 site were extracted. Within alpha, the 2-Hz-wide frequency displaying the strongest suppression during action “execution” was used to define the band of interest for each participant (Babiloni et al. 2002; Muthukumaraswamy et al. 2004). Finally, power in the band of interest during action observation relative to rest was calculated to generate a raw mu-suppression ratio, and then log-transformed to ensure a normally distributed mu-suppression index in the sample (Oberman et al. 2005).

**Music-Rating Task**

Participants who performed the music-rating task in the context of a social interaction containing mimicry or antimimicry were covertly videotaped during the social interaction, but due to a technical problem with the camcorder, not all of those videos were retained for offline analysis. Two naïve observers watched the intact videos (n = 8 mimicry; n = 7 antimimicry) and coded for: 1) duration of the music-rating task, 2) number of times the experimenter was not sitting still during the social interaction (i.e., total movements), and 3) the number of those deviations that were imitative (i.e., mimicry movements; classified as a similar posture, gesture, mannerism to the participant). Coding was performed reliably for duration (α = 1), total movements (α = 0.74), and mimicry movements (α = 0.83); therefore, aggregate scores were computed for each variable. For participants in the CPU condition, duration of the music-rating task was extracted from the Superlab data files.

**Results**

**Behavioral and Questionnaire Data**

**Music-Rating Task**

Prior to conducting our main analyses, some preliminary results were examined. Regardless of whether participants completed
the music-rating task in the context of a social interaction containing mimicry (M = 299.38 s, SD = 108.15 s), antimimicry (M = 301.79 s, SD = 121.80 s), or on a computer (M = 287.30 s, SD = 28.83 s), the task took a similar duration to complete [F(2, 27) < 1; Fig. 2A]. To ensure that any effects of our mimicry manipulation were not driven by differences in exposure to another person’s motor behaviors rather than mimicry per se, we compared the total number of movements between the mimicry (M = 17.19, SD = 3.06) and antimimicry (M = 21.86, SD = 5.61) conditions, and actually found a trend toward a larger number of movements in the antimimicry condition, but this difference was not significant [F1,13 = 4.16, P < 0.1; Fig. 2B]. Importantly, social interactions in the mimicry condition contained a larger number of movements that were classified by the naïve coders as “imitative” (M = 8.94, SD = 2.53) than were present in the antimimicry condition (M = 4.50, SD = 2.48; F1,13 = 11.70, P < 0.01, η² = 0.47; Fig. 2C).

In addition to comparing observed and mimicry movements between conditions, we also wanted to determine how our mimicry manipulation affected social interaction quality. The presence of mimicry during social interactions has been reported to increase liking and rapport between interaction partners after mimicry, leading to the hypothesis that it acts as a form of “social glue” (Lakin et al. 2003). Therefore, to ensure that our experimental treatment had a similar downstream consequence to what would be predicted from the social psychology literature, the composite liking/rapport measure was contrasted between the mimicry and antimimicry conditions. Crucially, this measure was significantly higher for the mimicry condition (M = 79.90, SD = 7.56; t(18) = 2.61, P < 0.05, d = 1.17) and mimicry [M = 79.90, SD = 5.82; t(18) = 2.65, P < 0.05, d = 1.18] groups. As the action execution condition was merely included to define a frequency band of interest for the mu-suppression analysis, however, this group difference would not affect our main analyses.

**EEG Data**

An exclusion criterion of 2.5 standardized residuals was applied to the EEG data, resulting in the removal of one individual (SD = −2.75), and a final sample of 29 participants (10 mimicry, 9 antimimicry, 10 CPU).

Before examining pre/post-test patterns in our EEG data, it was crucial to establish that the action observation task leads to mu-suppression, our indirect EEG metric for HMS activity, in our experimental groups. To establish this, the normalized μ-suppression index was compared with zero at pretest for each group. Indeed, all groups displayed a significant degree of μ-suppression prior to our experimental treatment [mimicry: M = −0.08, SD = 0.12, t(9) = −2.23, P < 0.05, d = 0.67; antimimicry: M = −0.21, SD = 0.17, t(9) = −3.71, P < 0.01, d = 1.23; CPU: M = −0.29, SD = 0.11, t(9) = −8.31, P < 0.001, d = 2.63]. Unexpectedly, at pretest, there was a trend toward a difference between the mimicry and antimimicry conditions (P = 0.07) and the music-rating task in the context of a social interaction containing mimicry (M = 299.38 s, SD = 108.15 s), antimimicry (M = 301.79 s, SD = 121.80 s), or on a computer (M = 287.30 s, SD = 28.83 s), the task took a similar duration to complete [F(2, 27) < 1; Fig. 2A]. To ensure that any effects of our mimicry manipulation were not driven by differences in exposure to another person’s motor behaviors rather than mimicry per se, we compared the total number of movements between the mimicry (M = 17.19, SD = 3.06) and antimimicry (M = 21.86, SD = 5.61) conditions, and actually found a trend toward a larger number of movements in the antimimicry condition, but this difference was not significant [F1,13 = 4.16, P < 0.1; Fig. 2B]. Importantly, social interactions in the mimicry condition contained a larger number of movements that were classified by the naïve coders as “imitative” (M = 8.94, SD = 2.53) than were present in the antimimicry condition (M = 4.50, SD = 2.48; F1,13 = 11.70, P < 0.01, η² = 0.47; Fig. 2C).

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**Action Observation Task**

During the action observation/EEG task, participants counted either the number of observed/executed ball squeezes (action observation and execution conditions), or the number of seconds the condition lasted (rest condition). Behavioral data for each task were reported verbally to the experimenter at the end of each block, and this data did not change systematically from pretest to post-test (all Ps > 0.1), therefore group comparisons were made on the behavioral responses across EEG sessions. None of the mimicry treatment groups varied in terms of the number of seconds reported for the rest condition [Moverall = 63.29 s, SDoverall = 13.20 s; F(2, 27) = 1.29, P > 0.2], nor did they report different numbers of observed squeezes during the action observation condition [Moverall = 61.99, SDoverall = 5.73; F(2, 27) < 1]. Unexpectedly, there was a group difference in executed squeezes [F(2, 27) = 3.68, P < 0.05, η² = 0.21], as participants in the CPU group executed significantly less squeezes (M = 63.53, SD = 2.11) than the antimimicry [M = 83.98, SD = 7.56; t(18) = 2.61, P < 0.05, d = 1.17] and mimicry [M = 79.90, SD = 5.82; t(18) = 2.65, P < 0.05, d = 1.18] groups. As the action execution condition was merely included to define a frequency band of interest for the mu-suppression analysis, however, this group difference would not affect our main analyses.

**Figure 2.** (A) Participants in all 3 experimental treatment groups engaged in the music-rating task for a similar duration (ns = P > 0.7). (B) The antimimicry group was exposed to marginally more total movements performed by the interaction partner than the mimicry group (ns = P < 0.1); yet (C) crucially, the mimicry group was exposed to far more imitative movements by the interaction partner than the antimimicry group (**P < 0.01).
a significant difference between the mimicry and CPU conditions [$t(18) = 4.07, P = 0.001, d = 1.82$]. However, since we were primarily concerned with the change in mu-suppression from pretest to post-test, this was not fatal to our main analyses.

The primary analysis in the present experiment was a mixed-model ANOVA on the normalized mu-suppression data, with one within-subjects factor (session: pretest, post-test), and one between-subjects factor (treatment: mimicry, antimimicry, or CPU). In line with our hypothesis, there was an interaction between the 2 factors [$F_{2,26} = 3.40, P < 0.05, \eta^2 = 0.21$]. Mu-suppression was significantly enhanced from pre- to post-test in the mimicry group [$M_{diff} = 0.05, SD_{diff} = 0.08; t(9) = 2.04, P < 0.05, d = 0.64$], was unchanged in the antimimicry group [$M_{diff} = -0.03, SD_{diff} = 0.18; t(9) = -0.45, P > 0.6$], and was reduced in the CPU group [$M_{diff} = -0.09, SD_{diff} = 0.10; t(9) = 0.92, P > 0.05, d = -0.92$] (Fig. 4). Neither the effect of session [$F(1,26) = 0.84, P = 0.37$], nor of condition [$F(1,26) = 0.84, P = 0.37$] had a significant impact on mu-suppression.

When contrasting the pre- to post-test change between groups, participants in the mimicry group displayed a significant increase in mu-suppression relative to the CPU group [$t(18) = 3.54, P < 0.01, d = 1.54$], but did not differ from the antimimicry group ($P > 0.1$). Crucially, the difference between the mimicry and CPU groups cannot be attributed to variations in raw alpha power during either the action observation (Pretest: $M_{mimicry} = 0.49, SD_{mimicry} = 0.47$ vs. $M_{CPU} = 0.29, SD_{CPU} = 0.17, P > 0.2$; Post-test: $M_{mimicry} = 0.59, SD_{mimicry} = 0.86$ vs. $M_{CPU} = 0.35, SD_{CPU} = 0.23, P > 0.3$) or rest (Pretest: $M_{mimicry} = 0.60, SD_{mimicry} = 0.49$ vs. $M_{CPU} = 0.57, SD_{CPU} = 0.36, P > 0.8$; Post-test: $M_{mimicry} = 0.72, SD_{mimicry} = 0.72$ vs. $M_{CPU} = 0.59, SD_{CPU} = 0.36, P > 0.5$) conditions. Instead, the effects were driven by pre- to post-test changes in the pattern of mu-suppression during action observation as a function of our mimicry manipulation.

**Subset Analysis**

As the mimicry and CPU conditions were characterized by different levels of extant mu-suppression before the mimicry manipulation occurred, we analyzed a subset of our sample to allay the potential concern that the pre- to post-test changes in our data might reflect a regression to the mean in one of the 2 groups. The subsets selected were defined post hoc and contained the 5 participants in the mimicry group who displayed the most pretest mu-suppression, and the 5 participants in the CPU group who displayed the least mu-suppression. In this subset of the data, the level of mu-suppression was similar at pretest for the mimicry ($M = -0.16, SD = 0.12$) and CPU ($M = -0.22, SD = 0.09, P > 0.4$) groups. In a targeted comparison of the pre- to post-test change in mu-suppression between these groups, the mimicked participants displayed a lower change value ($M = -0.08, SD = 0.10$) than the subset of participants in the CPU condition [$M = 0.10, SD = 0.08; t(9) = 3.51, P < 0.01, d = 1.99$]. Therefore, the results from our sample-wide analysis hold in a subset of participants that were matched for pretest levels of mu-suppression.

**Discussion**

The present study reasoned that, if the HMS is functional for social mimicry, this system should be more sensitive to others’ actions following recent experience being imitated. To the extent that HMS activity can be inferred from suppression of
the rolandic mu-rhythm during action observation, our data vindicate this hypothesis: Being mimicked during a reciprocal social interaction results in increased HMS activity during subsequent action observation.

One possible explanation for the present results is that participating in an interaction containing mimicry increases the general level of social attunement, such that perceptual systems are more sensitive to input from the same category of stimulus as was encountered in the interaction. At the broadest level, the stimulus category would be “human.” Thus, by this view, brain regions involved in the visual perception of others, such as posterior superior temporal sulcus (pSTS), may simply be more tuned to input from any human stimulus after an interaction involving mimicry. Given that the pSTS is widely thought of as an “input node” to the HMS, increased sensitivity of the pSTS to human input could lead to greater downstream mirroring of that stimulus, which would produce the kind of result we observe. We have previously referred to this type of account as an “input modulation” (Obhi et al. 2011; Hogeveen and Obhi 2012).

Beyond a repetition-driven enhancement of input to the HMS, the present results could also represent a finding that is functionally equivalent to a priming effect. Behaviorally, priming refers to any situation where exposure to a stimulus at time A improves (often, accelerates) processing of the same stimulus item or category at a later time B (Tulving and Schachter 1990). At the neural level, the dominant finding in the priming literature is reduced event-related hemodynamic or electrocortical activity when an item or category is repeated. Such repetition suppression effects are thought to reflect more efficient engagement of the same process when the primed item or category is repeated (Henson 2003). Yet, a number of fMRI and EEG studies have paradoxically found enhanced activity, suggesting that behavioral priming effects are sometimes accompanied by the recruitment of a new process upon repetition (Henson 2003; Gruber and Müller 2005; Morel et al. 2009). Assuming similar engagement of the HMS during both social mimicry and passive action observation, the present results could represent a repetition enhancement of the HMS after mimicry. The contrast between the mimicry and CPU conditions supports this view: a decrease in mu-suppression for the CPU group may represent a standard repetition-suppression effect, which is counteracted by an expanded cortical network for processing observed actions at post-test following the experience of being mimicked, to the point of repetition enhancement in the mimicry group.

The input modulation and priming accounts both state that exposure to a stimulus facilitates processing of another stimulus downstream, they simply place the locus of that facilitation at earlier and later stages of processing, respectively. Further work will be needed to clarify whether one, both, or neither of these accounts are correct, but, in either circumstance, attention should be paid to “why” such facilitation takes place. Given the prosocial consequences of being mimicked (Chartrand and Lakin 2013), and the finding that watching someone being mimicked activates reward-related brain areas (Kühn et al. 2010), the rewarding nature of mimicry could have driven the present results. In this view, positive affect would accompany mimicry, which would enhance subsequent HMS activity as a function of the reward value of the mimetic experience. This argument fits nicely with our finding that being mimicked led to enhanced liking and rapport for the interaction partner.

Regardless of how the present results do or do not fit the priming literature, the varied nature of the “input” during the action observation task and the reciprocal social interaction has interesting implications concerning the nature of imitative representations. Whereas the majority of researchers describing the HMS have emphasized the direct match between observed and executed actions (Catmur et al. 2007; Obhi and Hogeveen 2010; Oosterhof et al. 2013), here the effect of being mimicked would appear to be action-independent. The mimicked behavior was dynamically set by the participants’ motor output in the social interaction, and was not matched to the hand action displayed in the pre- and post-test action observation sessions. Beyond direct matching, then, being mimicked appears to exert a more general influence on the HMS.

One explanation for an action-independent effect of being mimicked on the HMS is the level of distinction between self and other in the motor system. Whereas motor representations for voluntary actions are activated by self-related processes, when we observe someone else mimicking our own movements the HMS would lead to a shared representation of action between self and other (Georgieff and Jeannerod 1998). Despite mimicry’s ubiquity, effective social interactions involve a “normal” amount of imitation, evidenced by the finding that hyperimitation is an occasional symptom of autism and schizophrenia, disorders characterized by profound social impairments (Chapman and McGhie 1964; Rutter 1974; Spengler et al. 2010). For the HMS to exist without invariable imitation, the system requires a complementary network for disambiguating self-from other-activated motor representations. Current research suggests that 2 particular brain regions—medial prefrontal cortex and temporoparietal junction—are functionally involved in maintaining one’s own motor plan and attributing observed actions to another agent, and thereby controlling imitative response tendencies (Brass et al. 2009). Considering the entire imitation control network, then, being mimicked might reduce connectivity between regions involved in self-other control and the HMS, effectively blurring the self-other distinction and leading to enhanced HMS activity at post-test. This argument is supported by recent findings that improved control of co-activated self- and other-related representations improves one’s ability to inhibit automatic imitative responses (Santiesteban, Banissy, et al. 2012; Santiesteban, White, et al. 2012).

As with any between-groups experiment, there is the potential limitation that some a priori difference between treatment conditions affected the present results. Indeed, the groups did not show equivalent pretest levels of mu-suppression, and the group with the weakest pretest mu-suppression was the critical mimicry condition. However, we do not feel the issue is fatal to the present conclusions since this limitation is protected by the pretest/post-test design. That the mimicry showed the weakest HMS activation at pretest might suggest that, if anything, those participants would be the least responsive to being imitated during the reciprocal social interaction. While we admit that the ideal sample would contain groups matched in terms of their degree of mu-suppression, different levels of suppression between-subjects does not affect the critical conclusion that being mimicked enhanced mu-suppression within-subjects.

To summarize, we assessed the impact of being mimicked on HMS activity during subsequent action observation. Our findings indicate that social mimicry enhances mu-suppression when participants passively view actions at a later time. To the
extent that mu-suppression indexes HMS activity, our results provide the most direct evidence to date for a functional link between behavioral social mimicry and the HMS.

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**References**


