

Social Interaction Enhances Motor Resonance for Observed Human Actions

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Understanding the neural basis of social behavior has become an important goal for cognitive neuroscience and a key aim is to link neural processes observed in the laboratory to more naturalistic social behaviors in real-world contexts. Although it is accepted that mirror mechanisms contribute to the occurrence of motor resonance (MR) and are common to action execution, observation, and imitation, questions remain about mirror (and MR) involvement in real social behavior and in processing nonhuman actions. To determine whether social interaction primes the MR system, groups of participants engaged or did not engage in a social interaction before observing human or robotic actions. During observation, MR was assessed via motor-evoked potentials elicited with transcranial magnetic stimulation. Compared with participants who did not engage in a prior social interaction, participants who engaged in the social interaction showed a significant increase in MR for human actions. In contrast, social interaction did not increase MR for robot actions. Thus, naturalistic social interaction and laboratory action observation tasks appear to involve common MR mechanisms, and recent experience tunes the system to particular agent types.

Introduction

In addition to the obvious utility of human social interaction, its importance is also underscored by several ontological and evolutionary arguments. For example, Tomasello (1999) suggests that social interaction facilitates cultural transmission of adaptive abilities, and it is thought that the yearning for social interaction in newborns satisfies emotional and cognitive needs (Spitz, 1965; Bowlby, 1969, 1982; Rochat, 2008). It has even been proposed that the need to belong is a fundamental human motivation, satisfied through social interactions (Baumeister and Leary, 1995).

Detecting and responding to biological stimuli is a fundamental and adaptive capability (e.g., responding to predators or potential mates). Perhaps due to this, brain areas such as the posterior superior temporal sulcus (pSTS) are biased for processing biological motion. The pSTS and the parietofrontal mirror system form part of a wider action observation network (AON), which is thought to underlie many social abilities (Sinigaglia and Rizzolatti, 2011; Oberman and Ramachandran, 2007; Decety and Sommerville, 2008).

The mirror system is active when observing others act (Iacoboni, 2005; Rizzolatti and Sinigaglia, 2010). Thus, mirror mechanisms should be important for social interactions. Mirror

mechanisms might also contribute to the tendency to mimic the gestures and bodily movements of social interaction partners, although this has not been explicitly tested (Chartrand and Bargh, 1999; Chartrand and van Baaren, 2009). Motor resonance (MR) is the activation of matching motor representations during observation of action(s) made by others, and could index mirror activity within the wider AON (Fadiga et al., 1995, 2005; Cross et al., 2010; Press, 2011). The mirror system is also implicated in automatic imitation and action observation tasks (Iacoboni, 2009; Obhi and Hogeveen, 2010; Heyes, 2011; Hogeveen and Obhi, 2011; Obhi et al., 2011). We refer to the mirror and wider AON mechanisms enabling motor resonance as “the motor resonance system (MR system).” Research suggests that the MR system is, in general, biologically tuned (Press, 2011; but see Gazzola et al., 2007), although recent experience seems to tune the system to a particular agent type (Press et al., 2007).

Despite considerable research on MR in action observation tasks, there is a lack of research on the MR system in naturalistic social interactions. One way to examine whether common mechanisms operate in naturalistic social interactions and action observation tasks is to combine the two task types into a single experiment. Using this approach, we investigated whether naturalistic social interaction modulates MR during a subsequent action observation task involving a human or a robot.

Separate groups of participants engaged or did not engage in a social interaction before observing a human or robot squeezing a rubber ball. We assessed MR via transcranial magnetic stimulation (TMS)-elicited motor-evoked potentials (MEPs). We predicted more MR for human versus robotic actions, and that this biological tuning would increase for participants who underwent prior social interaction. Given the suggested relationship between nonconscious mimicry and the mirror system, we further hy-

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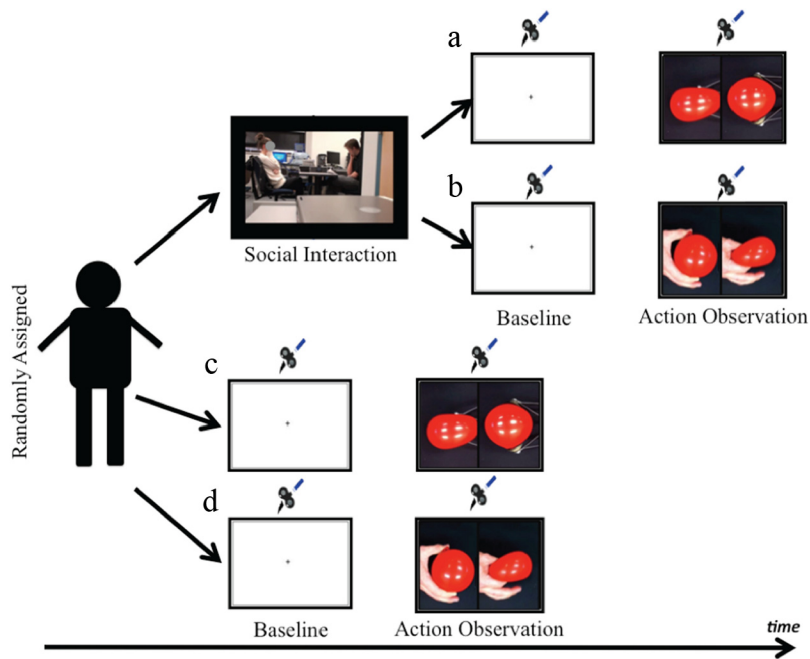


Figure 1. Breakdown of the experimental stimuli and conditions. Before arriving on the day of the study, participants were assigned to one of four conditions: 25% of participants were assigned to the social interaction followed by robotic action observation condition (*a*), 25% of participants were assigned to the social interaction followed by human action observation condition (*b*), 25% of participants were assigned to the immediate robotic action observation condition (*c*), and 25% of participants were assigned to the immediate human action observation condition (*d*).

pothesized that participants who demonstrated mimicry in the interaction would show more MR compared with nonmimickers.

Materials and Methods

Participants

Forty participants (28 female) between the ages of 18 and 21 years (mean, 18.5 years) participated in the study for course credit. Before arriving on the day of the study, participants were randomly assigned to one of four groups: no social interaction/robot observation ($n = 10$), no social interaction/human observation ($n = 10$), social interaction/robot observation ($n = 10$), and social interaction/human observation ($n = 10$). Unfortunately, a technical error with the video camera occurred for one participant in the social interaction/human observation condition, leaving data from the mimicry session at $n = 9$ for that group. Two of the participants were left-handed, and all had normal or corrected-to-normal vision.

Apparatus and stimuli

The social interaction was programmed using Superlab v.4 (Cedrus) and run on a desktop PC (Dell) with stimuli displayed on a 20" LCD monitor. TMS was performed with a figure-eight coil attached to a Rapid² system (Magstim). Electromyographic (EMG) data were recorded using a psychophysiological recording system (Biopac Systems). Digital pulses were sent from the computer running Superlab to the Biopac system, which in turn was used to trigger TMS pulses through a solid-state relay drive. The EMG signal was acquired with a 5 kHz sampling rate, amplified (to 5.0 mV) and filtered (bandpass 10–500 Hz), and sent to a laptop computer for offline analysis. Offline EMG analysis was conducted using AcqKnowledge v.4.1 (Biopac Systems).

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Experimental stimuli were videos depicting either a right hand (palm facing upward) or an E-Z grabber reaching tool (Arcoa) squeezing a ball on a black background. The E-Z grabber stimulus was matched with the human stimulus for approximate size, squeeze intensity, and velocity profile. The velocity profile was matched by equating the number of frames in the three phases of the video for each stimulus: compression (666.67 ms), pause at maximum flexion (299.97 ms), and opening (366.63 ms). Participants were told that the E-Z grabber stimulus was a robot, and an informal debrief revealed that all participants believed this instruction. Video editing was performed using Adobe Premiere Pro CS4 (Adobe Systems). All inferential statistical analysis was performed using SPSS statistics v.17 (SPSS).

Procedure

Social interaction. On entering the laboratory, participants in the social interaction condition were told that they would begin the experiment with a music rating task (cf. van Baaren et al., 2003), which was ostensibly unrelated to the subsequent TMS experiment. The experimenter then left participants alone in the room for 1 min while they went to retrieve the iPod dock, which was purposely left at another lab. During this time, participants were covertly videotaped to determine a baseline measure of face-touching behavior. The experimenter then reentered the lab and explained that they

would be listening to four music fragments, which participants were told might be used as stimuli in a future study. Participants were asked to provide three adjectives they would use to describe the music fragments. During the interaction, the experimenter touched his face approximately once every 10 s. Participants' rate of face-touching behavior during the interaction, compared with baseline, was coded offline to index behavioral mimicry (Fig. 1). To clarify, determination of the degree to which the participant mimicked the experimenter allows for investigation of not only global social interaction effects, but also the specific effects of mimicry on subsequent motor resonance.

Previous researchers have used the number of times a target movement occurs during a social interaction to quantify mimicry (Chartrand and Bargh, 1999; van Baaren et al., 2003). However, this measure would place equal weight on every target movement, regardless of how long each movement lasts. For example, in the present study, if the participant touches their face and holds the position for 5 s, traditional mimicry analyses would weigh that movement equally to a slight scratch of the same area, which may be <1 s in duration. We reasoned that it would be more precise to quantify the amount of time spent performing the target movement, which would be indicative of the presence of that target throughout the interaction. Specifically, two time periods were analyzed for each participant: the total number of milliseconds before the interaction began (baseline total) and the total number of milliseconds spent interacting with the experimenter (interaction total). The coder identified the total number of milliseconds participants touched their face during the baseline (baseline target) and the interaction (interaction target). Ratios were calculated to determine the rate of face touching during the baseline (baseline ratio = baseline target/baseline total) and interaction (interaction ratio = interaction target/interaction total). Our dependent measure from the interaction, mimicry ratio, is the rate of face touching during the interaction divided by that of the baseline (mimicry ratio = interaction ratio/baseline ratio).

TMS procedures. For the TMS set-up, participants were seated with their right arm resting on a wrist pad positioned in front of the computer monitor. A cardboard box and black fabric were used to occlude vision of their hand. MEPs were measured with pairs of 8 mm surface electrodes

placed in a belly–tendon arrangement over the abductor pollicis brevis (APB) muscle, and a ground was placed on the ulnar styloid of participants' right wrist. Vertex was located using theinion–nasion line and preauricular points at the posterior end of each zygomatic arch as landmarks. TMS was delivered through a figure-eight coil, held normal to the scalp and 45° to midline, with current flowing in a posterior–anterior direction over left M1. Stimulation began at 70% of stimulator output and the coil was moved incrementally until the site eliciting the greatest MEP in the right APB muscle was identified. The optimal location was marked on a Lycra swim cap worn by participants, and a mechanical arm was used to hold the coil in a fixed position. Once the optimal location for MEPs was identified, stimulator output was lowered at 2% intervals until the minimum intensity capable of eliciting MEPs of ~1 mV peak-to-peak amplitude on 50% of TMS pulses had been identified (Lepage et al., 2010; Obhi et al., 2011). Stimulator output was held constant at this intensity for the rest of the experiment (i.e., baseline and action observation blocks), ranging from 55% to 83% (mean, 64%) in the present sample.

Once the localization procedure was complete, baseline motor corticospinal excitability was assessed by delivering 30 TMS pulses at random intervals (between 3000–5000 ms) while participants passively viewed a fixation cross (Fig. 1). After the baseline block, half of the participants observed 75 trials containing the human hand stimulus, while the other half observed the same number of trials containing the robot effector stimulus. Action observation trials contained a fixation cross (2000 ms) and videos consisting of a single squeeze repeated three to seven times (4270–9940 ms; Fig. 1). TMS pulses were delivered at points of maximum flexion during one of the observed squeezes on 40% of trials. To ensure attention to the action, participants were instructed to covertly count the number of squeezes in each video. At the end of the experiment, all participants were asked questions from a standard funneled debrief, designed to inquire about any perceived connections between the music rating and action observation tasks (cf. Chartrand and Bargh, 2000). After the funneled debrief, the purpose, hypotheses, and methods of the study were explained in an informal debrief.

Pooled data: methods

One comparison of interest for the present study—whether mimicry of a human interaction partner has an effect on subsequent motor resonance to a human action—was based on a sample that was possibly too small to detect real differences. Therefore, an additional group of participants (pooled group: $n = 10$; five female; age range 18–39) were added to the present sample for purposes of a more powerful mimicker versus non-mimicker comparison. Participants from the pooled group engaged in a photo description task with a female confederate (cf. Chartrand and Bargh, 1999), which was ostensibly unrelated to the TMS experiment. All the details of the mimicry assessment procedure for the pooled group were identical to the procedure used for the present sample. The only difference was that the target mimicry behavior was foot shaking instead of face touching. In the photo-description task, participants were asked to spend 1 min describing each photograph to the confederate, and, during the interaction, the confederate shook her right foot approximately once every 10 s. Again, in a manner identical to the analysis of the present sample, the degree to which participants increased their foot-shaking between the baseline and interaction phases was coded offline as an index of behavioral mimicry.

After engaging in the social interaction, the pooled group engaged in a TMS/action observation session in which the TMS localization and stimulation procedures/parameters were the same as for the present sample. The action observation task contained the same number of trials, same percentage of TMS trials, and a similar stimulus involving a hand squeezing a rubber ball. It is noteworthy to mention that the gender of the interaction partner and the action observation stimulus was matched for both the pooled group and the present sample.

Results

Motor resonance

MEPs were defined as the maximum EMG peak-to-peak amplitude in a 15–40 ms epoch after the delivery of TMS. MEPs greater

than 3 SDs from the participants' mean for each condition were omitted from statistical analysis. In total, this procedure resulted in the removal of 1.92% of the data.

Motor resonance was quantified by calculating MEP ratios—i.e., average MEP amplitudes in the action observation condition divided by the baseline.

Comparison of MEP ratios to 1

To confirm the presence of motor resonance during the action observation session, MEP ratios were compared with a mean of 1 using a one-sample t test for each condition. Because we had a clear directional prediction—larger MEP ratios (i.e., >1) during movement observation—all subsequent t tests are one-tailed. Participants in the no-interaction condition who observed the robot stimulus displayed a trend toward resonance during action observation (mean, 1.26; SD, 0.474; $t_{(9)} = 1.713$, $p = 0.061$), whereas participants who engaged in the social interaction before observing the robotic stimulus did not display motor resonance (mean, 1.04; SD, 0.330; $t_{(9)} = 0.450$, $p = 0.332$). In contrast, both participants who went immediately into the human observation task (mean, 1.32; SD, 0.438; $t_{(9)} = 2.274$, $p = 0.024$) and participants who engaged in the social interaction before observing the human stimulus (mean, 2.17; SD, 0.995; $t_{(9)} = 3.706$, $p = 0.003$) displayed significant MEP facilitation during action observation.

Motor resonance in the experimental conditions

MEP ratios were analyzed in a 2 (action stimulus: robot, human) \times 2 (social interaction: yes, no) univariate ANOVA. There was a significant main effect of action stimulus ($F_{(1,36)} = 9.140$, $p = 0.005$). Specifically, participants displayed significantly greater motor resonance to the human (mean, 1.74; SD, 0.866) compared with the robotic (mean, 1.15; SD, 0.412) action stimulus ($t_{(38)} = 2.744$, $p = 0.009$). However, the main effect of social interaction was not significant ($F_{(1,36)} = 2.711$, $p = 0.108$). Critically, there was a significant interaction between the two factors ($F_{(1,36)} = 7.427$, $p = 0.010$; Fig. 2).

A series of planned one-tailed comparisons were conducted, enabling further exploration of the interaction. These tests revealed a significant difference in MEP ratios as a function of the action stimulus for participants in the social interaction condition (robot: mean, 1.05; SD = 0.330; vs human: mean, 2.17; SD = 0.995; $t_{(18)} = 3.372$, $p = 0.002$). However, no difference was found for participants in the no interaction condition (robot: mean, 1.26; SD, 0.474; vs human: mean, 1.32; SD = 0.438; $t_{(18)} = 0.284$, $p = 0.390$). Therefore, motor cortical output appears to be initially indifferent to the biological status of the observed action, but social interaction configures the motor system to selectively resonate with the socially relevant human stimulus.

Mimicry and motor resonance

In the present experiment, mimicry was not an experimentally manipulated factor, but rather a spontaneous tendency displayed by participants to various extents. However, to assess whether there was a difference in motor resonance between those participants that mimicked during the social interaction and those that did not, we treated “the presence of mimicry” as if it were an experimental factor for the mimicry analysis.

Coding mimicry

An independent judge who was not involved in the experiment coded the social interaction videos for mimicry (for details of mimicry coding, see Materials and Methods, above). A second

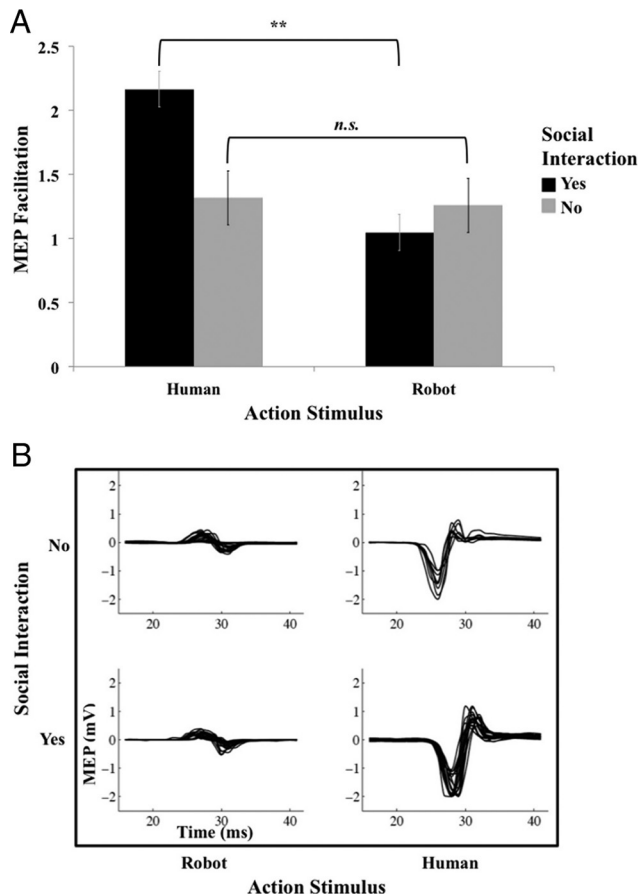


Figure 2. *A*, MEP ratio data. Data reported refers to a ratio increase between the action observation and baseline phases of the experiment. Only participants in the social interaction group displayed an effect of action stimulus, whereas the no social interaction group displayed similar patterns of MEP facilitation to the human and robotic stimuli. Therefore, the social interaction enhanced biologically tuned motor resonance (** $p = 0.002$; *n.s.*: $p = 0.390$). *B*, Raw MEP amplitudes. MEPs that were within 1 SD of the mean for four representative participants, depicted in their respective conditions.

judge coded a sample of the videos ($n = 8$) to ensure strong interrater reliability ($r = 0.994$, $p < 0.001$).

Mimicry and MR: present sample analysis

To assess whether participants who observed the human action were influenced by prior mimicry, we separated our data into two groups: mimickers (i.e., mimicry ratio > 1) and nonmimickers (i.e., mimicry ratio ≤ 1), and compared MEP ratios between the two groups. A comparison between mimickers ($n = 6$) and nonmimickers ($n = 3$) revealed no significant difference in MEP ratios for the human stimulus after mimicking the experimenter (mimickers: mean, 2.36; SD = 1.16; vs nonmimickers: mean, 2.10; SD, 0.70; $t_{(7)} = 0.348$, $p = 0.369$). For the robotic stimulus, mimickers ($n = 3$; mean, 0.78; SD, 0.41) showed less motor resonance than nonmimickers ($n = 7$; mean, 1.16; SD, 0.24; mimickers vs nonmimickers; $t_{(8)} = 1.903$, $p = 0.047$).

Mimicry and MR: pooled data analysis

Due to the low statistical power of the mimicker versus nonmimicker comparison, we pooled the results from the current study with data from an additional group of participants who took part in a social interaction followed by an action observation task (see Materials and Methods, above). Specifically, as outlined in the

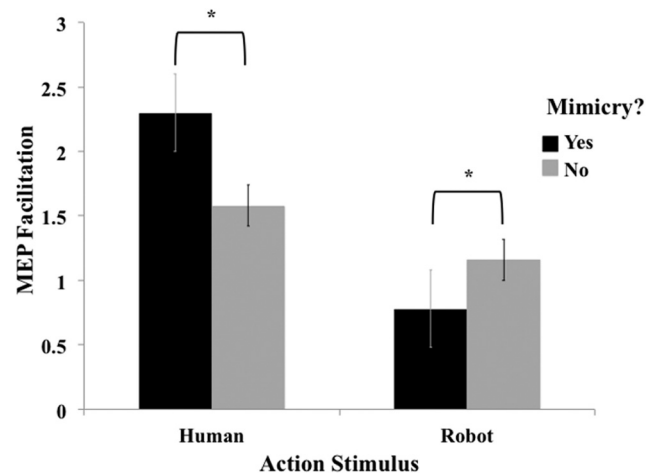


Figure 3. MEP ratio comparison of mimickers versus nonmimickers. Participants who displayed behavioral mimicry before observing a human action displayed significantly more MEP facilitation than those who did not mimic before observing a human action. However, participants who mimicked before observing a robotic action displayed significantly less MEP facilitation than those who did not mimic ($*p < 0.05$).

Materials and Methods, a second group of participants engaged in a similar social interaction before engaging in a nearly identical action observation session. Mimicry in this group was quantified in the same way (i.e., ratio of time spent performing the target behavior during the interaction compared with baseline), MEP facilitation was indexed in the same way (i.e., ratio of MEP amplitudes during action observation compared with baseline), and MEPs were induced during the observation of the same action (i.e., rubber ball squeeze). The only apparent difference between the two paradigms was the use of a different target mimicry behavior for the pooled group. Therefore, we pooled data from the two human observation groups and examined whether or not mimicry *per se* had an effect on downstream motor resonance in an action observation task. This comparison showed that MEP facilitation was significantly higher for mimickers ($n = 10$; mean, 2.30; SD, 1.06) than nonmimickers ($n = 9$; mean, 1.58; SD, 0.94; $t_{(17)} = 1.815$, $p = 0.044$; Fig. 3). Overall, it appears that mimickers display a larger increase in MEP facilitation to human stimuli after mimicking the experimenter than nonmimickers do.

We report the pooled data simply to convey the effects of mimicry on motor resonance given all the data we have available. Readers should be aware that data from the smaller samples of mimickers and nonmimickers did not show the same effect as the larger sample of pooled data. It was not possible to pool data for robot observation because our pooled group did not take part in a robot observation condition.

Discussion

Given the importance of social interaction for humans, it is imperative to understand the ways in which social interaction changes the brain, and how this affects subsequent information processing. The goal of the current study was to determine the effects of a naturalistic social interaction on motor resonance in a subsequent action observation task. First, we wanted to elucidate the effects of the social interaction *per se* on subsequent motor resonance during observation of a human or functionally equivalent robotic action. Second, we wanted to determine whether participants who displayed mimicry during the social interaction showed greater levels of motor resonance in the subsequent observation task than those who did not display mimicry.

Overall, motor resonance was greater during human observation than during robot observation. However, the interaction effect suggests that this difference is driven by the social interaction. That is, participants who did not engage in the social interaction showed statistically similar levels of MR for human and robot actions, whereas those who engaged in the social interaction showed significantly greater levels of MR for human actions. Thus, social interaction facilitates MR for subsequent action observation involving humans, but not robots. Furthermore, when we pooled mimicry data from an additional group of participants run through a similar procedure with mimicry data from the current study, it became clear that participants who mimicked during the social interaction (mimickers) displayed an even greater increase in motor resonance compared with those who did not mimic (nonmimickers). These results are the first to show that naturalistic social interaction (and mimicry) changes the manner in which the brain processes subsequent stimuli. Our results provide some of the strongest evidence to date that mimicry and action observation rely on the same motor resonant mechanisms.

These results strongly suggest that common mechanisms operate in naturalistic social interactions and laboratory-based action observation tasks. This link has often been inferred, but until recently has not been explicitly investigated (Chartrand and van Baaren, 2009; Iacoboni, 2009; Obhi and Hogeveen, 2010; Heyes, 2011; Hogeveen and Obhi, 2011; Obhi et al., 2011). Typically, social psychologists have concerned themselves with the form and function of more naturalistic social interaction (Baumeister and Leary, 1995; Chartrand and Bargh, 1999), whereas cognitive neuroscientists have limited their considerations to well controlled laboratory contexts involving action observation. By combining both approaches, we have demonstrated what appears to be functionally equivalent to a priming effect of social interaction on the motor resonance system. Our work adds to the small number of studies explicitly linking naturally occurring social phenomena to neurophysiological-dependent measures (Kourtis et al., 2010; Knoch et al., 2008).

Previous research had suggested a privileged status for biological agents (Kilner et al., 2003; Tsai and Brass, 2007). In their experiment, Kilner et al. (2003) found that observation of incongruent biological actions interfered with ongoing actions made by participants. In contrast, observation of incongruent robotic actions produced no interference. Later work by the same group reported interference for a nonbiological stimulus moving in a different direction to the participant's movement, but also found interference effects that depended on the biological motion of an observed human movement (Kilner et al., 2007). More recent evidence has suggested that exposure to biological or nonbiological stimuli directly impinges on the degree of corepresentation that takes place in a joint Simon task (Müller et al., 2011). Specifically, Müller et al. (2011) either exposed participants to a video containing a biological agent (a human) or a nonbiological agent (Pinocchio). The participants exposed to a human stimulus showed a joint Simon effect only when paired with a human partner, whereas the reverse was found for participants who were exposed to, and able to form a vivid image of, the nonbiological agent. Similarly, Press et al. (2007) showed that recent experience making actions while observing robotic actions eliminated the bias for human stimuli in an automatic imitation task. Thus, the idea that an observed action must have biological status for corepresentation to occur, and by extension for motor resonance to occur during observation, is not supported. In contrast, the idea that underlying mechanisms are tuned by virtue of experi-

ence seems sensible (Catmur et al., 2007, 2008, 2009; Gillmeister et al., 2008; Heyes, 2010).

The mimicry analysis of the pooled data suggests that active interaction with a particular type of agent, defined by spontaneous social mimicry, is associated with increased motor resonance compared with more passive interaction (i.e., interaction unaccompanied by mimicry). To be clear, participants who mimicked during the social interaction showed greater increases in motor resonance in the human action observation task than those who did not mimic, but nevertheless took part in the social interaction. This result makes sense given findings from brain imaging experiments of the mirror system, which have shown increased mirror system activity in imitation compared with observation of actions (Iacoboni et al., 1999). Furthermore, in the sample from the present study, mimickers showed significantly less MR to robot actions than nonmimickers. Thus, recent experience and interaction with a biological agent appears to tune the system to biological actions, and relatively suppress resonance for nonbiological actions.

How exactly can such tuning be achieved? One idea is that the motor resonance system is crucial for social interactions, and by virtue of engagement during interaction, the system is primed to process subsequent human actions. This priming effect does not extend to robotic actions, even if they depict the same goal (squeezing a ball in the current experiment).

We have recently proposed several ways in which activity in the mirror system could be modulated (Obhi et al., 2011). Briefly, top-down processes or bottom-up processes (i.e., expectation effects, or detector warm-up effects) may result in input modulation, whereby the entry node to the human mirror system, the pSTS, is biased toward specific stimulus types (Corbetta et al., 1990; Luks and Simpson, 2004). In the present experiment, a recent encounter with a human seemed to increase the bias for human stimuli, possibly via greater activation in the pSTS and frontoparietal mirror system. It remains to be seen whether recent experience with a robot can reverse the apparent preference of the pSTS for biological stimuli, but previous work suggests this might be possible. For example, Press et al. (2007) reported a change in the bias toward human actions in automatic imitation tasks when repeated exposure to a robot was provided. Recent results from Müller et al. (2011) also showed that exposure to and vivid imagery of a nonbiological agent resulted in corepresentation of that agent's actions, and a corresponding suppression of corepresentation of human actions. Of course, whether these effects are mediated by changes at the level of the pSTS is unknown, but this is a possibility. A second possibility is a direct modulation process whereby motor resonance for recently encountered agents is increased directly via prefrontal inputs to premotor cortex (Miller, 2000; Amodio and Frith, 2006). Of course, a combination of input modulation and direct modulation accounts could also produce the observed effects.

In summary, we have shown that social interaction enhances biological tuning of the motor resonance system and our pooled data suggest that mimicry during the social interaction increases this effect. Whereas observation of robot and human actions in the absence of a previous social interaction produced similar levels of motor resonance, previous social interaction dramatically increased resonance for the human action only. We suggest that the motor resonance system is configured by recent experience and that it may be capable of coding the actions of a multitude of agent types.

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