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Research Report

The role of the left inferior frontal gyrus in social perception: An rTMS study

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ABSTRACT

Perceiving and interpreting social information richness is something that humans do automatically whenever they engage in social interactions. Numerous studies have identified neural substrates, including mirror neurons that may enable such social perception. In this study, we temporarily disrupted activity in the left inferior frontal gyrus (LIFG) using repetitive transcranial magnetic stimulation (rTMS). We investigated whether this cortical region, that is hypothesized to include mirror neurons, plays a central role in social perception. The LIFG was stimulated in the experimental condition ($n=18$), the vertex was targeted in the control condition ($n=19$). Disrupting LIFG, but not vertex, increased reaction times during an emotion recognition task, and eliminated the suppression of the 8–12 Hz EEG μ rhythm, postulated as an index of mirroring activity. The results of this study provide further evidence for the role of the human mirror neuron system (MNS) in social perception, and indicate that the MNS can be measured with EEG.

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1. Introduction

Substantial parts of daily life are characterized by social interactions. An important part of such behavior is the ability to recognize and understand the social information provided by conspecifics (Iacoboni and Mazziotta, 2007). To manage and deal with this rich set of information, Tager-Flusberg and Sullivan (2000) have proposed a multi-domain model that divides social information processing into a social cognitive and social perceptive domain. The social cognitive domain is characterized as higher-order and slower offline reasoning about behavior that is not always perceived, whereas social perceptive domain is defined as the ability to make rapid online judgments about another person's emotional state. The

underlying processes of social perception have triggered a long line of research (Insel and Fernald, 2004), and most recently in social cognitive neuroscience.

1.1. Mirror neurons and social perception

During the last decade, the processes falling under the social perception domain have often been linked to the activity of a distinct mirror neuron system (MNS) in the human brain (Rizzolatti and Craighero, 2004; Iacoboni et al., 2005). The MNS core network has been proposed to consist of the superior temporal sulci, inferior parietal lobe and the bilateral inferior frontal cortex (Aziz-Zadeh et al., 2006). The human MNS is presumably involved in action understanding and imitation

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by facilitating the ability to simulate an action (Carr et al., 2003; Iacoboni, 2005; Lyons et al., 2006; Aziz-Zadeh, et al., 2006). Current theories suggest that mirror neurons provide a link between passive action observation and the encoding of social perception (Lyons et al., 2006) and are assumed to be necessary to encode action understanding and intentionality (Cattaneo et al., 2007; Rizzolatti and Sinigaglia, 2007). Despite criticism (Dinstein et al., 2007; Hickok, 2009; Lingnau et al., 2009), one can reasonably hold that, based on a substantial body of research (Rizzolatti and Craighero, 2004), the action understanding properties of the mirror neuron system serve as a foundational cornerstone for higher order perspective taking such as empathy (Oberman and Ramachandran, 2007; Iacoboni, 2009).

1.2. Measuring the MNS activity with EEG

A non-intrusive way of indirectly measuring the involvement of the MNS involves the recording of the μ rhythm using the electroencephalographic (EEG) signal (Altschuler et al., 2000; Rizzolatti and Craighero, 2004). The μ rhythm reflects the activation of the primary sensorimotor regions (Pfurtscheller and Neuper, 1997; Oberman et al., 2007). When at rest, neurons in this region fire in synchrony producing large EEG oscillations in the 8–12 Hz frequency band, which can be recorded at C3 and C4 electrode sites on the scalp (Klimesch et al., 1998). When participants perform, observe, or imagine an action, the oscillations in μ rhythm diminish, which likely reflect the downstream modulation of the primary sensorimotor cortex by mirror neurons (Pineda, 2005). This modulation hinges on cortico-cortical connections between the central premotor cortex and the primary sensorimotor cortex, evidenced in anatomical and psychological studies that have included humans and non-human primates (Oberman et al., 2007).

There has been some discussion about which EEG frequencies in the 8–25 Hz range actually index mirror neuron activity (Hari and Salmelin, 1997; Pineda, 2005; Egner and Serman, 2006). Some argue for the use of the 12–15 Hz frequency band called the sensorimotor rhythm (SMR). Research on felines has shown that the SMR can be measured when the feline is motionless but attentive. The SMR is blocked when the feline moves, reflecting the engagement of motor neurons and possibly mirror neurons (Howe and Serman, 1972). Others argue that both the μ rhythm in the alpha range (8–12 Hz) and the 15–25 Hz in the beta range should be used since the latter could be the harmonic of the fundamental frequency of the former rhythm (Hari and Salmelin, 1997).

1.3. The current study

The first hypothesis that is tested in the present study is that the left inferior frontal gyrus (LIFG) is involved in social perception. The other hypothesis is that the LIFG modulates the μ rhythm. The present experiment builds upon a pilot study conducted by Elfenbein et al. (2007), reporting that disruption of the LIFG using repetitive transcranial magnetic stimulation (rTMS) for 5 minutes preserved μ oscillations, that is, the expected μ suppression did not occur while viewing biologically relevant movements. In contrast, disruption of the left occipital pole did lead to μ suppression. The current study expanded the design by not only investigating whether a

relationship exists between LIFG function, μ rhythm and social information processing. It also investigates whether this relationship is reflected in the alpha μ rhythm (8–12 Hz), the SMR (12–15 Hz), and/or the beta μ rhythm (15–25 Hz). We had several reasons for choosing the LIFG as the target site. First, the pars opercularis of the IFG is considered to be the human homolog of the monkey area F5, which is the area where mirror neurons were first reported (Geyer et al., 2000). Second, previous research has shown that rTMS over LIFG disrupts processes attributed to a MNS (Heiser et al., 2003; Pobric and Hamilton, 2006; Elfenbein et al., 2007). Third, it is hypothesized that the μ oscillation is dependent on IFG activity (Pineda, 2005). Finally, we tested whether typically developing participants show impaired social perception (and preserved social cognition) following disruption of the LIFG compared to stimulation of a control site.

2. Results

2.1. Psychometric measurements

The LIFG and the vertex group did not differ on the psychometric tests, as is shown in Table 1, suggesting homogeneous populations. This is essential since the current study uses a between subject design. Both participant groups were stable in their PANAS scores between the first and the second session (LIFG: $t(17)=0.18, p>0.05$; Vertex: $t(18)=0.28, p>0.05$).

2.2. Videos

The EEG data from the middle 45 seconds of each video was used to determine single mean power (voltage amplitude squared) for the three different frequency bands (μ , SMR, beta). Overall, there was no main effect of stimulation site on μ power as the vertex group and the LIFG group did not differ significantly $F(1)=0.48, p>0.05$. However, there were highly significant main effects of video $F(2.15)=4.96, p<0.01$ and frequency band on μ power

Table 1 – Demographic variables, Means (and standard deviations) and test statistics for the Vertex versus LIFG stimulation group.

	Vertex	LIFG	
Age	20.5 (1.1)	19.8 (1.52)	$t(34)=-1.658, p=0.107$
Ravens Progressive Matrices test	45.66 (6.49)	48.29 (6.21)	$t(35)=1.396, p=0.171$
SQ ^a	59.38 (8.1)	58.09 (10.72)	$t(33)=-0.641, p=0.526$
EQ ^a	50.62 (7.75)	51.54 (7.61)	$t(35)=-0.622, p=0.538$
AQ	17.11 (4.43)	16 (5.78)	$t(34)=0.164, p=0.87$
PANAS			
Session one ^b	2.58 (0.78)	2.37 (0.7)	$t(35)=-0.534, p=0.597$
PANAS			
Session two ^b	2.47 (0.91)	2.22 (0.63)	$t(34)=-0.972, p=0.338$

^a Scores are transformed to a normal distribution based on Wakabayashi et al. (2006).

^b Scores are the ratio between the overall positive score divided by the overall negative score.

$F(1.66)=59.36, p<0.001$. Interaction effects were also found between video and frequency $F(4.2)=11.172, p<0.001$, electrode site and frequency $F(1.75)=3.408, p<0.05$, between group, video, electrode site and pre- and post-stimulation $F(2.6)=2.88, p<0.05$.

The data recorded from the C4 electrode were used for further analysis because this electrode showed more mirror neuron modulated activity in response to the videos than C3 before stimulation. For instance, the μ frequency measured at C3 did not differ between the non-biological motion video and the imitation video before stimulation $t(13)=-2.62, p>0.05$ in the LIFG group. Also, the μ frequency recorded at C3 did not differentiate between non-biological motion and simple biological motion $t(12)=2.25, p>0.05$ or between non-biological motion and complex biological motion $t(13)=1.19, p>0.05$ in the LIFG group.

2.2.1. Mu rhythms (8–12 Hz)

The only significant difference between the vertex group and the LIFG group was in terms of the non-biological motion video that was shown before rTMS stimulation $t(20.21)=2.09, p=0.05$ in which the vertex had a lower mean voltage amplitude. Since we took the relative differences between videos for groups this baseline difference cannot be considered a confound. As illustrated in Fig. 1, when examining the data within the LIFG group before stimulation, the differences were as expected. That is, significantly higher mean amplitudes were found for the non-biological video compared to the imitation video $t(14)=-4.48, p<0.01$, the simple biological motion videos $t(13)=2.29, p<0.05$ and the complex biological motion videos $t(13)=3.92, p<0.01$. Additionally, planned pairwise comparisons showed that the imitation video elicited a significantly lower mean amplitude than the simple biological motion videos $t(13)=-0.22, p<0.01$. Following LIFG stimulation, the only significant effect was that the non-biological motion videos elicited a higher mean amplitude than the imitation video $t(14)=3.13, p<0.01$. In the vertex group, the non-biological motion videos had a higher mean voltage amplitude than the imitation video $t(14)=-3.62, p<0.01$ and the imitation video had a lower mean amplitude than the simple biological motion video $t(13)=-2.96, p<0.05$ before stimulation. After stimulation of the vertex, only the imitation video elicited a significantly lower mean amplitude than the complex biological motion videos $t(13)=-3.3, p<0.01$.

2.2.2. SMR rhythms (12–15 Hz)

No main effect of stimulation site was found for the SMR data. The LIFG group showed significant differences between the non-biological motion videos and the imitation video $t(13)=-4.48, p<0.01$, indicating that the imitation video yielded more SMR suppression before stimulation, and these differences remained significant after stimulation $t(14)=-3.13, p<0.01$. In contrast, in the vertex group, the non-biological motion videos were significantly different from the imitation video $t(14)=-3.06, p<0.01$ before stimulation, where the imitation video showed greater SMR suppression, but this difference disappeared following stimulation $t(14)=-1.25, p>0.05$.

2.2.3. Beta rhythms (15–25 Hz)

There were no differences between videos within either the vertex or the LIFG group for the beta rhythms, nor were there any effects between the groups.

2.3. Behavioral performance

Before stimulation, the LIFG group and the vertex group did not differ in accuracy on the behavioral tasks (emotion recognition: $t(34)=0.26, p>0.05$, gender recognition: $t(34)=0.65, p>0.05$, mental causation: $t(34)=0.83, p>0.05$, physical causation: $t(34)=-0.001, p>0.05$). Before stimulation, vertex group showed faster responses for all the behavioral tasks compared to the LIFG group (emotion recognition task $t(21.65)=2.91, p<0.01$, gender recognition task $t(23.74)=2.549, p<0.05$, mental causation task $t(26.93)=2.096, p=0.05$, the physical causation task $t(34)=2.8, p<0.01$). Because of these RT differences between the LIFG group and the vertex group before stimulation, the post-stimulation data were divided by the pre-stimulation data in order to examine relative effects instead of absolute effects of rTMS stimulation. Finally, the ratios were normalized by a log transformation, to control for differences in task difficulties. T-tests on the ratio between post-stimulation and pre-stimulation did not result in any significant differences between the vertex and the LIFG group nor were there any differences between tasks within the vertex or LIFG group. This was the case for both accuracy rates and RTs.

2.4. Effect of presentation order on behavioral performance

Because the temporal dynamics of rTMS have not been studied extensively, the influence of presentation order on the accuracy and the RTs for the behavioral tasks was investigated. T-tests were performed on the log transformations of the ratio-scaled data for each task and each sequence location separately to see if the stimulation groups differed in their performance. There were no significant differences in accuracy between the LIFG group and the vertex group within any of the four tasks presentation orders. However, the groups differed in RT on the emotion recognition task when it was presented as the second task $t(6)=3.43, p<0.05$. There was an overall linear decline of the log ratio of RT for the vertex on emotion recognition $r=0.53, p<0.05$ but this was not observed for the LIFG group. See Fig. 2 for the differences in rTMS over presentation order.

3. Discussion

The present study investigated the relationship between the LIFG function, various EEG frequency bands in the 8–25 Hz range that are thought to reflect mirror neuron activity and social information processing. It was hypothesized that of the alpha (8–12 Hz) μ rhythm, SMR (12–15 Hz) and beta (15–25 Hz) rhythms, the 8–12 Hz μ rhythm would most likely reflect mirror neuron activity. Furthermore, it was expected that disruption of the LIFG after rTMS, interferes with the performance on a social perception task.

3.1. The effects of rTMS on the EEG frequency bands

It was expected that μ suppression would be largest when participants had to imitate a movement, somewhat less when they observed a video containing complex biological movement, even less still when these movements were simple, and lowest when the movement was non-biological (Oberman et al., 2007). Fully in line with these predictions, our results indicate that the

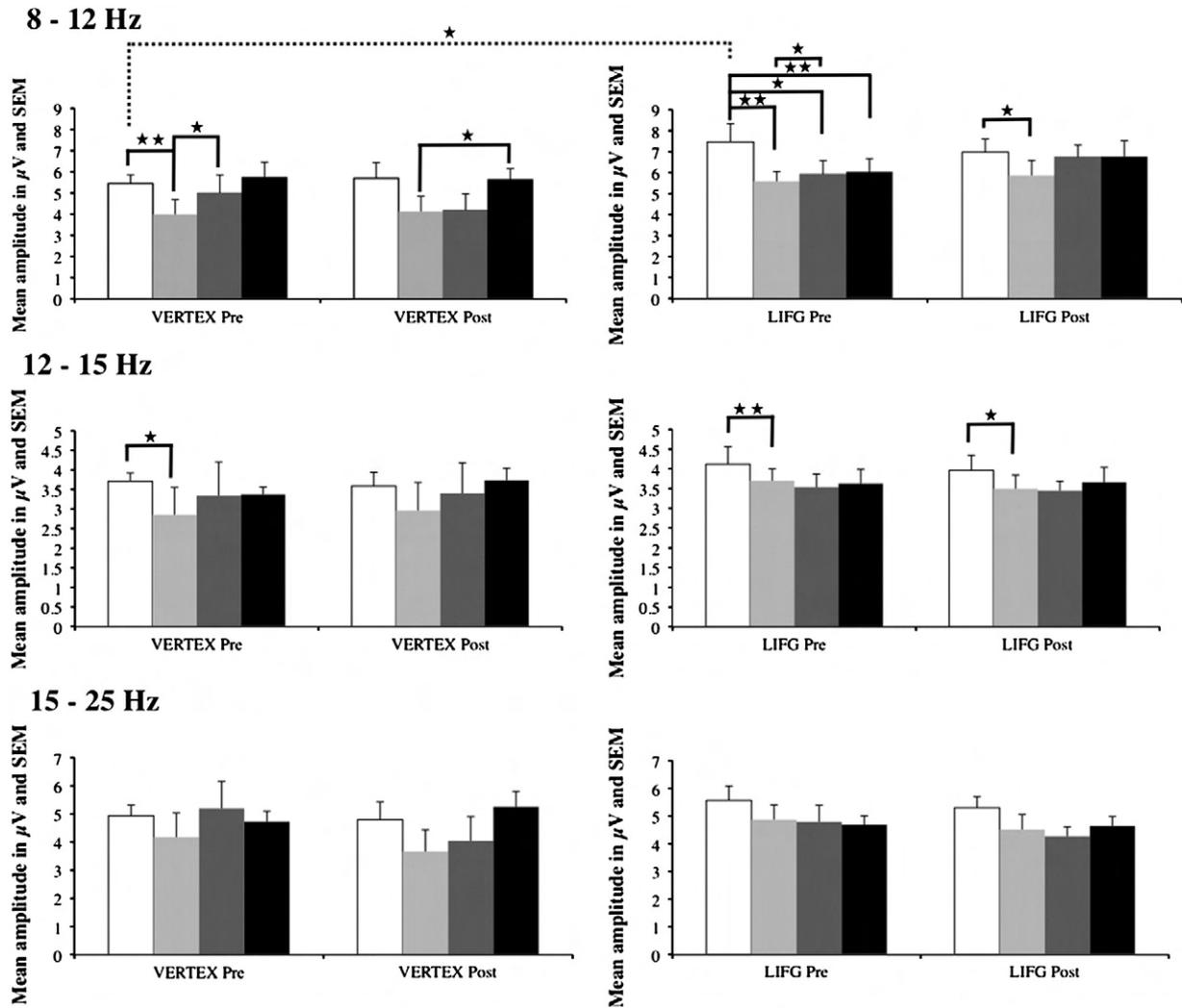


Fig. 1 – The mean amplitude of the μ (8–12 Hz), SMR(12–15 Hz) and beta (15–25 Hz) frequency for C4 before and after rTMS stimulation in the LIFG and vertex group in response to the videos. White is the non-biological motion, light gray is the imitation video, dark gray is the simple and black is the complex biological video. * $p < 0.05$, ** $p < 0.01$.

8–12 Hz μ rhythm could be used as a reliable index of such mirror neuron related activity.

Consistent with expectations, the LIFG group showed enhanced μ suppression in the imitation condition before rTMS stimulation, as well as in the complex and simple biological movement conditions compared to the non-biological movement condition. Greater μ suppression in the imitation condition compared to the simple biological motion videos was also found. Similar results were found for the vertex stimulation group, except that the simple and complex videos did not elicit more μ suppression than the non-biological motion videos. It was hypothesized that following rTMS stimulation directed at the LIFG, the μ rhythm would not differ between the imitation video and the passive viewing of all other videos since the MNS would be impaired. The results support our hypothesis since a significant difference between the imitation video and the non-biological motion videos was the only effect found. While videos were not presented in a counterbalanced order to avoid visual effects on imitation, the fact that following stimulation the suppression effect in the μ

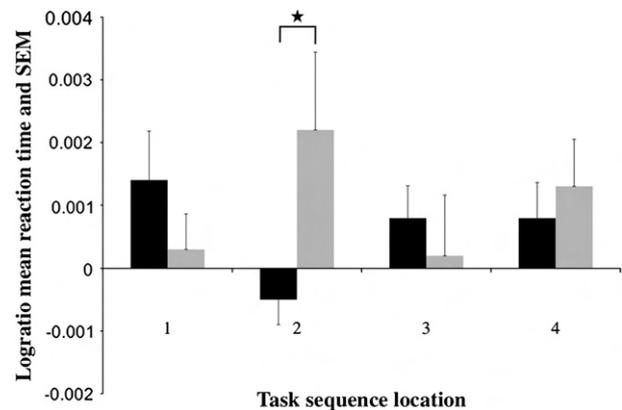


Fig. 2 – Log ratio reaction time emotion recognition for the vertex (black) and LIFG (grey) over task sequence location. * $p < 0.05$.

rhythm is abolished to all the observation videos suggests a real physiological effect irrespective of presentation order. Congruent with our hypothesis, there was no differentiation between the non-biological and biological motion videos after rTMS stimulation of the LIFG. The observation that the μ patterns differed between imitation and the non-biological video could be explained in two ways: The μ rhythm may reflect the activity of mirror neurons and motor neurons in the LIFG. The fact that μ suppression occurs for the imitation video both before and after LIFG stimulation argues against selective suppressive effects due to repetition of the same video. It does support the idea that although the mirror neuron population may be affected, the motor neuron population producing suppression is not. A less likely explanation is that the imitation video engages more mirror neurons than the other biological movement videos and that the rTMS stimulation parameters were not effective enough to disrupt the amount of mirror neurons involved during imitation. It is not possible to dissociate between these two interpretations on basis of the present experimental design providing an open question for further research. Following rTMS stimulation over the vertex, imitation still elicited more μ suppression than the complex biological motion videos.

Taken together, our results support the general hypotheses that the change in μ frequency is primarily due to rTMS effects on mirror neurons in the LIFG and that this frequency could be used as a non-invasive indirect index of mirror neuron activity as previously argued by [Oberman et al., \(2007\)](#) and [Pineda \(2005\)](#). When considering the SMR rhythms, it was observed that during pre rTMS stimulation the mean amplitudes were different between the non-biological motion videos and the imitation video, within both groups. For the LIFG group this effect remained significant after stimulation, but it disappeared in the vertex group. This was in accordance to our expectations arguing that the SMR reflects motor neuron activity and not mirror neuron activity. No significant differences were found in the beta rhythm. Since neither the SMR nor the beta frequency showed changes to observation-based stimuli that are normally used to elicit changes in mirror neuron activity, these results challenge the notion that they can be reliable indices for mirror neuron activity ([Howe and Serman, 1972](#); [Hari and Salmelin, 1997](#)). This study therefore indicates that the LIFG modulates the μ frequency and the μ frequency likely reflects mirror neuron activity.

3.2. Effects of rTMS on social perception

Based on the pilot study of [Oberman et al. \(2007\)](#) we predicted that stimulation of the LIFG would cause an overall impairment in social perception as reflected by lower accuracy rates and higher RTs. The data did not support this hypothesis. This could reflect the fact that rTMS was applied for only 5 minutes, which has an estimated half-life of influence of about 2.5 minutes, whereas the behavioral tasks lasted up to 20 minutes after stimulation. This possible confound is unlikely for reasons described in [Experimental procedures](#) section. However to test whether these behavioral null findings were caused by the possible limited effect of rTMS stimulation in the temporal domain, the role of presentation order on performance was investigated. This analysis revealed that the LIFG group had

longer RT than the vertex group on the emotional recognition task after rTMS stimulation as a function of temporal order. That is, the effect is present when the task is second in the temporal order and thus closer to the effective time window of stimulation. Thus, whereas no overall effect on social perception was found perhaps because of these temporal constraints, this analysis adds support to the hypothesis that the LIFG is indeed involved in social perception, and not in social cognitive skills such as theory of mind ([Pineda and Hecht, 2008](#)). A possible confound between the behavioral tasks and their control conditions is that the emotion recognition task has four response alternatives, while the control (gender recognition) condition only has two response alternatives. Therefore, any differences between these tasks could be due to differences in task difficulty. However, this explanation seems unlikely since we used the relative difference of each task and nor does it explain why no such effects occur in the mental versus physical causation tasks.

3.3. Social-cognitive versus social-perceptive domains

Categorizing social information into at least social-cognitive and social-perceptive domains gives rise to the possibility that both domains may be working in parallel, and that each domain might have its own neural substrate, as proposed by [Tager-Flusberg and Sullivan \(2000\)](#). That is, the social perceptive domain is conceptualized to involve the amygdala, medial temporal cortex, superior temporal cortex and the IFG. The latter structure being relevant to facial recognition, as well as processing emotions and intentional motion. This speculation stems from previous research showing that bilateral IFG is selectively active when emotional facial cues are processed ([Dapretto et al., 2006](#)). In contrast, the social cognitive domain is assumed to consist of the medial frontal and orbitofrontal cortices ([Tager-Flusberg and Sullivan, 2000](#)).

Human MNS brain regions show a high degree of overlap with brain areas thought to be involved in the social perceptive and social cognitive domains. This overlap could indicate that the functions ascribed to the MNS are similar to functions in the social perceptive domain.

3.4. Possible different interpretation of MNS

Recently, several authors have argued for a different interpretation of the MNS literature. Some argue that there is no such thing as MNS in humans whereas others argue that instead of being essential for action understanding and therefore social perception, the MNS actually is involved in facilitating the motor system due to learned associations between the semantic representation of actions and the motor programs that generate the movement ([Lingnau et al., 2009](#); [Hickok, 2009](#)). However as [Kilner et al. \(2010\)](#) and [Perkins et al. \(2010\)](#) argued, the absence of an MNS in humans could be due to several methodological issues or due to misinterpretation of the literature ([Rizzolatti and Sinigaglia, 2010](#)). Furthermore, since the current study reports differences in a modality that requires the understanding of another person's mental state (i.e. expressed emotion), our findings can be interpreted within the human MNS framework.

In conclusion, results from the current study support the theory that the human MNS is involved in processing specific

social information, and that the EEG μ rhythm can be used as an index for mirror neuron activity.

4. Experimental procedures

4.1. Participants

Forty-five self-reported right-handed male college students (mean age: 20.4, SD: 2.0, range: 18–29 years) were recruited for the experiment. Four participants were excluded during screening based on their medical history. Four other participants did not show up for the second session and were excluded from the analysis. Of the remaining participants, eighteen participants were randomly assigned to the experimental (LIFG) stimulation condition and nineteen participants were enrolled in the control (vertex) stimulation condition. The study was approved by the UCSD institutional review board (IRB) and the VA Hospital ethical commission.

4.2. Stimuli

4.2.1. Psychometric measurements

Five psychometric tests were administered, of which only the Positive And Negative Affect Schedule (PANAS) was administered during both the first and the second session of the experiment. This test was used to evaluate current mood status (Watson et al., 1988). The short versions of the Systemizing Quotient (SQ) and the Empathizing Quotient (EQ) were administered to measure levels of systematizing and empathizing, as these personality traits could be important factors in social cognition (Wheelwright, et al., 2006). The autism quotient (AQ) test by Baron-Cohen et al. (2001b) was included to control for differences in autistic traits between the control and experimental group. Finally, the Advanced Ravens Progressive Matrices test (Raven et al., 1998) was used to measure general fluid intelligence. This test requires minimal instructions and has the ability to distinguish individuals from a highly educated group to test if the group is homogeneous.

4.2.2. Videos

A total of seven different videos were used to investigate the relationship between rTMS stimulation over the two sites, μ rhythm suppression, the blocking of SMR frequency, and possible changes in beta frequency. These videos were selected from an independent study in which the participants were asked to rate the videos in terms of sociality (Oberman et al., 2007), indicating that μ frequency amplitude was strongly correlated with video rating scores.

Silent videos were presented for 60 seconds, with only a few seconds in between videos. Participants were shown five videos with biological movement and two with non-biological movement. One of the five biological movement videos required the participant to imitate the manual movement depicted in the video. This video showed a right hand opening and closing seen from an egocentric perspective. Two different videos were used to depict simple biological movement: one involving a right hand taking a cigarette from a cigarette pack. The other video showed a woman mimicking the picking up of

a phone and putting it down again. The final two videos involved complex biological movement: one showed a man and woman in an apparent argument. The other video showed three people throwing a ball to one another or sometimes towards the camera. Two different videos were used that illustrated non-biological motion: one showed two white balls (32.9 cd/m^2) on a black background (1.0 cd/m^2) moving vertically towards each other, then touching in the middle of the screen and finally moving apart to their initial starting position. The balls subtended 2° of visual angle when touching in the middle of the screen and 5° at their maximal point of separation. This motion is visually equivalent to the trajectory taken by the tips of the fingers and thumb in the imitation video. The other non-biological motion video showed a moving contraption of ordinary objects (e.g., a tire) affecting other objects. All the videos had occasional brief pauses (approximately 1 second) that the participants were asked to count to control for attention effects. Participants were presented with the same imitation video in the first and the second EEG sessions. The other six videos were divided over the two sessions and counter-balanced over participants. The non-biological motion videos were used as a baseline condition.

4.3. Behavioral tasks

Four behavioral tasks were used to determine if LIFG stimulation had an effect on social perception or social cognition. The social perception task is a modification of the Eyes task and involved identifying facial expressions based on photographs of only the eye region of the face (Baron-Cohen et al., 2001a). As shown in Fig. 3, a word was shown in each corner of the display describing a possible emotion that was expressed, along with a number below the word, which corresponded to the response keys. A gender discrimination task served as control task. That is, the same set of eyes was presented but now the images had the words “male” and “female” in the two corners of the display below the image. Below these words, a number was depicted corresponding to the response keys. For each task, participants were shown a total of 37 gray-scaled images of eyes, 19 of which were male. During both the emotion and gender discrimination tasks, the stimuli were presented for three seconds after which the participants had five seconds to respond. For the social cognition task, a variation of the Cartoons task developed by Brunet et al. (2000) was used. This task involves mental attribution of intentions and beliefs and included control blocks for physical causation and object involvement. Participants were shown 28 sets of black and white captionless cartoons. As illustrated in Fig. 3, a set consisted of three images showing a causal sequence with a person as the active agent. This was followed by a second set of three new images beneath the original sequence. The participant had to choose which of the three new images followed logically from the original sequence by pressing the corresponding number that was depicted below each of the three images. As a control task for the mental causation condition, participants were shown 15 sets of black and white cartoons, which were similar to those of the mental causation condition, but now followed the rules of physics instead of having a biological agent causing the sequence. Each causal sequence was presented for three seconds after which

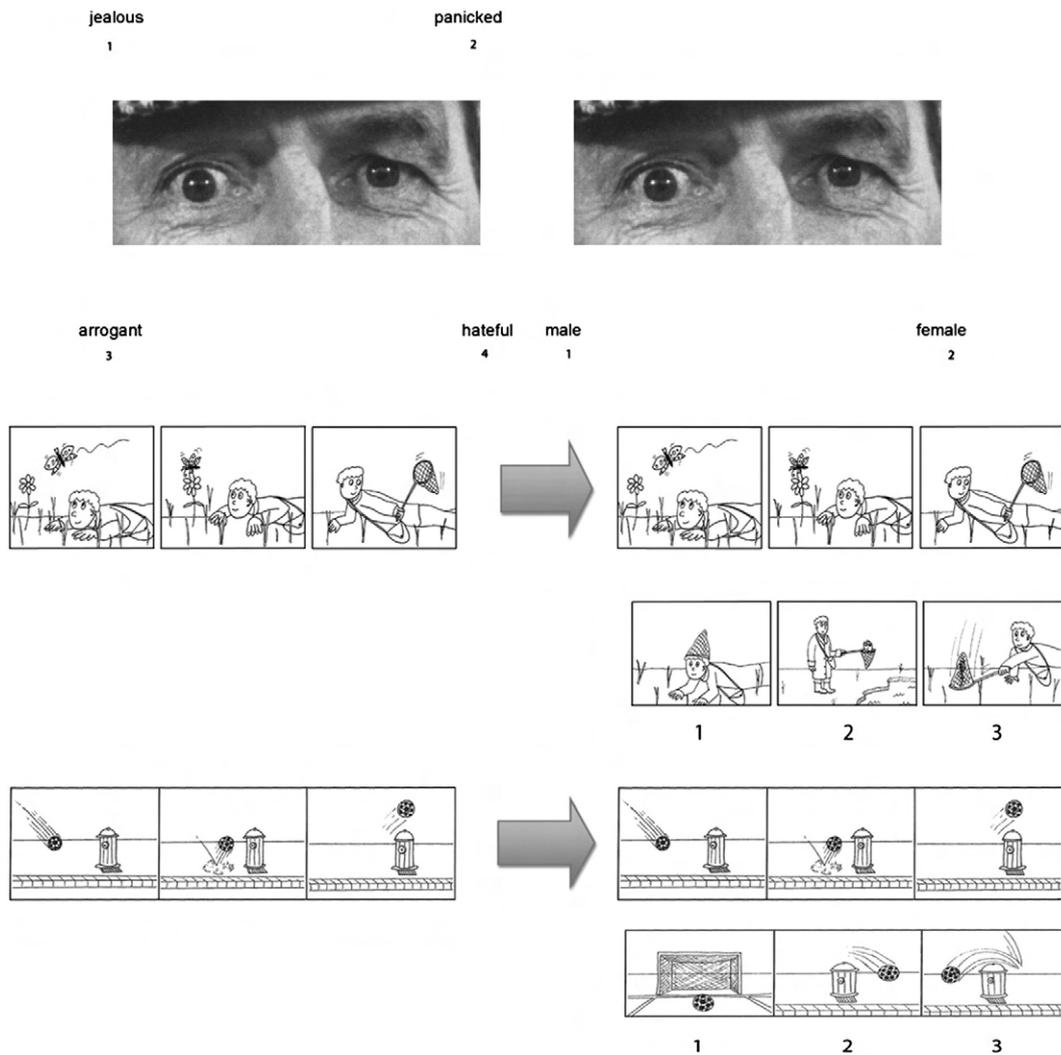


Fig. 3 – Left upper corner shows an example of the emotion recognition task, right upper corner an example of the gender recognition task. Middle row is an example of the mental causation task and lower row is an example of the physical causation task.

the three images were shown below this sequence from which the participants had to pick one that depicted a logical continuation of the sequence. The participants had five seconds to respond. All stimuli for all tasks were divided into two sets, the presentation order of which was counterbalanced across participants over pre- and post-stimulation sessions. All the participants were instructed to respond as quickly as possible.

4.4. Procedure

The experiment was divided into two sessions on separate days. During the first session, the experimental procedure was explained to the participants, and the informed consent forms were signed. This was followed by administration of the five psychometric pen and paper tests. When participants returned for the second session they were comfortably seated behind a laptop. A summary of the experimental procedure was given, and again the PANAS was administered. Next, the circumference of the participant’s head was measured and marked for EEG electrode placement. Once the EEG electrodes were placed at C3,

C4, the mastoids and forehead (ground electrode), the first part of the experiment could start.

In this part the participants watched four short videos in the following order: imitation video, non-biological movement video, simple biological movement video, complex biological movement video. Videos were not randomized in order to minimize visual effects on the imitation condition. At the end of each video, participants were asked to press the number on the keyboard corresponding to the number of pauses. When the video tasks were completed, the four behavioral tasks were presented, randomized across participants. After a short rest interval, rTMS stimulation was administered for five minutes. rTMS was applied either over the vertex or over the LIFG. After stimulation, the second part of the experiment would follow, similar to the first part, but now each task included a different set of stimuli.

4.5. Apparatus and EEG recordings

Presentation software (Version 13) was used for stimulus presentation and response recording. For EEG data recording a BrainMaster EEG amplifier model 2E, Ag-AgCl electrodes and

Bioexplorer software (Version 1.4) were used. EEG was recorded using an online bandpass filter of 1–30 Hz at a sampling rate of 512 Hz, with the impedance at all the electrodes kept below 10 K Ω . The EEG band frequencies were calculated by using a Fast Fourier Transformation analysis. The time epochs used for the EEG analysis were the middle 45 seconds of each video trial, which were averaged to a single mean power (voltage amplitude squared). This was done separately per participant and per electrode for the 8–12 Hz, 12–15 Hz and the 15–25 Hz frequency bands. Data analysis was performed with SPSS for Macintosh (version 17).

4.6. rTMS

4.6.1. Apparatus

The rTMS machine used in the study was a monophasic Cadwell MES-10 Magnetic Stimulator (Cadwell, 1989). The stimulation coil was a Cadwell Corticoil for Highly Localized Stimulation (Cohen et al., 1990).

4.6.2. Stimulation intensity

To determine the stimulation intensity for the current study, we compared other studies using 1 Hz rTMS stimulation in the vicinity of the LIFG to see if there was some agreement in the level of stimulation intensity. Based on this literature review (Topper et al., 1998; Sparing et al., 2001; Hansenne et al., 2004; Nixon et al., 2004; Gough et al., 2005; Andoh et al., 2006), a 1 Hz monophasic pulse was chosen with a fixed intensity of 45% maximum output of the stimulator, which generates a peak magnetic field of 0.99 T across subjects. The reason for this was that monophasic pulses seem to need a lower intensity (Topper et al., 1998).

4.6.3. The duration of low frequency rTMS stimulation

Several studies (Mottaghy et al., 2003; Hansenne et al., 2004; Lang et al., 2006; Nyffeler et al., 2006; Eisenegger et al., 2008) have argued for a rule of thumb that applies to the duration of rTMS effects: that the offline effect has a duration half of the total stimulation time and that this depends on the stimulus parameters, experimental design and coil characteristics. Since participants in the present study had to complete four behavioral tasks that lasted for approximately 20 minutes total following stimulation, it meant that total stimulation should have lasted for 40 minutes. However, in a pilot study by Elfenbein et al. (2007) in which similar stimulus intensities were used that are comparable to those in the present, impairment on the social perception task was found well over 20 minutes following 5 minutes of LIFG stimulation. This finding could be explained by the rTMS machine that both Elfenbein et al. (2007) and we used, which sends out a monophasic pulse. As Sommer and Paulus (2003) argued, monophasic pulses are more effective in inducing a longer lasting corticospinal inhibition than biphasic pulses. Therefore, we decided to apply rTMS over the LIFG for only 5 minutes at 45% of maximum output of stimulator.

4.6.4. Stimulation and recording sites

The international 10/20 system for EEG electrode placement was used to determine both the rTMS stimulation sites (Cz for vertex and F7 for LIFG) as well as the EEG recording sites (C3 and C4). A measuring tape was used to determine the appropriate

positions on the head. The control group received rTMS stimulation at Cz, corresponding to the location of the Vertex. The vertex was chosen as a control site since this site is frequently used to test for non-specific rTMS effects (Nyffeler et al., 2006; Nowak et al., 2008). The vertex corresponds to the Cz electrode in the standard 10/20 EEG system. The experimental group received rTMS stimulation at F7, in order to stimulate the posterior part of the LIFG (Pascual-Leone et al., 1991; Herwig et al., 2003; Okamoto et al., 2004).

4.7. Statistical analyses

According to accepted standards (Hair et al., 1998) a Z score of 2.5 was used as the cutoff point for classifying outliers, which led to the rejection of 4.39% of the total data. The data were checked for normality using one-sample Kolmogorov–Smirnov statistics. All data groups were compared with each other using a two-sample Kolmogorov–Smirnov statistics to check for equal distributions. To control for individual differences between and within groups, the data were transformed to ratios by dividing post rTMS stimulation data over pre rTMS stimulation data, thus using the relative change between the two measurements. The ratio data had a lower bound of zero but no higher bound, thereby violating the normal distribution. To normalize the data, a log₁₀ transformation was used. One-way mixed repeated ANOVA, with stimulation site (LIFG, Vertex) as the between subject variable, and electrode site (C3, C4), video, behavioral tasks, session (pre and post rTMS stimulation) and frequency as the within subject variables were used. For the within-subject variables the Huynh–Feldt correction for violation of sphericity was used. The dependent variables were the single mean voltage amplitude of the three different frequency bands measured during the videos, and the accuracy rates and the RTs for the behavioral tasks. A Bonferroni correction was used to control for multiple comparisons for an alpha value of 0.05.

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