The human mirror neuron system: A link between action observation and social skills

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The discovery of the mirror neuron system (MNS) has led researchers to speculate that this system evolved from an embodied visual recognition apparatus in monkey to a system critical for social skills in humans. It is accepted that the MNS is specialized for processing animate stimuli, although the degree to which social interaction modulates the firing of mirror neurons has not been investigated. In the current study, EEG mu wave suppression was used as an index of MNS activity. Data were collected while subjects viewed four videos: (1) Visual White Noise: baseline, (2) Non-interacting: three individuals tossed a ball up in the air to themselves, (3) Social Action, Spectator: three individuals tossed a ball to each other and (4) Social Action, Interactive: similar to video 3 except occasionally the ball would be thrown off the screen toward the viewer. The mu wave was modulated by the degree of social interaction, with the Non-interacting condition showing the least suppression, followed by the Social Action, Spectator condition and the Social Action, Interactive condition showing the most suppression. These data suggest that the human MNS is specialized not only for processing animate stimuli, but specifically stimuli with social relevance.

INTRODUCTION

Social interaction is an essential part of being human. Some believe that we are born with an innate desire and ability for social interaction (Meltzoff and Moore, 1997). The intrinsic necessity for social interaction has been suggested as evolution's motivating factor for uniquely human skills including art, language, theory of mind and empathy (Ramachandran, 2000).

One system proposed to underlie many aspects of social cognition is the mirror neuron system (MNS) (Gallese et al., 2004). While recording single neurons in the macaque premotor cortex (Area F5), Rizzolatti and colleagues discovered a unique set of premotor neurons that appeared to respond both when a monkey performed an action and when it sat motionless observing another individual performing an action (Di Pellegrino et al., 1992; for a review, see Rizzolatti et al., 2001). These neurons were named 'mirror neurons' for their unique property of firing to both observed and performed actions.

Although single-unit recording is not typically performed in the human brain, indirect population-level measures support the existence of a functionally analogous system to the macaque MNS in the human inferior frontal gyrus (IFG) (Fadiga et al., 1995; Parsons et al., 1995; Iacoboni et al., 1999). Additionally, fMRI studies suggest that the frontal MNS in humans may be one part of a broader network of brain regions including the inferior parietal lobule (Parsons et al., 1995; Buccino et al., 2001;), the superior temporal sulcus (Iacoboni et al., 2001) and regions of the limbic system (Wicker et al., 2003; Singer et al., 2004; Morrison et al., 2004). This broader network, with its ability to match perceptions of the environment to internal sensorimotor representations, may play a key role in multiple aspects of social cognition from biological action perception to empathy.

Researchers speculate that the MNS in lower primates largely functions to facilitate action understanding (Rizzolatti et al., 2001), while in higher primates this same system is thought to have evolved to support imitation via on line activation of the motor properties of the mirror neurons (Rizzolatti and Arbib, 1998). In humans, it is speculated that mirror neurons further evolved to represent not only the physical aspects of an action but also the underlying intentions, thoughts and feelings that motivated that action, possibly through reciprocal connections with other brain regions such as the limbic system or medial prefrontal cortex. It has been suggested that this evolutionary bootstrapping provided the foundation for arguably unique human social skills such as theory of mind, empathy, and language (Gallese, 2001).

In support of the involvement of the MNS in understanding of intentions, a recent study found that activity in the IFG may be modulated by the underlying intention of an observed action (Iacoboni et al., 2005). Specifically, subjects were presented with the same action embedded in two different contexts (implying two different purposes for the

action), and researchers found significant differences in the levels of activation between the two contexts. Further support for the role of the human MNS in social skills comes from studies on individuals with autism spectrum disorders (ASD). Following preliminary data from our laboratory suggesting a dysfunction of the MNS in individuals with ASD (Altschuler et al., 2000), five independent laboratories have published neurophysiological evidence supporting this claim (Nishitani et al., 2004; Dapretto et al., 2006; Oberman et al., 2005; Theoret et al., 2005; Villalobos et al., 2005).

Previous studies in our laboratory (Altschuler et al., 1997; Altschuler et al., 2000; Pineda et al., 2000; Oberman et al., 2005;) and other laboratories (Muthukumaraswamy and Johnson, 2004; Muthukumaraswamy et al., 2004) have investigated MNS in humans through analysis of electro-encephalography (EEG) mu frequency band oscillations. At rest, sensorimotor neurons spontaneously fire in synchrony (Gastaut, 1951), leading to large-amplitude EEG oscillations in the 8–13 Hz (mu) frequency band recorded over scalp locations C3, Cz, and C4 (for a review see Pineda, 2005).

The use of mu suppression as an index of mirror neuron activity is validated by anatomical and physiological evidence of strong cortico–cortico connections between human and non-human primate ventral premotor cortex (including the region thought to contain mirror neurons) and primary sensorimotor cortex where the mu rhythm is generated and recorded (Muakkasa and Strick, 1979; Godschalk et al., 1984; Matelli et al., 1986; Ghosh et al., 1987; Nishitani and Hari, 2000; Tokuno and Nambu, 2000; Dum and Strick, 2002; Shimazu et al., 2004).

Functional correlations also support the use of mu suppression as an index of mirror neuron activity. First, studies dating back to 1954 find that, similar to mirror neurons, mu oscillations respond specifically to self-performed, observed and imagined actions (Gastaut and Bert, 1954; Cochin et al., 1998; Babiloni et al., 2002; Pineda et al., 2000). Additionally, both mirror neurons (Rizzolatti and Fadiga, 1998) and mu oscillations only respond to animate stimuli (Altschuler et al., 1997; Oberman et al., 2005), and respond more to target-directed actions as compared to non-goal-directed actions (Muthukumaraswamy et al., 2004). Finally, both mirror neurons (Buccino et al., 2001) and mu oscillations seem to respond in a somatotopic manner (Pfurtscheller et al., 1997). Taken together, these findings suggest that changes in mu suppression can provide an inexpensive, non-invasive method to study human mirror neuron functioning (Oberman et al., 2005; Muthukumaraswamy et al., 2004).

In the original studies of mu suppression by Gastaut and Bert (1954), it was reported that the amount of suppression was related to the degree to which the observer related to the image on the screen. Although it is widely accepted that the MNS is selective for animate stimuli and proposed to be involved in many aspects of social cognition, the degree to which the MNS is sensitive to differences in degree of social interaction is unclear.

One study, conducted by Iacoboni et al. (2004), which largely highlights the role of the dorsomedial prefrontal and medial parietal cortex (the 'default state areas') in the processing of social interactions also finds differences in the degree of activity in the IFG when an observer watches a scene depicting two individuals interacting as compared to a scene depicting one individual engaging in everyday activities. However, as these scenes differed in complexity, content, as well as degree of social interaction, it is hard to discern what property of the stimulus the IFG was sensitive to. The goal of the current study was to highlight the role of the MNS in the processing of social stimuli. Specifically, we investigated both the degree to which the mu rhythm would be modulated based on the degree of social content of a given human action as well as the degree to which the observer is involved in the observed scene.

MATERIALS AND METHODS
Subjects
The sample was composed of 20 college students (10 male, 10 female) ranging in age from 18–34 years (mean = 21.05 years, s.d. = 3.38) recruited from the University of California, San Diego Psychology Department subject pool. Participants received class credit for their participation, and all gave written consents & to participate in the study. This study was reviewed and approved by the University of California, San Diego Human Research Protections Program.

Procedure
EEG data were collected while subjects watched four different videos: (1) Visual White Noise: full-screen television static (mean luminance 3.7 cd/m^2) was presented as a baseline condition; (2) Non-interacting: three individuals tossed a ball up in the air to themselves; (3) Social Action, Spectator: three individuals tossed a ball to each other; and (4) Social action, Interactive: similar to video 3 except occasionally the ball would be thrown off the screen, seemingly toward the viewer, as if the viewer were part of the game. All videos were 80 s in length and were matched for low-level visual properties such as amount of movement and complexity of the scene. All conditions were presented twice in order to obtain enough clean EEG data for analyses and the order of the conditions was counterbalanced across subjects.

To ensure that the participants attended to the video stimuli, during all of the conditions except the baseline, they were asked to engage in a continuous performance task. Between four and six times during the 80 s video, the actors in the video stopped throwing the ball and would simply hold it in their hands for a period of 2 s. Subjects were asked

to count the number of times the ball stopped being thrown and report the number of stops to the experimenter at the end of the block.

EEG data acquisition and analysis

Disk electrodes were applied to the face above and below the left eye to monitor the electrooculogram (EOG) and behind each ear (mastoids) for use as reference electrodes. Data were collected from 13 electrodes embedded in a cap, at the following scalp positions: F3, Fz, F4, C3, Cz, C4, P3, Pz, P4, T5, T6, O1 and O2, using the international 10–20 method of electrode placement. Following placement of the cap, electrolytic gel was applied at each electrode site and the skin surface was lightly abraded to reduce the impedance of the electrode–skin contact. The impedances on all electrodes were measured and confirmed to be less than $5\,k\Omega$ both before and after testing. Once the electrodes were in place, subjects were seated inside an acoustically and electromagnetically shielded testing chamber. EEG was recorded and analyzed using a Neuroscan Synamps system (band pass 0.1–30 Hz). Data were collected for approximately 160 s per condition at a sampling rate of 500 Hz.

EEG frequency oscillations in the 8–13 Hz range recorded over occipital cortex are influenced by states of expectancy and awareness (Klimesch *et al.*, 1998). Since the μ frequency band overlaps with the posterior alpha band, it is possible that recordings from C3, Cz and C4 might be contaminated by this posterior activity. In order to reduce this influence, the first and last 10 s of each block of data were removed from all subjects to eliminate the possibility of attentional transients due to initiation and termination of the stimulus. A 1 min segment of data following the initial 10 s was obtained and combined with the other trial of the same condition, resulting in one 2 min segment of data per condition. Eye blink and head movements were manually identified in the EOG recording and EEG artifacts during these intervals were removed prior to analysis according to standard criteria (Goldensohn *et al.*, 1999). Data were only analyzed if there was sufficient clean data with no movement or eye blink artifacts.

Although data were obtained from electrodes across the scalp, mu rhythm is defined as oscillations measured over sensorimotor cortex; thus, only data from C3, Cz and C4 are presented. A repeated-measures within-subject ANOVA was conducted to compare the suppression values across the three experimental conditions.

Data were segmented into epochs of 2 s beginning at the start of the segment. Fast Fourier transforms in the 8–13 Hz range were performed on the cleaned and epoched data (1024 points). A cosine window was used to control for artifacts resulting from data splicing. Mu suppression was calculated as the ratio of the power during the experimental conditions relative to the power during the baseline condition. A ratio was used to control for variability in absolute mu power as a result of individual differences such as scalp thickness and electrode placement and impedance, as opposed to mirror neuron activity. Since ratio data are inherently non-normal as a result of lower bounding, a log transform was used for analysis. A log ratio of less than zero indicates suppression, whereas a value of zero indicates no suppression and values greater than zero indicate enhancement.

RESULTS

Behavioral performance

All subjects performed with 100% accuracy on the continuous performance task during all conditions. We infer that any differences found in mu suppression are, therefore, not due to differences in attending to the stimuli.

Mu suppression

A highly significant main effect of condition was obtained (Figure 1) ($F(2,58) = 17.75$, $P < 0.0001$). Follow-up pair wise comparisons revealed a linear trend with the Social Action, Interactive condition, showing the greatest amount of suppression ($M = -0.22$) followed by the Social Action, Spectator condition ($M = -0.15$) with the Non-interacting condition ($M = -0.08$) showing the least amount of suppression.

Experimental manipulation confirmation

In order to assess whether subjects perceived the stimuli as containing different levels of social content, a separate group of 20 individuals rated the videos on social content on a 5-point Likert scale. A highly significant main effect of condition was obtained (Figure 2): ($F(2,18) = 57.86$, $P < 0.0001$). Follow-up pair wise comparisons revealed a linear trend with the Social Action, Interactive condition, rated as having the greatest social content ($M = 3.55$) followed by the Social Action, Spectator condition ($M = 3.25$), with the Non-interacting condition ($M = 2.15$) being rated as the least social.

DISCUSSION

Results of this study, showing modulations in mu wave suppression to observed actions based on the degree of social interaction, suggest that MNS is sensitive to the presence of social cues in a stimulus. The finding that the system is most active (resulting in the greatest amount of mu wave suppression) when the stimulus is not only social but interactive is consistent with the anecdotal report by Gastaut and Bert (1954) that the blocking of the mu wave occurs when an individual 'identifies himself with an active person represented on the screen' as well as with the previous fMRI data showing increased activity in IFG in response to social interaction (Iacoboni *et al.*, 2004). These findings suggest that the greater the degree of identification of the viewer with the stimuli, the greater the degree of social interaction perceived.
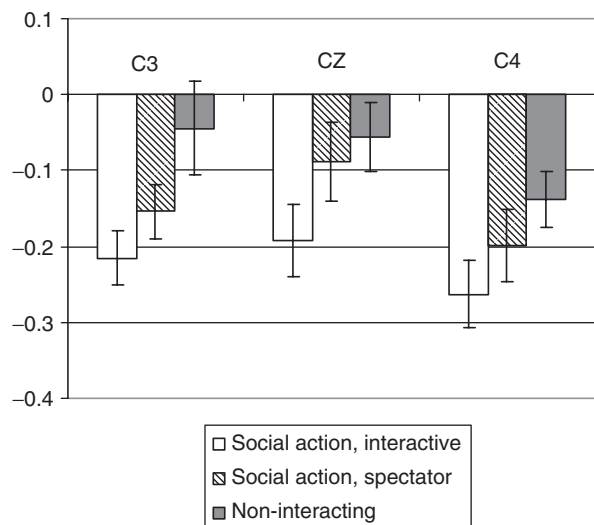
Fig. 1 Mu suppression during the observation of human action. Bars represent the mean log ratio of power in the mu frequency (8–13 Hz) during the Social Action, Interactive (white), Social Action, Spectator (gray stripe), and Non-interacting (dark gray) over the power in the baseline condition for scalp locations C3, Cz and C4. Error bars represent the standard error of the mean. For all values, a mean log ratio less than zero indicates mu suppression.
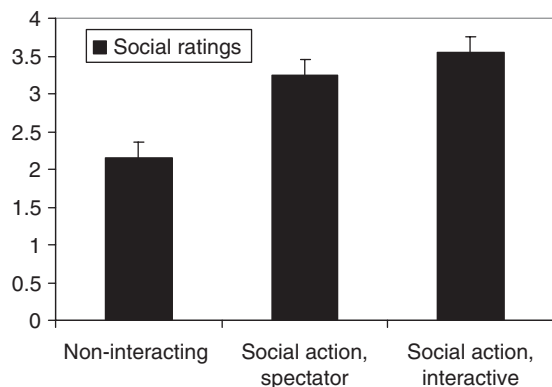

Fig. 2 Ratings of perceived social content. Bars represent the mean rating on a 5-point Likert scale of social content of the three experimental videos. Error bars represent the standard error of the mean. Zero on the Likert scale was labeled 'No Social Content,' while 5 was labeled 'Extremely Social.'

This study provides the necessary link between the known action observation/execution properties of the monkey MNS and the theorized social functions of the human MNS. The selectivity of the human MNS for animate stimuli had been previously suggested based on studies finding no significant mu suppression to the observation of inanimate stimuli matched for low-level visual properties (Altschuler *et al.*, 1997; Oberman *et al.*, 2005). Additionally, previous fMRI studies had indicated that the human MNS was sensitive to intentions and goals, with the IFG modulating its degree of activity based on the intention of the observed action (Iacoboni *et al.*, 2005). The current study suggests that this system is also sensitive to the degree of sociality, as evidenced

by modulations in the degree of mu suppression between the three experimental conditions. This characteristic may provide a necessary link between simple action observation and more complex social skills such as theory of mind, empathy and language.

Since the mu frequency band overlaps the posterior alpha band, it is possible that, despite efforts to control for this, recordings from C3, Cz and C4 might be contaminated by this posterior activity. As all conditions involved visual stimuli and the eyes were open throughout the study, we would not expect a systematic difference between conditions in posterior alpha activity. Additionally, by eliminating the first and last 10 s of each block and including a continuous performance task during all three experimental conditions, we reduced the possibility of confounds such as changes in attention affecting our mu power results. Consistent with this, no electrodes other than C3, Cz and C4 showed a consistent pattern of suppression in the frequency band of interest. These results suggest that the modulations of mu rhythms observed in C3, Cz and C4 were not likely to be mediated by posterior alpha activity or differences in attentional demands between the three experimental conditions.

Although mu wave suppression is considered a valid index of mirror neuron activity (Muthukumaraswamy *et al.*, 2004; Oberman *et al.*, 2005), owing to the low spatial resolution of EEG it is difficult to differentiate between activity selective to the premotor MNS and activity in other regions that are part of a larger action observation/execution network that may modulate the activity in the premotor MNS (Muthukumaraswamy and Johnson, 2004; Muthukumaraswamy *et al.*, 2004). Further investigations with higher-spatial-resolution techniques, such as fMRI and high-resolution EEG, may be able to dissociate between these two sources of activation and confirm at what stage of processing the information regarding social content is processed.

Conflict of Interest

None declared.

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