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Mirroring and mu rhythm involvement in social cognition: Are there dissociable subcomponents of theory of mind?

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ABSTRACT

Tager-Flusberg and Sullivan [Tager-Flusberg, H., Sullivan, K., 2000. A componential view of theory of mind: evidence from Williams syndrome. Cognition 76, 59–90] have argued for a distinction between the social-perceptive component of theory of mind (ToM), involving judgment of mental state from facial and body expressions, and the social-cognitive component, which is representation-based and linked to language and theory-building. This is analogous to the distinction made by others [Gallese, V., Keysers, C., Rizzolatti, G., 2004. A unifying view of the basis of social cognition. Trends in Cognitive Science 8, 396–403] between representing the mental state of another as if it was one's own (simulation theory), which requires involvement of the mirror neuron system, and explicit or declarative reasoning about mental states (theory theory), which does not. This componential view of ToM was tested by examining mirroring, as indexed by EEG mu rhythm suppression, in subjects performing tasks assumed to tap both dimensions. Mu suppression was positively correlated with accuracy on the social-perceptual task but not in the social-cognitive task. In a ToM control task requiring judgments about person–object interactions accuracy was correlated with mu suppression. This implies that mirroring is involved in making judgments about emotions and person–object interactions. However, mirroring is insensitive to the distinction between correct and incorrect inferences in the social-cognitive task suggesting that additional mechanisms are needed to make mental attributions of beliefs and intentions. These results are consistent with a refined componential view of ToM.

1. Introduction

Impairments in theory of mind (ToM) have been hypothesized to underlie the social interactions, communications, and behavioral symptoms of autism. This hypothesis (Baron-Cohen et al., 1985; Colle et al., 2007) centers on an impairment in the ability to conceive of mental states and to use mental state concepts to interpret and predict one's own and other people's behavior. At the same time, a large body of evidence points to mirror neuron system (MNS) activity as a potential neural mechanism for the understanding of such mental states. More specifically, mirror neurons have been implicated in understanding action (Umilta et al., 2001; Iacoboni et al., 2005), viewing and imitating facial expressions (Dapretto et al., 2006), and language (Rizzolatti and Arbib, 1998). Furthermore, the MNS appears to be anatomically and functionally impaired in autism, a disorder characterized by social and emotional deficits (Oberman et al., 2005; Dapretto et al., 2006; Williams et al., 2001; Hadjikhani et al., 2006). This has led to proposals that such a system may constitute a neurobiological substrate for theory of mind (ToM). This cognitive function has been operationalized in tasks ranging from attributing false beliefs to others, to recognizing facial expressions of emotion, to identifying social faux pas (Tager-Flusberg and Sullivan, 2000; Baron-Cohen et al., 1997; Shamay-Tsoory et al., 2003). Some of the processes involved in each of these abilities likely overlap, and in order to assess mirror neuron involvement in these abilities, mirror neuron activity must be directly compared in experiments that dissociate the neural processes involved in these disparate tasks.

Several recent proposals posit that cognition about others is composed of at least partially independent processes (Saxe, 2006; Saxe and Powell, 2006; Uddin et al., 2007; Keysers and Gazzola, 2006; Gobbini et al., 2007; De Lange et al., 2008). One such theoretical framework by Tager-Flusberg and Sullivan (2000), which is based on the evidence from Autism Spectrum Disorders and Williams Syndrome, proposes distinct social-cognitive (SC)

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and social-perceptive (SP) dimensions mediated by distinct neural substrates. The hypothesized SP subcomponent involves "on-line attribution of intentional, emotional or other person-related knowledge." It is hypothesized to be connected to the affective system, and its inputs may include facial and body expressions, vocal expression, motion and actions. Its proposed neurobiological substrate is the amygdala and medial temporal cortex, and is involved in biological motion and face perception (Bonda et al., 1996; Vuilleumier and Pourtois, 2007). In contrast, the SC subcomponent appears later in development, is assumed to be representation-based, and includes abilities that are typically identified as ToM, including the identification of false belief. The SC subcomponent may be linked to language and theory-building but it may not be totally independent of social-perceptual processing. Its proposed substrate is the prefrontal cortex, including orbitofrontal cortex and medial frontal cortex.

Tager-Flusberg and Sullivan support their componential view of ToM with evidence for dissociation in two neuropsychological populations, Williams Syndrome (WS) and Autism Spectrum Disorders (ASD). One task believed to specifically tap SP abilities is the Eyes task, in which subjects judge facial expressions of emotion based on photographs of only the eye region of the face (Baron-Cohen et al., 1997, 2006). The neural substrate for the SP dissociation between WS and ASD subjects may be the amygdala, medial temporal cortex, and superior temporal cortex. Children with ASD, which has been linked to amygdala and superior temporal lobe abnormalities (Pierce et al., 2001; Aylward et al., 1999), perform significantly below average on this task (Baron-Cohen et al., 1997, 2006). Furthermore, rCBF in superior temporal lobe has been found to be inversely correlated with autism severity (Gendry et al., 2005). Children diagnosed with Asperger's Syndrome, a mild form of autism, perform poorly on this task as well. They do not activate the amygdala during the Eyes task and show functional disconnection of the medial temporal lobe (Welchew et al., 2005). Additionally, typically developing individuals with acquired damage to the amygdala perform poorly on the Eyes task (Adolphs et al., 2002). In contrast, WS children have intact amygdala and medial temporal lobe and their performance on this task is indistinguishable from typically developing children's (Bellugi et al., 1999).

Both ASD and WS children appear to perform poorly on the standard Sally–Anne false belief task and the "Smarties" unexpected contents task, two consistently used and well-defined behavioral tests that are thought to require a representational understanding of other minds (Baron-Cohen et al., 1985). While children with Asperger's Syndrome can sometimes succeed at tasks involving a representational understanding of mind, they do not show the normal activation of medial frontal cortex during these tasks and therefore may be relying on different mechanisms (Happe and Frith, 1996).

Tager-Flusberg and Sullivan's distinction between perceptive and cognitive components has recently been echoed by similar distinctions between emotional and cognitive empathy (Blair, 2005), early- and late-developing components of theory of mind (Saxe and Powell, 2006), automatic/reflexive and controlled/reflective processes (Lieberman, 2007), and simulation and mentalizing (Gallese et al., 2004; De Lange et al., 2008). Thus social-cognitive neuroscience appears to be converging on a dual-process model of cognition about other minds. This is supported by a growing body of evidence suggesting two distinct neural circuits for social cognition. The frontoparietal mirror neuron system bridges the gap between the physical self and others through embodied motor simulation, and cortical midline structures and the temporal–parietal junction engage in self–other processing at a more evaluative level (Uddin et al., 2007; Saxe, 2006; Saxe and Powell, 2006; Keysers and Gazzola, 2006; Gobbini et al., 2007; De Lange et al., 2008).

Tager-Flusberg and Sullivan's social-cognitive/social-perceptive distinction has particularly interesting similarities to the distinction made by Gallese et al. (2004) between declarative reasoning about others' actions and mirror-neuron-based "simulation" of those actions. Mirror neurons are active both when an individual observes and performs an action (di Pellegrino et al., 1992; Rizzolatti and Craighero, 2004). These perception–action mechanisms have been associated with a variety of processes thought to be related to theory of mind, including action comprehension and attribution of motivation (Kohler et al., 2002; Iacoboni et al., 2005), language (Rizzolatti and Arbib, 1998), understanding facial expressions of emotion (Carr et al., 2003; Gallese et al., 2004; Leslie et al., 2004), empathy (Leslie et al., 2004), and social relevance (Oberman et al., 2007; Iacoboni et al., 2005). They are thought to allow "simulation" of a perceived action within the observer's own neural circuitry as if the observer were performing the action herself (Gallese et al., 2004). Simulation theory proposes that understanding the actions of others, including their mental states, is achieved through modeling those states within one's own mind (Gordon, 2005). From this perspective, understanding of another mind is immediately available through understanding of one's own mind without the use of explicit mental representations. The functions of the social-perceptual subcomponent appear similar to mirror neuron-based simulation. First, the SP component appears early in development, and newborn infants imitate adult facial expressions within hours of birth (Meltzoff, 1999). Second, the proposed substrate of the SP component is the medial temporal cortex. Subregions of this area are known to process facial expressions of emotion and biological motion, and mirror neurons are sensitive to such stimuli (Leslie et al., 2004; Iacoboni and Dapretto, 2006).

In contrast to simulation theory, the "theory theory" holds that individuals reason about other's minds using explicit mental representations (Gopnik and Schulz, 2004). This type of high-level processing appears more comparable to Tager-Flusberg and Sullivan's late-developing, language- and representation-based social-cognitive subcomponent (Meltzoff, 1999). That is, the SC component is proposed to appear later in development, and children do not reliably pass false belief tests until preschool age (Wellman and Liu, 2004; Wellman et al., 2001). Second, the SC component is hypothesized to be based on representational thinking and language. Language causally influences preschool-age children's performance on false belief tasks (Lohmann and Tomasello, 2003).

In order to address mirror neuron involvement in ToM a noninvasive approach is needed to assess the electrophysiology in humans. While mirror neuron activity cannot be directly monitored in humans, a number of recent studies have indicated that mirroring activity may be reflected in the mu frequency band of the EEG (alpha: 8–13 Hz and beta: 15–20 Hz, measured over sensorimotor cortex) (Altschuler et al., 1997; Muthukumaraswamy et al., 2004; Oberman et al., 2005; Pineda, 2005; Hari et al., 2000). Sensorimotor neurons fire synchronously at rest, leading to high-amplitude mu oscillations, and asynchronously during self-movement, leading to reduced amplitude of the mu band (mu suppression) (Pineda, 2005). Mu suppression during action observation, but in the absence of self-performed action, appears to reflect downstream modulation of sensorimotor neurons by premotor mirror neurons (Muthukumaraswamy et al., 2004; Oberman et al., 2005; Pineda, 2005). The use of mu suppression as a potential though indirect index of mirror neuron activity is supported by anatomical and physiological evidence of strong cortico–cortico connections in human and non-human primates between ventral premotor cortex (including the region thought to contain mirror neurons) and primary sensorimotor cortex where the mu rhythm is generated and recorded (Shimazu et al., 2004).

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Studies with human mu suppression closely parallel primate single-cell recordings in object-directedness and other aspects, providing further evidence that mu suppression is consistent with the notion that there are mirror neurons in humans and that their activity is reflected in EEG oscillations recorded over sensorimotor areas (Muthukumaraswamy et al., 2004).

The present study was designed to compare mirror neuron involvement in the social-cognitive and social-perceptive components of ToM. We measured mu suppression as an index of mirror neuron activity while subjects performed tasks of the type that dissociate between these components in ASD and WS. We reasoned that in typically developing control subjects, the social-perceptive and social-cognitive components should interact fluidly. Both components might be activated in some of our tasks, but if a particular task relies more heavily on mirror neurons, mirror neuron activation should predict the proportion of correct responses in that task. Recent evidence suggests that the mirror neuron system is involved in evaluating the correctness of the actions of others (Koelewijn et al., 2008). On the other hand, mirror neuron activation that is uncorrelated with accuracy would indicate that the task involves mirror neurons, but that additional neural systems are required for accurate performance. Simulation theory predicts that mirror neurons should be active only to reasoning about mental states through self-modeling of those states. Therefore, we hypothesize that if these processes are independent, then mirror neuron activity ought to be more predictive of accuracy during SP tasks than during SC tasks. Determining the specific involvement of mirror neurons in ToM could inform the general model of how we mentally represent other minds, as well as have implications for diagnosis and treatment for clinical populations.

2. Methods

2.1. Subjects

Twenty-three healthy right-handed college students, 12 male and 11 female (mean age = 21.3 ± 1.8 years), were recruited to participate in the study. Exclusionary criteria included diagnosis of a mental disorder and stimulant use within the 2 h prior to the experiment. All subjects were compensated with class experimental credit. The University of California, San Diego's IRB approved this experimental protocol.

2.2. Experimental paradigm

Subjects performed tasks that tapped either the SP or SC dimension of ToM, as well as control tasks, while in an acoustically and electronically shielded, dimmed room. EEG was recorded from 16 channels using a NeuroScan Synamps system with standard 10–20 electrode placement. EEG recordings were referenced to electronically linked mastoids and grounded at FPz. Bandpass filtering was set at 0.1–30 Hz (half-amplitude, −3 dB/octave roll-off). Vertical (VEOG) and horizontal electrooculogram (HEOG) channels were recorded to remove blinks and horizontal scanning movements. Stimuli were presented in blocks on a computer screen with 2-min breaks between blocks. Responses were made on a normal computer keyboard.

The experimental protocol (see Fig. 1) included presentation of a blank screen for 3 s between trials. Each trial was preceded by a fixation cross for 2 s. A cue graphic (which included three panels in one task) appeared at the top of the screen for 5 s. Three additional graphics then appeared at the bottom of the screen, marked A, B, and C. Subjects were instructed to press the keyboard button corresponding to the graphic that matched the cue. All four graphics remained on the screen for upto 14 s or until a response was made. The 5-s stimulus presentation time was determined in pilot experiments to be enough time for subjects to fully evaluate the stimulus so that when the option to respond was made available, responses were more or less immediate.

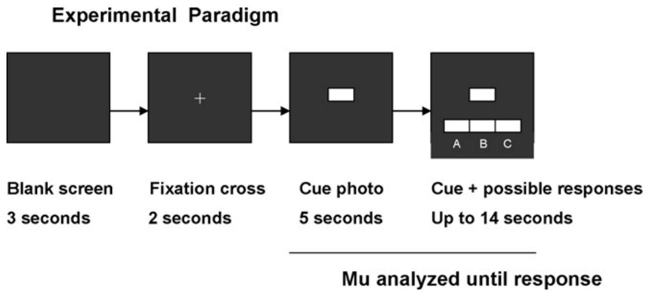

Fig. 1. Experimental paradigm: schematic diagram illustrating the time course of stimulus presentation. Each trial ended with subject response but could last up to 24 s.

2.2.1. Social-perceptual task

As shown in Fig. 2, the task used to tap SP abilities was a modification of the Eyes task (Baron-Cohen et al., 2006, 1997), which involves identifying facial expressions based on photographs of only the eye region of the face. Tager-Flusberg and Sullivan (2000) remark that the Eyes task may be a sensitive measure of the SP component because of its perceptual ambiguity. Performance on this task is relatively spared in Williams Syndrome but is impaired in ASD (Baron-Cohen et al., 1997, 2006). However, the Eyes task does not include enough separate trials for EEG data collection. Therefore, additional eye regions of the face were cropped from the MacBrain Face Stimulus Set, which include photographs of Caucasian and African-American males and females depicting seven different facial expressions: angry, afraid, happy, surprised, neutral, disgusted, and sad. The task format followed the scheme illustrated in Fig. 1: a cue graphic appeared at the top of the screen for 2 s, followed by three additional graphics. In one block of 28 trials, subjects matched based on facial emotion, selecting the graphic on the bottom of the screen that matched the emotion depicted by the cue (Emotion Matching task). In the other two blocks of 14 trials each, subjects matched faces based on race (Race Matching task) or gender (Gender Matching task).

2.2.2. Social-cognitive task

While Tager-Flusberg and Sullivan (2000) identify false belief tasks as a basic test of SC ability, normal children pass false belief tasks easily by age 3 or 4. Since this study involved normal adults, we used the Cartoons task developed by Brunet et al. (2000), which involves mental attribution of intentions and beliefs and includes control blocks for physical causation and object involvement. This task, as shown in Fig. 3A–C, involves viewing three blocks of captionless cartoons. In one block of 28 trials, cartoons required an attribution of intention in order to be interpreted (Mental Attribution task). In the other two blocks of 14 trials each, cartoons involved physical causation with no characters (PC-NC), or physical causation with characters (PC-C). Timing of stimulus presentation and signal analysis were exactly as in the SP task. That is, for all cartoons, subjects were first shown a cue picture containing three panels depicting a sequence of events and then asked to choose the panel at the bottom of the screen (labeled A, B, or C) that most logically followed the sequence. This task has the advantage of being similar to the Sally–Anne task in that it has a non-verbal, visual presentation and it tests the ability to make attributions of mental state. However, the required judgments are more complex and thus more fitting for adults. The original stimuli used in the current study were obtained from Brunet et al. (2000).

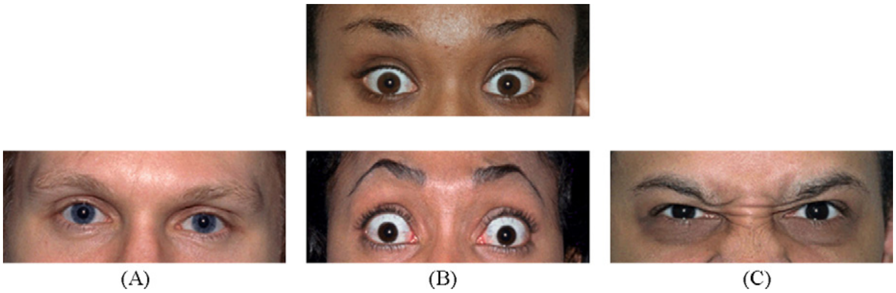

Fig. 2. Sample trial from the Emotion Matching block in the Eyes task (adapted from Baron-Cohen et al., 1997, 2006). Top image is the cue and bottom images represent the three targets, only one of which is the correct match (B is the correct response).

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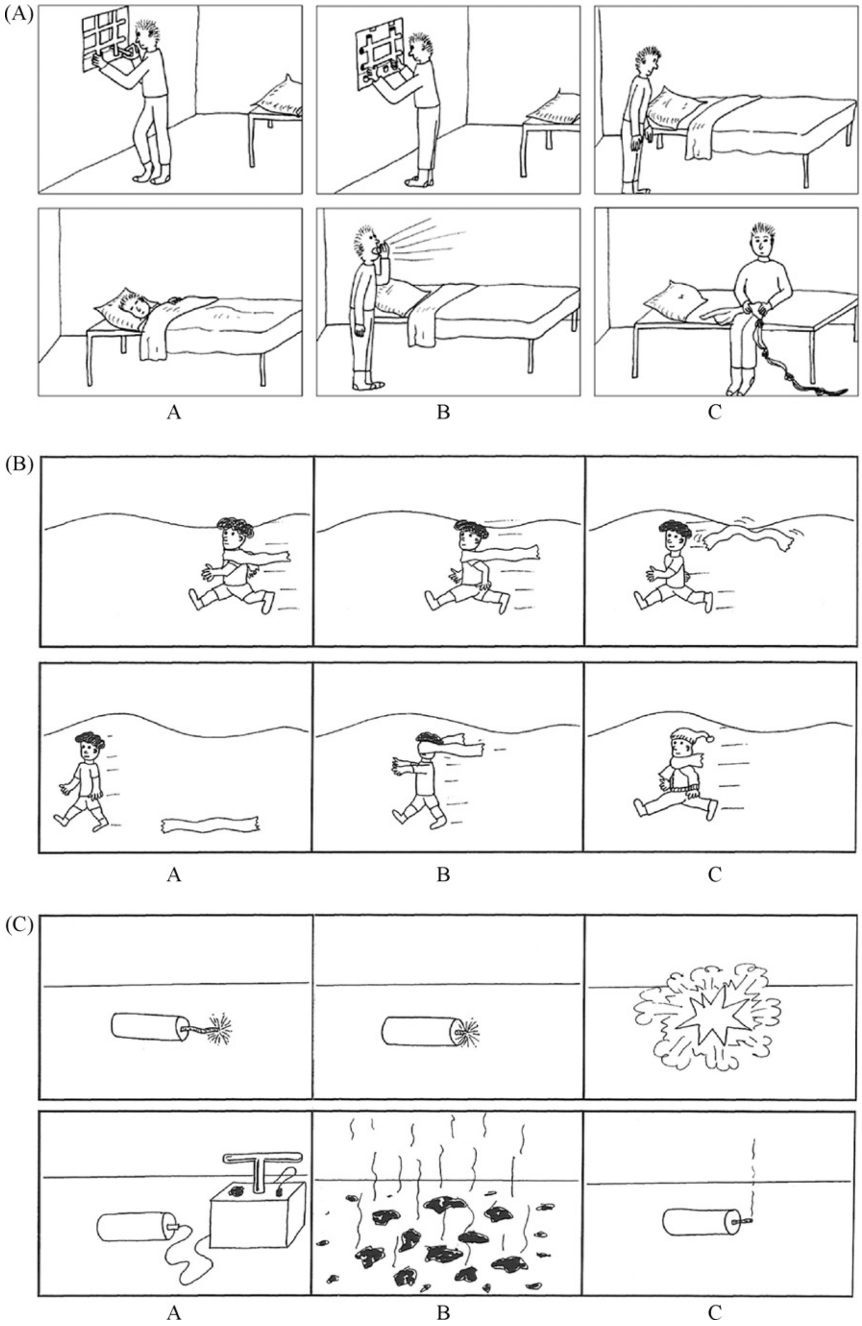

Fig. 3. Three examples of the Cartoons task (adapted from Brunet et al., 2003). (A) Mental Attribution task. Top three panels are the initial cue and bottom three panels represent the targets, only one of which is the correct answer (C is the correct response); (B) Physical Causation-with Characters (PC-C) (A is the correct response); (C) Physical Causation-without Characters (PC-NC) (B is the correct response).

2.2.3. Baseline task

To assess mu rhythm responsiveness while mirror neurons would presumably be inactive, subjects viewed a 2-min video of two circles moving up and down. This stimulus was previously found not to produce mu suppression and was the control task in Oberman et al. (2005). Occasionally, the motion of the circles paused and subjects were instructed to press a keyboard button when this occurred.

3. Data analysis

Eye blinks and both eye and head movements were digitally identified in the EOG recording and removed. Other EEG artifacts were also automatically and manually removed prior to analysis. Data were only analyzed if sufficiently "clean" EEG, with no movement or eye blink artifacts, were present. For each cleaned segment the integrated power in the 8–13 Hz mu range was computed using a Fast Fourier Transform over electrode sites C3, Cz and C4 since these are the sites where mu rhythm is typically most robust. Data were segmented into epochs of 2 s beginning at the start of the segment. Fast Fourier Transforms were performed on the epoched data (1024 points). A cosine window was used to control for artifacts resulting from data splicing.

Mu power was calculated for the baseline task and separately for correct trials and incorrect trials in each condition. These values were used to calculate mu suppression, computed as the ratio of mu power during the experimental tasks to power during the baseline task. A ratio was used to control for variability in absolute mu power as a result of individual differences in scalp thickness and electrode impedance, as opposed to absolute differences in electrical activity. Since ratio data are inherently non-normal as a

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result of lower bounding, a log transform was used. A log ratio of less than zero indicates suppression whereas a value of zero indicates no suppression and values greater than zero indicate enhancement.

For the Eyes task, a repeated-measures ANOVA was used to analyze the data, with response (correct, incorrect), block (emotion, gender, race), and electrode site (C3, Cz, C4) as within-subject factors and gender as a between-subjects measure. Similarly, for the Cartoons task, a repeated-measures ANOVA was used, with response (correct, incorrect), block (Mental Attribution, Physical Causation with Characters, Physical Causation without Characters), and electrode site (C3, Cz, C4) as within-subject factors and gender as a between-subjects measure. Step-down ANOVAs were used to assess any obtained differences while Greenhouse-Geisser corrections were applied to the degrees of freedom with only the corrected probability values reported. For each task block, the correlation between an individual's overall mu suppression and behavioral performance was also calculated. A Bonferroni correction was used to correct for multiple comparisons. Finally, percent correct and incorrect trials were analyzed using one-way repeated measures ANOVA with factors of task (6) with gender as a between-subjects factor. Pairwise comparisons were done using Tukey's Honest Significant Difference (HSD).

4. Results

Behavioral performance. Analysis of subjects' behavioral responses revealed a general effect of task ($F(5, 105) = 9.883$, $p < 0.001$), as illustrated in Fig. 4. In the SP version of the paradigm, the Emotion Matching task produced the lowest percent correct responses compared to Race and Gender Matching tasks, suggesting it was a more difficult task. Pairwise comparisons showed that percent correct in the Emotion Matching (0.85) was only significantly different from Race Matching (0.92) ($p < 0.05$). In the SC version where response rates were much higher, the Mental Attribution task produced a smaller percent correct responses compared to PC-C and PC-NC tasks. Pairwise comparisons indicated that percent correct in the Mental Attribution task (0.91) was statistically different from both PC-NC (0.96) and PC-C (0.97) ($p < 0.05$). No effect of gender was detected.

Mu suppression. The SP version of the paradigm showed a significant main effect of block ($F(2, 42) = 4.685$, $p < 0.05$). Pairwise comparisons showed that mu rhythms were statistically more suppressed in the Race Matching compared to Emotion Matching tasks ($p < 0.01$). There was no significant difference in mu suppression between Race and Gender Matching ($p = 0.09$) or between Gender and Emotion Matching ($p = 1.0$). There was a response × block interaction ($F(2, 42) = 4.657$, $p < 0.05$). As Fig. 5 (top) illustrates, mu suppression values during the Emotion Matching block were greater for correct than in incorrect trials at the three electrode sites. Individual ANOVAs showed that this difference in mu suppression was marginally significant in the Emotion Matching block ($p = 0.065$). Fig. 6 shows that performance accuracy during the Emotion Matching block was negatively correlated with mu suppression for both correct and incorrect trials ($p < 0.01$), suggesting that greater accuracy correlated with increased mu suppression. In the Gender Matching block, there was no significant difference in mu suppression between correct and incorrect trials ($p = 0.71$), and accuracy was not correlated with mu suppression ($r^2 = 0.015$, $p = 2.33$). However, in the Race Matching block, mu suppression was actually greater for *incorrect* compared to correct trials ($F > 1$, $p = 0.036$), and accuracy was significantly positively correlated with mu suppression ($r^2 = 0.069$; $p = 0.014$), suggesting that that greater accuracy was correlated with *decreased* mu suppression.

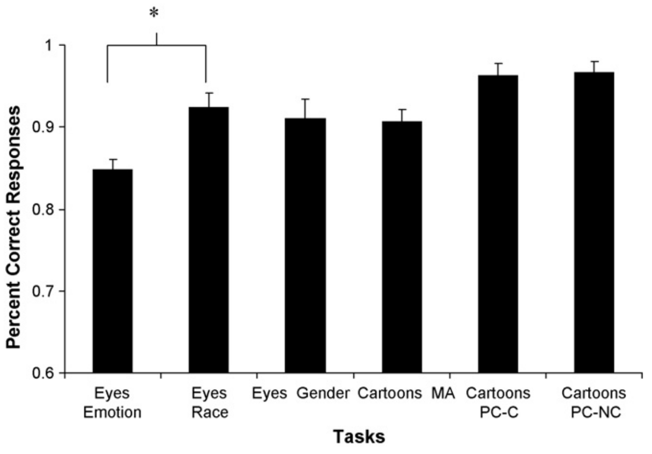

Fig. 4. Response accuracy performance on both the Eyes task and Cartoons task. Note the reduction in accuracy for the experimental condition in both groups, compared to control blocks. $^*p < 0.05$.

The SC version of the paradigm showed a marginally significant main effect of response ($F(1, 21 = 4.087$, $p = 0.056)$, such that overall there was tendency for greater suppression during correct trials. There was a statistically significant response × block × electrode ($F(4, 84) = 6.85$, $p < 0.01$). However, as shown in Fig. 5 (bottom), the Mental Attribution block showed no significant difference in mu suppression between correct and incorrect trials ($r^2 = 0.0006$, $p = 0.78$). Furthermore, as illustrated in Fig. 7, accuracy on this block was not correlated with mu suppression. In contrast, significantly more mu suppression occurred in correct versus incorrect trials in the PC-C block ($p < 0.01$; Fig. 5 bottom). Accuracy in the PC-C block was also negatively correlated with mu suppression for both correct and incorrect trials ($r^2 = 0.096$, $p < 0.01$; Fig. 8) suggesting that greater accuracy was correlated with more mu suppression. In the Physical Causation without Characters (PC-NC) block, there was no significant difference in mu suppression between correct and incorrect trials ($p = 0.96$), and accuracy on this block was not correlated with mu suppression ($r^2 = 0.041$, $p = 0.075$). There were no mu suppression differences between PC-NC and Mental Attribution, nor between PC-NC and PC-C blocks ($p > 0.1$).

Comparisons between accuracy and mu suppression across the different blocks of the Eyes and Cartoons tasks showed that accuracy on the Emotion Matching block correlated significantly with mu suppression in the PC-C block of the Cartoons task ($r^2 = 0.063$, $p < 0.01$); and conversely, accuracy on the PC-C block of the Cartoons task correlated significantly with mu suppression on the Emotion Matching block of the Eyes task ($r^2 = 0.126$, $p < 0.01$). This suggested some common mechanism mediating the processing in both of these tasks. There were no statistically significant effects of gender for any of the tasks.

5. Discussion

The present results indicate that mirror neuron activity, as reflected in mu rhythm suppression, is more relevant while individuals make social-perceptual judgments about emotional facial expressions (Emotion Matching task) and physical interactions between people and objects (Physical Causation with Characters task) than during gender discrimination (Gender Matching) or during social-cognitive tasks requiring attribution of belief (Mental Attribution). These differences are not due to task difficulty since both the Emotion Matching and Mental Attribution tasks appeared to be more difficult than the other tasks, as indicated by the lower percent correct responses in each relative to the control tasks. The differences in mu suppression to correct and

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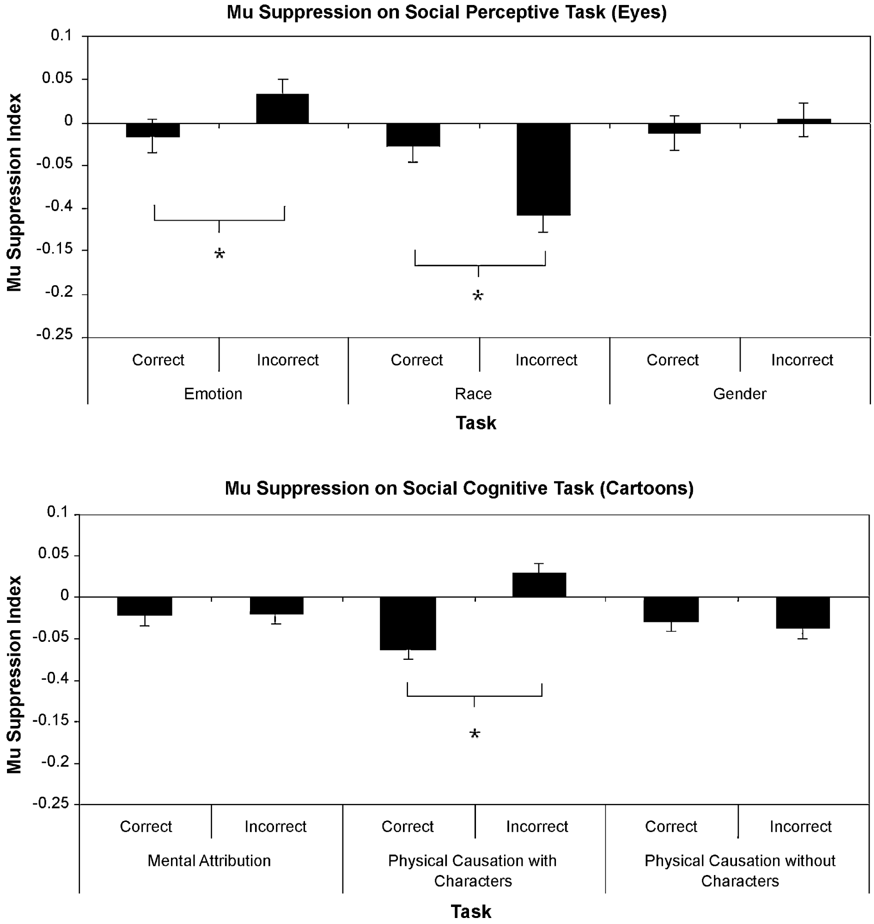

Fig. 5. Top: Mu suppression index (MSI) for the social perceptual (SP) or Eyes task for correct and incorrect trials during the Emotion, Race, and Gender Matching blocks. Bottom: Mu suppression index (MSI) for the social cognitive (SC) or Cartoons task for correct and incorrect trials during the Mental Attribution, Physical Causation with Characters (PC-C), and Physical Causation without Characters (PC-NC) blocks.

incorrect trials in the Emotion Matching and Physical Causation with Characters compared to the Mental Attribution blocks implies that the mirror neuron system is differentially active between these two tasks. To the extent that these tasks recruit SP and SC processes, this is consistent with the SP and SC distinction in ToM suggested by Tager-Flusberg and Sullivan (2000). However, because mu suppression still occurs during the SC task, it suggests that SP and SC are not totally independent processes, but that additional mechanisms must be engaged during mental attribution tasks.

A possible explanation for the difference in mu suppression between correct and incorrect trials is that there may be a stronger

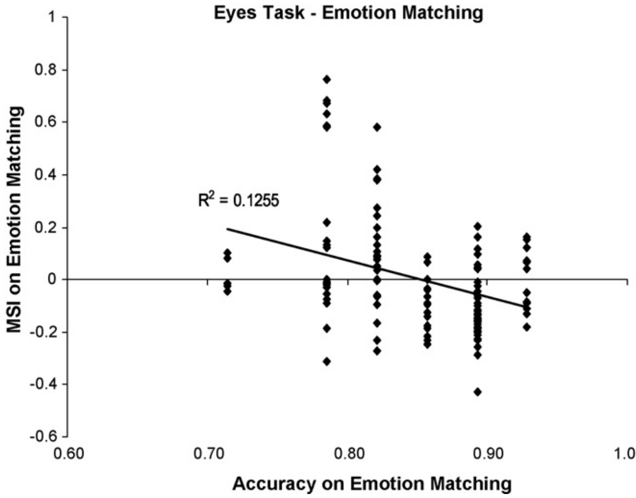

Fig. 6. Correlation between mu suppression at electrodes C3, CZ and C4 and accuracy during the Emotion Matching block ($R = -0.539$, $p < 0.01$).

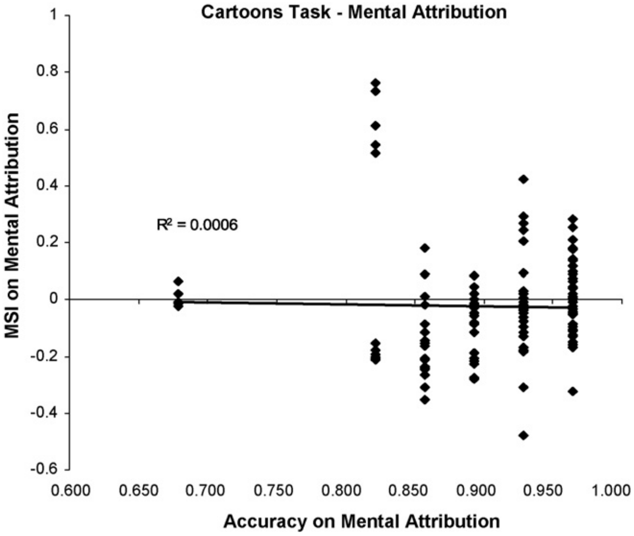

Fig. 7. Correlation between mu suppression at electrodes C3, CZ and C4 and accuracy during the Mental Attribution block ($R = -0.025$, $p = 0.39$).

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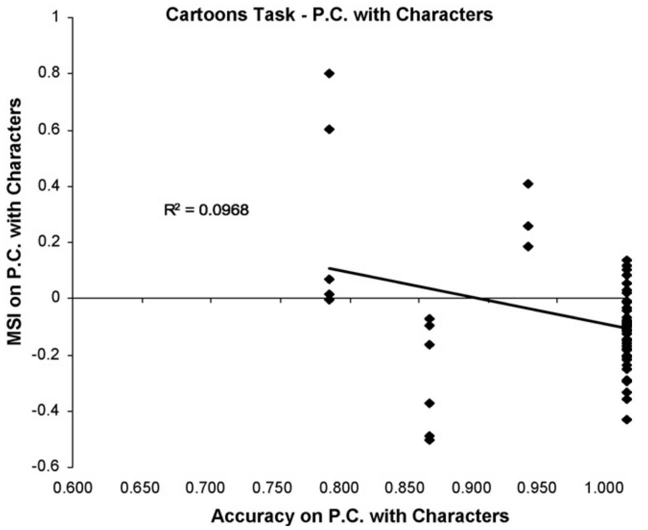

Fig. 8. Correlation between mu suppression at electrodes C3, CZ and C4 and accuracy during the Physical Causation with Characters block ($R = -0.311$, $p < 0.01$).

rebound effect for incorrect trials, which could reflect motor evaluation following recognition of an error. A similar finding was recently reported for the beta end of the mu rhythm. It suggests that mu rhythms not only reflect motor activity modulated by action observation, but that the modulation increases when the observed action is erroneous. This would be consistent with the idea that the MNS is involved in evaluating the correctness of the actions of others (Koelewijn et al., 2008). However, this seems unlikely to be the major factor in mu suppression in our experiment given that MSI differed between correct and incorrect trials in some tasks but not others.

Mu suppression was greater for correct than incorrect trials in the Emotion Matching block of the Eyes task and in the Physical Causation with Characters (PC-C) block of the Cartoons task. This is in line with previous research showing that mirror neurons are active during the viewing of facial expressions of emotion (Dapretto et al., 2006) and object interaction (Rizzolatti and Craighero, 2004), and that lesions of somatosensory cortex impair perception of emotional facial expressions (Adolphs et al., 2000). Studies also reveal that when people are exposed to emotional facial expressions, they spontaneously react with distinct facial electromyographic (EMG) reactions in emotion-relevant facial muscles (Magnee et al., 2007). These reactions appear to reflect, in part, a tendency to mimic the facial stimuli.

In the present experiment, accuracy on each of the tasks correlated with mu suppression on that task. Finally, accuracy in one task (Emotion Matching) correlated with mu suppression in the other task (PC-C). Similarly, accuracy on the PC-C task also correlated with mu suppression on Emotion Matching task. This suggests the existence of a common mechanism involved in these two tasks, which we hypothesize involve mirror neuron-based simulation. There is evidence for mirror neuron-based simulation of both facial expression and human-object interactions (Gallese, 2007; Molnar-Szakacs et al., 2006). Simulation of facial expressions occurs subconsciously and automatically and individuals spontaneously mimic observed facial expressions, even when the stimuli are presented subliminally (Wallbott, 1991; Dimberg et al., 2000). Simulation of object interactions was the first discovered function of mirror neurons, and arguably its most basic (Rizzolatti and Craighero, 2004).

The lack of a significant difference in mu suppression between correct and incorrect trials in the Mental Attribution block of the Cartoons task suggests that making such mental attributions of belief involve mapping another's actions onto the observer's own motor system (i.e., simulation) but is not sufficient for an accurate response and must therefore require additional neural mechanisms. This insensitivity in mu suppression to mental attribution of belief could be attributed to the use of cartoons and the lack of biological realism. Previous work has shown that certain nonbiological actions that lack an implication of agency (e.g., simple ball movements) do not cause mu suppression in humans (Oberman et al., 2005), while nonbiological movements where agency can be inferred, such as robot movements, do cause mu suppression (Oberman and Ramachandran, 2007). However, this explanation is contradicted by the finding of differential mu suppression in the PC-C task, where similar cartoon stimuli were used. These differences between ball movement and the PC-C task may instead result from the complexity of the stimuli in the cartoons task and the depiction of agency and not its nonbiological nature.

These results are not at odds with the general idea that mirror neurons encode the goal of an action. Previous research showing that mirror neurons are involved in understanding others' intentions have involved actions in which the goal is related to the object in a simple way, similar to the Physical Causation with Characters cartoons (e.g., Umilta et al., 2001; Iacoboni et al., 2005). In contrast, the goals in the Mental Attribution cartoons were either related to the objects in a complex way (putting wet shoes by the fire to dry them out) or sometimes not directly related to object interactions at all (realizing a pie in the oven is burning by looking at the clock). Thus the Mental Attribution task involves more complex, higher-order judgments of mental state than either the PC-C task or the tasks in Umilta et al. (2001) and Iacoboni et al. (2005).

The differential brain activity evoked during the Emotion Matching and Physical Causation with Characters versus Mental Attribution blocks indicates that there are likely separate mental processes subserved by distinct brain processes for making judgments about emotional expressions and object interaction, compared to making mental attributions of belief. This is consistent with Tager-Flusberg and Sullivan (2000) componential view of theory of mind, as well as other related two-component research (Saxe, 2006; Saxe and Powell, 2006; Uddin et al., 2007; Keysers and Gazzola, 2006; Gobbini et al., 2007; De Lange et al., 2008). It seems probable that aspects of both theory–theory and simulation theory may be true, since if all social cognition were achieved using either theorizing or simulation, brain activity in both conditions would have been similar. We hypothesize that the explicit, logical hypothesizing described by theory–theory may be responsible for social-cognitive tasks like making judgments about mental states, and the implicit, self–other mapping described by simulation theory may be responsible for social-perceptual tasks like making judgments about emotional facial expressions. It is critical that future research investigate this possibility using other social-cognitive and social-perceptual tasks, such as false belief, voice tone, and body language, with stimuli that are as ecologically valid as possible. Furthermore, the significant mu suppression in the Race Matching block, despite a lack of mu suppression in the Gender Matching block, was unexpected and warrants further investigation. Nonetheless, it suggests that judgments about race may involve self–other mapping and/or recruit emotional systems in a way that gender matching does not.

Importantly, the current results only support a distinction between theory of mind subcomponents in as much as correlating neural activity with accuracy is a reliable way of identifying the neural processes on which a task relies. It is possible that SC processes as well as SP processes were recruited during some tasks. Future research could monitor neural markers of both the SP and

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SC components to determine the extent to which they are used independently. In addition, while facial mimicry was not monitored during the Eyes task, this would be an interesting additional marker of mirroring.

Taking into account the proposed dissociation between social-perceptual and social-cognitive abilities in autism and Williams Syndrome disorders (Tager-Flusberg and Sullivan, 2000), it is possible to generate predictions regarding mu suppression in these populations. A link between mirror neurons and theory of mind has been postulated in the context of autism (Williams et al., 2001, 2006), and autistic individuals, who appear to have deficits in the SP component of theory of mind, show a lack of mu suppression in response to observed movement (Oberman et al., 2005) as well as a lack of BOLD signal during facial imitation in Brodmann's area 44 (Dapretto et al., 2006). It has been shown that individuals with autism do not have inferior frontal gyrus activation during observation or imitation of emotional facial expressions (Dapretto et al., 2006). Therefore, it is predicted that individuals with autism will have problems with the two subcomponents of ToM and will not show mu suppression during observation of emotional facial expressions or other social-perceptual stimuli. Conversely, it is predicted that individuals with Williams Syndrome will only have problems with one of the subcomponents of ToM (Sullivan and Tager-Flusberg, 1999). They will likely show normal mu suppression for emotional facial expressions or other social-perceptual stimuli, but have problems with stimuli involving social-cognitive events, which require representational attribution of mental states such as belief.

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References

Adolphs, R., Baron-Cohen, S., Tranel, D., 2002. Impaired recognition of social emotions following amygdala damage. Journal of Cognitive Neuroscience 14, 1264–1274.

Adolphs, R., Damasio, H., Tranel, D., Cooper, G., Damasio, A.R., 2000. A role for somatosensory cortices in the visual recognition of emotion as revealed by three-dimensional lesion mapping. Journal of Neuroscience 20, 2683–2690.

Altschuler, E.L., Vankov, A., Wang, V., Ramachandran, V.S., Pineda, J.A., 1997. Person see, person do: human cortical electrophysiological correlates of monkey see monkey do cells. Soc. Neurosci. Abstr. 23 (2), 1848.

Aylward, E.H., Minshew, N.J., Goldstein, G., Honeycutt, N.A., Augustine, A.M., Yates, K.O., et al., 1999. MRI volumes of amygdala and hippocampus in non-mentally retarded autistic adolescents and adults. Neurology 53, 2145–2150.

Baron-Cohen, S., Jolliffe, T., Mortimore, C., Robertson, M., 1997. Another advanced test of theory of mind: evidence from very high functioning adults with autism or asperger syndrome. Journal of Child Psychology and Psychiatry 38, 813–822.

Baron-Cohen, S., Leslie, A.M., Frith, U., 1985. Does the autistic child have a "theory of mind"? Cognition 21, 37–46.

Baron-Cohen, S., Ring, H., Chitnis, X., Wheelwright, S., Gregory, L., Williams, S., et al., 2006. fMRI of parents of children with Asperger Syndrome: a pilot study. Brain and Cognition 61, 122–130.

Bellugi, U., Adolphs, R., Cassady, C., Chiles, M., 1999. Towards the neural basis for hypersociability in a genetic syndrome. Neuroreport 10, 1653–1657.

Blair, R.J., 2005. Responding to the emotions of others: dissociating forms of empathy through the study of typical and psychiatric populations. Consciousness and Cognition 14, 698–718.

Bonda, E., Petrides, M., Ostry, D., Evans, A., 1996. Specific involvement of human parietal systems and the amygdala in the perception of biological motion. Journal of Neuroscience 16, 3737–3744.

Brunet, E., Sarfati, Y., Hardy-Bayle, M.C., 2003. Reasoning about physical causality and other's intentions in schizophrenia. Cognitive Neuropsychiatry 8, 129–139.

Brunet, E., Sarfati, Y., Hardy-Bayle, M.C., Decety, J., 2000. A PET investigation of the attribution of intentions with a nonverbal task. Neuroimage 11, 157–166.

Carr, L., Iacoboni, M., Dubeau, M.C., Mazziotta, J.C., Lenzi, G.L., 2003. Neural mechanisms of empathy in humans: a relay from neural systems for imitation to limbic areas. Proceedings of the National Academy of Sciences of the United States of America 100, 5497–5502.

Colle, L., Baron-Cohen, S., Hill, J., 2007. Do children with autism have a theory of mind? A non-verbal test of autism vs. specific language impairment. Journal of Autism and Developmental Disorders 37, 716–723.

Dapretto, M., Davies, M.S., Pfeifer, J.H., Scott, A.A., Sigman, M., Bookheimer, S.Y., et al., 2006. Understanding emotions in others: mirror neuron dysfunction in children with autism spectrum disorders. Nature Neuroscience 9, 28–30.

De Lange, F.P., Spronk, M., Willems, R.M., Toni, I., Bekkering, H., 2008. Complementary systems for understanding action intentions. Current Biology 18, 454–457.

di Pellegrino, G., Fadiga, L., Fogassi, L., Gallese, V., Rizzolatti, G., 1992. Understanding motor events: a neurophysiological study. Experimental Brain Research 91, 176–180.

Dimberg, U., Thunberg, M., Elmehed, K., 2000. Unconscious facial reactions to emotional facial expressions. Psychological Science 11, 86–89.

Gallese, V., 2007. Before and below 'theory of mind': embodied simulation and the neural correlates of social cognition. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences 362 (1480), 659–669.

Gallese, V., Keysers, C., Rizzolatti, G., 2004. A unifying view of the basis of social cognition. Trends in Cognitive Sciences 8, 396–403.

Gendry, M.I., Zilbovicius, M., Boddaert, N., Robel, L., Philippe, A., Sfaello, I., et al., 2005. Autism severity and temporal lobe functional abnormalities. Annals of Neurology 58, 466–469.

Gobbini, M.I., Koralek, A.C., Bryan, R.E., Montgomery, K.J., Haxby, J.V., 2007. Two takes on the social brain: a comparison of theory of mind tasks. Journal of Cognitive Neuroscience 19, 1803–1814.

Gopnik, A., Schulz, L., 2004. Mechanisms of theory formation in young children. Trends in Cognitive Sciences 8, 371–377.

Gordon, R.M., 2005. Simulation and systematic errors in prediction. Trends in Cognitive Sciences 9, 361–362.

Hadjikhani, N., Joseph, R.M., Snyder, J., Tager-Flusberg, H., 2006. Anatomical differences in the mirror neuron system and social cognition network in autism. Cerebral Cortex 16, 1276–1282.

Happe, F., Frith, U., 1996. The neuropsychology of autism. Brain 119 (Pt 4), 1377–1400.

Hari, R., Levanen, S., Raij, T., 2000. Timing of human cortical functions during cognition: role of MEG. Trends in Cognitive Sciences 4, 455–462.

Iacoboni, M., Dapretto, M., 2006. The mirror neuron system and the consequences of its dysfunction. Nature Reviews. Neuroscience 7, 942–951.

Iacoboni, M., Molnar-Szakacs, I., Gallese, V., Buccino, G., Mazziotta, J.C., Rizzolatti, G., 2005. Grasping the intentions of others with one's own mirror neuron system. PLoS Biology 3, e79.

Keysers, C., Gazzola, V., 2006. Towards a unifying neural theory of social cognition. Progress in Brain Research 156, 379–401.

Koelewijn, T., van Schie, H.T., Bekkering, H., Oostenveld, R., Jensen, O., 2008. Motor-cortical beta oscillations are modulated by correctness of observed action. Neuroimage 40, 767–775.

Kohler, E., Keysers, C., Umilta, M.A., Fogassi, L., Gallese, V., Rizzolatti, G., 2002. Hearing sounds, understanding actions: action representation in mirror neurons. Science 297, 846–848.

Leslie, K.R., Johnson-Frey, S.H., Grafton, S.T., 2004. Functional imaging of face and hand imitation: towards a motor theory of empathy. Neuroimage 21, 601–607.

Lieberman, M.D., 2007. Social cognitive neuroscience: a review of core processes. Annual Review of Psychology 58, 259–289.

Lohmann, H., Tomasello, M., 2003. The role of language in the development of false belief understanding: a training study. Child Development 74, 1130–1144.

Magnee, M.J., Stekelenburg, J.J., Kemner, C., de, G.B., 2007. Similar facial electromyographic responses to faces, voices, and body expressions. Neuroreport 18, 369–372.

Meltzoff, A.N., 1999. Origins of theory of mind, cognition and communication. Journal of Communication Disorders 32, 251–269.

Molnar-Szakacs, I., Kaplan, J., Greenfield, P.M., Iacoboni, M., 2006. Observing complex action sequences: the role of the fronto-parietal mirror neuron system. Neuroimage 33, 923–935.

Muthukumaraswamy, S.D., Johnson, B.W., McNair, N.A., 2004. Mu rhythm modulation during observation of an object-directed grasp. Brain Research. Cognitive Brain Research 19, 195–201.

Oberman, L.M., Hubbard, E.M., McCleery, J.P., Altschuler, E.L., Ramachandran, V.S., Pineda, J.A., 2005. EEG evidence for mirror neuron dysfunction in autism spectrum disorders. Cognitive Brain Research 24 (2), 190–198.

Oberman, L.M., Ramachandran, V.S., 2007. The simulating social mind: the role of the mirror neuron system and simulation in the social and communicative deficits of autism spectrum disorders. Psychological Bulletin 133, 310–327.

Oberman, L.M., Pineda, J.A., Ramachandran, V.S., 2007. The human mirror neuron system: A link between action observation and social skills. Social Cognitive and Affective Neuroscience 2, 62–66.

Pierce, K., Muller, R.A., Ambrose, J., Allen, G., Courchesne, E., 2001. Face processing occurs outside the fusiform 'face area' in autism: evidence from functional MRI. Brain 124, 2059–2073.

Pineda, J.A., 2005. The functional significance of mu rhythms: translating "seeing" and "hearing" into "doing". Brain Research. Brain Research Review 50, 57–68.

Rizzolatti, G., Arbib, M.A., 1998. Language within our grasp. Trends in Neurosciences 21, 188–194.

Rizzolatti, G., Craighero, L., 2004. The mirror-neuron system. Annual Review of Neuroscience 27, 169–192.

Saxe, R., 2006. Uniquely human social cognition. Current Opinion in Neurobiology 16, 235–239.

Saxe, R., Powell, L.J., 2006. It's the thought that counts: specific brain regions for one component of theory of mind. Psychological Science 17, 692–699.

Shamay-Tsoory, S.G., Tomer, R., Berger, B.D., haron-Peretz, J., 2003. Characterization of empathy deficits following prefrontal brain damage: the role of the right ventromedial prefrontal cortex. Journal of Cognitive Neuroscience 15, 324–337.

Shimazu, H., Maier, M.A., Cerri, G., Kirkwood, P.A., Lemon, R.N., 2004. Macaque ventral premotor cortex exerts powerful facilitation of motor cortex outputs to upper limb motoneurons. Journal of Neuroscience 24, 1200–1211.

Sullivan, K., Tager-Flusberg, H., 1999. Second-order belief attribution in Williams syndrome: intact or impaired? American Journal of Mental Retardation 104, 523–532.

Tager-Flusberg, H., Sullivan, K., 2000. A componential view of theory of mind: evidence from Williams syndrome. Cognition 76, 59–90.

Uddin, L.Q., Iacoboni, M., Lange, C., Keenan, J.P., 2007. The self and social cognition: the role of cortical midline structures and mirror neurons. Trends in Cognitive Sciences 11, 153–157.

Umilta, M.A., Kohler, E., Gallese, V., Fogassi, L., Fadiga, L., Keysers, C., et al., 2001. I know what you are doing. A neurophysiological study. Neuron 31, 155–165.

Vuilleumier, P., Pourtois, G., 2007. Distributed and interactive brain mechanisms during emotion face perception: evidence from functional neuroimaging. Neuropsychologia 45, 174–194.

Wallbott, H.G., 1991. Recognition of emotion from facial expression via imitation? Some indirect evidence for an old theory.. British Journal of Social Psychology 30 (Pt 3), 207–219.

Welchew, D.E., Ashwin, C., Berkouk, K., Salvador, R., Suckling, J., Baron-Cohen, S., et al., 2005. Functional disconnectivity of the medial temporal lobe in Asperger's syndrome. Biological Psychiatry 57, 991–998.

Wellman, H.M., Cross, D., Watson, J., 2001. Meta-analysis of theory-of-mind development: the truth about false belief. Child Development 72, 655–684.

Wellman, H.M., Liu, D., 2004. Scaling of theory-of-mind tasks. Child Development 75, 523–541.

Williams, J.H., Waiter, G.D., Gilchrist, A., Perrett, D.I., Murray, A.D., Whiten, A., 2006. Neural mechanisms of imitation and 'mirror neuron' functioning in autistic spectrum disorder. Neuropsychologia 44, 610–621.

Williams, J.H., Whiten, A., Suddendorf, T., Perrett, D.I., 2001. Imitation, mirror neurons and autism. Neuroscience Biobehavioral Reviews 25, 287–295.

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