Contents lists available at ScienceDirect

Biological Psychology

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

J.A. Pineda [a,b,*], E. Hecht [c]

[a] Department of Cognitive Science, University of California, San Diego, La Jolla, CA 92093-0515, USA
[b] Department of Neuroscience, University of California, San Diego, La Jolla, CA 92093-0515, USA
[c] Neuroscience Department, Emory University, Atlanta, GA 30339, USA

ARTICLE INFO

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.

© 2008 Elsevier B.V. All rights reserved.

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)

* Corresponding author at: UC San Diego, 9500 Gilman Drive, La Jolla, CA 92093-0515, USA. Tel.: +1 858 534 9754; fax: +1 858 534 1128.
E-mail address: pineda@cogsci.ucsd.edu (J.A. Pineda).

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 orbito-frontal 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).