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Review

A systems level analysis of the mirror neuron hypothesis and imitation impairments in autism spectrum disorders

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ABSTRACT

Although several studies suggest an imitation deficit as a key feature of autism, questions have been raised about the consistency of this finding and about the component skills involved in imitation. The primary aim of this review is to examine the uneven profile of imitation deficits found in autism in the context of the mirror neuron system (MNS) dysfunction hypothesis. We use the cortical underconnectivity framework (Just et al., 2004) to examine the coordination of brain areas that orchestrate the communication between the component skills underlying imitation. A comprehensive account of imitation deficit in autism should take into account the regions that are at the core of the MNS (e.g., IFG and IPL) and related regions that feed into the MNS (e.g., STS, Cerebellum) in their functioning and in their coordination. Our findings suggest that the MNS may be associated with mediating familiarity, attention, self-other matching, and social relevance, which may be vital in characterizing the imitation deficits in autism. Such an analysis may have greater clinical and therapeutic value.

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1. Introduction

From children dressing up like their favorite TV characters to adults mirroring each other's body posture at a board meeting, imitation is a ubiquitous and fundamental aspect of human social behavior. Indeed, imitative behavior begins very early in life. As early as 42 h after birth, newborn infants have been found to mirror simple actions of others, such as tongue protrusion, lip smacking, and mouth opening (Meltzoff and Moore, 1983). These automatic imitation behaviors have been shown to decrease around two months of age (Abravanal and Sigafoos, 1984; Field et al., 1986; Fontaine, 1984) and reappear with increased complexity around one year of age (Meltzoff and Moore, 1992), suggesting that rudimentary imitation ability is present very early in life but may develop and change significantly over time.

Early imitation is thought to play a substantial role in the development of motor control, communication, and social abilities (Tomasello et al., 1993). For example, as children begin to speak,

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imitation of mouth movements is thought to teach them how to manipulate their own articulators (Jordan and Rumelhart, 2002). Imitation has also been implicated in the comprehension of others' behavior (Goldenberg and Karnath, 2006), with its earliest forms acting to provide a sense of connectedness between an infant and its world. In other words, imitation provides the child with information about the actions and intentions of the physical and the social world, which assists in the process of social learning (Rogers et al., 2003), and forms the foundation for future social development.

2. Mirror neuron system (MNS)

Because of the developmental significance of imitation, recent interest has centered on the neural substrates that mediate imitation. Specifically, the discovery of mirror neurons in nonhuman primates has offered promising clues to how we perform actions and perceive the actions of others. In nonhuman primates, neurons dedicated to the visual processing of the actions of others were identified mainly in area F5, and in area PF (Rizzolatti and Craighero, 2004). These neurons not only fire when a monkey performs an action but also when a monkey watches an action being performed (Gallese et al., 1996; Rizzolatti et al., 1996). While it may be difficult to directly study the existence of mirror neurons in humans, a substantial number of fMRI and EEG studies have found evidence that a homologue of the monkey mirror neurons exists in humans (Iacoboni and Dapretto, 2006; see Turella et al., 2009 for alternate perspective), where the monkey F5 is thought to loosely correspond to the human inferior frontal gyrus (IFG), and the monkey PF is thought to loosely correspond to the human inferior parietal lobule (IPL). An electrical stimulation study provided more direct evidence for the existence of mirror neurons in humans. Specifically, electrical stimulation of the senosorimotor cortex of a 36-month-old child undergoing epilepsy surgery resulted in sensorimotor hand reactions, and this same area was found to be activated by simply observing hand movement (Fecteau et al., 2004). Furthermore, an fMRI adaptation of it revealed that areas of the IPL in humans activated both during the observation and during the execution of actions (Chong et al., 2008).

In addition to simulation, the MNS may provide us with the tools for action understanding. Indeed, human beings are adept not only at interpreting the actions of oneself and that of others but also at reasoning about such actions with causal explanations. This may involve identifying the agent and object in an event and inferring the intention behind a certain action. Although the neural basis of action understanding is complex, the involvement of the mirror neuron circuitry in this process is relatively well established (Lestou et al., 2008). The role of MNS in action understanding has been explained by differing accounts. Gallese (2001, 2003) argues that what mirror neurons code is the relationship, in motor terms, between the agent and the object of action, whereas Knoblich and Jordan (2002) propose that mirror neurons code the perceived effect an action exerts on an object. While the former leans toward a maximalist role of mirror neurons, the latter tends to be minimalistic (see Pacherie and Dokic, 2006). Despite these differing views of the functions of mirror neurons in action understanding, the important role MNs play in action understanding is undeniable. Thus, the MNS does not simply respond to visual stimuli alone; it can reflect the understanding of intentions through the understanding of a motor act (Kohler et al., 2002). It has also been found that the MNS is sensitive to the timing of observed actions as well. The MNS therefore codes a goal-directed action and the separate movements which lead to the achievement of that goal (Rizzolatti and Craighero, 2004). These separate movements seem collectively stored in a sort of 'action bank' in the observers' mind. When viewing an action being performed, one must look into their 'action bank' for a match to the action and then apply their understanding of the intention behind the action (Sinigaglia and Sparaci, 2010).

Even though the significance of the MNS is still debated (see Hickok, 2009), many researchers believe that this system directly influences imitation (Iacoboni et al., 1999; Koski et al., 2002, 2003; Heiser et al., 2003), and appropriate understanding of actions appears to be an important prerequisite for imitation where one has to represent the model and then plan and execute the imitative action. Therefore, it has been hypothesized that individuals with autism who have deficits in imitation (Williams et al., 2004) may also have a malfunctioning MNS (Oberman and Ramachandran, 2007; Williams et al., 2001). Indeed, the "mirror neuron dysfunction hypothesis of autism" has received widespread attention, with quite a few studies suggesting atypicalities of the MNS in persons with autism contributing to autism symptomatology (for recent reviews, see Williams, 2008 or Bernier and Dawson, 2009).

Recent evidence of impairments in action understanding in persons with autism may be associated with atypical functioning of the MNS in this population. Understanding an action may involve two important aspects: (a) comprehending the motor action (*what*), and (b) inferring the intention behind the action (*why*). It is argued that a mirror mechanism may be involved in both these aspects (Rizzolatti et al., 2009). In a recent study, Boria et al. (2009) examined the *why* and *what* of action understanding in autism and found that children with autism had difficulty in figuring out the intention behind an action by relying on motor information.

In addition to the perceptual and intentional elements of action understanding, several other factors may also contribute to action understanding which may be altered in people with ASD. For instance, Zalla et al. (2010) found individuals with autism exhibiting greater numbers of temporal inversions when presented with an action and asked to predict the outcome. The authors suggested that these temporal inversions disrupt the ability of individuals with autism to both understand and predict the actions of others. In addition, previous literature has pointed to the need of familiarity, not just with the action, but also with the actor for appropriate action understanding in individuals with autism (Le Bel et al., 2009). Action understanding also involves appropriate visual attention, a topic of debate in individuals with autism (see Section 6.1). According to Vivanti et al. (2008), individuals with autism showed similar patterns of visual attention when observing a demonstrator perform an action but showed reduced attention to the demonstrator's face. Such difficulties in attention may be linked to dysfunction in appropriate affective coordination in ASD.

It has also been suggested that the way we understand actions of others is through our own first person ability for action and emotion. Perhaps this allows us to share the emotional aspects of other's gestures and actions; the lack of this appropriate mirroring (through the MNS) may impair appropriate action understanding as well as affective coordination in autism (Sinigaglia and Sparaci, 2010). If others' actions are truly understood by connecting to our own actions and emotions, then a breakdown in the MNS and/or empathy would hinder appropriate action understanding. This is of particular relevance to autism as several studies have indicated that a dysfunction in the MNS in autism may be at the core of their difficulty to empathize (Buccino and Amore, 2008). Deficits in MNS may also have an impact on theory of mind (ToM) in autism. For instance, Pineda and Hecht (2009) found that the mirroring system was primarily involved with two aspects of ToM, emotion and person–object interaction, both of which are suggested in previous literature to be necessary for appropriate action understanding. Thus, there is substantial evidence to suggest that people with ASD may have difficulty with action understanding and that this difficulty may be related to MNS impairments.