



Review

An integrative neural model of social perception, action observation, and theory of mind



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ARTICLE INFO

Article history:

Received 13 November 2014
 Received in revised form 13 January 2015
 Accepted 23 January 2015
 Available online 3 February 2015

Keywords:

Social neuroscience
 Neural systems
 Social information processing
 Social perception
 Action observation
 Mirror system
 Imitation
 Theory of mind
 Mentalizing
 Posterior superior temporal sulcus
 Functional connectivity
 Autism spectrum disorder
 Psychiatric disorders

ABSTRACT

In the field of social neuroscience, major branches of research have been instrumental in describing independent components of typical and aberrant social information processing, but the field as a whole lacks a comprehensive model that integrates different branches. We review existing research related to the neural basis of three key neural systems underlying social information processing: social perception, action observation, and theory of mind. We propose an integrative model that unites these three processes and highlights the posterior superior temporal sulcus (pSTS), which plays a central role in all three systems. Furthermore, we integrate these neural systems with the dual system account of implicit and explicit social information processing. Large-scale meta-analyses based on Neurosynth confirmed that the pSTS is at the intersection of the three neural systems. Resting-state functional connectivity analysis with 1000 subjects confirmed that the pSTS is connected to all other regions in these systems. The findings presented in this review are specifically relevant for psychiatric research especially disorders characterized by social deficits such as autism spectrum disorder.

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1. Introduction

The field of social neuroscience is rapidly evolving and with it our understanding of the neural basis of social information

processing. Different branches of research within the field have been instrumental in describing specific components of typical and aberrant social information processing. However, these findings are heterogeneous and the field as a whole is lacking a comprehensive model of social information processing. In the following review we outline existing research related to the neural basis of three key neural systems underlying social information processing: social perception, action observation, and theory of mind. We propose an integrative model of social information processing that

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unites these three central processes and highlight the common brain region implicated in them, the posterior superior temporal sulcus (pSTS) region. We also show that the pSTS region is functionally interconnected to all key regions in the “social brain” for social information processing.

The findings presented in this review are highly relevant for psychiatric research especially regarding a wide variety of seemingly disparate disorders characterized by social deficits (Kennedy and Adolphs, 2012), such as autism spectrum disorder (ASD), Williams syndrome, behavioral-variant frontotemporal dementia, Fragile X, developmental prosopagnosia, Capgras syndrome and psychopathy. To demonstrate how our model can be applied to neuropsychiatric disorders, we use ASD as an example and we review relevant evidence suggesting that one or more of the key regions in our model are abnormal in ASD. As defined in DSM-5, ASD is a disorder characterized by persistent and prominent deficits in social communication and social interaction as well as restricted and repetitive behavior (APA, 2013). We also discuss the implications of our model for research on ASD, highlighting the temporal integration role of the pSTS and a recent hypothesis that posits that ASD can be understood as a disorder of temporal prediction (Sinha et al., 2014). Our model also suggests that the pSTS region may serve as a target for interventions designed to improve social functioning in ASD (e.g., Ventola et al., 2014).

2. A neural system for social perception

Humans are inherently social creatures as evidenced by a range of social behavior that typically emerges early in infancy. Infants preferentially orient to social signals such as facial expressions and by the age of three months recognize their mother's face and tone of voice (Johnson et al., 1991; Kovacs et al., 2010; Kurzweil, 1988; Valenza et al., 1996). Expertise in social perception, defined as the ability to decode another person's mental states based on basic behavioral signals, is evolutionarily adaptive due to its reflexive and highly efficient nature (Allison et al., 2000; Beauchamp et al., 2008; McArthur and Baron, 1983). Basic social perception precedes more effortful and explicit processes which emerge later in development (Carpenter et al., 1998; Low and Perner, 2012).

Similar social behavior is observable in monkeys and thus primate research serves as a useful model for understanding social perception in humans. Chimpanzees and corvids, for example, are able to understand what conspecifics know in the context of food competition (Brothers, 1996; Call and Tomasello, 2008; Emery and Clayton, 2009; Premack and Woodruff, 1978). Interestingly, chimpanzees can also use information about others' intentions to help conspecifics and humans (Melis et al., 2011) and there is evidence suggesting that rhesus monkeys are able to infer what others perceive on the basis of what others can see (Flombaum and Santos, 2005) and hear (Santos et al., 2006). The brain regions supporting social perception in primates and humans are largely overlapping (Brothers, 1996). Dynamic social perception mainly implicates the pSTS, the amygdala (AMY), the orbital frontal cortex (OFC) and the fusiform gyrus (FFG) (Allison et al., 2000). These regions have been found to have reciprocal connections within the primate brain and to be sensitive and selective to social stimuli in monkeys and humans (Brothers, 1989, 1996; Brothers and Ring, 1993; Ku et al., 2011).

The pSTS plays a key role in the social perception network. It receives direct input from primary visual and auditory regions in primates and humans and has been implicated in extracting and representing dynamic information in these regions (Belin et al., 2000; Brothers, 1996; Hoffman and Haxby, 2000; Jastorff et al., 2012; Kreifelts et al., 2009). The pSTS is sensitive to and selective for social stimuli that signal intention in humans (Jastorff et al., 2012).

It is selectively activated to static social (i.e. faces) vs. non-social stimuli (i.e. objects) as well as complex dynamic social information, such as changes in the direction of eye gaze or facial expression (Gobbini and Haxby, 2007; Watson et al., 2014). The pSTS is selective for intentional human actions that are more socially meaningful than non-goal directed movements (Bahnmann et al., 2010). In the auditory domain, the pSTS plays an important role in processing affective speech (Wildgruber et al., 2006). Using dynamic causal modeling, Ethofer et al. (2006) demonstrated that the pSTS is the input region of the affective voice processing system, where affective information is extracted and represented. In terms of somatosensory input, mimicking the type of touch during close social interactions by stroking skin areas with C-tactile (CT) nerves, such as the forearm, with a soft brush has been shown to activate the pSTS region (Bjornsdotter et al., 2014; Gordon et al., 2013).

Interestingly, not all social perception studies show pSTS involvement. One possible explanation for this is that some studies did not report a contrast between a relatively social vs. relatively non-social sensory experience. For example, in a study that examined somatosensory experience during an affective touch experiment, Gazzola et al. (2012) had the participants believe that the caresser was either female or male and found that the perceived sex of the caresser (female vs. male) activated the somatosensory cortices but not the pSTS region. The sex effect testing (i.e., female vs. male caresser) involves a contrast of different kinds of social sensory experience, but does not seem to involve a contrast of a relatively social vs. relatively non-social experience (e.g., biological motion vs. scrambled motion). The latter type of contrast is critical for demonstrating pSTS activation because the pSTS is particularly sensitive to the degree of social vs. non-social meaning in the behavioral signals.

The FFG, along the ventral-temporal cortex houses several distinct but adjacent regions that are involved in visual aspects of social perception. Among them, the fusiform face area (FFA) selectively responds to face stimuli, whereas the fusiform body area (FBA) selectively responds to body stimuli (Schwarzlose et al., 2005). The FFA is sensitive to the typical pattern of saccades and fixations observed during implicit facial processing (Morris et al., 2007a, 2007b). Furthermore, the FFA is involved in facial identity recognition (Pitcher et al., 2011), and goal-directed action recognition (Gobbini et al., 2007, 2011; Schultz et al., 2003; Shultz and McCarthy, 2012).

The AMY encodes the emotional salience of social information (Costafreda et al., 2008), particularly when such information requires rapid and reflexive processing (Adolphs, 2009). For instance, the AMY supports gaze orientation toward socially relevant facial features (i.e. the eyes) (Adolphs et al., 2005), particularly when facial expressions communicate fear (Adolphs, 2008).

The OFC has been associated with reward coding of environmental sensory cues, a crucial aspect of behavioral planning in humans as well as primates (Watson and Platt, 2012). Due to the OFC's central role in value-based decision-making, it has been implicated in attention to socially rewarding stimuli and ultimately helps to determine an individual's interest in engaging in social interactions and responding to social cues (Ethofer et al., 2013; Kahnt et al., 2010; Wallis, 2012).

Studies investigating social perception in individuals with ASD have tremendously advanced our understanding of the typical development of social perception and the social deficits of individuals with ASD. Infants with ASD attend less to social cues, such as faces and voices, compared to typical babies (Chawarska et al., 2010, 2012, 2013). Furthermore, unlike typically developing toddlers at the age of two years, toddlers with ASD fail to orient to the social significance of biological motion; instead, they tend to focus on non-social, physical contingencies, which are disregarded by their

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