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Review

# The past, present and future of social neuroscience: A European perspective

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ABSTRACT

This review provides an overview of the field of social neuroscience from a European perspective and focuses mainly on outlining research topics which originated in European laboratories. After a brief historical synopsis of the emergence of this young field, the most relevant findings related to the investigation of the neural networks underlying our capacity to understand the minds of others are summarized. More specifically, three routes of social cognition are distinguished: (1) our capacity to mentalize, or to infer intentions and beliefs of others, (2) our capacity to mimic and understand other's motor actions, and (3) our capacity to empathize, or to share and understand the feelings of others. More recent studies focusing on social emotions such as love, compassion, revenge or our sense of fairness will be discussed linking the field of social neuroscience to the even younger field of neuroeconomics, with the focus on the study of human social interactions using game theoretical paradigms. Finally, the use of a multi-method and multi-disciplinary research approach combining genetic, pharmacological, computational and developmental aspects is advocated and future directions for the study of interactive minds are discussed.



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## Introduction

In the last few decades, the field of cognitive neuroscience has made enormous advances in our understanding of a variety of human primary sensory functions such as vision, hearing, taste and touch, as well to our insight into higher cognitive functions such as memory, problem solving, executive functioning, complex planning and even consciousness (Gazzaniga, 2009). However, for quite a while, cognitive neuroscience primarily focused on the investigation of the human brain in isolation, thereby neglecting the inherently social nature of humans. Thus, typical experiments in cognitive neuroscience involved subjects lying in a scanner or being plugged into an EEG cap having been presented abstract shapes, word lists or asked to perform simple motor tasks. However, in real-life, humans are usually engaged in social interactions and occupied with thoughts and feelings about themselves and their relationships to others. The importance of human sociality is reflected in the so-called 'social brain hypothesis' which was developed in the 1990s by Dunbar and colleagues in the UK (Dunbar, 1992, 1995, 1998). The theory suggests that the large brains observed in primates evolved not only to process information of ecological relevance but mostly to meet the required computational demands associated with living in large complex social groups, a feature which distinguishes primates from most other animal species. In fact, studies have shown that neocortex volume correlates with group size (Dunbar, 1995, 2009).

With the emergence of the new field of social neuroscience around the turn of the century, the study of human sociality finally captured the interest of cognitive neuroscience. Although the first

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articles and books referring to the 'social brain' had appeared years earlier in the early 1990s (Baron-Cohen, 1995; Brothers, 1997; Brothers et al., 1990; Cacioppo and Berntson, 1992; di Pellegrino et al., 1992; Frith and Frith, 1999; Frith et al., 1991; Grafton et al., 1996; Rizzolatti et al., 1996), social cognitive neuroscience, as a new interdisciplinary endeavor, now combining approaches from various disciplines including developmental-, clinical-, comparative- and social psychology, cognitive neurosciences and (neuro)economics, biology, evolutionary anthropology and philosophy, only really took off as broader movement a decade later around the turn of the century. In 1999, Ralph Adolphs published an influential overview article on 'social cognition and the human brain' (Adolphs, 1999), which was followed in 2001 by the first edited volume on social neuroscience by Cacioppo and colleagues, the same authors who had coined the term years before (Cacioppo and Berntson, 1992). Also in 2001, Ochsner and Lieberman published an influential article in the American Psychologist titled 'The emergence of social cognitive neuroscience'. This was followed by the inaugural 'Social Cognitive Neuroscience' conference in California in 2001 organized by the authors. The popularity of the new field was attested to by a rapidly growing number of focused conferences, special issues of journals, and books (e.g., Adolphs, 2003; Allison et al., 2000; Cacioppo, 2001; Harmon-Jones and Devine, 2003; Heatherton and Macrae, 2003; Ochsner and Lieberman, 2001) and, in 2006, by the founding of two independent journals devoted to topics around social cognition in neuroscience: *Social Neuroscience* and *Social Cognitive and Affective Neuroscience* (SCAN).

Although the origin of social neuroscience cannot easily be traced back to any specific country or continent, nevertheless there seem to be some topics that have been preferentially studied in Europe and others largely in the US. Whereas the investigation of different routes of social cognition and the question of how we understand other people's minds (Theory of Mind), feelings (empathy) and actions (action observation and 'mirror neuron systems') have traditionally been the focus of research in Europe, social neuroscientists in the US have historically focused on questions concerning the self, the process of stereotyping and our capacity for emotion regulation. Even though such a rather artificial continent-based divide can only take the risk of being proven wrong by many counterexamples, for reasons of simplicity, the following article will mainly focus on summarizing streams of research that have strong associations with European labs, whereas Matthew Liebermann in the same volume will complement this article with a US perspective. Note, that other areas such as the Asian continent have recently developed a great interest in this new field. Furthermore, again for pragmatic reasons, this review will specifically focus on summarizing neuroimaging work in healthy human adults in the domain of social neuroscience. The reader should, however, be aware of the existence of a large body of work highly relevant to the domain of social neuroscience including studies in developmental social neuroscience (see review from Sarah Blakemore in the same special issue), research including patients with social deficits such as patients with brain lesions (for example Adolphs et al., 1994; Beer et al., 2003; Koscik and Tranel, 2010) or patients with social deficits such as those observed in autism spectrum disorder, psychopathy, borderline or narcissistic personality disorders (Bird et al., 2010; Dziobek et al., 2008; Kiehl, 2006; Ritter et al., 2011). Furthermore, the large body of animal literature relevant to the domain of social neuroscience was not reviewed here due to space constraints (see for example excellent recent reviews on the effect of neuroendocrinology on social cognition and behavior Bos et al., 2011; Gordon et al., 2011; Insel, 2010; Meyer-Lindenberg et al., 2011; Ross and Young, 2009).

After summarizing research that has contributed to the identification of different neural systems underlying our ability to understand the minds, actions and feelings of others, a short overview of psychological, as well as neuroscientific, studies focusing on other social emotions such love and compassion follows. In this context, selected studies from the similarly young and neighboring field of neuroeconomics will be highlighted for their focus on processing of social emotions such as our sense of fairness and feelings of revenge and 'Schadenfreude' as well as their investigation of social interaction. Finally, challenges, open questions and future research directions in social neuroscience will be discussed.

## Theory of Mind or mentalizing

Before cognitive neuroscience started focusing on understanding how humans make sense of other human's minds, philosophy (Dennett, 1978; Dennett, 1987b), developmental psychology (Astington, 2001; Leslie, 1987; Wellman et al., 2001; Wimmer and Perner, 1983), clinical psychology (Baron-Cohen, 1995; Baron-Cohen et al., 1985) and primatology (e.g., Povinelli and Bering, 2002; Povinelli and Vonk, 2003; Premack and Woodruff, 1978; Tomasello et al., 2003; Tomasello et al., 1993) had already suggested that understanding other people's minds refers to a special cognitive ability that may or may not be present in other species, that only develops late in human ontogeny and that may be deficient in autistic children. This capacity that has also been termed 'Theory of Mind' (ToM), 'cognitive perspective taking', or 'mentalizing' (Baron-Cohen et al., 2000; Frith and Frith, 1999; Frith and Frith, 2003; Premack and Woodruff, 1978; Wimmer and Perner, 1983) refers to a person's ability to make attributions about mental states such as intentions, desires or beliefs to others (and oneself) and to understand that others have beliefs, desires and intentions that are different from one's own.

In the mid 1990s, after this first behavioral phase, research on ToM extended into the emerging field of cognitive neuroscience. These first imaging studies typically used stories, cartoons, picture sequences or animated geometric shapes to test the human ability to infer attributes about the minds of others in contrast to physical properties of the world (Brunet et al., 2000; Castelli et al., 2000; Fletcher et al., 1995; Gallagher et al., 2000; Gallagher et al., 2002; Goel et al., 1995; Schultz et al., 2003; Vogeley et al., 2001). The related and emerging field of neuroeconomics supplied another type of mentalizing experiments in which subjects are examined while playing strategic economic games with another person outside the scanning room. Brain activation elicited when playing against intentional versus non-intentional actors is compared (Gallagher et al., 2002; McCabe et al., 2001; Rilling et al., 2004; Singer et al., 2004a). Following this initial rather European-based generation of ToM studies, researchers such as Jason Mitchell and Rebecca Saxe made this a prominent topic in the US social neuroscience scene in the last years (Mitchell, 2009; Mitchell et al., 2005a, 2005b; Saxe, 2006; Saxe et al., 2004; Saxe and Kanwisher, 2003).

Several overview studies suggest that these Theory-of-Mind studies have consistently revealed a neural network comprising the posterior superior temporal sulcus (STS), extending into the temporoparietal junction (TPJ), the medial prefrontal cortex (mPFC), and sometimes the temporal poles (TP) (for reviews see Amodio and Frith, 2006; Frith and Frith, 1999, 2003; Gallagher and Frith, 2003; Mitchell, 2009; Saxe, 2006; Saxe et al., 2004). Although this network is commonly referred to as the Theory of Mind or mentalizing network, there are still numerous debates and speculations about the computational processes subserved by the single regions constituting this network. Recently, Rebecca Saxe has advocated that the broad region of right temporoparietal junction, referred to as rTPJ, specifically subserves inferences about mental states and beliefs. This rather domain-specific view of brain functioning has been challenged by others who point out that this region also subserves other rather low-level computations involved in attention and multi-sensory integration (e.g., Corbetta and Shulman, 2002; Decety and Lamm, 2007; Mitchell, 2008; but see Scholz et al., 2009). Jason Mitchell has conducted a series of studies