

Social Cognition and the Brain: A Meta-Analysis

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Abstract: This meta-analysis explores the location and function of brain areas involved in social cognition, or the capacity to understand people's behavioral intentions, social beliefs, and personality traits. On the basis of over 200 fMRI studies, it tests alternative theoretical proposals that attempt to explain how several brain areas process information relevant for social cognition. The results suggest that inferring temporary states such as goals, intentions, and desires of other people—even when they are false and unjust from our own perspective—strongly engages the temporo-parietal junction (TPJ). Inferring more enduring dispositions of others and the self, or interpersonal norms and scripts, engages the medial prefrontal cortex (mPFC), although temporal states can also activate the mPFC. Other candidate tasks reflecting general-purpose brain processes that may potentially subservise social cognition are briefly reviewed, such as sequence learning, causality detection, emotion processing, and executive functioning (action monitoring, attention, dual task monitoring, episodic memory retrieval), but none of them overlaps uniquely with the regions activated during social cognition. Hence, it appears that social cognition particularly engages the TPJ and mPFC regions. The available evidence is consistent with the role of a TPJ-related mirror system for inferring temporary goals and intentions at a relatively perceptual level of representation, and the mPFC as a module that integrates social information across time and allows reflection and representation of traits and norms, and presumably also of intentionality, at a more abstract cognitive level. *Hum Brain Mapp* 30:829–858, 2009. © 2008 Wiley-Liss, Inc.

Key words: social neuroscience; trait inference; theory of mind; goal inference; intentionality

INTRODUCTION

Functional neuroimaging has played a crucial role in seeking to isolate brain regions specific to social cognition. Social cognition broadly includes the cognitive processes used to understand and store information about other persons including the self, and about interpersonal norms and scripts (or procedures) to navigate efficiently in the social

world. Essentially, it requires that perceivers extract and understand the behavioral motives and stable dispositions of themselves and other persons and groups. Humans draw on “social intelligence” to ascribe dangerous behavior to aggressive goals (she wants to hurt me) and traits (she is always so aggressive). To do this, we often refer to the other's thoughts and beliefs, as if we can read their mind. This capacity is known as theory of mind (ToM) or mentalizing. Although many species including primates can accurately predict the goals of their conspecific's behavior, it appears that only humans can separate a mental perspective of their own actions from that of others' actions [Emery, 2005]. When explaining a person's behavior in terms of a goal, desire, or trait, we recognize that this mental representation does not necessarily correspond to our own interpretations or to reality.

Social cognition, and mentalizing in particular, is a high-level capacity. It has been studied from various theoretical and methodological perspectives, most notably social psy-

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chology and social neuroscience. Social psychologists have investigated how we perceive and interpret our social environment including other persons, groups, and the self, how we build social knowledge structures that reflect the norms and values of society, and how this is influenced through conscious and unconscious processing mechanisms, which sometimes lead to biased judgments [e.g., Gilbert and Malone, 1995; Trope and Gaunt, 2000; Van Rooy et al., 2003]. Neuroscientists have analyzed which structures in the brain support the mental processes involved in social cognition. It is commonly assumed that the capacity to mentalize depends on cognitive brain mechanisms that are potentially dedicated specifically to social reasoning. Neurological evidence from studies of brain lesions [Apperly et al., 2004; Wood et al., 2005] and autism [Baron-Cohen, 2006; Frith and Frith, 1999, 2001] supports this hypothesis. The advance of brain imaging and especially functional magnetic resonance imaging (fMRI) which allows unprecedented precision and validity in the localization of brain activity, provides a powerful tool for increasing our understanding of the neural activity in the brain that is associated with social cognition processes [for an introduction to fMRI, see Huettel et al., 2004].

The main goals of this article are to explore the brain areas that are held responsible for social reasoning, to analyze what specific sub processes or functions are computed in these areas, and to look for other brain systems that may support this social cognition capacity. Although there have already been reviews and perspectives on the neural correlates of social cognition, most of them lack an exhaustive overview of the available evidence. Therefore, this article presents a meta-analysis on a larger scale of many processes involved in social cognition that have been explored with fMRI since the turn of the millennium. It focuses on “cold” processes of social reasoning, and only touches briefly on “hot” or affective processes.

Because a purely data-driven approach would undoubtedly miss some important questions and insights that have already been developed earlier, this analysis will start with an overview of recent theoretical insights and perspectives. Functional neuroimaging can provide answers to these theoretical debates and questions because it demonstrates whether two tasks or processes engage common or distinct brain mechanisms. This relies on the key assumption that different areas are related to qualitative differences in psychological processes. However, this assumption is not necessarily correct [Henson, 2006; Saxe et al., 2004a]. Each brain region may contain thousands of neurons with distinct functions that cannot be teased apart with the current techniques. Hence, when two tasks activate the same area, it may well be that the fMRI technique is too rough and that what seems a common area may in fact reflect a distinct location and different processes. Conversely, even if we assume that the same brain area and process is involved, it may be that this region is more strongly recruited for social cognition than for any other process, as if the underlying general neural architecture has become

specialized for a particular social function. In conclusion, a single study is unlikely to be decisive, and an exhaustive overview of evidence might potentially provide more reliable answers.

Theoretical Perspectives on Social Cognition

Most social and developmental psychologists conceive social cognition as involving a plethora of different social inferences. Cross-cutting these finer distinctions, however, one can divide social processes in two major types of mental inferences: (1) inferences of transitory states (goals and intentions) and (2) inferences of enduring characteristics (personality traits and social scripts). It is generally believed in social and development psychology that transitory goal inferences are more perceptual in nature and directly related to observed behaviors, whereas enduring dispositions involve abstract inferences that require a more mature capacity to mentalize.

The division parallels many similar distinctions in social psychology. Perhaps, the most popular view is that observers first identify and categorize a person’s behavior (e.g., helpful gesture) and then attribute the corresponding trait to the actor [e.g., he or she is helpful; Gilbert and Malone, 1995; Trope and Gaunt, 2000]. A related perspective is that we first identify the intentions, desires, or motives of an actor spontaneously [Fein, 1996; Hassin et al., 2005; Heider, 1958; Malle, 1999; Read and Miller, 1993] and that this process shapes the trait inferences we subsequently make. For instance, when an actor engages in helpful behavior, we wonder which reasons or motives may have compelled the actor to do so (out of sincere desire to help or to ingratiate?) and this influences whether we make a trait attribution of helpfulness or insincerity [Malle and Knobe, 1997; Malle et al., 2000; Reeder et al., 2002, 2004].

This division is also reflected in children’s development of social mentalizing. Infants of 5- to 8-month-old have a sense of goal-directed behavior and look longer when the target of a movement changes than when the path towards the same target changes [Woodward, 1998]. At the age of 18 months, children can complete an action that they have seen an adult attempt, but did not finish [Frith and Frith, 1999]. At the age of 3 or 4 years, children describe representational mental states or beliefs of others, distinct from their own, with a limited repertoire of mental concepts, such as desires and perceptions [Saxe et al., 2004a]. However, it is only by the age of 7 or 8 years that they show a marked increase in the use of personality traits and begin to appreciate that people have stable dispositions that help to predict future behaviors across different situations and that should be distinguished from situational pressures [Hagá and Garcia-Marques, 2007; Rholes et al., 1990].

A mentalizing capacity is perhaps most clearly demonstrated in “false” belief tasks, because this task requires distinguishing between own and other beliefs. A typical example of a false belief task is when, in a verbal or car-

toon story, unbeknown to an actor (but in full view to the participant) an object (e.g., sweet) is switched between two boxes (or the boxes are switched), so that after returning, the actor points to the wrong box when asked where the sweet lies. The participant must then identify where the actor (falsely) believes the sweet is. For instance, a child's mother moves a chocolate from the green to the blue cupboard while the child is outside playing. The participant is then asked to report the content of the actor's belief (Where does the child think the chocolate is?) or to predict the actor's action (Where will the child look for the chocolate?). Most children before the age of 4 are unable to distinguish the actual location of the chocolate (blue cupboard) from the actor's false beliefs on the former location (green cupboard), and use the actual location to infer the actor's belief. However, children of all ages perform better on false beliefs tasks when the (true) location of the target object is less salient, such as when the chocolate is eaten [Saxe et al., 2004a; Wellman et al., 2001]. Patients with lesions in the temporo-parietal junction, who generally fail on false belief tasks, are able to indicate the correct box when the actor does not point at the wrong location [Apperly et al., 2004]. These children or patients have difficulties dissociating the actor's false goal from their own correct goal, but less so when their own (true) goal location is absent or less salient.

The diversity in social inferences is consistent with neuroscientists' modular view on the brain, where social cognition is seen as a neural circuit with a set of related and highly intertwined, but separate processes that are each specialized in some aspect of the social mentalizing system. Brain imaging techniques have identified two main areas responsible for human social cognition—the temporo-parietal junction (TPJ) and the medial prefrontal cortex (mPFC; see Fig. 1A,B). According to some authors, mentalizing is a high-level mental process that is subserved mainly by cortical midline structures, especially the mPFC [e.g., Amodio and Frith, 2006; Gallagher and Frith, 2003]. On the other hand, an increasing number of authors suggest that the TPJ has specific social functions of its own, in particular for identifying the goals or intentions behind behaviors, together with the aid of "mirror neurons" [e.g., Gallese et al., 2004; Keysers and Gazzola, 2007; Saxe and Powell, 2006; Uddin et al., 2007].

I begin with a brief review of the functions of the temporo-parietal cortex and the mirror system, followed by the functions of the mPFC. This overview is based on the most recent perspectives in this area based on brain imaging data and additionally supported by data from single-cell recordings and lesion studies. There are probably as many different theoretical perspectives as there are major researchers in the social neuroscience field, so that it is impossible to include all relevant views here. Next, the meta-analysis is presented and the results are discussed in view of the theoretical claims made earlier. I end with a short discussion of topics that are of interest for social psychology and social neuroscience.

How the Temporo-Parietal Cortex identifies Action Goals: The Mirror System

Mirror neurons in the motor and associative cortex of humans and monkeys discharge not only when specific actions are executed, but also when these same actions are observed in other animals or humans [Gallese et al., 2004; Keysers and Perrett, 2004]. They allow identifying the underlying goals of a biological movement, by matching the perceived behavior with one's own behavior, and the most common goals associated with it.

This mirror mechanism is a very attractive proposal because it provides a very simple and elegant explanation for automatic inferences of self and other's intentions. How does it work? As depicted in Figure 1C, single-cell recording studies with monkeys and fMRI studies with humans has revealed that the mirror system consists of a cortical structure involving the superior temporal sulcus (STS), the inferior parietal lobe (IPL) or parietal mirror system, and the premotor cortex (PMC) including the inferior frontal gyrus (IFG) or frontal mirror system [homologous to the F5 in monkeys; Gallese et al., 2004; Iacoboni, 2005; Keysers and Perrett, 2004]. Visual information in the STS is propagated to the IPL (~60% of the neurons in the monkey), where it is passed to the PMC (~20% of the neurons). The PMC region is responsible for action execution. There the perceived action, its future path and intention is recognized and identified by its resemblance to one's own actions, and this information is passed back to the IPL [Iacoboni, 2005; Keysers and Perrett, 2004]. Thus, the shared representation of other and self movements and intentions supplements observed visual input with inferences about what is not immediately visible but very likely to occur next. In a sense, the IPL "sees" the intentions behind other's actions by "simulating" or "matching" the actions of others in a shared representation [but see Jacob and Jeannerod, 2005, for a different view]. Perhaps, the mirror system developed this social function on top of an earlier and more basic function for fine-tuning one's movements on the basis of visual feedback from one's own movements [Keysers and Perrett, 2004].

The mirror system implies that goals and intentions do not require a high-level propositional or symbolic representation. Instead, a rudimentary coding of the anticipated spatial end-state of an action may suffice. Single-cell recordings in macaque monkeys demonstrate that different mirror neurons discharge when a movement (e.g., grasping) is part of different end-state. Thus, when a monkey reaches for food and brings it to the mouth (e.g., for eating), different mirror neurons are activated than when the monkey places the food aside [e.g., for placing; Fogassi et al., 2005]. Similar goal identifying brain regions have been documented in the IFG of the human brain [Iacoboni et al., 2005]. Yet, some authors hypothesized that the left IPL is connected to the language motor system (Broca area) via the mirror system, so that a more symbolic representation may

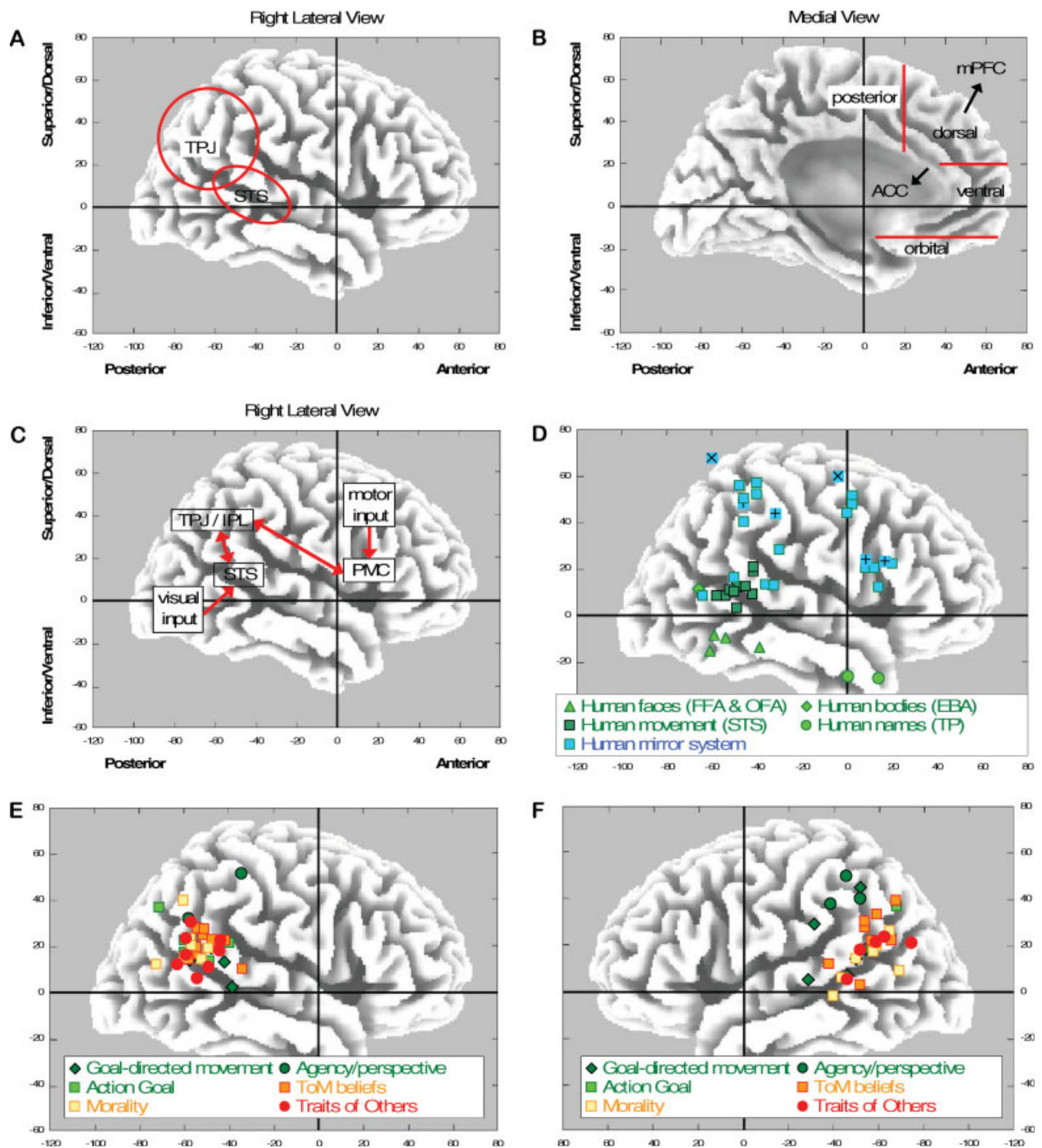


Figure 1.

[A,B] The anatomy of the human brain, and the major areas involved in social cognition, placed in x-y-z stereotactic atlas. Left-right (not shown) reflects the anatomical x-axis, posterior-anterior at the bottom reflects the anatomical y-axis, and inferior-superior (or ventral-dorsal) on the left reflects the anatomical z-axis. [C] The mirror system: Visual input in the STS is propagated to the TPJ/IPL, and further to the PMC where it is compared with own action schemas and associated goals. The matched goal behind the action detected at the PMC is sent back to the TPJ/IPL (for goal identification) and STS (for agency

identification). [D] How a human, its body (parts), movements and name are represented in the brain in the FFA (Fusiform Face Area), OFA (Occipital Face Area), EBA (Extrastriate Body Area), STS (Superior Temporal Sulcus) and the anterior Temporal Pole, and how the mirror system is recruited for observing (posterior areas) and executing (anterior areas) movements of mouth/face [+], hand/arm [□] or foot [×]. [E,F] The TPJ involved in social inferences of intentionality and traits; right and left lateral view, respectively. The studies involved in D-F can be identified via the y-z coordinates in Table I.

facilitate reasoning on other's goals and intentions [Iacoboni, 2005; Rizzolatti and Arbib, 1998].

It is important to note that although many mirror neurons in the STS respond to the same degree for other and own movement, a selective number of mirror neurons discharge only to visual information on other's movements, and tend to be inhibited by own movements and kinesthetic information [Keysers and Perrett, 2004]. These viewpoint-other mirror cells allow the brain to resolve the issue of the identity of the actor. This provides us with a direct and automatic sense of agency or ownership, or the experience that body and movements are one's own or from someone else.

If the IPL mirror area is capable to infer the motor intentions of others on the basis of simple action observations, then it appears very plausible that the IPL or a related parietal mirror region could identify intentions that are of a more complex social nature. As this meta-analysis will reveal, the TPJ which extends from the STS to the IPL, is the most likely candidate for such a mirror area of social cognition. If true, the TPJ should be involved in making the following inferences:

- Inferring the intention underlying a perceived social movement or behavior.
- Identifying the agent of a social action as the self, or as distinct from the self.
- Distinguishing social intentions of the self from those of someone else, even when they diverge.

The mirror system goes a long way towards explaining action and intention understanding. However, evidence for the involvement of a mirror system in more abstract and long-term forms of mentalizing is lacking. Instead, the prefrontal cortex seems to be more involved in the processing of long-term traits of self and others, and interpersonal knowledge on norms and scripts [Keysers and Gazzola, 2007; Uddin et al., 2007].

How the mPFC Identifies Social Beliefs, Traits, and Scripts

Long-lasting social dispositions and interpersonal knowledge such as personality traits and social rules involve the capacity to remember the behaviors of people over a long stretch of time under multiple circumstances, to recognize the common goal in these behaviors and to link them to the actors' most likely plan of past and future actions. For instance, to infer whether a person is socially skilled, one needs to observe his or her behaviors under easy and difficult circumstances (e.g., talking to one person or before an audience), and infer how he or she reacts under various goals (e.g., under free choice or coercion). There is growing evidence indicating that attributing traits and scripts involves the mPFC. This brain area has a high degree of interconnectivity through connections from the dorso-lateral prefrontal cortex (PFC), the anterior STS, the TPJ, and other brain regions. Therefore, the mPFC can handle considerable neural input, and this may contribute

to the capacity of the mPFC to implement more abstract inferences [e.g., Amodio and Frith, 2006; Leslie et al., 2004; Northoff and Bermpohl, 2004]. Unfortunately, there is as yet no computational account of the mechanisms that underlie this mentalizing ability.

In social psychology, trait inferences have been typically viewed in terms of internal causal attributions that obey the general-purpose causality principles of contingency or covariation [Kelley, 1967] in much the same way as causal attributions for physical events. These theories emphasize the causal role of the actor in producing the behavior, unless external environmental factors constrain his or her freedom and mitigate his or her causal role. Perceivers automatically attribute the behavior to a correspondent trait of the actor, and discount the inference to the actor on the basis of situational circumstances if present and relevant [although this is sometimes done insufficiently; Gilbert and Malone, 1995; Gilbert et al., 1988; Trope and Gaunt, 2000]. This is typically seen as a high-level reflective reasoning process involving "an iterative or even simultaneous evaluation of the various hypotheses before reaching a conclusion" [Trope and Gaunt, 2000, p. 353].

In social neuroscience, a number of general-purpose evaluative and executive brain functions in the medial or lateral areas of the PFC have been proposed as subserving or facilitating trait inferences. Several authors have even suggested that maintaining different representations of self and other's intentions or beliefs is a high-level capacity mediated by the PFC [e.g., Amodio and Frith, 2006; Decety and Chaminade, 2003; Frith and Frith, 2001; Gallagher and Frith, 2003; Leslie et al., 2004]. The following functions have been proposed and are explored in this meta-analysis:

- Emotional inputs (i.e., from the amygdala and orbital part of the PFC) may aid the formation of positive or negative evaluations about the self or others, which are a key component of trait inferences.
- Monitoring one's behavior and in particular inhibiting irrelevant cues [e.g., Amodio and Frith, 2006] may help to discard one's own beliefs and contemplate beliefs from others.
- Focusing one's attention selectively on others instead of the self has also been suggested as a crucial process subserving mentalizing [e.g., Leslie et al., 2004].
- Working memory may aid in the representation of different perspectives of self and others and in the decoupling of mental states from reality.
- Episodic retrieval may aid trait inferences of self and others.

Alternatively, recent neurological evidence suggests that neurons in the mPFC are uniquely oriented to time and fire over extended periods of time and across events [Huey et al., 2006; Wood and Grafman, 2003]. This has led to the hypothesis that the mPFC serves the integration of social information over time, by storing this information in

traits or scripts [Huey et al., 2006]. Evidence from single-cell recordings in rats [Runyan et al., 2004] documented that the mPFC is crucially involved in the learning of long-term storage of information associating multimodal but temporally disconnected events. The neurons can continuously fire during an interval between an input and a delayed output. The mPFC stores these temporally disconnected events before or in parallel to hippocampal memory (believed to be the typical storage for episodic events). Likewise, Matsumoto and Tanaka (2004) reviewed several single-cell studies with monkeys and reported that mPFC cells show increasing activation during the initial steps of learning a novel sequence of actions, and this activity avoids rejection of early steps that go unrewarded initially, but when maintained are rewarded in the final steps. A lesion study involving rabbits [McLaughlin et al., 2002] demonstrated that lesions to the mPFC delay trace conditioning (that requires forming associations between intervals that extend several seconds), but not conditioning at shorter intervals. In a lesion study with humans, Wood et al. (2005) documented that patients with lesions in the right ventral PFC (who show socially inappropriate behavior in their everyday life) are impaired to inhibit inappropriate parts of a social script sequence.

This meta-analysis seeks evidence for these alternative accounts of the social cognition process in the mPFC, and explores to what extent each of them receives support. It does so by identifying the brain areas in the mPFC that subserve social inferences of traits and scripts and comparing them with the areas involved in general-purpose functions to assess how much they might contribute to social inference. If general-purpose functions of causality, emotion, and supervisory execution are core components of social reasoning, their activations should overlap considerably with social activations in the mPFC. On the other hand, if they only aid and facilitate social inferences, they will overlap less.

METHOD

The studies reviewed in this article were identified by searches in PubMed, ScienceDirect, and PsychInfo by the term “fMRI” along with at least one of the following terms “person,” “self,” or “social” in the title or abstract (or keywords when available to search). The search was confined between January 2000 and April 2007. For more complete coverage, I inspected several review articles from which I identified additional articles [Amodio and Frith, 2006; Beer and Ochsner, 2006; Decety and Chaminade, 2003; Frith and Frith, 2001; Gallagher and Frith, 2003; Grèzes and Decety, 2001; Matsumoto and Tanaka, 2004; Mitchell, 2006; Northoff and Bermpohl, 2004; Ochsner et al., 2004a; Olsen et al., 2007; Saxe et al., 2004a; Todorov et al., 2006]. In addition, to augment these studies with other functions that might be relevant to social cognition and that might activate the same brain areas, additional fMRI studies which also appeared between January 2000 and April 2007

besides those identified in the general search, were included for the following tasks:

- Script sequences learning and response sequences learning (excluding motor sequence learning) identified by searches in PubMed and ScienceDirect by the term “fMRI” along with at least one of the following terms “sequence,” “script,” or “trace” in the title or abstract (or keywords when available to search).
- Causal attribution identified by searches in PubMed and ScienceDirect by the term “fMRI” along with at least one of the following terms “cause,” “causal,” or “attribution” in the title or abstract (or keywords when available to search).
- Emotional judgment and processing by including the studies listed in the review by Ochsner et al. (2004a).
- Response conflict and inhibitory control by including the studies listed in the meta-analysis by Neumann et al. (2008).
- Executive and memory functions of the prefrontal cortex by including the brain coordinates from the meta-analysis by Gilbert et al. (2006; their article search was confined between January 1999 to October 2004; the peak coordinates are reported in that article).

Studies were included only if they investigated unmedicated healthy children or adults, used fMRI scanning (unless reported otherwise), and reported the coordinates of activations in the space of the MNI template [Collins et al., 1994] or the atlas of Talairach and Tournoux (1988). When activations were reported in MNI space they were transformed into Talairach and Tournoux coordinates, using a nonlinear transformation (<http://imaging.mrc-cbu.cam.ac.uk/imaging/MniTalairach>) so that all coordinates were in a common stereotaxic framework. I restricted the brain areas to the regions of interest, including the superior temporal sulcus (STS), temporo-parietal junction (TPJ) bilaterally, lateral prefrontal cortex (PFC) bilaterally, and medial prefrontal cortex (mPFC). For convenience, I included the anterior part of the cingulate cortex in the mPFC throughout this review (see Fig. 1B). I included all the studies that reported a priori defined tasks, even if their peak activation coordinates did not fall within any of these expected regions so that the proportion of studies satisfying the expected localization could be estimated. The reported activations were restricted to significant contrasts involving a comparison between an experimental versus base-line control task or, in a limited number of studies, a parametric correlation with an experimental variable. If both types of outcomes were available in a single study, then only the coordinates involving the more relevant parametric correlation with the task of interest is reported. The contrast involved either increase or decrease in activation.

Task categories were identified that included components that were most identical among a set of similar studies, to create large enough samples of comparable functions of mental processes. Additional features of the

studies were also categorized. The stimulus material was categorized as visual versus verbal (see Table I), and the instructions were coded either as directing the participants explicitly to the process under study, or not and involving implicit social inferences (see “SSI” in Table I). When the description of tasks, stimuli, and especially instructions was not clear-cut (e.g., no example or verbatim reports), the characterization by the authors was used for categorization. Classification of all studies proceeded in two steps. The first classification was provisional after the first reading of each article. A second and third classification was made about 1 and 3 months later, after rereading the relevant article sections and a decision was made to maintain or alter the original classification. This second and third reading generally confirmed the initial subdivision of task categories, although a few initial subcategories were collapsed or removed due to an insufficient number of studies to permit reliable conclusions. Table I lists all the studies included in this meta-analysis under the heading of each task category as classified in the final round. As can be seen, each task category incorporates a number of highly similar task components and control conditions.

Activations were accepted as significant according to the criteria set by each study. To ensure that the activation peaks entered into the meta-analysis resulted from independent contrasts, the reported coordinates were restricted to one per study and task category. In a limited number of cases, two activations were reported, one for each different task components of interest (e.g., two separate negative emotions) or different sample of participants. The retained coordinates involved the most significant activation peak for each of the regions of interest. Each activation peak was classified as medial when its distance on the x -axis (left-right axis) did not exceed 20 mm (although most studies were within a 12 mm distance, see Table I). For simplicity and coherence, a few small exceptions beyond the 20 mm limit were occasionally allowed if the majority of the conditions/studies were in the medial area, and vice versa for the lateral categorization (indicated in bold in Table I). Conventional t -tests confirmed that the mean x -coordinate for each task category was never significantly different from zero for the medial localization and significantly different from zero for the lateral localization (see Table I).

Because statistical tests were computed on dichotomous codings (i.e., presence or absence of activation), all tests were nonparametrical. Comparisons between brain areas involved Cochran’s Q , and between sets of studies (e.g., task categories) involved Kruskal-Wallis analysis of variance (ANOVA). Correlations were computed using Goodman-Kruskal’s gamma (Γ). All these tests are implemented in Statistica 7.0.

RESULTS

All the coordinates involved in this meta-analysis are listed in Table I, and the main results and statistical tests are summarized in Table II. As shown in Table II, Cochran

tests revealed that most tasks elicit differential activation across the various regions of interest, consistent with the idea that different areas are preferentially engaged in distinct processes (i.e., tasks) of social cognition. In addition, Kruskal-Wallis’ ANOVAs reveal to what extent these activations are consistent or different throughout similar task categories that span action intentionality (Tasks 1–5), trait inferences and scripts (Tasks 6–10), emotions and other general-purpose functions (Tasks 11–18).

Table III lists the nonparametric Goodman-Kruskal Γ between the presence of activation and (visual-verbal) material or (explicit-spontaneous) instructions. These two latter extraneous variables are largely independent, $\Gamma = 0.06$, ns. Table III demonstrates that for social inferences (Tasks 1–10), in general, the TPJ is more engaged given visual material and spontaneous instructions, whereas the mPFC as a whole is more engaged for verbal material. However, with respect to instructions, the dorsal part of the PFC is more engaged during spontaneous inferences (in line with the TPJ) while the ventral part is more engaged during explicit inferences. The right PFC is more engaged given visual material and the left PFC is more implicated during explicit instructions (perhaps reflecting a rehearsal of verbal instructions). It is obvious that material and instruction have a significant influence on brain activation beyond the social tasks involved, and this is further discussed in the following sections when appropriate.

Where We Aim to: Action Goals and Intentions

Recent fMRI research has revealed that the perception of social information and in particular goal-directed behavior is supported by (a) incoming information from the visual system that detects and represents biological information, such as human faces, bodies, and movements, and (b) the mirror system that identifies the goals behind these behaviors. Although this issue is not part of this meta-analysis, it is informative to sketch a relevant background against which social information is processed. Therefore, I first briefly describe this visual and mirror system.

Identifying the social other

Where and how is the visual input on biological or social stimuli and movements represented and analyzed by the human brain? I selected an illustrative fMRI study by Grossman and Blake (2002) as well as other studies that reported several distinct areas from the primary visual system and the temporal cortex that are involved in identifying humans and human movement (for a more extensive review, see Allison et al., 2000). In addition, I included a number of illustrative studies highlighting the brain areas involved in the mirror system for identifying simple movement (see Fig. 1D).

- The recognition of human faces involves two regions known as the fusiform and the occipital face area [FFA and OFA; but see also Turk et al., 2005];

TABLE 1. Major task categories, stimuli, instructions and corresponding Talairach coordinates

Study	Year	Stimuli	Instruction	Target	Control	Talairach Coordinates												
						IFFA&OFA	rFFA&OFA	IFFA&OFA	rFFA&OFA	IEBA	rEBA	ISTS	rSTS	iIPL	rIPL	iPMC	rPMC	
Human faces (Frontal & Occipital Face Areas - FFA & OFA)																		
Summerfeld et al.	2006	face picture	viewing	human faces	objects (human-made)	-34	-78	-15	46	-59	-9	44	-61	-15				
Turk et al.	2005	face picture	viewing	name (identity)	occupation	-34	-40	-15	38	-39	-14							
Grossman and Blake	2002	face picture	viewing	human faces	bodies (or objects)	-35	-55	-12	38	-54	-10							
Grossman and Blake	2002	face picture	viewing	human faces	bodies (or objects)	0.00	0.75	0.00	0.00	1.00								
Human bodies (Extrastriate Body Area - EBA)																		
Grossman and Blake	2002	pictures & videos	viewing	(headless) bodies	objects	-39	-70	14	41	-66	11							
Human movement (Superior Temporal Sulcus - STS)																		
Carter and Peephay	2006	animation	viewing	human + robot movement	non-biological	-45	-56	14	59	-42	19							
Grossman and Blake	2002	point light video	viewing	body movement	random movement	-41	-52	11	46	-49	12							
Bonds et al. (PET)	1996	point light video	viewing	body movement	random movement				56	-54	8							
Saxe et al.	2004	body video	viewing	body movement occluded	body movement visible				54	-42	9							
Mosconi et al.	2005	animated gaze by other	viewing	gaze toward target cue	gaze away from target cue				60	-52	11							
Schibach et al.	2006	animated gaze by other	viewing	gaze towards self	gaze away from self				42	-42	21							
Peephay et al.	2004	animated gaze by other	viewing	gaze towards self	gaze away from self				-50	10								
Puce et al.	1998	animation	viewing	gaze movement	no gaze movement	-46	-53	5	49	-49	3							
Wicker et al. (PET)	1998	video	viewing	gaze movement	no gaze movement	-44	-68	4	42	-58	8							
Puce et al.	1998	animation	viewing	mouth movement	no mouth movement	-47	-50	2	50	-49	3							
Peephay et al.	2004	animation	viewing	grasping movement	incorrect grasp	-47	-77	14	56	-45	12							
Human names (temporal pole)																		
Sugiura et al.	2006	names	(un)familiar name?	personal (or famous)	unfamiliar	-32	10	-29	28	14	-28							
Sugiura et al.	2006	names	(un)familiar name?	personal (or famous)	unfamiliar	-55	-5	-27	55	1	-27							
Human mirror system																		
Iacoboni et al.	2005	hand movement	viewing / imitate	intention	movement													
Molnar-Szakacs et al.	2005	hand movement	viewing + imitate (both)	intention	movement													
Van der Graag et al.	2007	facial movement	viewing + imitate (both)	movement	no movement	-34	-52	49	34	-46	48							
Grèzes et al.	2003	hand movement	viewing + imitate (both)	not object-related	no movement	-32	-44	50	30	-46	50							
Grèzes et al.	2003	hand movement	viewing + imitate (both)	object-related	no movement	-34	-48	56	32	-48	56							
Koski et al.	2003	finger movement	viewing / imitate	imitation	observation													
Koski et al.	2002	finger movement	viewing / imitate	imitation	observation													
Iacoboni et al.	2001	finger movement	viewing / imitate	imitation	observation													
Iacoboni et al.	2001	finger movement	viewing / imitate	imitation	observation													
Iacoboni et al.	1999	finger movement	viewing / imitate	imitation	observation													
Buccino et al.	2001	mouth movement	viewing	object-related	no movement	-36	-52	56	52	-32	44							
Buccino et al.	2001	hand/arm movement	viewing	object-related	no movement	-36	-40	52	40	-40	52							
Buccino et al.	2001	foot movement	viewing	object-related	no movement	-32	-64	60	24	-60	68							
						0.15	0.00	0.38	0.00	0.46	0.00	0.62	0.00	0.77	0.00	0.77	0.00	

TABLE 1. (Continued)

		ITPJ	rITPJ	dmPFC	vmPFC	IFC	rPFC	rPFC
1. Goal-directed movement								
Fornuft	2003	animations with shapes	s	movement / causality judgment	causality judgment	movement judgment		
Hamilton & Grafton	2006	in press video	s	SSI (viewing)	goal of action	hand movement	12 63 20	42 12 16
Hamilton & Grafton	2006	video	s	SSI (viewing)	goal of action (with objects)	hand movement		
Schultz et al.	2004	animations with shapes	s	SSI (viewing)	chases goal of target object	chases path of target object		
Cherishi et al.	2004	animations with shapes	s	SSI (viewing)	goal-directed reactivity	hand movement		
Martin & Weisberg	2003	animations with shapes	s	SSI (viewing)	goal-directed reactivity	physical reactivity	4 56 25	36 17 25
Blakemore et al.	2003	animations with shapes	s	movement / causality judgment	goal-directed reactivity	physical reactivity	1 41 -13	
Blakemore et al.	2001	animations with shapes	s	movement / causality judgment	physical reactivity	no physical reactivity		
				0.14	0.73	0.00	0.63	0.00
								0.29
2. Agency/perspective								
David et al.	2006	virtual ball toss	s	who is producing movement?	other	self		
Farrer & Frith	2002	moving joystick	s	who is producing movement?	other	self	57 -34 51	
Aichorn et al.	2006	visual scenes	s	take perspective of	other	self	-48 -52 40 44 -58 32	-51 23 30 44 6 46
Vogelley et al.	2004	visual scenes	s	take perspective of	other	self	-40 -46 50	-38 28 48
				0.00	0.75	0.08	0.50	0.50
								0.50
3. Action Goal								
Blakemore et al. (Adults)	2007	action/event stories	b	SSI (choose story ending)	intentional action	physical event		
Blakemore et al. (Young)	2007	action/event stories	b	SSI (choose story ending)	intentional action	physical event	-42 -68 37 48 -71 37	-9 62 8
Völlm et al.	2006	action/event cartoons	b	SSI (choose story ending)	intentional action	physical event	-45 -68 37 48 -60 22	0 53 17
den Ouden et al.	2005	action/event stories	b	SSI (choose story ending)	intentional action	physical event	-53 -57 19 53 -60 17	15 37 51
Walter et al.	2004#1	action/event cartoons	b	SSI (choose story ending)	intentional action	physical event	-42 -68 37 48 -71 37	-9 62 8
Walter et al.	2004#2	action/event cartoons	b	SSI (choose story ending)	intentional action	physical event	56 -48 14	6 33 18
Saxe & Wexler	2005	desire stories	b	SSI (reactions to story ending)	social background violating	compatible desire	6 49 -13	-42 31 -14
				0.00	0.71	0.00	1.00	0.14
								0.86
								0.14
								0.00
4. ToM beliefs								
Saxe & Powell	2006	action/object stories	b	SSI (read)	true belief	physical appearance		
Ferri & van Cramon	2002	action/object stories	b	identify with actors	true belief	unrelated event	-50 -54 28 56 -55 17	0 46 42 -9 50 0
Sommer et al.	2007	action cartoons	b	action actor expected?	false belief	true belief	-50 -65 25	-19 49 30
Perner et al.	2006	action/object stories	b	several questions	false belief	outdated photo	34 -51 25	
Saxe et al.	2006	action/object stories	b	several questions	false belief	outdated photo	-48 -54 30 53 -54 28	-15 54 30
Saxe & Kanwisher	2003#1	action/object stories	b	SSI (one-back matching)	false belief	physical event	-45 -68 38 56 -54 18	0 56 8
Saxe & Kanwisher	2003#2	action/object stories	b	several questions	false belief	outdated photo	-53 -57 22 50 -51 27	6 56 14
Vogelley et al.	2001	action/object stories	b	several questions	false belief	physical event	-48 -60 33 53 -49 19	6 56 26
Gallagher et al.	2000	action cartoons	b	several questions	false belief	physical event	-54 -66 22 60 -46 22	-56 28 16
Wang et al. (adults)	2006	action/event stories	b	did speaker meant it?	irony (false communication)	no irony	6 56 26	22 46 46
Wang et al. (children)	2006	action/event stories	b	did speaker meant it?	irony (false communication)	no irony	-10 48 12	42 8 46
Grèzes et al.	2006	videos of people lifting box	s	misled about weight?	pretended action	perpetuator of deceit	-12 50 -10	
Grèzes et al.	2004	videos of people lifting box	s	misled about weight?	pretended action	true action	2 44 -10	
German et al.	2004	videos of short actions	s	SSI (video complete?)	pretended action	true action	4 48 20	53 14 7
Spiers & Maguire	2006	virtual taxi driving	s	SSI (thoughts measured later)	thoughts on others	no thoughts while driving	-50 -52 3 56 -58 14	-39 14 -13 33 20 -11
				0.00	0.60	0.00	0.73	0.13
								0.00
								0.33

TABLE I. (Continued)

				ITPJ	rTPJ	dmPFC	vmPFC	IPFC	rPFC
5 Morality									
Heekeren et al.	2005	action stories		-55 -59 20	57 -57 23		3 57 8		
Heekeren et al.	2003	action stories	moral	-49 -59 21		6 61 27		-42 34 -6	
Borg et al.	2006	action stories	moral	-53 -59 9	50 -72 12		-12 49 -10	-42 46 25	
Moll et al.	2002	statements	moral	-47 -40 -2			-10 46 -12		
Moll et al.	2001	statements	moral		47 -60 15		4 54 3	-28 57 19	41 56 13
Robertson et al.	2007	action stories	moral	-59 -50 14	65 -52 14	2 48 29			
Greene et al.	2004	action stories	moral-personal	-45 -58 17	46 -49 19		0 54 18		
Greene et al.	2001#1	action stories	moral-personal	-48 -55 25	50 -57 20		1 52 17		45 38 24
Fiddick et al.	2005	moral norms	normviolating judgment		55 -60 40	0 45 42		-51 23 -8	51 23 -8
Berthoz et al.	2002	action stories	normviolating	-50 -44 6			-8 52 18	-52 32 2	
				0.00 0.80 0.00	0.70 0.27	0.30 0.26	0.70 0.00	0.50 0.00	0.30
6 Traits of Others									
Mitchell et al.	2006	face-action stories	person judgment			-12 40 45			
Mitchell et al.	2005c	face-action stories	person judgment			-9 54 30	0 40 -17	-53 21 7	50 26 -9
Mitchell et al.	2004	face-action stories	person judgment			-12 51 31			
Mitchell et al.	2005a	trait words	person judgment		50 -57 30	9 54 30			
Ochsner et al.	2005#2	trait words	person judgment	-50 -59 21	51 -59 23	-12 48 31	-10 51 1	-38 12 44	
Mason et al.	2004	action words	person judgment			10 48 34			26 16 45
Mitchell et al.	2002	noun-trait pairs	person judgment	-51 -75 21	48 -63 12	0 54 21	3 39 0		
Mitchell et al.	2005b	faces	pleasantness judgment	-50 -46 5	56 -49 11	-9 51 31		-45 12 16	
Heberlein & Saxe	2005	point light video	person (trait) judgment	-53 -63 23	59 -44 22		-10 47 6		
Turk et al.	2004	faces	person preference judgment		40 -59 16	0 40 16			36 23 -1
Harris et al.	2005	action stories	person judgment		60 -44 18	-2 46 28	5 50 0		25 50 19
Mitchell et al.	2006	face-action stories	trait-diagnostic			-3 49 42			
Todorov et al.	2006	face-action stories	trait-diagnostic			-5 50 37		-14 31 31	
Iacoboni et al.	2004	video clips	2 persons interacting	-38 -52 18		-2 52 26			56 22 0
Plante et al.	2004	mind in eyes test	mind in eyes test			5 34 57		-46 28 19	42 22 47
				0.00 0.33 0.00	0.53 0.16	0.93 0.50	0.33 0.00	0.33 0.00	0.40
7 Person in games									
Fukui et al.	2006	chicken game	human opponent			-8 43 35			
Tomlin et al.	2006	trust game	human opponent	-57 -51 28		0 35 10			
Rilling et al.	2004	ultimate & PD games	human opponent		48 -55 27	3 44 20			
Gallagher et al.	2002	stone-paper-scissors	human opponent			-10 50 30	8 54 12		
Elliott et al.	2006	gambling game	human opponent	-48 -60 31		-6 51 28		-45 51 -9	45 36 30
Berns et al.	2005	mental rotation	conform to others		24 -65 38				
Akitsuki et al.	2003	gambling game	4 wins (or 4 losses)			12 58 22			
				0.28	0.29	0.67 0.86	0.14	0.14	0.14
8 Close others									
Mitchell et al.	2005b	faces	s describe person				9 55 0		
Ochsner et al.	2005#2	trait words	close other			-2 55 16			
Schmiz et al.	2004	trait words	close other			-4 56 1			
Heatherton et al.	2006	trait words	close other (friend)		0 16 42	3 32 -22		-30 29 -22	
Zhu et al. (Western)	2007	trait words	close other (mother)			-4 35 -2			
Zhu et al. (Chinese)	2007	trait words	close other (mother)			2 55 3		-22 59 15	
Segar et al.	2004	food names	close other (friend)			-2 53 18		-28 20 49	
Gobbini et al.	2004	faces	close other	-36 -63 30	49 -55 19		-4 53 18	-22 12 44	38 4 31
Kumaran & Maguire	2005	2 persons	s SSI (one-back recognition)	-48 -51 24		-3 48 39	-6 48 3	-33 24 -24	33 24 -24
			close other			1.00 0.50	0.22 0.58	1.00 0.00	0.56
				0.22	0.11	0.50	0.22 0.58	1.00 0.00	0.56

TABLE I. (Continued)

9 Self-reference		ITPJ	rTPJ	dmpFC	vmPFC	IPFC	rPFC
Zhu et al. (Western)	2007	trait words		-2 33 30	0 51 3		
Zhu et al. (Chinese)	2007	trait words		-6 36 20	8 55 6	-24 57 12	
Heatherton et al.	2006	trait words					48 32 -12
Ochsner et al.	2005#2	trait words			26 41 2		
Moran et al.	2006	trait words			-6 53 6		
Fossati et al.	2004	trait words			10 52 14		
Lieberman et al.	2004	trait & profession words			-4 58 -12		
Macrae et al.	2004	trait words			-9 50 0		
Schmitz et al.	2004	trait words			6 56 4		
Fossati et al.	2003	trait words			10 49 16		
Kelley et al.	2002	trait words			10 52 2		
Kircher et al.	2002#1	trait words					
Kircher et al.	2000	trait words	-49 -42 31				
Johnson et al.	2002	trait statements					
Paulus & Frank	2003	food pictures			0 53 5		
Vogelley et al.	2001	action stories			-9 50 4		
Kircher et al.	2002#2	trait words	58 -56 12		6 54 -4		
Johnson et al.	2006#1	none					
Johnson et al.	2006#2	none	-42 -74 24		1 45 4		
Maguire & Frith	2003	event statement			2 39 -1		
Bhatt & Camerer	2005	dominance game			-3 52 -3		
Platak et al.	2006	faces			6 42 0	-27 48 9	
Platak et al.	2004	faces			6 46 -12		42 22 47
Kircher et al.	2001#1	faces			6 42 -2	-32 31 20	
Kircher et al.	2000	faces	-49 -42 31		6 42 -2		
Lawrence et al.	2006	silent videos	-49 -42 31		4 37 -7		25 33 -7
Phan et al.	2005	pictures (IAPS)			-6 37 -6		
			0.00	0.15	0.05	0.07	0.11
					0.07	0.13	0.05
10 Social Scripts		ITPJ	rTPJ	dmpFC	vmPFC	IPFC	rPFC
Krueger et al.	2007	scripted activities			3 54 -5		
Ferri et al.	2005	action stories			-23 47 12	-45 15 20	
Wood et al.	2005	scripted activities	43 -53 26		4 54 -6		
Wood et al.	2003	scripted activities (1 person)					
Wood et al.	2003	scripted activities (>1 pers.)			-8 48 31		
Reis et al.	2007	scripted activities			-3 62 25		56 28 29
Fiddick et al.	2005	scripted activities			0 45 42	-51 23 -8	51 23 -8
				0.14	0.26	0.43	0.61
			0.00				0.24
							0.57
11 Response sequence		ITPJ	rTPJ	dmpFC	vmPFC	IPFC	rPFC
Desrebois et al. (PET)	2005	artificial grammar learning			-4 35 -8		26 15 -11
Aizenslein et al.	2004	artificial grammar learning	-40 -25 38			-54 26 25	52 14 19
Desrebois et al. (PET)	2003	artificial grammar learning			-16 41 0	-32 28 23	48 38 20
Dreher et al.	2002	sequence of tasks			0 64 8		
Koechlin et al.	2002	sequence of tasks			-20 44 0	-48 12 32	
Koechlin et al.	2000	sequence of tasks			9 42 -6		
			0.33	0.00	0.00	0.02	0.50
					1.00	0.04	0.50

TABLE I. (Continued)

12 Emotionality		ITPJ	rTPJ	dMPF	vMPF	IPFC	rPFC
Ochsner et al.	2004a pictures (IAPS)						
Ochsner et al.	2004a pictures (IAPS)						
Cunningham et al.	2003 names of famous people						
Cunningham et al.	2004 social concepts						
Phan et al.	2004 pictures (IAPS)						
Winston et al.	2003 emotional faces						
Gur et al.	2002 emotional faces						
Gusnard et al.	2001 pictures (IAPS)						
Ochsner et al.	2002 pictures (IAPS)						
Zyset et al.	2003 statements						
Zyset et al.	2002 statements						
		-54 -63 27					
		0.08 0.00	0.42	0.06 0.41	0.75 0.01	0.33 0.00	0.33
13 Positive emotions		ITPJ	rTPJ	dMPF	vMPF	IPFC	rPFC
Heinzel et al.	2005 pictures (IAPS)						
Cunningham et al.	2004 social concept words						
Cato et al.	2004 (none)						
Cunningham et al.	2004 social concepts						
Kim et al.	2004 face + action stories						
Hutcherson et al.	2005 films						
Goldin et al.	2005 films						
Hutcherson et al.	2005 films						
Britton et al.	2006 films + pictures						
Kringelbach et al.	2003 emotional faces						
Kilgore & Yurgelun-Todd	2007 emotional faces						
Sato et al.	2004 emotional faces						
Harris & Flake	2006#1 pictures of social groups						
Farrow et al.	2001 action stories						
		-57 51 24					
		0.07	0.14 0.48	0.43 0.38	0.43 0.00	0.43 0.00	0.29
14 Negative emotions		ITPJ	rTPJ	dMPF	vMPF	IPFC	rPFC
Tabert et al.	2001 emotional words						
Cunningham et al.	2004 social concept words						
Cato et al.	2004 (none)						
Ochsner, Ray et al.	2004b pictures (IAPS)						
Kim et al.	2004 face + action stories						
Cunningham et al.	2003 names of famous people						
Kilgore & Yurgelun-Todd	2007 emotional faces						
Britton et al.	2006 films + pictures						
Goldin et al.	2005 films						
Hutcherson et al.	2005 films						
Hutcherson et al.	2005 films						
Eisenberger et al.	2003 cyberball game						
		54 -56 20					
		0.07	0.14 0.48	0.43 0.38	0.43 0.00	0.43 0.00	0.29

TABLE I. (Continued)

Author	Year	Task	Stimuli	Outcome	Region	Activation (t)	Region	Activation (t)	Region	Activation (t)	Region	Activation (t)
Sanfey et al.	2003	ultimatum game	offers from opponent	unfair	ITPJ	-30	ITPJ	30	ITPJ	30	ITPJ	-30
Pfahn et al.	2003	pictures (IAPS)	emotion judgment	aversion	dMPFC	4	dmPFC	20	vmPFC	4	vmPFC	20
Britton et al.	2006	films + pictures	emotion judgment	disgust	dmPFC	3	dmPFC	54	vmPFC	3	vmPFC	54
Harris & Fiske	2006	pictures of social groups	emotion judgment	disgust	ITPJ	61	ITPJ	-26	ITPJ	1	ITPJ	6
Todorov, Gobbini et al.	2007	faces + action stories	SSI (one-back-recognition)	disgust	ITPJ	50	ITPJ	-38	ITPJ	-10	ITPJ	47
Ochsner et al.	2006	hand in very hot water	emotion judgment	fear	ITPJ	0.03	ITPJ	0.00	ITPJ	0.32	ITPJ	0.38
Sato et al.	2004	emotional faces	SSI (passively viewing)	fear	ITPJ	0.16	ITPJ	0.00	ITPJ	0.55	ITPJ	0.52
15 Reward learning												
Daw et al.	2006	bandit dilemma	reward (financial)	reward magnitude	vmPFC	-3	vmPFC	28	vmPFC	-3	vmPFC	28
Knutzen et al.	2005	visual stimuli	reward (financial)	reward magnitude	ITPJ	-4	ITPJ	48	ITPJ	-4	ITPJ	48
O'Doherty et al.	2006	visual stimuli	reward (taste)	reward prediction	ITPJ	0	ITPJ	30	ITPJ	0	ITPJ	30
Tanaka et al.	2004	markov decision task	reward (financial)	reward prediction	ITPJ	-4	ITPJ	44	ITPJ	-4	ITPJ	44
Ellis et al.	2004	visual stimuli	reward (financial)	reward	ITPJ	9	ITPJ	57	ITPJ	9	ITPJ	57
Gottfried et al.	2003	visual stimuli	reward (olfactory)	reward	ITPJ	0	ITPJ	51	ITPJ	0	ITPJ	51
O'Doherty et al.	2001	visual stimuli	reward (financial)	reward	ITPJ	-12	ITPJ	49	ITPJ	-12	ITPJ	49
O'Doherty et al.	2004	monetary choices	reward (financial)	reward - immediate	ITPJ	-4	ITPJ	48	ITPJ	-4	ITPJ	48
McCure et al.	2004	visual stimuli	reward (taste)	reward - delayed	ITPJ	-8	ITPJ	47	ITPJ	-8	ITPJ	47
O'Doherty et al.	2003	visual stimuli	reward (taste)	reward prediction error	ITPJ	-21	ITPJ	45	ITPJ	-21	ITPJ	45
McCure et al.	2003	food items	reward (taste)	reward prediction error	ITPJ	20	ITPJ	34	ITPJ	20	ITPJ	34
Berns et al.	2001	food items	reward (taste)	unexpected reward	ITPJ	-10	ITPJ	29	ITPJ	-10	ITPJ	29
Corticelli et al.	2005	financial game	reward (financial)	reward loss	ITPJ	0.06	ITPJ	0.20	ITPJ	0.06	ITPJ	0.20
16 Physical causality												
Fugelsang & Dunbar	2005	medical issue	predict medical outcome	uncertain (low relation)	ITPJ	9	ITPJ	22	ITPJ	9	ITPJ	22
Corlett et al.	2004	food items	predict medical outcome	revaluation error	ITPJ	-26	ITPJ	72	ITPJ	-26	ITPJ	72
Turner et al.	2004	food items	predict medical outcome	preventive learning	ITPJ	32	ITPJ	-56	ITPJ	32	ITPJ	-56
Fletcher et al.	2001	drug items	predict medical outcome	unexpected trials	ITPJ	-36	ITPJ	-56	ITPJ	-36	ITPJ	-56
Foerde et al.	2006	weather prediction	predict weather outcome	single task	ITPJ	6	ITPJ	13	ITPJ	6	ITPJ	13
Voiz et al.	2004	competition game	rule learning	prediction uncertainty	ITPJ	-45	ITPJ	-56	ITPJ	-45	ITPJ	-56
Kuperberg et al.	2006	several sentences	describe relationship	causal	ITPJ	0.02	ITPJ	0.38	ITPJ	0.02	ITPJ	0.38
Satpute et al.	2005	pairs of words	describe relationship	causal	ITPJ	0.13	ITPJ	0.13	ITPJ	0.13	ITPJ	0.13
17 Social causality												
Harris et al.	2005	action stories	describe cause	internal cause (person)	ITPJ	60	ITPJ	-44	ITPJ	60	ITPJ	-44
Blackwood et al.	2003	action stories	describe cause	internal cause (self)	ITPJ	-2	ITPJ	46	ITPJ	-2	ITPJ	46
Blackwood et al.	2000	statements	describe cause	internal cause (self)	ITPJ	-46	ITPJ	-50	ITPJ	-46	ITPJ	-50
Fontpujt	2003	animations with shapes	describe cause	causality judgment	ITPJ	12	ITPJ	63	ITPJ	12	ITPJ	63
18 Response conflict												
Miham & Banich	2005	stroop task	color identification	incongruent	dmPFC	6	dmPFC	20	dmPFC	6	dmPFC	20
Kenns et al.	2004	stroop task	color identification	incongruent	dmPFC	3	dmPFC	14	dmPFC	3	dmPFC	14
Fan et al.	2003	stroop task	color identification	incongruent	dmPFC	-3	dmPFC	28	dmPFC	-3	dmPFC	28
Miham et al.	2003a	stroop task	color identification	congruent	dmPFC	-44	dmPFC	16	dmPFC	-44	dmPFC	16
Miham et al.	2003b	stroop task	color identification	congruent	dmPFC	-30	dmPFC	20	dmPFC	-30	dmPFC	20

TABLE I. (Continued)

Potenza et al. (Normal)	2003	stroop task	b	color identification	incongruent	congruent	-1	11	42	-43	7	35
Milham et al. (Old)	2002	stroop task	b	color identification	incongruent	congruent	2	12	52	-44	40	8
Milham et al. (Young)	2002	stroop task	b	color identification	incongruent	congruent	4	10	54	-48	44	8
Peterson et al.	2002	stroop task	b	color identification	incongruent	congruent	11	17	22	-41	30	8
Banich et al.	2001#1	stroop task	b	color identification	incongruent	congruent	6	18	40	-46	6	26
Banich et al.	2001#2	stroop task	b	color identification	incongruent	congruent	4	16	48	-38	12	40
Milham et al.	2001	stroop task	b	color identification	incongruent	congruent	0	10	44	-42	2	36
Ruff et al.	2001	stroop task	b	color identification	incongruent	congruent	28	18	47	-55	13	32
Ruff et al.	2001	stroop task	b	color identification	incongruent	congruent	24	22	50	-51	9	33
Siegel et al.	2001	stroop task	b	color identification	incongruent	congruent	-3	36	26	-48	28	17
Zyset et al.	2001	stroop task	b	color identification	incongruent	congruent	1	26	42	-38	5	30
Carter et al.	2000	stroop task	b	color identification	incongruent	congruent	0	15	41	-38	5	30
MacDonald et al.	2000	stroop task	b	color identification	incongruent	congruent	4	1	43	-41	18	28
Biasi et al.	2006	flanker task	s	arrow identification	incongruent	congruent	4	10	46	-45	14	-5
Roelofs et al.	2006	flanker task	s	arrow identification	incongruent	congruent	-4	30	36	-22	48	36
Fan et al.	2003	flanker task	s	arrow identification	incongruent	congruent	-8	28	21	-34	53	7
Casey et al.	2000	flanker task	s	arrow identification	incongruent	congruent	-8	22	32	-5	18	57
Biasi et al.	2006	flanker task	s	arrow identification	response inhibition	congruent	19	7	60	-48	30	22
Bunge et al.	2002	flanker task	s	letter identification	incongruent	congruent	14	24	43	-34	9	35
Peterson et al.	2002	simon task	s	arrow identification	incongruent	congruent	11	17	21	-39	34	9
de Zubicaray	2001	semantic interference task	s	picture identification	incongruent	congruent	24	42	20	-30	58	-3
							0.29	0.52	0.00	0.88	0.00	0.73

The entries reflect the x , y , and z coordinates, respectively, on a Talairach and Tournoux (1988) template of peak activations that are significantly different in the target condition in comparison with the control condition. Empty cells indicate that there was no significant brain activity reported. The last row of each task category depicts the P -value of a t -test against the hypothesis that the x -coordinate is null (on the left) and the proportion of significant activations in that region (on the right). I IPL = left IPL, rIPL = right IPL; lTPJ = left TPJ, rTPJ = right TPJ; lPFC = left PFC, rPFC = right PFC; s = visual material; b = verbal material; SSI = spontaneous social inference; # = experiment number, IAPS = International Affective Picture System (Lang et al., 1998).

- The recognition of a stationary body of other people involves the extrastriate body area (EBA), and recent research suggests that one's own body movements (e.g., of hand and foot) can also involve the EBA [Astafiev et al., 2004; Jeannerod, 2004];
- More importantly, human motions such as body, gaze, and hand movements involve the superior temporal sulcus (STS). This is most often identified at the right hemisphere (all studies reported in Table I or 100%) and less so at the left hemisphere (55%). It is important to note that fMRI responses to human movement have been shown not only with films of human actors, but also with robots that mimic human movements as well as with point-lights that display movements with only a handful small dots at the major human joints while all the rest is invisible. Our familiarity with human and biological movement render these moving light dots so compelling that they are perceived as natural movements in comparison with dots moving randomly [Bonda et al., 1996; Grossman and Blake, 2002].
- Somewhat separated from the previous regions, the names of known people are represented in the lower anterior part of the temporal lobe. It has been suggested that this region is implicated in a neural circuit for person identity [Sugiura et al., 2006].
- The mirror system for identifying simple hand, mouth, face or foot movements (e.g., grasping an object) is composed of the STS, IPL (extending to the superior parietal lobe) and PMC. To elucidate the location of this mirror system in humans, researchers typically sought for brain areas common to action observation and execution (i.e., imitation) as opposed to static positions, for areas that were more strongly recruited during imitating as opposed to viewing movements, or that were more strongly engaged during goal-directed movements as opposed to movements without goal involvement. Of interest is that the parietal lobe and PMC reveal a rough somatotopic organization, much in line with the classic homunculus of the motor system, with foot movements at superior areas and mouth/face movements at inferior areas, with hand movements in-between. This somatotopic organization has been revealed also for auditory input [Gazzola et al., 2006]. Two recent studies also identified the IFG (an inferior part of the PMC) as an area involved in identifying the goals of hand movements (e.g., during behaviors like drinking and cleaning) as opposed to action execution alone [Iacoboni et al., 2005; Molnar-Szakacs et al., 2005]. That the mirror system codes predominantly goals rather than movements themselves, has been demonstrated by the activation of this region during observation of hand movements even when the specific details of the movement are outside the motor vocabulary of the observer: hand actions for participants born without hands [Gazzola et al., 2007a] and robotic actions for

TABLE II. An overview of major task categories and corresponding brain areas

Task category	ITPJ	rTPJ	dmPFC	vmPFC	IPFC	rPFC	Cochran Q
Action intentionality (temporary)							
Goal-directed movement	0.75	0.63	0.25	0.13	0.00	0.25	<i>0.007</i>
Agency/perspective	0.75	0.50	0.00	0.00	0.50	0.50	<i>0.202</i>
Action Goal	0.71	1.00	0.14	0.86	0.14	0.00	<i><.001</i>
ToM beliefs	0.60	0.73	0.53	0.53	0.13	0.33	<i>0.025</i>
Morality	0.80	0.70	0.30	0.70	0.50	0.30	<i>0.141</i>
Kruskal-Wallis ANOVA	<i>0.859</i>	<i>0.401</i>	<i>0.192</i>	<i>0.009</i>	<i>0.059</i>	<i>0.418</i>	
Traits and scripts (enduring)							
Traits of Others	0.33	0.53	0.93	0.33	0.33	0.40	<i>0.005</i>
Person in games	0.29	0.29	0.86	0.14	0.14	0.14	<i>0.035</i>
Close others	0.22	0.11	0.22	1.00	0.56	0.22	<i><.001</i>
Self-reference	0.15	0.07	0.07	0.85	0.11	0.11	<i><.001</i>
Social Scripts	0.00	0.14	0.43	0.57	0.29	0.29	<i>0.282</i>
Kruskal-Wallis ANOVA	<i>0.386</i>	<i>0.012</i>	<i><.001</i>	<i><.001</i>	<i>0.083</i>	<i>0.276</i>	
Other functions							
Response sequence	0.33	0.00	0.00	1.00	0.50	0.50	<i>0.004</i>
Emotionality	0.08	0.42	0.08	0.75	0.33	0.33	<i>0.005</i>
Positive emotions	0.08	0.15	0.46	0.46	0.46	0.31	<i>0.165</i>
Negative emotions	0.17	0.28	0.56	0.11	0.22	0.39	<i>0.015</i>
Reward learning	0.00	0.00	0.08	0.85	0.23	0.15	<i><.001</i>
Physical causality	0.38	0.13	0.25	0.13	0.88	0.63	<i>0.009</i>
Social causality	0.25	0.25	0.50	0.25	0.25	0.25	<i>0.956</i>
Response conflict	0.00	0.00	0.92	0.00	0.88	0.73	<i><.001</i>
Kruskal-Wallis ANOVA	<i>0.035</i>	<i>0.012</i>	<i><.001</i>	<i><.001</i>	<i><.001</i>	<i>0.022</i>	

Cell entries denote the proportion of studies where activation in that region was identified. The cell entries of the Kruskal-Wallis ANOVA and Cochran Q (in italic) refer to the significance level *P* of these tests. Additional Kruskal-Wallis tests reveal that the left and right TPJ activations do not differ for each of the tasks listed.

typically developed participants [Gazzola et al., 2007b].

All these areas of human visual perception, with the exception of person names, are located in a specific and limited part of the superior temporal and parietal cortex (see Fig. 1D). The human mirror system additionally recruits the PMC, especially for goal identification of behaviors.

Identifying action intention

Contrary to simply action identification which recruits the IPL, social human behavior recruits the TPJ, which

stretches between the IPL and STS involved in the visual detection of biological movement (Fig. 1A). As noted in the introduction, there is large agreement that the human visual information detected at a lower level in the STS as well as verbal information, informs the higher-level analysis at the TPJ. If our suggestion is correct that the TPJ is a key mirror site for social cognition, than the TPJ should be involved in the identification of the goals and intentions of humans. Kruskal-Wallis ANOVAs in Table II confirm that inferences of action intentionality (Tasks 1–5) consistently engage the TPJ, although the mPFC is also involved in some tasks. The activation of the left and right TPJ does not differ significantly between each other, as also revealed

TABLE III. Gamma correlations between tasks and activation in specific brain areas

Stimulus type	ITPJ	rTPJ	dmPFC	vmPFC	IPFC	rPFC
Visual-Verbal						
Tasks 1–5 (<i>n</i> = 44)	0.43*	0.13	−0.13	0.85**	0.40	−0.54*
Tasks 6–10 (<i>n</i> = 65)	−0.55**	−0.46*	0.46*	−0.15	0.01	−0.46*
Tasks 11–18 (<i>n</i> = 100)	−0.04	−0.10	0.05	−0.09	0.31*	0.41**
All Tasks (<i>n</i> = 209)	−0.04	−0.11	0.10	0.25**	0.14	−0.07
Explicit-Spontaneous						
Tasks 1–5 (<i>n</i> = 44)	0.47*	0.63**	0.13	−0.10	−0.52*	−0.40
Tasks 6–10 (<i>n</i> = 65)	0.55**	0.30	0.75***	−0.82***	0.19	0.30
Tasks 11–18 (<i>n</i> = 100)	−1.00	0.31	−0.35	−0.53*	−0.61**	−0.01
All Tasks (<i>n</i> = 209)	0.56***	0.59***	0.11	−0.35**	−0.45***	−0.16

The more verbal or spontaneous, the stronger a positive correlation is **P* < 0.05; ***P* < 0.01; ****P* < 0.001.

by additional Kruskal-Wallis tests. This is true for all tasks listed in Table II.

Figure 1E,F depicts the TPJ coordinates of a large set of fMRI studies in which the critical task is to infer intentionality by the actor, either close at the perceptual level by inferring the expected end-goal or actor (Task 1–2), or at a higher cognitive level by inferring the actor’s beliefs on the desired outcome (Task 3–5). As can be seen in Table I, the task stimuli involve mostly verbal and visual material like short stories or sentences, or visual material like cartoons or videos, as well as interactive games with real humans. This is consistent with the notion that the TPJ has a multi-modal functionality, that is, it reacts to visual as well as verbal material (e.g., stories).

- **Goal-directed Movement:** At the most basic perceptual level perhaps, participants are viewing animations of shapes that move in a human-like manner in comparison to random movements. This is reminiscent of a classic study by Heider and Simmel (1944) in which observers ascribe human intentions to moving circles and triangles (such as chase, follow etc.). Given their human-like nature, observers perceive them as biological movements that are directed towards a goal, resulting in TPJ activation (75% and 63% of the studies in Table I, for the left and right hemisphere, respectively). It is interesting to note that these animations are so compelling that they create greater activity in the TPJ than goal-directed hand manipulations of an object (cup, hammer, telephone etc. Ohnishi et al., 2004).
- **Agency and Perspective:** In these studies, participants observe a visual scene or movements involving different persons and identify the relative locations of the objects from the perspective of the self or other, or identify whether the other (versus the self) is initiating the movement. Although these tasks are only somewhat similar and could have been separated in two task distinct categories (if more studies were available), they both require the perceiver to distinguish own action perspective and goal from those of other persons. Nevertheless, these tasks consistently engage the TPJ (75% and 50%), in agreement with several similar PET studies that also reveal the TPJ as major site of brain activation [Chaminade and Decety, 2002; Chaminade et al., 2002; Decety et al., 2002; Farrer et al., 2003; Ruby and Decety, 2001].
- **Action Goals:** Participants are requested to identify the likely or desired end state of a story in comparison with mere physical consequences (e.g., a gulf destroying a sand castle at the beach). Although many earlier reviews have tended to confound this task with ToM inferences (see below), we isolated it as theoretically distinct and important, because it only requires identifying the implied goal of an action, without an understanding or insight of the actor’s own beliefs. Goal inferences lead to activation in the TPJ (71% and 100%).

ToM Beliefs: At a somewhat higher inferential level, participants must not only realize that others’ movements and behaviors involve goals and intentionality, they must also identify these intentions. This requires the understanding that the protagonist acted the way he or she did, only because of a distinct goal in mind, a capacity called theory of mind (ToM). Several tasks have been devised to measure this capacity. In tasks that involve a “true” belief, the observer simply needs to identify the protagonists’ belief or intention. However, the ToM capacity becomes most evident when own and other intentions diverge in “false” belief tasks described earlier, or when participants have to detect false from true actions or communications (as in irony) because these tasks require distinguishing between own and other beliefs.

Earlier studies using the false belief task took physical events as control tasks, whereas more recent studies apply carefully matched controls, such as stories involving photos that are “false” in the sense that they became outdated after some critical event [Perner et al., 2006; Saxe et al., 2006]. Similarly, in other tasks, videotapes show actors who on some occasions pretend to lift objects that are heavier than they actually are in comparison with the same action without deceit of the objects’ weight [German et al., 2004; Grèzes et al., 2004, 2006; see Table I]. Many of these tasks lead to increased TPJ activation (60% and 73%).

- **Moral Judgments:** The transition from false beliefs to unjust or unfair beliefs or intentions appears to be a close one. This is attested by the fact that the TPJ is also strongly involved in judgments of morality. Participants are given stories or dilemmas with different levels and types of moral injustice (e.g., commissions of unjust actions or omissions of just actions; where a person is critically involved or not; where a moral dilemma is left open or the wrong-doing has been committed). What is common in all these tasks is the intentional act of wrongdoing. Moral, personal, or norm violating stories elicit more activation in the TPJ than nonmoral, impersonal or normal activities, respectively (80% and 70%). Thus, when confronted with a moral dilemma, we seem to base our decisions on right or wrong intentions to act or effortful action, rather than on a logical analysis of death count and so on. This emphasis on intentionality is also seen in the law (e.g., difference between premeditated murder and accidental manslaughter).

Summary and discussion

The studies in this overview support the contention that the TPJ is crucially involved in the identification and representation of action goals. However, as can be also inspected on Figure 2A, many tasks on intentionality also engage the mPFC. This has led to the view that the mPFC

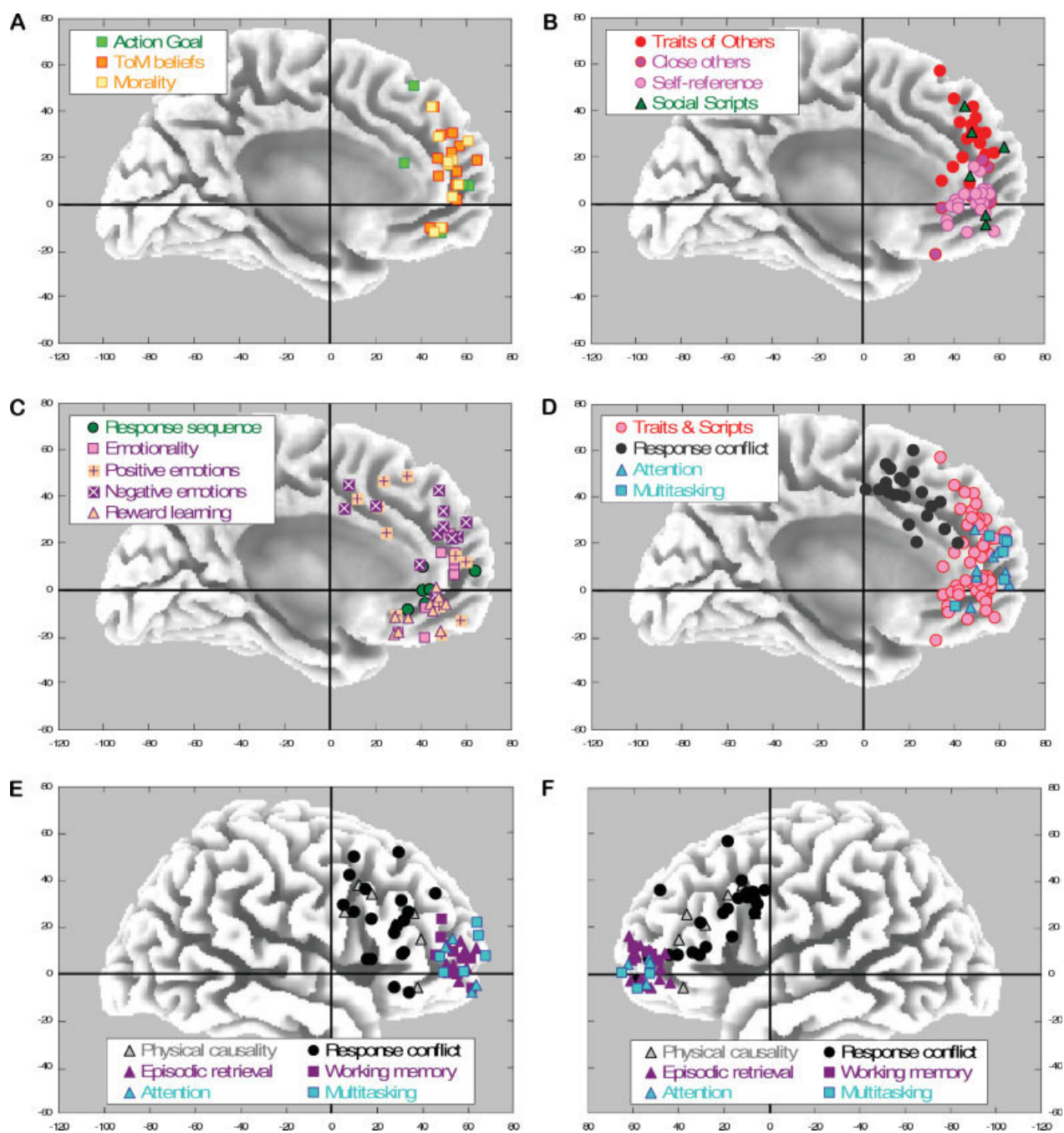


Figure 2.

[A] The mPFC involved in social inferences of intentionality. [B] The mPFC involved in social inferences of traits (other and self) and scripts. Social inferences during interpersonal games are included in the trait inferences of others. [C] The mPFC involved in sequence learning and emotional responses. [D] The

medial PFC involved in executive functions, in comparison with social inferences of traits and scripts (copied from Fig. 2B). [E,F] The lateral PFC involved in causal learning and executive functions; right and left lateral view, respectively. The studies involved in A-F can be identified via the y-z coordinates in Table I.

is the key region in mentalizing and aids in the realization of different perspectives for tasks that require decoupling other's perspective from one's own or reality [Frith and

Frith, 2001; Gallagher and Frith, 2003]. However, true belief tasks do not require holding in mind diverging beliefs or intentions, and yet they also tend to activate the

mPFC [Ferstl and von Cramon, 2002; Saxe and Powell, 2006; see also Table I]. More importantly, Saxe and Powell (2006) found that the TPJ was more strongly activated in relation to beliefs for inferred events (that could be false, e.g., “his dog broke loose so he guessed that the leash had come untied”) versus true events (e.g., “he was sick, felt weak and had a high fever”). In contrast, the mPFC was equally activated in these two conditions. Similarly, Sommer et al. (2007, see Table I) found stronger activation of the TPJ for false beliefs in comparison with true beliefs, while the mPFC was not differentially engaged. Lesion studies with humans have demonstrated that patients with frontal lobe lesions make more mistakes on difficult false belief and deception tasks than patients with other brain lesions, although they make no more errors on the simplest of the false belief tasks [Stuss et al., 2001]. Hence, holding in mind different perspectives seems not the key explanation for the involvement of the mPFC.

Closer inspection of the data suggests another reason for the engagement of the mPFC. Inferences on goal-directed movement and agency (Tasks 1–2, see Table I) are based on visual stimuli, while the other intentionality and belief judgments (Tasks 3–5) are predominantly based on verbal action stories, and this difference is highly significant, Kruskal-Wallis $H(1, N = 44) = 23.17, P < 0.001$. More importantly, a nonparametric correlation between the presence of verbal material and the engagement of the mPFC is highly significant, not only for the ventral part as listed in Table III ($\Gamma = 0.85, P < 0.001$), but also when the ventral and dorsal parts are taken together ($\Gamma = 0.90, P < 0.001$). This suggests that the mPFC is additionally engaged when there is no immediate visual substrate on which to base intentionality judgments.

But why is the mPFC engaged under such circumstances? Perhaps, verbal stories may require more cognitive or complex processing subserved by the mPFC. This is consistent with many perspectives that stress this region as major site of social cognition [Amodio and Frith, 2006; Leslie et al., 2004; Northoff and Bermpohl, 2004]. Alternatively, verbal stories are typically richer in socially relevant context, and therefore may have induced participants not only to infer action goals, but also traits of the actors involved. For instance, by hiding a desired object from view in a false belief scenario, one might be tempted to infer that the actor is unreliable or unfriendly. Social psychology research has since long established that we often make trait inferences automatically with little awareness or intention on the basis of short behavioral descriptions [see Uleman, 1999, for a review]. This interpretation is supported by a significant nonparametric correlation revealing that spontaneous judgments across all social task categories (denoted “SSI” for Tasks 1–10 in Table I) elicit more activation not only in the left and right TPJ ($\Gamma = 0.58$ and $0.54, P < 0.001$), but also in the dorsal mPFC ($\Gamma = 0.42, P < 0.01$) which is believed to subserve trait inferences about others (see below). Because none of these studies were designed to control for spontaneous trait

inferences, it is unclear to what extent this interpretation is correct.

Taken together, there is strong evidence that the TPJ is a necessary substrate for inferring the goals of others even if they diverge from one’s own, but perhaps the mPFC may be involved in more complex and explicit meta-representations and distinctions of social inference, when rich verbal material is available or when we (spontaneously) make additional trait inferences about others. The parietal area is known as an association cortex responsible for the analysis and identification of higher-order information with respect to spatial location (the “where” system). One type of spatial information is the expected end-point of a movement, that is, its goal. This is a basic capacity of many fast-moving organisms, which enables perceivers to orient themselves in order to avoid unwanted collisions, or to approach and collaborate with each other efficiently. We can therefore label the TPJ as the “where-to” system. A recent study by Mitchell (2008) provides support for this idea. Participants performed typical ToM tasks as well as an attentional orienting task. This is a simple task where an arrow cues the participants towards the position of a forthcoming target stimulus. It was found that the same area of the TPJ was implicated in the ToM task as well as in the orientation task when participants were miscued and their expectations on the target location were violated. This shows that this region is involved in a variety of other nonsocial tasks that require participants to (re)orient their attention to a task-relevant direction or end-point. Future research may perhaps identify separate sub areas in the TPJ dedicated to social and nonsocial orientation functions.

Who We Are: Inferences of Traits and Social Scripts

As noted in the introduction, enduring social dispositions and interpersonal knowledge, such as personality traits and social rules, involve the capacity to remember the behaviors of people over a long stretch of time under multiple circumstances, to recognize the common goal in these behaviors and to link them to the actors’ most likely plan of past and future actions. Permanent characteristics tell us what kind of a person someone is, and social scripts tell us to what kind of group we belong.

It has been hypothesized that the mPFC is crucially involved in the formation of such enduring inferences. The mPFC is a large brain structure that can be functionally subdivided (see Fig. 1B) into a posterior part, a dorsal part (dmPFC) which lies above the 20 mm coordinate of the inferior-superior z-axis, a ventral part (vmPFC) which lies below it, and an orbital part which lies below the –15 mm coordinate of the z-axis. The dorsal and ventral parts are the core regions of social cognition.

Identifying the traits of others and self

In large agreement with most theoretical positions, enduring social judgments uniformly involve the ventral

or dorsal part of the mPFC (see Table II). This is attested by a nonsignificant Kruskal-Wallis $H(4, N = 65) = 4.86$, ns, when considering these two parts of the mPFC together. The TPJ is also engaged, but only in one task (i.e., inferring traits of others; Kruskal-Wallis $H(4, N = 65) = 12.96$, $P < 0.05$; see also Fig. 1E,F). The tasks that engage the mPFC are depicted in Figure 2B and detailed in Table I.

- **Trait Inferences:** These studies require participants to make judgments in terms of enduring traits (instead of immediate action goals) about actors on the basis of short stories, sentences or on the basis of single trait words (studies that also involve self judgments were excluded from this category, as this might induce a different mind set than mere judgments about others). All these tasks activate the dorsal part of the mPFC, except for the study by Heberlein and Saxe (2005) who made a somewhat unusual comparison between trait and emotion inferences and found an increased activation in the ventral part of the mPFC (although close to the dmPFC). Tasks that require participants to make unrelated judgments (e.g., memory tasks) suggest that trait inferences were also made spontaneously (see “SSI” in Table I) for trait-implicating actions compared to non trait-implicating actions, as the former lead to greater activation in the mPFC [Iacononi et al., 2004; Mitchell et al., 2006; Todorov et al., 2007].
- **Interactive Games:** Trait impressions of others are presumably also spontaneously made in interactive games because to win a game, it is important to make an accurate guess on the next moves of the opponent. To do so, one must develop an impression on the trust, cooperativeness or competitiveness of the other. Quite often in these tasks, the control condition is a computer instead of a human opponent, which seems to induce other strategy considerations. In other studies, a first win or loss is compared against long-term wins or losses (which presumably induce more trait inferences). A great majority of these games involve the mPFC (100%; the majority or 86% in the dorsal part).
- **Close Others:** The more ventral part of the mPFC is activated when people make trait inferences about familiar others, such as mother, relatives, and friends (100%). Given that close others are often experienced as very similar to the self, it is perhaps quite plausible that judgments of close others is located in the same brain area as judgments about the self (see later). Similarity to the self was parametrically analyzed by Mitchell et al. (2005b) and their results indicated that when others are judged similar to the self, this strongly activates the vmPFC (see also Table I).
- **Self-references:** A plethora of studies explored all sorts of inferences about the self, from pure trait ratings and permanent descriptions that are applicable to the self, thinking about one’s hopes or memories about

the self, to involvement of the self in viewing of one’s face, or in interaction games. Although these latter tasks are not directly about traits, it is easily imaginable that while seeing one’s face or other self-relevant material or while thinking about one’s hopes and choices, many characteristics and dispositions of the self are spontaneously generated, retrieved, or compared. Of the more than 20 studies listed in Table I, 85% elicit the ventral part of the mPFC. Note also in Figure 2B that all judgments of self and close others are located at the vmPFC and never surpass the 20 mm z-coordinate (with one exception). Contrary to some alternative theoretical views, no other regions are systematically engaged in the representation, evaluation or description of the self.

- **Social Scripts:** These studies do not focus on a single actor, but rather on social scripts that describe adequate social action for all actors. Participants are asked to check for an incorrect versus correct sequence order within scripted stories. These tasks require activating and employing interpersonal knowledge on social rules and scenarios by checking the correct chronological order. In all these studies, social scripts consistently engage the mPFC, both in the ventral or dorsal part (100%).

Summary and discussion

Undoubtedly, there is a great deal of consistency in the location of trait inferences and social script knowledge, as the amount and consistency of the empirical evidence is impressive. In all these enduring social judgments, the mPFC is almost uniquely engaged. Trait information about unfamiliar others selectively engages the dorsal part of the mPFC, whereas the ventral part is implicated when making trait inferences about familiar others or the self. The dmPFC can thus be considered the neural substrate of trait processing of other people, whereas the vmPFC can be considered the anatomical substrate of core experiences of the self and close others. Knowledge on social scripts involves both parts of the mPFC.

No other regions of interest are reliably implicated (<35%), except for the rTPJ which is also engaged in trait inferences about others (Task 6). This can be explained by the tendency for enduring social judgments (Tasks 6–10) to engage the TPJ more when visual task material is provided, as attested by a significant nonparametric correlation ($\Gamma = 0.45$ and 0.55 for right and left TPJ, respectively, $P < 0.05$). This parallels the opposite effect of temporary goal inferences (Tasks 1–5) discussed earlier where verbal material additionally engages the mPFC. Hence, the conclusion that enduring trait and norm inferences crucially involve the mPFC seems overwhelmingly supported by the empirical data, whereas the TPJ seems additionally engaged for processing visual material about others. This provides support for the view that the understanding of humans as enduring organisms with permanent social and

psychological properties such as traits and norms is a crucial common element that engages the mPFC.

Is Social Cognition Subserved by Other Brain Functions?

As we have seen in the introduction, a plethora of hypotheses have been offered on how mentalizing in the mPFC is served by other complex brain functions involving time integration, emotionality, causality, or executive processing (e.g., inhibition of one's own beliefs in favor of other's beliefs by supervisory control or attentional mechanisms; working memory processes in differential perspective taking and the decoupling of mental states from reality; episodic retrieval in the service of self-references). An analysis of these functions provides us with a sense of how much they are selectively used for social cognition. If the activation of a function falls within the ventral and dorsal areas of mPFC, then there is reason to believe that it is a core process of social cognition. If not, and the overlap is only partial, then this function more likely aids social processes, but is not an integral part of it. The selection of studies on these additional task categories was based on the general literature search and additional searches detailed in the Method section.

- **Response Sequence:** It has been hypothesized that enduring social inferences and knowledge on traits and scripts require the integration of chronological sequences over larger time intervals, and that this time integration is performed in the mPFC [Huey et al., 2006; Wood and Grafman, 2003]. This implies that the mPFC is engaged in several form of sequence learning, not only in social script learning. Given the paucity of fMRI experiments on sequence learning, PET studies on this topic were also included in this analysis (see Table I). Sequence learning tasks do not require to generate motor sequences, but to respond to observed stimulus sequences with an appropriate response. Perhaps, the most well-known example of a response sequence task is artificial grammar learning [Destrebecqz et al., 2003, 2005]. Participants respond to the spatial locations of stimuli (e.g., left or right whenever the stimulus appears somewhere left or right on the screen), which are presented in a predictable order or sequence of about 15 locations long. After some time, participants may become sensitive to this sequence of responses. Destrebecqz et al. (2003, 2005) measured the participants' brain activation when they are requested to generate the sequence and are consciously aware of it. As shown in Table I and depicted in Figure 2C, these and similar studies identified provide evidence that sequence learning engages the ventral part of the mPFC (100%), although in some studies activation extends to the lateral PFC.
- **Emotions:** What is the role of emotions in "cold" social cognition processes? As shown in Table I and

Figure 2C, emotional compared to nonemotional judgments (82%), as well as the experience of positive (79%) and negative (63%) emotions activate the dorsal and ventral regions of the mPFC, although they seem to engage the superior part of the mPFC as well. All these studies use verbal as well as visual material, and explicit or implicit instructions. In addition, other studies examining how people learn to discriminate stimuli that are financially or sensory rewarding as opposed to nonrewarding or punishing also implicate the vmPFC, extending further to the orbital mPFC (85%). As emotions and evaluations on our self and other people are part of how we form traits about them, it is perhaps not surprising to see that both the ventral and dorsal parts of the mPFC are involved. However, emotional responses engage regions that extend also to more orbital and superior regions of the mPFC.

- **Causality Detection:** In traditional theories of social psychology, trait inferences are interpreted in terms of internal causal attributions that obey the classical causality principles of contingency or covariation [Kelley, 1967] in much the same way as causal attributions for physical events. To assess the possible role of covariation and causal reasoning in trait inferences, several studies were explored that require participants to assess causal contingencies of physical (i.e., nonsocial) and social events.

For nonsocial causal attributions, participants learn, for instance, to predict the possibility of a medical outcome (e.g., an allergic reaction) by extracting the covariation between food items and the presence of allergic reactions after reading several medical cases. As can be seen in Figure 2E,F and Table I, quite surprisingly, none of these physical causality tasks engaged the mPFC, but rather the lateral PFC (88% and 63% at the left and right, respectively). The strongest activation is reported at unexpected trial outcomes or when the learning error or uncertainty was greatest (so that learning opportunities at subsequent trials are largest).

In contrast, the location of social causality judgments is less specific. Participants are requested to give the internal (personal) versus external cause of several social behaviors depicted in short stories or animations. Contrary to BlackWood et al. (2003) who found activation in the lateral PFC for stories involving self attributions, Harris et al., (2005) found activation in the mPFC, just as we had seen earlier for trait inferences. Perhaps, this difference is due to the fact that Blackwood used short behavioral sentences, while Harris et al. (2005) provided additional information summarizing the covariation across other people, circumstance, or time [cf., Kelley, 1967]. This may have rendered the whole action description more socially rich, leading to more trait inferences and the activation of the mPFC.

- **Response Conflict:** Many authors speculated that mentalizing is in part directed by the ability to monitor one's behavior and inhibit irrelevant cues. This would allow inhibiting one's own intention beliefs in favor of

other people's beliefs in false belief tests [e.g., Amodio and Frith, 2006]. Response Conflict and inhibition is typically investigated in Stroop and flanker tasks. For instance, in a Stroop task, participants report the color of a word in ink, and this task requires inhibition of the semantic meaning of the word when it involves an incongruent color (e.g., the word "red" written in blue ink). The activity of the mPFC reported in these studies (see Fig. 2D) overlaps entirely with the mean peak activity observed in an extensive meta-analysis on response conflict by Barch et al. (2001; Talairach coordinates 3, 19, 35) and by Neumann et al. (2008). As can be seen in Figure 2D, although action monitoring is located at the midline PFC, it often engages more posterior/superior regions outside the dorsal ventral regions implicated in social cognition, and also extends in the lateral regions (Fig. 2E,F).

- **Executive Functions:** Other roles for executive functions in social cognition have been put forward, including the capacity to focus one's attention on others versus the self [e.g., Leslie et al., 2004], as well as other executive and memory functions of the PFC, including dual attention and episodic retrieval. To assess these possibilities, I plotted all coordinates on executive brain functions from the recent meta-analysis by Gilbert et al. (2006) in Figure 2D–F. As can be seen, none of the coordinates of these executive and memory functions are located at the mPFC, except for a small portion of the multitasking and attention studies that tend to be located at a more anterior part of the mPFC, and extend also to the lateral PFC. In a recent study comparing directly mentalizing and attention tasks, Gilbert et al. (2007) confirmed that attention was located more anterior (at the tip of the mPFC) than mentalizing functions. Although a number of fMRI and PET studies revealed a substantial overlap between autobiographic memory [Graham et al., 2003; Maguire and Frith, 2003; Maguire and Mummery, 2003] and self-references in the vmPFC, the results seem to indicate that this has little to do with episodic memory per se, which shows little overlap. Given the limited number of autobiographic studies identified and the high degree of self-involvement they share with self-reference studies, it remains unclear whether autobiographic memory is a separate memory system or whether it is involved in a larger social self system.

Summary and discussion

Of the many additional functions explored in this analysis that involve the PFC, only sequence learning seems to overlap completely within the ventral or dorsal areas of the mPFC implicated in inferences of enduring traits and scripts. This is consistent with the idea put forward by Grafman and colleagues that the mPFC is especially tuned towards the integration of relevant stimuli over time

[Huey et al., 2006; Krueger et al., 2007; Wood and Grafman, 2003; Wood et al., 2005]. In the social domain, this takes the form of traits and scripts of social behavior. Thus, there is strong evidence that time integration is a core component of enduring social inferences that is accomplished in the mPFC, although that region is not selectively used for social processing, as it is also implicated in nonsocial time-related processes.

No other brain function seems to selectively subserve social inferences, because the overlap between their activation and the ventral and dorsal mPFC is limited (with the exception perhaps of autobiographic memory). Because the brain areas implicated in emotional experiences extend beyond the ventral and dorsal parts of the mPFC, it seems more likely that emotionality is not a subsystem of trait impression formation per se [see also Amodio and Frith, 2006, Heberlein and Saxe, 2005], but rather a different neural circuit (involving also subcortical areas, such as the amygdala) of which the input to the mPFC presumably modulates and enriches trait inferences with affective associations. Interestingly, it is tempting to speculate that the close proximity of the reward system in the orbito-frontal cortex explains the ventral position of trait inferences of self and familiar others (who typically generate more warmth and emotionality) relative to the more dorsal positions of the same judgments for unknown people.

Given the minimal overlap with the ventral and dorsal mPFC, the current meta-analysis suggests that physical causality detection, action inhibition, attention and other executive or episodic memory functions may perhaps influence social cognition, but do not play a crucial role in it. This contradicts earlier proposals that endowed these functions a greater role in social cognition [e.g., Amodio and Frith, 2006; Leslie et al., 2004; Northoff and Bermpohl, 2004].

CONCLUSIONS

This overview covers more than 100 fMRI studies on human social cognition as well as about 100 fMRI studies involving potentially related functionalities. Based on past research in social and developmental psychology, I distinguished two major types of social judgments: (1) Temporary inferences involving the detection and identification of a person's goals and goal-related beliefs, and (2) enduring inferences of personality traits and interpersonal scripts and norms. This distinction is also revealed in the progressive mastery of social capacities by young children up to the age of eight [Rholes et al., 1990], and in social research on the processing stages from goal identification to trait inference [Malle and Knobe, 1997; Malle et al., 2000; Reeder, et al., 2002, 2004]. For instance, when an actor engages in harmful behavior, we wonder which reasons or motives may have caused this behavior (out of a motive to harm or after provocation?), and this will determine whether we see this person as violent or not. The

data in this meta-analysis are consistent with this framework, and can perhaps be best interpreted as revealing a neural circuit starting from the more posterior TPJ, where immediate goals and desires are inferred, towards the more anterior mPFC associated with inferences of a more explicit nature of temporary goals and of more enduring traits and scripts.

Intentionality and Goals

This review provides strong support for the claim that the TPJ is a necessary substrate for inferring the goals of others, even if they diverge from one's own as in a false belief task. The data document that this neural system is sufficient to identify the direction and goal of behaviors that are visually available, and I therefore labeled the TPJ the "where-to" system in analogy with the "where" spatial system in the parietal lobe. It is still a matter of debate whether the TPJ is sufficient when behaviors are presented in a verbal (including a mixed cartoon-like) format, because in these cases the mPFC is also involved. It is possible that the greater complexity of such stimulus material requires additional processing in mPFC for representing explicit meta-representations. Alternatively, such verbal material is richer in social content and context, which perhaps allows for more spontaneous trait inferences that engage the mPFC. Research that controls for such spontaneous inferences is currently lacking, but is much needed if we want to learn more about the role of the mPFC in inferences of the goals and intentions of others.

The major role played by the TPJ for inferring goals and intentions is consistent with idea of a mirror circuit for identifying intentionality in the human brain as suggested by Keysers and Perrett (2004) and Iacoboni (2005), although this region is more caudal and inferior to the IPL which was identified in studies on the mirror properties of simple movements. As far as I am aware, evidence on the mirror properties of the TPJ for complex social behavior is currently lacking, and research on this crucial topic is needed. Also lacking is evidence on the role of the PMC as the "matching" site of the mirror system for identifying and representing intentions underlying complex social behaviors.

Enduring Traits and Scripts

In contrast to the somewhat equivocal role of the mPFC in immediate goal inferences, the meta-analysis showed robust empirical evidence consistent with the idea that understanding humans as enduring organisms with permanent social and psychological properties such as traits and norms is a crucial common element that engages the mPFC. This analysis also demonstrated that trait information about unfamiliar others selectively engages the dorsal part of the mPFC, whereas the ventral part is implicated when making trait inferences about familiar others or the self [see also Mitchell et al., 2005b]. Knowledge on social

scripts involves both parts of the mPFC. No other regions analyzed in this meta-analysis are reliably engaged, except the rTPJ during trait inferences of other persons. It was, however, argued, that this is most likely due to the visual information which tends to engage the TPJ.

However, this does not imply that no other functions are subserved by the mPFC. However, of the many brain functions explored, only sequence learning seems to be tied intimately to social cognition, as both areas of activation overlap entirely. This provides support for the idea that the mPFC is crucially involved in the integration of information across time, be it social or not (Huey et al., 2006; Krueger et al., 2007; Wood and Grafman, 2003; Wood et al., 2005). This meta-analysis also documented a substantial overlap with emotional and reward processing, which confirms the long-held idea that the mPFC is strongly involved in the integration of different sort of information. However, the data suggest that emotionality is a not a subsystem of trait impression formation per se [see also Amodio and Frith, 2006, Heberlein and Saxe, 2005], but rather that it provides input to the mPFC to modulate and enrich social inferences with affective associations. Other general-purpose functions engage areas of the PFC that are not activated during social cognition, and are therefore very unlikely to constitute a core process of social inference, contrary to ideas put forward by many authors in the social neuroscience literature [e.g., Amodio and Frith, 2006; Leslie et al., 2004; Northoff and Bermphohl, 2004] and social psychology [cf. Kelley, 1967]. These distinct functions are physical causality, action monitoring and inhibition, divided and directed attention, episodic memory, and working memory.

OPEN QUESTIONS

The amount of research devoted to social cognition in the last decade has been impressive. Nevertheless, a large number of unresolved questions have not yet been answered. Below, I briefly list a number of them that strike me as particularly interesting for future research. Some of these novel questions have recently been taken up in new research.

Different Types of Judgments on Individuals and Groups

- Are inferences of goals and traits of other persons subserved by a sequential posterior-anterior neurological circuit as suggested, and if so, in what ways? To uncover the primacy of one process over the other, we probably need time-sensitive methods like event-related potentials (ERPs). Can this sequence explain why humans are so prone to the well-known fundamental attribution bias, that is, the pervasive tendency to put more weight to the actor in explaining behavior and less to the external environment [Gilbert and

Malone, 1995; Trope and Gaunt, 2000]? More generally, can social neuroscience help to unravel the sources of other cognitive heuristics and biases in social cognition?

- What are the neurological substrates of other social inferences that have received relatively little attention in social neuroscience, including inferences at the individual level like ulterior motives (which are similar to false beliefs and deceit explored in neurological research, e.g., Grèzes et al., 2004), and at the group level like categorization, stereotyping or norm learning [Tomelleri et al., 2007]?
- Can we differentiate various types of enduring inferences at the neurological and psychological level? For instance, is the difference between trait inferences of others and self due to actual differences in mPFC processes or rather due to differences in informational sources such as the emotional warmth and closeness generated by familiar others (including the self; from the reward area located at the ventral and orbital mPFC) or greater autobiographic memory [located at the ventral mPFC, see Graham et al., 2003; Maguire and Frith, 2003; Maguire and Mummery, 2003]? As another example, do trait inferences and social script knowledge engage entirely identical brain areas as suggested by this meta-analysis?
- The present analysis suggests that social inferences are processed in a different manner than physical causality. However, which brain areas subserve explicit causality judgments on social events?

Spontaneity of Judgments

This meta-analysis suggests that spontaneous inferences preferentially engage the TPJ and dorsal mPFC, whereas explicit inferences preferentially engage the ventral mPFC. Many fMRI studies have relied on explicit instructions or questions, which pose less internal validity problems. But in everyday life, we more often make spontaneous social inferences. Can social neuroscience help to identify the processing elements in social cognition that are spontaneous and implicit, versus those that require mental reflection and resources [see also Keysers and Gazzola, 2007]?

- Are false beliefs inferred from other people made spontaneously or not [e.g., Apperly et al., 2006], and if so, which areas are engaged?
- Are trait inferences made spontaneously, and if so, which areas are involved? Mitchell et al. (2006) found no differences between spontaneous and intentional trait inferences, whereas Van Duynslaeger et al. (2007) found more involvement of the TPJ during spontaneous trait inferences, in line with the present analysis.
- Are group inferences made spontaneously? ERP data indicate that categorization of group members is spontaneous and fast, while the attribution of stereotypes

depends on minimal processing resources and goals [e.g., Tomelleri et al., 2007].

Social Judgments and Change

Given that social inferences are at times undesirable and derogative (e.g., negative stereotyping of minority groups), it is important to explore not only which conditions give rise to these inferences but also under which conditions they may change. Does change require a minimal amount of empathy in the other's mind? Does it require the deployment of automatic processes or of executive control and inhibition processes, or both? What are the mental brain processes involved in this? As far as I am aware, these questions are only beginning to be raised in social neuroscience [Achtzinger et al., 2007]. Nevertheless, insight in the brain processes that underlie change in social cognition has the potential to drastically alter our understanding on how the brain is responsible for our past successes and failures in attempting to change social minds and social behavior.

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