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General and specific contributions of the medial prefrontal cortex to knowledge about mental states

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Recent neuroimaging research (Mitchell, J.P., Heatherton, T.F., Macrae, C.N., 2002. Distinct neural systems subserve person and object knowledge. Proc. Natl. Acad. Sci. U. S. A. 99, 15238–15243.) has suggested that semantic knowledge about the psychological aspects of other people draws on a pattern of neural activity that differentiates social from nonsocial semantics. Although the medial prefrontal cortex (mPFC) clearly plays a central role in a range of such social–cognitive tasks, little is known about the precise contributions made by this region to social semantics. The current study addressed two outstanding questions regarding mPFC function. First, do mPFC contributions to processing words that refer to psychological states extend to other, nonhuman targets or are they specific to understanding the psychological experience of conspecifics? Second, does the mPFC respond generally to tasks that require processing another person, or is its activity specific to understanding psychological characteristics? To address these questions, participants were scanned using fMRI while judging the applicability of words to one of two types of targets: people or dogs. For each target, participants made one of two types of semantic judgment: does this word describe a potential psychological state of the target or does this word refer to a physical part of the target? Results demonstrated that greater mPFC activation accompanied judgments of psychological states than of body parts regardless of whether the target was a person or a dog, indicating that mPFC contributions to social semantics are specific for understanding psychological states–directly countering recent suggestions that mPFC responds generally to any judgment about another person–and that mPFC activity extends to targets other than conspecifics.

Keywords: Medial prefrontal cortex; Social–cognitive processing; fMRI.

Introduction

Humans possess a remarkable store of knowledge about the world in which they live. Even without considering areas of specialized expertise, most adult humans can identify and describe the function of thousands of artifacts, define the meaning of tens of thousands of words (e.g., native English speaking adults typically know the meaning of upwards of 25,000 words), and articulate a range of facts about such abstract topics as how physical or biological systems work (e.g., knowing that the movement of the sun across the sky is produced by the rotation of the earth and that penguins are birds that do not fly).

Understanding how such semantic knowledge is organized in the human brain has been a central question in much neuropsychological and functional neuroimaging works over the past two decades. Beginning with seminal observations by Warrington and colleagues in the 1980s (Warrington and McCarthy, 1983; Warrington and Shallice, 1984), research has consistently demonstrated that, rather than all aspects of semantics arising from a single system dedicated to understanding the world, semantic knowledge appears to be organized into discrete, category-specific domains. For example, individuals have been identified who demonstrate a selective inability to name or describe living things but preserved semantic knowledge of other domains, as well as patients with the reverse pattern of results (for a review, see Caramazza and Shelton, 1998). Consistent with these neuropsychological observations, recent fMRI experiments have identified distinct brain regions that respond maximally during semantic tasks for specific classes of stimuli, such as houses, faces, animals, or tools (Chao et al., 1999; Haxby et al., 2001; Martin, 2001; Martin et al., 1996).

Although some controversy exists regarding the precise organizing principles underlying this category specificity, some theorists have pointed out that, because different classes of objects are distinguished from one another by the relative importance of different types of features, neural representations of an object may involve the brain regions most important for processing the specific features unique to a class of object (Caramazza and Shelton, 1998). For instance, because most tools are defined by their function (and

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not some arbitrary physical property, such as color), motor regions–such as left premotor cortex–are involved in the representation of knowledge about tools (Martin, 2001). In contrast, because animals are differentiated from one another primarily on the basis of their visual features (rather than on the basis of function), semantic knowledge of animals appears to be represented by brain regions involved in the visual perception of animate objects and biological motion, such as middle temporal gyrus and a number of occipital regions (Chao et al., 1999; Damasio et al., 1996; Martin et al., 1996; Perani et al., 1995). Indeed, recent work has even suggested that subregions of the motor cortex that support movement of particular body parts (foot, hand, or tongue) are also recruited when people read words that are associated with movement of these body parts, such as *kick*, *throw*, or *chew* (Hauk et al., 2004).

Recently, we reported a similar dissociation for semantic knowledge about other people (Mitchell et al., 2002), in which we observed that the same brain regions implicated in making inferences about the mental states of others were also engaged during semantic judgments about words that denote such mental states. Specifically, participants were scanned while judging whether a given word could ever be used to describe either a person or an inanimate object (either a piece of fruit or an article of clothing). Half of the words could appropriately describe the psychological characteristics of a person (e.g., *assertive*, *energetic*), whereas the remaining half of the words could describe one class of objects, but not persons (e.g., *sundried*, *patched*). Although formally identical tasks, judgments of people and objects were associated with modulations in a qualitatively distinct set of brain regions. Importantly, semantic judgments about words that referred to the psychological characteristics of other people engaged brain regions previously observed during a variety of social–cognitive tasks that require understanding another person's mental states, most notably the mPFC. Similar mPFC regions have been linked to a range of social–cognitive tasks that involve mentalizing about the psychological characteristics of another person, such as making inferences about the mental states of characters in stories or cartoons (Fletcher et al., 1995; Gallagher et al., 2000; Gregory et al., 2002; Stone et al., 1998), judging whether a historical figure would know how to use various objects (Goel et al., 1995), encoding information about another's personality (Mitchell et al., 2004), and playing interactive games that require second-guessing an opponent (Gallagher et al., 2002; McCabe et al., 2001).

This earlier work leaves two important questions unresolved regarding mPFC involvement in person knowledge. First, does mPFC contribute to semantic knowledge about all aspects of other people or specifically to knowledge about psychological characteristics? In our earlier study (Mitchell et al., 2002), participants responded to words that either denoted the potential mental states of another person or to words that could not be used to describe people at all. As such, this earlier study cannot answer the question of whether additional mPFC activity would also accompany judgments about the nonmental (e.g., physical) aspects of other people–as suggested by recent researchers (Saxe and Kanwisher, 2003)–or whether such activity would be specific to processing mental states.

Second, does mPFC contribute to an understanding of mental states generally or is its involvement restricted to the mental states of other people? Although other humans are the paradigmatic case of stimuli that possess mental states, perceivers frequently extend social–cognitive attributions to animals, especially domestic pets such as dogs (Gosling et al., 2003). One possibility is that representing the psychological characteristics of other animals can be accomplished through the same mechanisms that allow perceivers to represent the psychological characteristics of other people (Mason et al., 2004). On the other hand, the richness of human social interaction and the particular importance of understanding and predicting the behavior of conspecifics may suggest that knowledge about the mental states of other people requires unique cognitive processing that does not extend to judgments of other targets.

The current study was designed to address these two interrelated questions. Adapting the task used in our earlier work (Mitchell et al., 2002), participants judged whether each of a series of words was applicable to a particular class of target stimulus, either people or dogs. These words referred to psychological states experienced by both dogs and people (e.g., *curious*, *frightened*), to body parts of which both dogs and people are composed (e.g., *artery*, *liver*), or to concepts and parts that were not applicable to humans or animals (e.g., *celestial*, *pedal*). Participants considered each word and simply indicated whether the word could apply to a target by either being a description of a potential psychological state or of a body part (or whether it could not describe the target).

Our current understanding of mPFC contributions to social knowledge would be informed by a number of possible patterns of results. On the one hand, mPFC activity may differentiate between the two types of semantic judgment (i.e., *psychological-state* > *body-part* words) regardless of the target of those judgments (persons or dogs). Such a result would suggest that mPFC both (i) specifically subserves knowledge about psychological states and not all aspects of social knowledge (e.g., knowledge about the physical aspects of other people) and (ii) subserves such psychological knowledge for mental agents in general, not just for other humans. In contrast, mPFC activity may instead differentiate between the two types of targets, but not the particular semantic judgments made about them. This alternative result would suggest that mPFC contributes to a wide range of semantic knowledge about other people, including an understanding of their physical characteristics, and that these contributions do not extend outside of knowledge about conspecifics specifically.

Method

Participants

Participants were 19 (12 female) right-handed, native English speakers with no history of neurological problems (mean age, 20.9 years; range, 19–24). Informed consent was obtained in a manner approved by the Committee for the Protection of Human Subjects at Dartmouth College.

Stimuli and behavioral procedure

Across 4 functional runs, participants judged whether each of a series of words was an appropriate descriptor of either a person or a dog. Each functional run began with a screen that read, "In the following run, you will be making judgments of a person [dog]," which indicated whether a person or dog would serve as the target for judgments in that particular run (2 person runs, 2 dog runs). The order of person and dog runs was determined randomly for each participant. Descriptors consisted of 12 *psychological-state* words referring to potential psychological characteristics of both people and dogs (e.g., *curious*, *energetic*) and 12 *body-part* words referring to body parts shared by people and dogs (e.g., *artery*, *liver*). Descriptors were pretested to ensure that they were equally applicable to both people and dogs. In addition, the stimulus set included 12 *abstract* words referring to abstract concepts that could not readily be used to describe people or dogs and that were matched for length with the psychological-state words (e.g., *celestial*, *marbelized*) as well as 12 *object-part* words referring to parts of inanimate objects that were matched in length with the body-part words (e.g., *bolt*, *pedal*) (Fig. 1).

Each trial consisted of one of these words presented for 4 s. Participants were instructed to press one of two buttons if the word could be used to describe a member of the target group (people or dogs) or if it referred to a body part of members of the target group; participants were instructed to press a different button if the word could not normally be used to describe or did not consitute a part of the target (because almost any abstract word could be used to describe a person metaphorically, participants were explicitly instructed to consider the literal connotation of words and not to base judgments on possible figurative meanings). Within each run, each descriptor word appeared twice, resulting in 48 'yes' responses (24 pyschological-state, 24 body-part) and 48 'no' responses (24 abstract, 24 object-part). To optimize estimation of the event-related fMRI response, trials were intermixed in a pseudo-random order and separated by a variable interstimulus interval of 500–7500 ms (Dale, 1999), during which participants passively viewed a fixation crosshair.

Imaging procedure

Imaging was conducted using a 1.5 T GE Signa scanner. Functional scanning used a gradient-echo echo-planar pulse sequence (TR, 2 s; TE, 35 ms; 3.75 × 3.75 in-plane resolution). Participants completed 4 functional runs of 256 acquisitions (25 axial slices; 5 mm thick; 1 mm skip) followed by a high-resolution T1-weighted structural scan (SPGR). Stimuli were projected onto a screen at the end of the magnet bore that participants viewed by way of a mirror mounted on the head coil. A pillow and foam cushions were placed inside the head coil to minimize head movements.

SPM99 software (Wellcome Department of Cognitive Neurology) was used for slice timing and motion correction, coregistration to the participant's high-resolution structural scan, normalization to the MN1305 stereotactic space (interpolating to 3 mm cubic voxels), and spatial smoothing (8-mm Gaussian kernel). Statistical analyses were performed using the general linear model in which the event-related design was modeled using a canonical hemodynamic response function, its temporal derivative, and additional covariates of no interest (a session mean and a linear trend). Contrasts of interest were implemented using a random-effects model. Specifically, regions-of-interest (ROIs) were defined using an automated algorithm that identified the peak voxel of clusters that comprised 10 or more contiguous voxels that each survived a statistical threshold of $P < 0.001$. ROIs were then subjected to a second-level analysis to test for differences between conditions; specifically, statistical comparisons between conditions were conducted using analysis-of-variance procedures on the parameter estimates associated with each trial type.

Results

Behavioral data

Response latencies were roughly comparable across trial types: psychological-state judgments of people (M = 1176 ms), psychological-state judgments of dogs (M = 1206 ms), body-part judgments of people (M = 1180 ms), and body-part judgments of dogs (M = 1155 ms). The only significant difference between any two conditions was observed for psychological-state and body-part judgments of dogs, $t(18) = 2.61$, $P < 0.02$ (all other pairwise comparisons, $t[18] < 1$, $p > 0.33$). In addition, the 2-way interaction of judgment type and target was significant ($F[1,18] = 8.37$, $P < 0.01$).

fMRI data

We adopted several complementary analytic strategies to examine differences in neural activation across the judgment tasks.

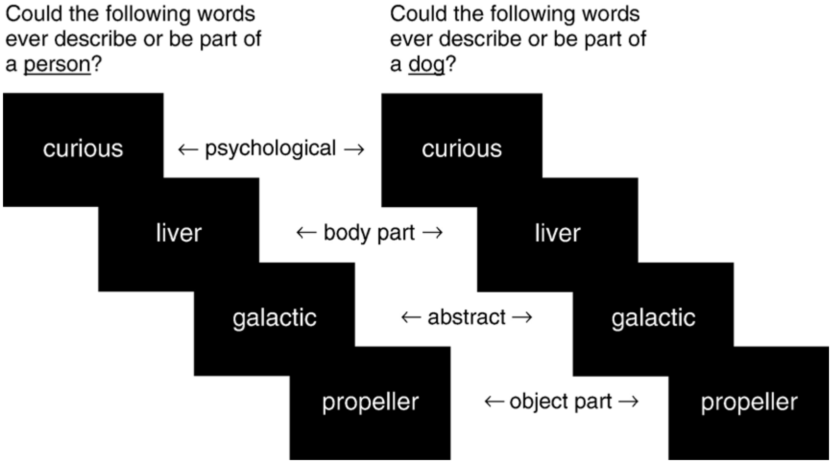

Fig. 1. Participants completed functional runs of two different types. During "person" runs, participants were asked to judge whether each of a series of words "could ever be used to describe or be part of a person." During "dog" runs, participants made the same judgments about a dog. Words could either appropriately describe the psychological states of (psychological-state trials), be a part of (body-part trials), or not describe/be part of (abstract and object-part trials) a person or dog. Importantly, the same items were equally applicable to both people and dogs and were used across runs of different types.

Table 1
Peak voxel and number of voxels for regions-of-interest obtained from the contrast of psychological-states > body-parts

Region	*x*	*y*	*z*	Max *t*	Voxels
Medial PFC	9	54	36	5.56	29
Angular gyrus	51	−60	30	5.56	23
Occipital cortex	−21	−87	−12	4.95	41
Precuneus	−6	−54	36	4.93	27
Inferior temporal gyrus	51	−30	−18	4.88	11
Superior frontal gyrus	6	21	48	4.14	11
	0	6	66	3.86	12

Note. t tests reflect the statistical difference between the two conditions, as computed by SPM99. Coordinates refer to the Montreal Neurological Institute stereotaxic space.

First, we directly contrasted *psychological-states* > *body-parts*, regardless of whether judgments were made for people or dogs. Consistent with earlier work (Mitchell et al., 2002), the maximum peak difference obtained from this contrast was located in dorsal mPFC (MNI coordinates: 9, 54, 36). This region was further interrogated for differences between person and dog trials. As displayed in Fig. 2, although activity in this mPFC region differentiated between judgment type, no meaningful difference was associated with the two types of targets for psychological-state and body-part trials: no main effect of target type was observed in this region, $F(1,18) = 0.29$, ns, and the difference between psychological-state and body-part trials was equivalent for persons and dogs (judgment type × target interaction, $F[1,18] = 0.16$, ns). Furthermore, the difference between psychological-state and body-part judgments was significant for both persons, $P < 0.002$ as well as dogs, $P < 0.01$. Additional regions obtained from this contrast included the angular gyrus, precuneus, inferior temporal gyrus, superior frontal gyrus, and medial occipital cortex (see Table 1 for coordinates). With one exception, each of these regions demonstrated the same pattern of activation as mPFC, i.e., greater activation for psychological-state than body-part judgments but no difference between dogs and persons. The only one of these regions in which we observed a difference between dogs and persons was in the medial occipital cortex, in which greater activation was observed for judgments about dogs than persons; interestingly, the coordinates of the peak activation in this region were highly similar to those reported by Chao et al. (1999) for the comparison of *animals* > *tools* (e.g., 12, −87, −7). No regions were observed for the reverse contrast, i.e., *body-parts* > *psychological-states*.

Additional regions in which brain activity differentiated between person and dog trials were identified from the direct contrast of *dog* > *person*, regardless of judgment type. This contrast revealed two regions that overlapped with earlier reports of the neural correlates of semantic knowledge for animals (Chao et al., 1999; Damasio et al., 1996; Martin et al., 1996; Perani et al., 1995): middle temporal gyrus (54, −51, −6) and inferior occipital gyrus (−21, −96, 3). In both regions, only a main effect of target type was observed, but no main effect of judgment or interaction between judgment type and target type (all P values > 0.20). At our a priori statistical threshold, no regions were revealed by the reverse contrast of *person* > *dog*; however, at a slightly relaxed statistical threshold ($P < 0.005$, 10 contiguous voxels), we observed a region of right superior temporal sulcus (51, −6, −9) in which activation was greater for person than for dog trials. No interaction was observed between target type and judgment in this region, although marginally greater activation was observed for psychological-state than for body-part judgments ($P < 0.08$).

Discussion

Following up on our earlier observation that greater mPFC activity accompanies semantic decisions about words that refer to the psychological states of other people (Mitchell et al., 2002), the current results simultaneously extend the scope of these earlier findings at the same time that they delineate the boundaries of mPFC contributions to social knowledge. Specifically, mPFC activity during the processing of psychological-state words extended beyond other people to include judgments of nonhuman animals that are believed to have mental states similar to those experienced by humans. Importantly, the same words were equally good descriptors of the mental states of persons and dogs. However, it is unlikely that participants were simply responding to dogs as if they were other people (i.e., surreptitiously imagining the target to be a person, regardless of the instruction to consider a dog). Although body-part words were also equally applicable to both targets, physical judgments were nevertheless associated with a number of significant differences as a function of the identity of the target. Specifically, whereas activity in middle temporal, medial occipital, and inferior occipital gyri was significantly greater for judgments of dogs than people, a (marginal) difference in the other direction was observed in superior temporal sulcus. Moreover, the association of these particular regions with judgments of dogs and

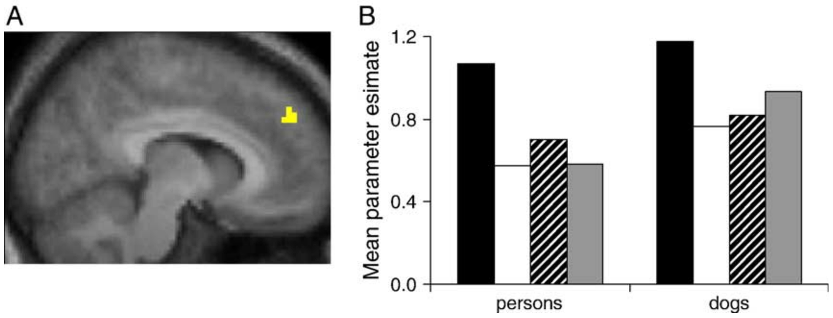

Fig. 2. The contrast of psychological-states > body-parts yielded a region of dorsal mPFC, displayed on a sagittal ($x = 9$) slice of participants' mean normalized brain (A). Although activation maps were obtained by analyzing only psychological-state and body-part words that could be used to describe the targets, panel (B) displays parameter estimates obtained for all four different types of judgment of persons and dogs: psychological-state words (leftmost solid black bars), body-part words (solid white bars, second from the left), abstract words that could not be used to describe either kind of target (striped bars, second from the right), and object-part words (rightmost solid gray bars). The zero-point on the graph represents baseline.

people parallels earlier work linking this former set of regions to semantic decisions about animals (Chao et al., 1999; Damasio et al., 1996; Martin et al., 1996; Perani et al., 1995) and the superior temporal sulcus to a range of social perception tasks (Allison et al., 2000). Together, these results most parsimoniously suggest that mPFC activity can also include the processing of mental agents other than conspecifics, such as nonhuman animals.

However, mPFC contributions to social knowledge were limited to judgments of the psychological states of such targets. Specifically, relatively little mPFC activity accompanied judgments about the body parts of either people or dogs, suggesting that mPFC activity was specific for processing semantic information about the potential psychological characteristics experienced by mental agents, but did not contribute substantially to processing information about the physical aspects of people or dogs. This latter result dovetails nicely with additional recent observations that mPFC activity can be modulated by the relative social–cognitive demands of a task, even under conditions in which the target stimuli remain constant. For instance, Mitchell et al. (2004) reported greater mPFC engagement when participants used a series of statements to form an impression of an unfamiliar person than when trying to memorize the same person–statement pairs without reference to their social–cognitive content. Likewise, some of our recent work (Mitchell et al., in press) has demonstrated that, whereas substantial mPFC activity accompanies judgments about the mental states of an individual (how pleased does this person look to have his photograph taken?), relatively little such activity accompanies judgments about the physical aspects of the same targets (how symmetrical is this person's face?). This constellation of findings strongly suggests that the mPFC does not respond preferentially to the presence of a person per se but rather specifically contributes to an understanding of the social–cognitive (i.e., psychological) aspects of other mental agents.

This conclusion directly conflicts with the earlier report of Saxe and Kanwisher (2003), who linked activity in dorsal mPFC to the processing of stories that were ostensibly limited to physical descriptions of another person; the peak coordinate of their dorsal mPFC region was quite similar (−3, 57, 39) to that of the mPFC region observed in the current study. However, it is unclear to what extent such physical descriptions necessarily suppressed mental-state processing in their participants. For example, the sample physical story provided in the appendix of Saxe and Kanwisher read, "Emily was always the tallest kid in her class. In kindergarten, she was already over 4 ft tall. Now that she is in college she is 6′4″. She is a head taller than the others" (p. 1841). Although this is clearly a physical description of a person, we suspect that stories like this may nevertheless provoke substantial consideration of the psychological experience of the target, for example, thinking about what it might feel like to be such a tall woman, imagining oneself as 6′4″, and so on. That is, these "physical" stories may have inadvertently induced participants to engage in a nontrival amount of mental state processing. Without a means of independently confirming that such physical descriptions successfully prevented participants from engaging in this kind of consideration of mental states, and in light of the current results, we find little support for the notion that the mPFC is a region that responds generally during consideration of a person per se. Rather, when participants in the current study were oriented to the physical aspects of another person and had no reason to consider mental states (i.e., body-part trials), mPFC activity was significantly greater for psychological-state trials than body-part trials, and body-part trials did not differ from judgments of words that could not be used to describe other people. As reviewed above, this view is consistent with a number of additional fMRI studies that also suggest that the mPFC subserves psychological inference about other people but does not contribute to person-relevant tasks that do not include a mentalizing component.

One intriguing, but poorly understood, feature of activity in dorsal mPFC consists of the "direction" of change observed in this region. Although, as in the current study, modulations in mPFC can occur as positive-going deflections in activity (i.e., "activations"), negative-going deflections from resting baseline states ("deactivations") are also frequently reported in this region (Gusnard and Raichle, 2001; Raichle et al., 2001; Shulman et al., 1997). In fact, in our earlier report of the neural correlates of person knowledge, modulations in a very similar mPFC region took the form of deactivations, although in the current study, they were clearly activations above baseline. The factors that account for this difference in the direction of change across studies remain unclear: both studies were completed using the same scanner in two samples from the same participant population (Dartmouth College students), and both used the identical baseline (passive viewing of a fixation crosshair) and scanning parameters (e.g., TR, slice orientation). One possibility is that the requirement to differentiate between people and other targets (dogs) might have increased processing demands in mPFC and led to activations above baseline (in our initial study, participants only needed to consider one kind of mental agent, i.e., other people). However, this mystery partially reflects a general lack of understanding regarding the potential functional significance of activations and deactivations; the best articulated theory of deactivations in regions like the mPFC is that such negative deflections represent suspension from a default state of cognitive processing important for social cognition (Gusnard and Raichle, 2001).

Notwithstanding questions regarding direction of modulation, the current results dovetail with an emerging view that semantics draws on a distributed, dynamic system of brain regions, the constituent parts of which depend on the type of semantic knowledge being accessed. For example, a number of studies have suggested that action verbs or nouns that imply particular actions (such as tools) engage premotor cortex (Chao et al., 1999; Dehaene, 1995; Ishai et al., 1999; Kellenbach et al., 2002; Martin et al., 1996), suggesting that motor regions contribute to the semantic representation of action-related words. Even more direct evidence for this proposition comes from recent work by Hauk et al. (2004), who observed greater activation in subregions of the motor cortex responsible for hand, foot, or tongue movements when participants read words that denoted an action typically performed with the corresponding body part (e.g., *throw*, *kick*, *chew*, respectively). In much the same way, the current study suggests that semantic judgments about words that refer to psychological states draw selectively on a brain region–the mPFC–consistently implicated in a wide range of social–cognitive tasks that require understanding the mental states of other people (Fletcher et al., 1995; Gallagher et al., 2000, 2002; Goel et al., 1995; Gregory et al., 2002; McCabe et al., 2001; Mitchell et al., 2004; Saxe and Kanwisher, 2003; Stone et al., 1998); (for reviews, see Adolphs, 2001; Frith and Frith, 1999; Gallagher and Frith, 2003). Although not employing the same passive reading task as Hauk et al., the current study does suggest that judging words that describe the psychological states of other mental agents draws on the same neural substrates as actively trying to apprehend those states in other people.

However, whereas a good deal is currently known about the organization of regions like ventral temporal cortex and motor/premotor cortex, a similar understanding of the principles underlying mPFC function has yet to emerge. That is, although researchers have repeatedly linked mPFC to social–cognitive processing, few hypotheses have been offered regarding such issues as whether discrete subregions of mPFC contribute to different aspects of social cognition and, if so, what different types of processing mark these separate subregions. Although some attempts at more precise specification of mPFC processing have begun to surface (Mitchell et al., in press), one important task for future research in this area will be to delineate the functional principles along which the mPFC is organized.

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