

Running Head: Person Knowledge

**Thinking About Actions:
The Neural Substrates of Person Knowledge**

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Abstract

Despite an extensive literature on the neural substrates of semantic knowledge, how person-related information is represented in the brain has yet to be elucidated. Accordingly, in the present study we used functional magnetic resonance imaging (fMRI) to investigate the neural correlates of person knowledge. Focusing on the neural substrates of action knowledge, participants reported whether or not a common set of behaviors could be performed by people or dogs. While dogs and people are capable of performing many of the same actions (e.g., run, sit, bite), we surmised that the representation of this knowledge would be associated with distinct patterns of neural activity. Specifically, person judgments were expected to activate cortical areas associated with theory of mind (ToM) reasoning. The results supported this prediction. Whereas action-related judgments about dogs were associated with activity in various regions, including the occipital and parahippocampal gyri; identical judgments about people yielded activity in areas of prefrontal cortex, notably the right middle and medial frontal gyri. These findings suggest that person knowledge may be functionally dissociable from comparable information about other animals, with action-related judgments about people recruiting neural activity that is indicative of ToM reasoning.

Key Words: Action Knowledge; fMRI; Social Cognition; Theory of Mind; Mentalizing.

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As other people are unquestionably the most important objects we encounter, it is surprising that little is currently known about the cortical representation of person-related knowledge. While neural regions that subserve important components of the person perception process (e.g., face perception, biological motion, emotion recognition, gaze detection) have been identified (Adolphs, 2003; Allison, Puce, & McCarthy, 2000; Hoffman & Haxby, 2000; Kanwisher, McDermott, & Chun, 1997; McCarthy et al., 1997; Puce et al., 1998), research has yet to consider how abstract knowledge about other people is represented in the brain (see Mitchell, Heatherton, & Macrae, 2002). This oversight is puzzling as much is known about the cortical representation of object-based knowledge. Both neuropsychological and functional neuroimaging investigations have confirmed that the extraction of knowledge about particular classes of inanimate stimuli (e.g., tools, musical instruments, houses) is associated with distinct regions of the brain (Caramazza, 2000; Caramazza & Shelton, 1998; Chao, Haxby, & Martin, 1999; Haxby et al., 2000, 2001; Martin, 2001; Martin, Ungerleider, & Haxby, 2000; Martin et al., 1996). But what of person knowledge?

One intriguing possibility is that the mind may have evolved dedicated neural circuits to deal with knowledge that has biological relevance or significance to people, such as information pertaining to plants, tools, and conspecifics (see Caramazza, 2000; Caramazza & Shelton, 1998). As Caramazza (2000, p. 1043) has argued, “evolutionary pressures resulted in specialized neural mechanisms for perceptually and conceptually distinguishing specific kinds of objects, leading to the categorical organization of knowledge in the brain. The range of categories that can be subsumed under this principle is very narrow—it is restricted to categories of objects whose rapid and accurate classification would have led to survival and reproductive advantages.” The benefits of such a distributed system lie in the rapid and

accurate manner in which conceptual knowledge can be accessed. Were distinct classes of knowledge to share a common neuroanatomical location, inter-item competition (e.g., interference) may compromise the selection process. Any impediment to this process could have debilitating consequences in task contexts that necessitate the rapid generation of behavioral responses. Person perception is just such a domain. The application of person knowledge demands a level of flexibility that is uncommon for most other classes of stimuli. Given therefore its importance, one might expect fundamental aspects of person knowledge to be functionally dissociable from comparable classes of information in the brain (Caramazza, 2000), a possibility we explored in the current investigation.

To elucidate the architecture of person knowledge, we examined the neural substrates of one important class of information—human action. Despite the demonstration that object-related actions (e.g., kettle – boil) are associated with activation in discrete regions of temporal cortex (see Klein et al., 1999; Martin, 2001; Martin et al., 1995; Petersen et al., 1988; Poline et al., 1996; Raichle et al., 1994; Warburton et al., 1996; Wise et al., 1991), studies have yet to identify cortical areas that support the representation of comparable person-based knowledge. Interestingly, some clues to the identity of these areas may be found in work that has investigated the neural correlates of mental state attribution (Baron-Cohen, 1995; Frith & Frith, 1999). Through the possession of a ToM, people are able to understand the goals and intentions that guide the behavior of others (Blakemore & Decety, 2001; Frith & Frith, 1999; Gallagher & Frith, 2003; Siegel & Varley, 2002). That is, people are able to infer the hidden internal states that give rise to human action.

Although distributed widely throughout the brain, the cerebral implementation of this capacity is known to involve a raft of frontal operations (Shallice, 2001). For example, observing action, adopting the perspective of another person, or inferring the mental state of an actor performing a social behavior produce patterns of activation in discrete regions of frontal cortex, notably the medial and middle frontal gyri (Brunet et al., 2000; Castelli et al., 2000; Fletcher et al., 1995a; Gallagher et al., 2000; Goel et al.,

1995; Vogeley et al., 2001). These regions and their associated cognitive operations are believed to play a pivotal role in mindreading, the process through which people infer the motives underlying human action (Gallagher & Frith, 2003). By extension, might these frontal areas also play a prominent role in the representation of action-based knowledge (Frith & Frith, 1999)? That is, might the neural areas that support an agentic interpretation of human action also contribute to the representation of this knowledge in the brain?

To investigate this possibility, we used event-related fMRI to measure brain activity while participants made a series of action-related judgments about people and dogs. Dogs were selected as the target of comparison as a large number of actions can be performed by both dogs and people (e.g., run, jump, lick). We surmised, however, that these common behaviors would be associated with distinct patterns of neural activity when paired with each target. Specifically, the frontal activity that is indicative of ToM reasoning—notably, activity in medial prefrontal cortex (MPFC)—was only expected to emerge when the actions were paired with people. When the same actions were paired with dogs, activity was expected to emerge in occipitotemporal regions that support visual and memorial processing (i.e., bringing images of dogs to mind, see Cabeza & Nyberg, 2000; Kosslyn, Ganis, & Thompson, 2001)

Method

Participants

Twenty participants (12 female & 8 male, age range: 18-33, mean age = 23.8) completed the experiment. All participants were right-handed, native English speakers with no history of neurological problems. All gave informed consent according to the procedures approved by the Committee for the Protection of Human Subjects at Dartmouth College. Data from three participants (1 male & 2 females) were discarded due to problems with the acquisition of images during the functional runs.

Stimulus Materials and Procedure

The stimulus materials were 144 action words. Of these items, 72 comprised actions that could be performed by both people and dogs (e.g., leap, sit, swallow) and 72 comprised actions that could be performed by neither target (e.g., ferment, dissolve, ripple). Participants responded to visually presented words by pressing one of two response buttons (yes/no) “if the action could be performed by a person (or a dog) or could not be performed by a person (or a dog).” On the person trials, the referent for the judgment task was a member of the opposite sex. Thus, female participants reported if a man could perform the actions and male participants reported if the actions could be performed by a woman. This instruction was included to prevent participants from using ‘self’ as the referent on the person trials. Debriefing confirmed that all participants followed the experimental instruction. Participants completed four runs (i.e., 2 person runs & 2 dog runs) and were instructed prior to each run whether the target was a person or a dog. Order of presentation of the runs was counterbalanced and the order of presentation of action words within each run was randomized for each participant. The words were presented using PsyScope (version 1.2.5) and back projected with an Epson (ELP-7000) LCD projector 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 within the head coil to minimize head movements. Each trial began with a fixation cross presented for 1000 ms. An action word (36-pt Geneva font) was then presented for 1500 ms. Each functional MRI run consisted of 36 trials in which the action could be performed by the target (i.e., person or dog) and 36 trials in which the action could not be performed by the target. A variable interstimulus interval (1000 ms – 8500 ms) was used to optimize estimation of the event-related BOLD response.

All images were collected using a 1.5T GE Signa scanner with standard head coil. T1- weighted anatomical images were collected using a 3-D sequence (SPGR; 128 sagittal slices, TR = 7 ms, TE = 3 ms, prep time = 315 ms, flip angle = 15°, FOV = 24 cm, slice thickness = 1.2 mm, matrix = 256 x 192).

Functional images were collected with a gradient echo EPI sequence (each volume comprised 25 slices; 4.5 mm thick, 1mm skip; TR = 2500 ms, TE = 35 ms, FOV = 24 cm, 64 x 64 matrix; 90° flip angle). Preprocessing and statistical analysis of the fMRI data were performed using SPM99 software (Wellcome Dept of Cognitive Neurology, London). Preprocessing included slice timing and motion correction, coregistration to each participant's anatomical data, normalization to the ICBM 152 brain template (Montreal Neurological Institute), and spatial smoothing with an 8 mm (full-width-at-half-maximum) Gaussian kernel. The hemodynamic response to the onset of each event type of interest was modeled with a canonical hemodynamic response function (HRF). Contrasts (t -tests, $p < .001$) for each voxel were run on individual participants and a random-effects model was then applied to the contrasts of all individual participants to obtain group activations.

Results

Behavioral data collected during scanning showed no difference in either the accuracy ($t(16) < 1$, ns – M s 91% vs. 91%) or time taken ($t(16) < 1$, ns – M s: 899 ms vs. 896 ms) by participants to make action judgments about people or dogs. Thus, it is unlikely that variability in the cortical activity associated with these judgments reflects differences in the difficulty of the respective tasks.

Insert Table 1 About Here

To examine whether action judgments about people and dogs were associated with different patterns of neural activity, we compared the event-related BOLD response associated with person trials to that associated with dog trials. This comparison revealed distinct patterns of brain activity for each type of target (see Table 1). Person > Dog comparisons yielded significant activations in the R. middle frontal gyrus, R. medial frontal gyrus, and R. anterior cingulate gyrus. In contrast, Dog > Person comparisons yielded significant activations in the L. and R. parahippocampal gyrus, L. superior occipital gyrus, R.

precuneus, L. uncus, L. cerebellum, and L. pulvinar. Figure 1 shows the significant activations that were observed in the R. medial and middle frontal gyri when person and dog judgments were directly compared. The hemodynamic time courses for each region are also shown. In both brain regions, the temporal profile of activity was comparable. While person and dog judgments showed significant deactivations below the resting baseline (i.e., fixating a crosshair), the effect was most pronounced for action-based judgments about dogs. Thus, the apparent positive activation of these regions in the direct comparison results from the difference between two decreases relative to baseline. Figure 1 also shows the significant activations that were observed in the R. parahippocampal gyrus and L. pulvinar in the direct comparison between person and dog judgments. In both of these regions person and dog judgments yielded activations above the resting baseline, but the effect was most pronounced for dogs.

Insert Figure 1 About Here

Discussion

The current results reveal that distinct areas of the brain subserved the representation of comparable action-related knowledge about people and other animals—namely, dogs. Whereas action-related knowledge about dogs was associated with increased activity in occipitotemporal regions that support visual and memorial processing (i.e., visual imagery), person-based knowledge prompted activity in areas of right prefrontal cortex, areas that have previously been implicated in ToM reasoning and mental state attribution (Brunet et al., 2000; Castelli et al., 2000; Fletcher et al., 1995a; Gallagher et al., 2000; Goel et al., 1995; Vogeley et al., 2001). An extensive literature has documented the role of the frontal lobes in ToM reasoning (Frith & Frith, 1999). Notwithstanding the wide range of experimental paradigms that have been used to investigate this topic (e.g., verbal vs. non-verbal), a consistent pattern of results has

emerged. The act of mentalizing routinely elicits activity in MPFC (Blakemore & Decety, 2001), activity that has been associated with people's attempt to interpret social information in an agentic (i.e., goal-directed) manner.

Comparable processes appear to have been operating in the current investigation. Although people and dogs routinely perform identical actions (e.g., sit, bite, sniff), they typically do so for quite different reasons. Whereas dogs respond primarily to environmental cues, people act in accordance with internal goals, desires, and intentions. Thus, observing a dog dash along the sidewalk is unlikely to elicit complex attributional processing. Witnessing a person perform the same action, however, is likely to trigger operations that furnish consciousness with candidate explanations for the behavior in question (e.g., perhaps the person has the goal of catching the bus). A basic feature of social-cognitive functioning may be that people continually strive to determine the hidden causes of human action (Frith & Frith, 1999). What is noteworthy about the present findings is that merely considering whether or not a person could perform particular actions was sufficient to activate frontal regions that have repeatedly been implicated in ToM reasoning (Blakemore & Decety, 2001; Gallagher & Frith, 2003; Siegel & Varley, 2002). In part, this further demonstrates the inherently social nature of the human mind and the ease with which the machinery of mental state attribution can be activated. Cortical areas that contribute to an agentic interpretation of human behavior (i.e., MPFC) also appear to be implicated in the representation of action-based knowledge in the brain (Frith & Frith, 1999; Gallagher & Frith, 2003).

It is important to note that the response observed in the MPFC in the current investigation differs from that which is typically referred to as an activation by researchers (i.e., an increase in activation relative to baseline). Responses in MPFC are almost always observed as decreases in activation relative to a resting baseline. While effects of this kind are generally difficult to interpret, recent work has attempted to elucidate why certain neural structures consistently deactivate in the presence of an active processing task (Binder et al., 1999; Gusnard et al., 2001; Raichle et al., 2001; Shulman et al., 1997; Stark & Squire,

2001). One possibility, noted by Raichle and colleagues (Raichle et al., 2001), is that structures such as the MPFC play a prominent role in default cognitive operations (e.g., stimulus-independent thought), hence deactivate when an external task is introduced. What is apparent from the present investigation, and other studies of this kind, is that MPFC plays a prominent role in fundamental aspects of social-cognitive functioning, such as the simulation of other minds, the use and representation of social knowledge, moral reasoning, and self-referential mental activity (Adolphs, 2001; Anderson et al., 1999; Castelli et al., 2000; Kelley et al., 2002; Milne & Grafman, 2001; Mitchell et al., 2002). Whilst these studies have typically reported increased activity in MPFC, it is important to note that these increases have consistently been observed relative to some other active task (Brunet et al., 2000; Castelli et al., 2000; Gallagher et al., 2000), thereby obscuring whether any changes occur relative to a resting baseline (but see, Gusnard et al., 2001; Kelley et al., 2002; Mitchell et al., 2002). As observed in the current investigation, if compared to a resting baseline task (e.g., fixating a crosshair), ToM reasoning may be associated with deactivations in MPFC.

In the only other study to date that has investigated the representation of abstract person-based knowledge, Mitchell et al. (2002) also reported activity in MPFC. These researchers speculated that activity in this region may subserve the specialized cognitive operations that are brought to bear when people think about conspecifics, such as when they represent the internal states of other social agents (Frith & Frith, 1999). The present findings are supportive of this viewpoint. The differential neural activity that was associated with action-related judgments about people and dogs may reflect the different cognitive strategies that participants use when they think about (i.e., judge) each type of target. Specifically, action judgments about dogs yielded activity in areas that have commonly been associated with memory-guided visual imagery (e.g., superior occipital gyrus, parahippocampal gyrus, precuneus - Cabeza & Nyberg, 2000; Fletcher et al., 1995b; Ishai, Haxby, & Ungerleider, 2002; Ishai, Ungerleider, & Haxby, 2000; Jeannerod, 2001; Kosslyn, Ganis, & Thompson, 2001), suggesting that task performance

may have been supported by this mental operation. Person judgments, in contrast, did not rely on mental imagery to the same degree, instead they were associated with prefrontal operations that are indicative of ToM reasoning (Blakemore & Decety, 2001; Siegel & Varley, 2002). Thus, whereas participants visualized animal (i.e., dog) action, they appeared to reason about comparable human behavior. This does not imply, however, that judgments about animals would never elicit ToM reasoning. One interesting possibility is that animal actions could enlist ToM reasoning, at least for certain individuals. Anecdotal evidence suggests that dog owners routinely construe canine behavior in an intentional, goal-directed manner. Thus, when considering the actions of a pet, one might expect these individuals to show modulations of MPFC that are indicative of mental state attribution (i.e., the intentional stance).

One of the most oft-reported findings in cognitive neuroscience is that different classes of knowledge are associated with distinct regions of the brain (Martin, 2001; Martin et al., 2000). Although the exact nature of this neuroanatomical localization remains open to debate, most researchers concur that the brain contains some kind of category-specific neural architecture. Based on this observation, some theorists have suggested that the mind may have evolved dedicated neural circuits to deal with fundamental aspects of social-cognitive functioning, such as person perception and the representation of person-based knowledge (Baron-Cohen, 1995; Caramazza, 2000; Caramazza & Shelton, 1998). Supporting this general viewpoint, recent research has shown that distinct neural systems subserve the representation of person and object knowledge—specifically, attributes that are descriptive of people and objects (Mitchell et al., 2002). As demonstrated in the present inquiry, the seemingly ‘special’ status of person knowledge may also extend to the representation of abstract action-related information. Compared to inferences about actions performed by dogs, identical judgments about human acts were accompanied by neural activity that is indicative of ToM reasoning. Construing human action in a mentalistic manner may therefore be an obligatory facet of social-cognitive functioning.

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Table 1

Regions of increased brain activity associated with accessing action knowledge.

People > Dog Activations					
Anatomical label	x	y	z	t value	
				Person	Dog
R middle frontal gyrus (BA 9)	34	35	35	-4.18*	-5.52*
R middle frontal gyrus (BA 6/8)	26	16	45	-5.35*	-6.92*
R medial frontal gyrus (BA 8/9)	10	48	34	-5.15*	-8.18*
R anterior cingulate gyrus (BA 32)	6	20	40	5.06*	2.71
Dog > People Activations					
Anatomical label	x	y	z	Person	Dog
R parahippocampal gyrus (BA 19/30)	24	-46	10	2.58	6.43*
L parahippocampal gyrus (BA 19)	-28	-52	4	3.18	6.73*
L pulvinar	-24	-29	14	1.88	4.63*
L pulvinar	-14	-32	16	3.45	5.88*
L superior occipital gyrus (BA 19)	-40	-78	33	-11.39*	-7.33*
R precuneus (BA 31)	26	-71	18	-5.87*	-5.22*
L cerebellum	-12	-39	-8	0.46	5.07*
L uncus (BA 28)	-12	6	-26	1.31	6.32*

Coordinates are from the Talairach and Tournoux (1998) atlas. Person and Dog columns display the t value associated with the area's peak hemodynamic response relative to passive baseline for Person and Dog trials, respectively; *, $p < .001$; L, left; R, right.

Fig. 1. Activation map showing brain areas to be more active during Person than Dog trials (red) and Dog than Person trials (blue) from the group analysis (n=17). Regions of modulation included the (A) right medial frontal gyrus (10, 48, 34), (B) right middle frontal gyrus (34, 35, 35), (C) right parahippocampal gyrus (24, -46, 10) and (D) left pulvinar (-24, -29, 14). The hemodynamic time courses associated with these areas are also depicted. Time courses (expressed as percent signal change relative to baseline) were computed for each condition within a 3-D region surrounding the peak voxel identified from the contrast statistical map (people vs. dogs). Regions were defined using an automated algorithm that identified all contiguous voxels within 6 mm of the peak that reached the significance level ($p < .0001$, uncorrected).

