

Watching social interactions produces dorsomedial prefrontal and medial parietal BOLD fMRI signal increases compared to a resting baseline

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Some human brain areas are tonically active in a resting state when subjects are not engaged in any overt task. The activity of these areas decreases when subjects are engaged in a wide variety of laboratory tasks designed to study cognitive operations. It has been suggested that these areas, among them the medial parietal and the dorsomedial prefrontal cortices, may support a “default state” of the human brain. Passive visual observation of laboratory stimuli typically yields no change in activity in these default areas compared to rest. Here we report functional magnetic resonance imaging (fMRI) data on normal subjects watching realistic movie clips depicting everyday social interactions. In contrast with previous findings on default state brain areas, the observation of the relational segment of the movie clip, during which two persons interact, yielded increased activity in the medial parietal (precuneus) and dorsomedial prefrontal cortices, compared to rest and to observation of the segment of the movie clip depicting a single individual engaged in everyday activities. To the best of our knowledge, this is the first report of joint increased activity in medial parietal and dorsomedial prefrontal cortices. We suggest that the default state areas may participate in the processing of social relations in concert with regions previously identified as critical for social cognition that were also activated by our stimuli, including the inferior frontal cortex, the superior temporal cortex, and the fusiform gyrus.

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Introduction

Recent neuroimaging research has suggested that some regions of the brain, among them the dorsomedial prefrontal cortex and medial parietal cortex (precuneus), are more active when people are at rest—not performing any overt task—than during almost any cognitive activity that psychologists have previously thought to test (Gusnard and Raichle, 2001; Raichle et al., 2001). Because these areas, collectively called the “default state” network, do not show reduced oxygen extraction fraction (a typical feature of neural activation) during rest, it is likely that they are tonically active and frequently deactivated by cognitive laboratory tasks rather than being activated by any specific demands of being in a resting state. Together, these regions may support the default activities of the human brain (Gusnard and Raichle, 2001; Raichle et al., 2001). Indeed, because few experiments have shown true increases in activation in these regions, tenuous hypotheses about functions of these brain regions have been based on laboratory tasks that deactivate these regions the least compared to a resting baseline (Mitchell et al., 2002).

Complex, culturally specified social relations are crucial for human survival; no other animal has such complex, diverse, and varied social relationships or is more dependent on them. Successful engagement in these relationships requires a sophisticated understanding of one’s social position, options, and prospects (Fiske and Haslam, in press; Haslam, in press). Studies of natural, everyday social cognition show that diverse cognitive processes are focused on people’s relationships with their acquaintances and associates (Fiske and Haslam, 1996, in press). Furthermore, virtually all human activity is shaped by social context or has social implications, resulting in a continuous need to monitor social contexts and meanings (Klin et al., 2003). It follows that humans may have evolved a cognitive adaptation consisting of (effortful or automatic) processing of social relations during “downtime”

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whenever other goals do not currently require cognitive resources. Thinking about social relations may therefore be a core ‘default’ activity of the human brain. If this is true, much social cognition should be based on relatively automatic processes that require no prompting, and indeed, a great deal of social cognition is automatic (Bargh and Chartrand, 1999). Additionally, true activations in the default network beyond the resting baseline should occur when subjects are engaged in processing actual (or realistic) social relations. In other words, if people are required to perform more of the cognitive processing they were already performing at rest, there should be true increases in activity in the regions responsible for those computations. This would be analogous to what occurs in the visual cortex, where visual perception increases activation compared to visual imagery. In short, one of the aspects of the default state of the human brain may be imagining or mentally processing social relationships. Nonsocial tasks are distractions that reduce social rumination and hence reduce activation of this default system. Indeed, an extensive body of research on subjective mental states in everyday life shows that complete engagement in very meaningful and challenging cognitive tasks (e.g., painting, rock climbing, music) results in a state of “flow” characterized by loss of normal social concerns and loss of awareness of the social context (Nakamura and Csikszentmihalyi, 2002).

To study neural and cognitive mechanisms for understanding social relations, we used functional magnetic resonance imaging (fMRI) while subjects were observing video clips depicting everyday social scenes. Subjects were simply instructed to watch movie clips of realistic social interactions. If social processing (effortful or automatic) is part of the ‘default state’ in humans, one would expect that some areas belonging to the default network would be more active during the social relational segments relative to the segments showing a single person acting alone. Moreover, during the social relational segments, these areas would be activated relative to a true resting baseline, indicating that processing social relations produces increased activation of those structures beyond their tonic default activity.

Methods

Subjects

Through newspaper advertisements we recruited 13 right-handed subjects (seven females, mean age: 27.2 ± 3.4). Participants gave informed consent following the guidelines of the UCLA Institutional Review Board. Handedness was determined by a questionnaire adapted from the Edinburgh Handedness Inventory (Oldfield, 1971). All were screened to rule out medication use, a history of neurological or psychiatric disorders, head trauma, substance abuse, or other serious medical conditions.

Image acquisition

Images were acquired using a GE 3.0 T MRI scanner with an upgrade for echo-planar imaging (EPI) (Advanced NMR Systems, Inc.). A 2D spin-echo image (TR = 4000 ms; TE = 40 ms, 256×256 , 4-mm thick, 1-mm spacing) was acquired in the sagittal plane to allow prescription of the slices to be obtained in the remaining sequences. This sequence also ensured the absence of structural abnormalities in the brain of the enrolled subjects. For each subject, a high-resolution structural T2-weighted EPI vol-

ume (spin-echo, TR = 4000 ms, TE = 54 ms, 128×128 , 26 slices, 4-mm thick, 1-mm spacing) was acquired coplanar with the functional scans. Nine functional EPI scans (gradient-echo, TR = 4000 ms, TE = 25 ms, flip angle = 90, 64×64 , 26 slices, 4-mm thick, 1-mm spacing) were acquired, each for a duration of 3 min and 16 s. Each functional scan covered the whole brain and was composed of 49 brain volumes. By design, the first four volumes were not processed due to initial signal instability in the functional scan. The remaining 45 volumes corresponded to five 20-s rest periods (blank screen) and four 20-s task periods (video clips). In each scan, there were two clips of Authority Ranking relationships and two clips of Communal Sharing relationships (see Stimuli and instructions). The order of presentation of Authority Ranking and Communal Sharing clips was counter-balanced across scans and subjects.

Data processing

GE image files were converted into Analyze files. Each functional volume was realigned to the T2-weighted structural volume within each subject using a rigid-body linear registration algorithm (Woods et al., 1998a). The T2-weighted structural volume of each subject was subsequently warped into a Talairach-compatible MR atlas (Woods et al., 1999) with fifth-order polynomial nonlinear warping (Woods et al., 1998b). Finally, the combination of the realignment of each functional volume onto the structural volume, and of the warping of the structural volume into the MR atlas, allowed reslicing of functional volumes into Talairach-compatible MR atlas space. Functional volumes resliced into the MR atlas space were smoothed using a Gaussian filter producing a final image resolution of $8.7 \times 8.7 \times 8.6$ mm.

Stimuli and instructions

Stimuli depicted two basic social relational models, Communal Sharing and Authority Ranking. Previous research has shown that these are two of four types of social relations that people in many cultures use to coordinate many kinds of social relationships and understand observed interactions (Fiske, 1991, 1992). Communal Sharing relationships are based on the perception that participants have something essential in common that makes them equivalent for certain social purposes (e.g., lovers or siblings). Authority Ranking relationships are based on the perception that, with respect to the current context, participants are differentiated in a linearly ordered hierarchy (e.g., boss and employee, or parent and children).

Stimuli consisted of a set of 36 video clips of everyday events that were professionally written, produced, acted, directed, digitally filmed, and edited. The video clips were interleaved with 20 s of blank screen (rest periods). Each clip was composed of a period (“alone”) of 12 s (corresponding to three brain volumes acquired with a TR = 4000 ms) during which a single actor is visible, followed by a “relational” period of 8 s (corresponding to two brain volumes acquired with a TR = 4000 ms) in which the first actor interacts with a second actor. Speech was present in both the alone and relational segments for about half of the clips. For the rest of the clips there was no speech in either segment. For half of the clips, the relational period reflected a Communal Sharing relationship between the actors. For instance, in one Communal Sharing clip, the two actors play a couple looking at family photos. For the other clips, the relational period reflects an Authority

Ranking relationship. For instance, in one Authority Ranking clip, the two actors are in a library and the librarian tells the student to “keep it quiet.” In pretesting, American subjects rated the Authority Ranking clips as more negative and less positive than the Communal Sharing clips.

The choice of a fixed order of presentation in which one actor alone always appeared before the relational segment of the clip (see in Discussion the interpretational limitations of our results) was motivated by the following consideration. We were concerned that if viewers watched a person alone after watching the same person interacting with another person, they would attribute to the person alone the same social relation they had just observed (i.e., a father is a father even when he is not currently interacting with his daughter). Thus, to avoid a null result that would be difficult to interpret, we opted for this not entirely ideal experimental design. By the same token, we opted not to show segments in which two actors are not interacting as a control condition for the relational segment. It seemed to us likely that viewers would anticipate or infer a relationship among people presented simultaneously on a split screen, even though these people were not directly interacting (indeed, this expectation is the basis for a cinematographic technique often used for just this purpose).

Subjects participating in the imaging study were instructed to simply watch the video clips. No explanation was given to them about Authority Ranking and Communal Sharing models. In a postimaging interview, some of the subjects stated that they were aware that the clips depicted different kinds of relationships, but none were able to clearly articulate the communal and hierarchical typology.

Statistical analyses

All statistical analyses were performed on group data after spatial normalization and smoothing. Contrast analyses were based

Table 1
Relational vs. alone segment

Hemisphere	Region	Talairach coordinates			<i>t</i> value
		<i>x</i>	<i>y</i>	<i>z</i>	
Left	DMPFC	−2	52	26	5.52
Left	Anterior STS	−62	−16	−2	6.61
Left	MT	−48	−68	12	9.00
Left	Cuneus	−4	−90	38	7.30
Left	Fusiform gyrus	−20	−72	−12	6.09
Right	Superior frontal gyrus	8	6	64	6.06
Right	PMC	48	6	40	5.88
Right	IFG	56	22	0	6.83
Right	Anterior STS	62	−10	−12	7.90
Right	Mid STS	52	−34	−4	8.16
Right	Posterior STS	66	−54	6	9.03
Right	Precuneus	4	−54	56	6.78
Right	Precuneus	4	−60	44	6.97
Right	MT	54	−68	8	12.32
Right	Fusiform gyrus	36	−82	−22	6.39
Right	Cuneus	6	−88	32	7.26

DMPFC = Dorsomedial Prefrontal Cortex, STS = Superior Temporal Sulcus, MT = Motion processing area, PMC = Premotor Cortex, IFG = Inferior Frontal Gyrus.

on an analysis of variance (ANOVA) model which factors out the between subject and the scan-to-scan variability in signal intensity (Iacoboni et al., 1999, 2001; Woods et al., 1996). The dependent variable of the ANOVAs was the blood-oxygenated level-dependent (BOLD) fMRI signal intensity at each voxel. The alpha level for each voxel was set at $P \leq 0.05$, corrected for multiple spatial comparison across the whole brain (Worsley et al., 1996). This extremely conservative approach means that even a single voxel classified as ‘activated’ with these criteria should be considered

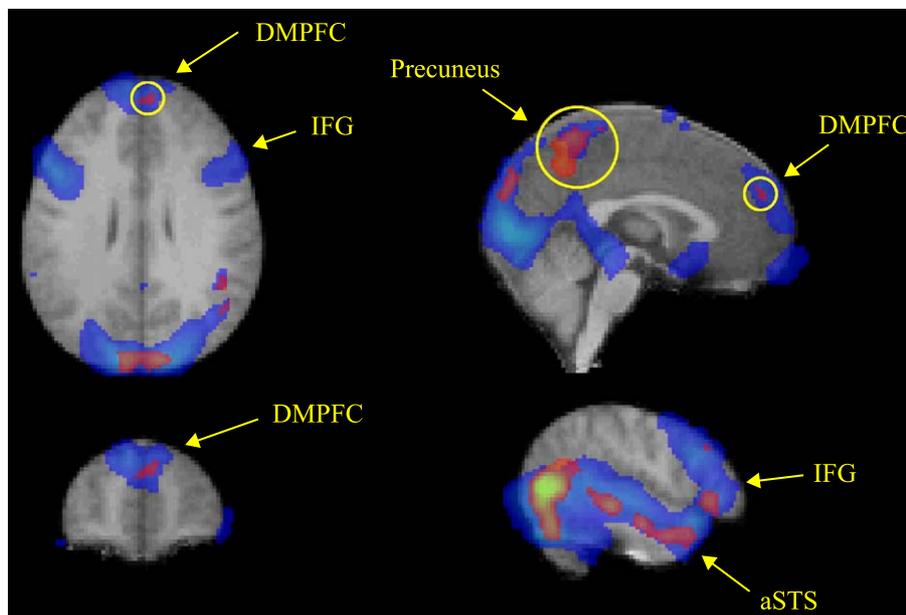


Fig. 1. In blue, voxels activated during observation of the relational part of the clip minus rest. In red-to-yellow, voxels activated during observation of the relational part of the clip minus observation of the alone part of the clip. The circled clusters of activated voxels belong to the ‘default state’ network. The left hemisphere is on the right side in the transverse and coronal views. DMPFC = Dorsomedial Prefrontal Cortex; IFG = Inferior Frontal Gyrus; aSTS = Anterior Superior Temporal Sulcus.

reliably activated. Moreover, the peaks we report and discuss in this paper represent clusters of several voxels (see below) that are each independently significant at $P \leq 0.05$ after this correction for multiple spatial comparisons across the whole brain.

Results

Preliminary analyses demonstrated no fMRI signal difference between the segments of the Authority Ranking and Communal Sharing clips showing one person alone. The comparisons of the relational segment of Authority Ranking and Communal Sharing clips vs. rest and vs. their relative alone segments yielded substantially identical results for the two types of relationship. For the sake of simplicity, therefore, we report the results of pooled data combining the Authority Ranking and Communal Sharing clips.

Fig. 1 and Table 1 summarize the areas reliably activated when the relational (interaction) segment was compared against the segment showing one actor alone. Two of the areas activated, the dorsomedial prefrontal cortex (a cluster of 48 voxels) and the precuneus in medial parietal cortex (a cluster of 545 voxels), belong to the default state network (Fig. 1).

Fig. 1 also summarizes the areas reliably activated when the relational segment of the clip was compared against rest. This subtraction is especially important because it assesses whether the previous subtraction (relational vs. alone) was the difference between two activations or two deactivations. In other words, the relational segment of the clip could have merely produced a smaller deactivation than the alone segment. The current subtraction (relational vs. rest) clearly shows that the relational segment of the clip reflects a true activation; all the regions activated by the relational segment compared to the alone segments were also activated in comparison to the resting baseline. In addition, large

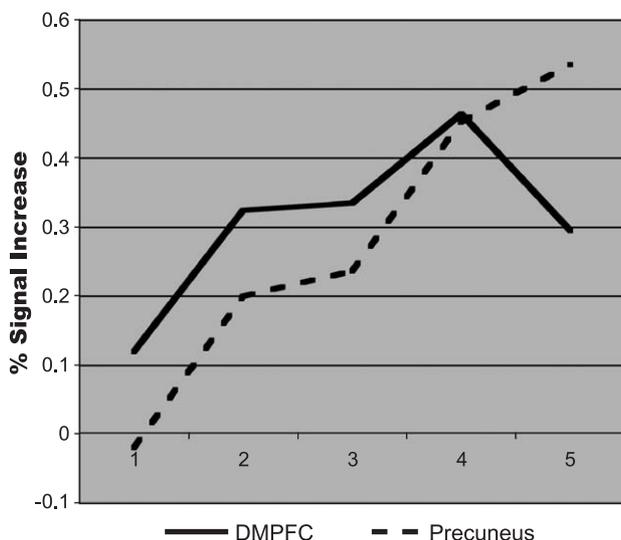


Fig. 2. Activity in the dorsomedial prefrontal cortex (DMPFC) and precuneus expressed in signal intensity normalized to the average signal intensity at rest in each region. The first three data points of the graph correspond to the observation of the alone segment of the clip (first three brain volumes with TR = 4000 ms), whereas the last two data points correspond to the observation of the relational segment of the clip (last two brain volumes with TR = 4000 ms).

activations in visual and auditory areas were observed, as expected. Fig. 2 shows the time course of the dorsomedial prefrontal and precuneus activity (normalized to the average activity in each region at rest) during the alone and the relational segments of the movies. Signal increases, compared to rest, occurred during both alone and relational segments of the clip, with higher signal increases during the relational segment.

A direct comparison between the relational segments of Authority Ranking and Communal Sharing clips yielded only bilateral increased signal in the anterior part of the superior temporal sulcus (STS) for the Authority Ranking stimuli. The relational segments of the Communal Sharing clips also activated this area compared to the alone segments and compared to rest, but less strongly than the Authority Ranking relational segments.

Discussion

To the best of our knowledge, this is the first report of a joint activation of the medial parietal and dorsomedial prefrontal cortices compared to rest. These two brain regions are part of the default state network (Greicius et al., 2003; Gusnard and Raichle, 2001). The increased activity in the medial parietal and dorsomedial prefrontal cortices cannot be accounted for simply by the fact that subjects were passively viewing the movie clips. In fact, passive observation of visual stimuli typically used in cognitive tasks does not typically yield increased activity in these regions compared to rest (Gusnard and Raichle, 2001; Raichle et al., 2001). Moreover, the medial parietal and medial prefrontal cortices show increased activity during the relational segments not only vs. rest, but also vs. the segment of the clip in which a single individual is engaged in everyday activities in the same context in which the social relation is going to occur. This pattern of activation suggests that the medial parietal and dorsomedial prefrontal cortices are specifically responding to social relationships, potential (in the alone segment) and actual (in the relational segment). Finally, the substantially identical response to Authority Ranking and Communal Sharing relations in the medial parietal and medial prefrontal cortices suggests that these two brain areas respond similarly (at the level of resolution of these fMRI images) to these two types of social interactions, although these particular two sets of clips differed in valence. All together, this suggests that the tonic activity of the medial parietal and medial prefrontal cortices may reflect the continuous processing of social relationships. Sustaining effective social relations may entail unreflective “day dreaming” and conscious meditation on the potential implications of past social events, imagining solutions to social relationship problems, and explicitly or implicitly planning for future eventualities (Lieberman et al., 2002).

Functional imaging experiments have been interpreted as suggesting that the medial parietal cortex (precuneus) may be concerned with retrieval of episodic memory (Cabeza and Nyberg, 2000a,b). Although these processes would appear to be important for attending to and processing social relations, in many of the previous studies, activation in the precuneus was not examined compared to a resting baseline (Cabeza et al., 2003; Zysset et al., 2002). Thus, it may be that tasks that have produced an apparent “activation” of the precuneus actually resulted in less deactivation than control tasks. Recently, it has been shown that reductions in activity in the precuneus vary parametrically with

task difficulty (McKiernan et al., 2003). Thus, an easier experimental task would yield less deactivation than a more difficult control task, even when both tasks actually deactivate this region relative to rest.

A number of recent imaging experiments have implicated the medial parietal cortex (and adjoining posterior cingulate) in processes of social cognition. For instance, across seven studies of self-knowledge, this region was the most commonly activated relative to a nonresting baseline (for review, see Lieberman and Eisenberger, *in press*). Social psychologists have long held that self-knowledge is primarily a result of social cognition and social comparison processes (Lieberman and Pfeifer, *in press*; Mead, 1934). Indeed, many imaging studies requiring subjects to compare oneself to another also consistently produce activation in the precuneus relative to a nonresting baseline (Farrow et al., 2001; Ruby and Decety, 2001, 2003).

Activation of the medial prefrontal cortex has often been reported in Theory of Mind (ToM) tasks (Frith and Frith, 2003). For example, in a recent study, greater activity in the medial prefrontal cortex was shown during a person-knowledge condition compared to an object-knowledge condition. However, relative to a resting baseline, both conditions produce deactivation (Mitchell et al., 2002). This study by Mitchell et al. clearly emphasizes the importance of a resting baseline in imaging studies using block designs and the necessity for plotting activity against time in reliably activated regions in event-related designs. For instance, a recent paper reviewing imaging studies using ToM tasks (Frith and Frith, 2003) suggests that the medial prefrontal cortex is crucial for ToM, but this conclusion is problematic because all the cited studies report greater activity of the medial prefrontal cortex in ToM tasks compared to some other active control tasks, without comparison to a true resting state (see Fig. 5 of Frith and Frith, 2003). If it turns out that, compared to rest, ToM tasks generally produce deactivation in regions activated by observation of realistic social stimuli, this would cast doubt on the centrality of ToM for understanding social relationships, which has been questioned on other grounds as well (see Haslam and Fiske, *in press*).

As indicated in the Methods section, we adopted a fixed order within each clip, such that the segment of the clip showing one actor alone always preceded the segment of the clip showing the interaction. We did so because we were concerned that viewers observing the interaction first would attribute the relational role (i.e., being a father) also to the actor observed alone. However, this fixed order entails some interpretational ambiguities. For instance, it is possible that these medial areas are responding to the continuous presence of one actor in the field of view. It is also possible that the additional response observed in the medial areas and also in the other areas listed in Table 1 is due to the presence of two actors in the relational segment rather than resulting from their social interaction. Here, too, our design cannot unequivocally disentangle this possibility from our main interpretation. We chose not to use two actors not interacting as a control for the relational segment because we anticipated that viewers would attribute some sort of relation to two people observed simultaneously, or think about relationships they might form, even though these people were not overtly interacting. These interpretational limitations, however, cannot detract from the fact that we report here for what we believe is the first time the simultaneous activation of medial prefrontal and medial parietal areas against a resting baseline.

Predictably, we also observed activation of the areas known to respond to the observation of socially relevant stimuli, such as actions and faces, in particular inferior frontal cortex, superior temporal cortex, and fusiform gyrus (Haxby et al., 2000; Iacoboni et al., 1999; Iacoboni et al., 2001; Kanwisher et al., 1997). However, it is notable that several previous studies on action observation have not reported activation, compared to rest, of the medial parietal and medial prefrontal cortices. Notably, a large fMRI dataset including 58 normal subjects showed no differences in the medial parietal and medial prefrontal cortices when action observation was compared to rest (Molnar-Szakacs et al., 2002). The lack of activation of the medial parietal and medial prefrontal cortices in previous action observation experiments is probably because the stimuli used in previous studies were simple motor actions not embedded in social relations. In those previous studies, a typical finding is the activation of the posterior sector of the superior temporal sulcus (STS) (Allison et al., 2000; Puce and Perrett, 2003), also activated here. Here, however, we also observed activation in more anterior more anterior-activated areas along STS (see Fig. 1 and Table 1). These anterior STS activations are anatomically more compatible with the single-unit recordings in the macaque describing STS neurons responding to biological motion (Jellema et al., 2000; Perrett et al., 1989). The anterior STS activations may have been driven by the use of complex stimuli that are closer to real-life situations (Klin et al., 2003) than previously used ones and may represent the integration of individual actions into a social context, giving the actions a social relational ‘meaning’. Thus, human STS may be conceptualized as divided in two broad sectors: a posterior STS sector connected mostly with the parietal lobe (Seltzer and Pandya, 1994) that processes the kinesthetic aspect of observed actions, and an anterior STS sector connected mostly with the frontal lobe (Barbas et al., 1999) that processes the social significance of the actions. The slightly greater response in anterior STS to the AR relations, compared to the CS relations, may simply reflect a greater perceived salience of the AR relations, generally not well received among our North American subjects; or it may have resulted from the fact that some of the AR scenes involved a problem or tension, while none of the CS scenes did, thus eliciting more processing.

Taken together, our data may be interpreted as suggesting that the human facility in understanding observed social relationships is provided by the combined activity of an action recognition system in the inferior frontal and superior temporal cortices, an anterior STS system that interprets the social significance of actions, and a dorsomedial prefrontal cortex and medial parietal cortex system that analyzes social relationships and considers their implications. The dorsomedial prefrontal cortex and medial parietal cortex system for thinking about social relationships is apparently part of the brain’s default state circuitry; it may continuously, often without effort or intention, assess and analyze past, present, or possible future social relationships whenever nonsocial tasks do not demand full attention. Given the complexity and pervasive importance of social relationships, this ongoing social processing may be crucial to sustaining adaptive social relations.

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