Watching Social Interactions Produces Dorsomedial Prefrontal and Medial Parietal

BOLD fMRI Signal Increases Compared to a Resting Baseline

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Abstract

Some human brain areas are tonically active in a resting state when subjects are not engaged in any overt task. The activity of these area 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 cortex, 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 data on normal subjects watching realistic movie clips depicting everyday social interactions. In contrast with previous findings on the 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 and dorsomedial prefrontal cortex, 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 cortex. 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.

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). Since 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 de-activated 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, since few experiments have shown true increases in activation in these regions, tenuous hypotheses about functions of these brain regions have been based on the 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 & 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 & Haslam, 1996; Fiske & Haslam, 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 (conscious or unreflective) processing of social relations during "downtime" 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 of social cognition should be based on relatively automatic processes that require no prompting, and indeed a great deal of social cognition has been shown to be 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. Non-social 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 awareness of the social context (Nakamura and Csikszentmihalyi, 2002).

To study the neural and cognitive mechanisms for understanding social relations, we used functional magnetic resonance imaging (fMRI) while subjects were observing videoclips depicting everyday social scenes. Subjects were simply instructed to watch movie clips of realistic social interactions. If social processing (conscious or unreflective) 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 (7 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 3.0T MRI scanner with an upgrade for echoplanar imaging (EPI) (Advanced NMR Systems, Inc.). A 2D spin-echo image (TR =

4000 ms; TE = 40 ms, 256 by 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 T2weighted EPI volume (spin-echo, TR = 4000 ms, TE 54 ms, 128 by 128, 26 slices, 4mm 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 by 64, 26 slices, 4-mm thick, 1-mm spacing) were acquired, each for a duration of 3 minutes and 16 seconds. 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-second rest periods (blank screen) and four 20-second 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 counterbalanced across scans and subjects.

Data processing

GE image files were converted into Analyze files. Each functional volume was re-aligned 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 re-alignment 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 the 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 mm by 8.7 mm by 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 (for example, 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 (for example, 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 seconds of blank screen (rest periods). Each clip was composed of a period ("alone") of twelve seconds (corresponding to three brain volumes acquired with a TR=4000 msec) during which a single actor is visible, followed by a "relational" period of eight seconds (corresponding to two brain volumes acquired with a TR=4000 msec) 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 the Discussion section 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 sometimes 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 post-imaging 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 the group data after spatial normalization and smoothing. Contrast analyses were based on an analysis of variance (ANOVA) model which factors out the between subject and the scan-to-scan variability in signal intensity (Woods et al., 1996; Iacoboni et al., 1999; Iacoboni et al., 2001). 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≤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 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≤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 versus rest and versus 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.

Figure 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 (a cluster of 545 voxels), belong to the default state network (Figure 1).

Figure 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 *de*-activation 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 activations in visual and auditory areas were observed, as expected. Figure 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.

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 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 medial parietal and dorsomedial prefrontal cortex, compared to rest. These two brain regions are part of the default state network (Gusnard and Raichle, 2001; Greicius et al., 2003). The increased activity in medial parietal and dorsomedial prefrontal cortex 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 cortex show increased activity during the relational segments not only versus rest, but also versus 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 medial parietal and dorsomedial prefrontal cortex 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 medial parietal and medial prefrontal cortex suggests that these two brain areas respond similarly (at the level of resolution of these fMRI images) to these two types of social interactions, despite the fact that these particular two sets of clips differed in valence. All together, this suggests that the tonic activity of medial parietal and medial prefrontal cortex 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 (Zysset et al., 2002; Cabeza et al., 2003). Thus, it may be that tasks that have produced an apparent "activation" of the precuneus actually resulted in less deactivation than the 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 medial parietal cortex (and adjoining posterior cingulate) in processes of social cognition. For instance,

across 7 studies of self-knowledge, this region was the most commonly activated relative to a non-resting baseline (for review, see Lieberman & Eisenberger, in press). Social psychologists have long held that self-knowledge is primarily a result of social cognition and social comparison processes (Mead, 1934; Lieberman & Pfeifer, in press). Indeed, a number of imaging studies requiring subjects to compare oneself to another also consistently produce activation in the precuneus relative to a non-resting baseline (Farrow et al., 2001; Ruby & 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 and colleagues 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 medial prefrontal cortex in ToM tasks compared to some other active control tasks, without comparison to a true resting state (see Figure 5 of Frith & 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 & 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 (Kanwisher et al., 1997;

lacoboni et al., 1999; Haxby et al., 2000; lacoboni et al., 2001). 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 cortex. Notably, a large fMRI dataset including 58 normal subjects showed no activation differences in the medial parietal and medial prefrontal cortex when action observation was compared to rest (Molnar-Szakacs et al., 2002). The lack of activation of medial parietal and medial prefrontal cortex in previous action observation experiments is probably due to the fact that 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 more anterior activated areas along STS (see Figure 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 (Perrett et al., 1989; Jellema et al., 2000). 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 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 non-social 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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References

- Allison, T., Puce, A., McCarthy, G., 2000. Social perception from visual cues: role of the STS region. Trends Cogn Sci 4, 267-278.
- Barbas, H., Ghashghaei, H., Dombrowski, S. M., Rempel-Clower, N. L., 1999. Medial prefrontal cortices are unified by common connections with superior temporal cortices and distinguished by input from memory-related areas in the rhesus monkey. J Comp Neurol 410, 343-346.
- Bargh, J. A., Chartrand, T. L., 1999. The unbearable automaticity of being. American Psychologist 54, 462-479.
- Cabeza, R., Nyberg, L., 2000a. Imaging cognition II: An empirical review of 275 PET and fMRI studies. J Cogn Neurosci 12, 1-47.
- Cabeza, R., Nyberg, L., 2000b. Neural bases of learning and memory: functional neuroimaging evidence. Curr Opin Neurol 13, 415-421.
- Cabeza, R., Dolcos, F., Prince, S. E., Rice, H. J., Weissman, D. H., Nyberg, L., 2003.

 Attention-related activity during episodic memory retrieval: a cross-function fMRI study. Neuropsychologia 41, 390-399.
- Farrow, T. F. D., Zheng, Y., Wilkinson, I. D., Spence, S. A., Deakin, J. F. W., Tarrier, N., Griffiths, P. D., & Woodruff, P. W. R. (2001). Investigating the functional anatomy of empathy and forgiveness. NeuroReport, 12, 2433-2438.
- Fiske, A. P., 1991. Structures of social life: The four elementary forms of human relations: Communal sharing, authority ranking, equality matching, market pricing. The Free Press, New York, NY.

- Fiske, A. P., 1992. The four elementary forms of sociality: Framework for a unified theory of social relations. Psych Rev, 99, 689-723.
- Fiske, A. P., Haslam, N., 1996. Social cognition is thinking about relationships. Curr Dir Psych Sci 5, 143-148.
- Fiske, A. P., Haslam, N., in press. The four basic social bonds: Structures for coordinating interaction. Forthcoming in Interpersonal Cognition, Mark Baldwin, Ed. Guilford.
- Frith, U., Frith, C. D., 2003. Development and neurophysiology of mentalizing. Philos

 Trans R Soc Lond B Biol Sci 358, 459-473.
- Greicius, M. D., Krasnow, B., Reiss, A. L., Menon, V., 2003. Functional connectivity in the resting brain: a network analysis of the default mode hypothesis. Proc Natl Acad Sci U S A 100, 253-258.
- Gusnard, D. A., Raichle, M. E., 2001. Searching for a baseline: functional imaging and the resting human brain. Nat Rev Neurosci 2, 685-694.
- Haslam, N., Ed., in press. Relational models theory: A contemporary overview.

 Mahwah, NJ: Erlbaum.
- Haslam, N., Fiske, A. P., in press. Social expertise: Theory of mind or theory of relationships? Forthcoming in Haslam, N., Ed., Relational models theory: A contemporary overview. Mahwah, NJ: Erlbaum.
- Haxby, J. V., Hoffman, E. A., Gobbini, M. I., 2000. The distributed human neural system for face perception. Trends Cogn Sci 4, 223-233.
- lacoboni, M., Woods, R. P., Brass, M., Bekkering, H., Mazziotta, J. C., Rizzolatti, G., 1999. Cortical mechanisms of human imitation. Science 286, 2526-2528.

- Iacoboni, M., Koski, L. M., Brass, M., Bekkering, H., Woods, R. P., Dubeau, M. C., Mazziotta, J. C., Rizzolatti, G., 2001. Reafferent copies of imitated actions in the right superior temporal cortex. Proc Natl Acad Sci U S A 98, 13995-13999.
- Jellema, T., Baker, C. I., Wicker, B., Perrett, D. I., 2000. Neural representation for the perception of the intentionality of actions. Brain Cogn 44, 280-302.
- Kanwisher, N., McDermott, J., Chun, M. M., 1997. The fusiform face area: a module in human extrastriate cortex specialized for face perception. J Neurosci 17, 4302-4311.
- Klin, A., Jones, W., Schultz, R., Volkmar, F., 2003. The enactive mind, or from actions to cognition: lessons from autism. Philos Trans R Soc Lond B Biol Sci 358, 345-360.
- Lieberman, M. D., & Eisenberger, N. I. (in press). Conflict and habit: A social cognitive neuroscience approach to the self. In: Tesser, A., Wood, J. V., & Stapel, D. A. (eds.), Psychological Perspectives on Self and Identity (vol. 4). Washington, D.C.: APA
- Lieberman, M. D., Gaunt, R., Gilbert, D. T., Trope, Y., 2002. Reflection and reflexion: A social cognitive neuroscience approach to attributional inference. In: Zanna, M., (Ed, Advances in Experimental Social Psychology Academic Press, New York, pp 199-249.
- Lieberman, M. D., & Pfeifer, J. H. (in press). The self and social perception: Three kinds of questions in social cognitive neuroscience. In: Easton, A. & Emery, N. (eds.), Cognitive Neuroscience of Emotional and Social Behavior. Philadelphia: Psychology Press.

- McKiernan, K. A., Kaufman, J. N., Kucera-Thompson, J., Binder, J. R., 2003. A parametric manipulation of factors affecting task-induced deactivation in functional neuroimaging. J Cogn Neurosci 15, 394-408.
- Mead, G.H., 1934. Mind, self, and society. University of Chicago Press, Chicago, IL.
- 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.
- Molnar-Szakacs, I., Iacoboni, M., Koski, L., Maeda, F., Dubeau, M. C., Aziz-Zadeh, L., Mazziotta, J. C., 2002. Action observation in the pars opercularis: Evidence from 58 subjects studied with FMRI. J Cogn Neurosci Suppl S, F118.
- Nakamura, J., Csikszentmihalyi, M., 2002. The concept of flow. In: Snyder, C. R., Lopez, S. J., Eds, Handbook of positive psychology Oxford University Press, London, pp 89-105.
- Oldfield, R. C., 1971. The assessment and analysis of handedness: the Edinburgh inventory. Neuropsychologia 9, 97-113.
- Perrett, D. I., Harries, M. H., Bevan, R., Thomas, S., Benson, P. J., Mistlin, A. J., Chitty, A. J., Hietanen, J. K., Ortega, J. E., 1989. Frameworks of analysis for the neural representation of animate objects and actions. J Exp Biol 146, 87-113.
- Puce, A., Perrett, D., 2003. Electrophysiology and brain imaging of biological motion.

 Philos Trans R Soc Lond B Biol Sci 358, 435-445.
- Raichle, M. E., MacLeod, A. M., Snyder, A. Z., Powers, W. J., Gusnard, D. A., Shulman, G. L., 2001. A default mode of brain function. Proc Natl Acad Sci U S A 98, 676-682.

- Ruby, P. & Decety, J. (2001). Effect of subjective perspective taking during simulation of action: a PET investigation of agency. Nature Neuroscience, 4, 546-550.
- Ruby, P. & Decety, J. (2003). What you believe versus what you think they believe: a neuroimaging study of conceptual perspective taking. Eur J of Neurosci, 17, 2475-2480.
- Seltzer, B., Pandya, D. N., 1994. Parietal, temporal, and occipital projections to cortex of the superior temporal sulcus in the rhesus monkey: a retrograde tracer study.

 J Comp Neurol 343, 445-463.
- Simpson, J. R., Jr., Snyder, A. Z., Gusnard, D. A., Raichle, M. E., 2001a. Emotion-induced changes in human medial prefrontal cortex: I. During cognitive task performance. Proc Natl Acad Sci U S A 98, 683-687.
- Simpson, J. R., Jr., Drevets, W. C., Snyder, A. Z., Gusnard, D. A., Raichle, M. E., 2001b.

 Emotion-induced changes in human medial prefrontal cortex: II. During anticipatory anxiety. Proc Natl Acad Sci U S A 98, 688-693.
- Woods, R. P., Iacoboni, M., Grafton, S. T., Mazziotta, J. C., 1996. Improved analysis of functional activation studies involving within-subject replications using a threeway ANOVA model. In: Myers, R., Cunningham, V., Bailey, D., Jones, T., Eds, Quantification of Brain Function using PET Academic Press, San Diego, CA, pp 353-358.
- Woods, R. P., Grafton, S. T., Holmes, C. J., Cherry, S. R., Mazziotta, J. C., 1998a.

 Automated Image Registration: I. General Methods and Intrasubject,

 Intramodality Validation. J Comput Assisted Tomogr 22, 139-152.

- Woods, R. P., Grafton, S. T., Watson, J. D. G., Sicotte, N. L., Mazziotta, J. C., 1998b.Automated Image Registration: II. Intersubject Validation of Linear andNonlinear Models. J Comput Assisted Tomogr 22, 153-165.
- Woods, R. P., Dapretto, M., Sicotte, N. L., Toga, A. W., Mazziotta, J. C., 1999. Creation and use of a Talairach-compatible atlas for accurate, automated nonlinear intersubject registration and analysis of functional imaging data. Hum Brain Mapp 8, 73-79.
- Worsley, K. J., Marrett, S., Neelin, P. A., Vandal, A. C., Friston, K. J., Evans, A. C., 1996.

 A unified statistical approach for determining significant signals in images of cerebral activation. Hum Brain Mapp 4, 58-73.
- Zysset, S., Huber, O., Ferstl, E., von Cramon, D. Y., 2002. The anterior frontomedian cortex and evaluative judgment: An fMRI study. NeuroImage 15, 983-991.

Table 1. Relational vs alone segment

Talairach coordinates t value

Region

Χ Ζ -2 52 **DMPFC** 26 Left 5.52 Left **Anterior STS** -62 -16 -2 6.61 Left MT -48 -68 12 9.00 38 7.30 Left Cuneus -4 -90 Left -20 -72 -12 Fusiform Gyrus 6.09 Right Sup Frontal Gyrus 8 6 64 6.06 Right **PMC** 48 6 40 5.88

56

62

52

66

4

4

54

36

6

22

-10

-34

-54

-54

-60

-68

-82

-88

6.83

7.90

8.16

9.03

6.78

6.97

12.32

6.39

7.26

0

-12

-4

6

56

44

8

-22

32

DMPFC= Dorsomedial Prefrontal Cortex

STS = Superior Temporal Sulcus

IFG

ΜT

Anterior STS

Posterior STS

Fusiform Gyrus

Precuneus

Precuneus

Cuneus

Mid STS

MT = Motion processing area

PMC = Premotor Cortex

Hemisphere

Right

Right

Right

Right

Right

Right

Right

Right

Right

IFG = Inferior Frontal Gyrus

Figure Legends

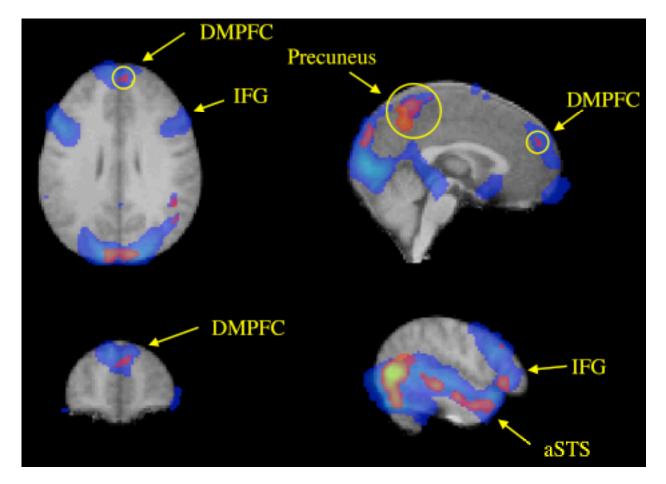


Figure 1. In blue, voxels activated during observation of the relational part of the clip minus rest. In red-to-yellow, voxels activated during observation of the relational part of the clip minus observation of the alone part of the clip. The circled clusters of activated voxels belong to the 'default 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.

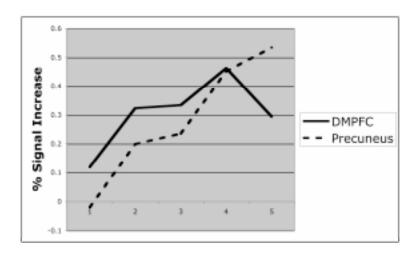


Figure 2. Activity in dorsomedial prefrontal cortex (DMPFC) and Precuneus expressed in signal intensity normalized to the average signal intensity at rest in each region. The first three data-points of the graph correspond to the observation of the alone segment of the clip (first three brain volumes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