

The neural bases of cooperation and competition: an fMRI investigation

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Cooperation and competition are two basic modes of social cognition that necessitate monitoring of both one's own and others' actions, as well as adopting a specific mental set. In this fMRI, study individuals played a specially designed computer game, according to a set of predefined rules, either in cooperation with or in competition against another person. The hemodynamic response during these conditions was contrasted to that of the same subjects playing the game independently. Both cooperation and competition stances resulted in activation of a common frontoparietal network subserving executive functions, as well as the anterior insula, involved in autonomic arousal. Moreover, distinct regions were found to be selectively associated with cooperation and competition, notably the orbitofrontal cortex in the former and the inferior parietal and medial prefrontal cortices in the latter. This pattern reflects the different mental frameworks implicated in being cooperative versus competitive with another person. In accordance with evidence from evolutionary psychology as well as from developmental psychology, we argue that cooperation is a socially rewarding process and is associated with specific left medial orbitofrontal cortex involvement.

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Introduction

Social cognition refers to the processes involved in understanding and interacting with conspecifics. Its evolution arose out of a complex and dynamic interplay between two opposite factors: on the one hand, cooperation among individuals to form groups can provide enhanced security against predators, better mate choice, and more reliable food resources; on the other hand, competition between group members provides individuals with selective advantages in terms of mate selection and food procurement. An evolutionary approach to social cognition therefore predicts mechanisms for cooperation, altruism, and other aspects of prosocial

behavior, as well as mechanisms for coercion, deception, and manipulation of conspecifics (Adolphs, 1999; Byrne and Whiten, 1988; Dunbar, 2003). Classical evolutionary theory emphasized competitive interactions based on the struggle for life and the survival of the fittest (e.g., see Spencer, 1870), but cooperation is also common between members of the same species and is indeed advantageous for the individuals because it increases their survival fitness (Eisler and Levine, 2002; Trivers, 1972). Among humans, in particular, cooperation seems to have been elevated to an integral part of society (Stevens and Hauser, 2004).

Cooperation and competition involve executive functions and mentalizing abilities, both of which play a crucial role during social interactions. Executive functions encompass several aspects of generating flexible behavior, including the ability to (a) choose a course of action in novel situations, (b) suppress a prepotent course of action that is no longer appropriate, and (c) monitor current ongoing action (Shallice, 1998). It is also worth noting that both cooperation and competition involve anticipating the behavior of one's social partner, which relies heavily on "mentalizing," that is, the ability to explain and predict the behavior of the other by attributing independent mental states to them, such as thoughts, beliefs, desires, and intentions, which are different from our own (Flavell, 1999). This is particularly true in competition when social partners have divergent goals.

Both cooperative and competitive interactions necessitate self–other monitoring, that is, the ability to guide thought and action in accord with both internal intentions and those of others (Decety and Sommerville, 2003). Furthermore, there is evidence from developmental psychology to suggest that this monitoring differs between collaborative and noncollaborative contexts. For instance, in one study, preschool children were significantly worse at recalling the agent of an action when they cooperated with an experimenter towards building a toy versus when they took turns working independently of the experimenter to build the toy (Sommerville and Hammond, 2003). This suggests that self–other merging is greater in cooperation conditions (see also DeCremer and Stouten, 2003).

Research in social psychology has demonstrated that people are motivated to form accurate impressions of persons they depend on for desired outcomes (Vonk, 1998). In cooperation, the outcomes of the perceiver and the other person rely on their collaborative accomplishments, whereas in competition, the outcomes of the perceiver are inversely related to those of the other person.

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study was approved by the local Ethics Committee (University of Oregon) and conducted in accordance with the Declaration of Helsinki.

The pattern game and conditions

During fMRI scanning, subjects played an online computerized game with a confederate. The game board consisted of a 5×5 grid on which players had to place circular colored tokens to build target patterns displayed above the grid (see Fig. 1). The spatial configurations of the patterns varied from trial to trial and were made of five tokens within a 3×3 matrix.

The objective of the game was to build the target pattern under one of three experimental conditions: alone (both subjects and confederate were playing independently of one another on the same board during independent trials), with the help of the other player (cooperation trials), or against another player (competition trials). Subjects and the experimenter took turns playing and were paced at 2000 ms per move. For half of the experimental trials, the subject was building the pattern, while for the other half, the experimenter was. The player (subject in the magnet or the experimenter) who is building the pattern is also the one who is placing the initial token onto the grid. One “trial” consisted of one game of eight moves (four per player). Trial time was set at 16,500 ms (note that these specifications were not given to the subjects). The tokens appeared automatically on the designated side of the player, above the grid. Players could control the horizontal movement of the tokens by means of a five-key MR-compatible response device (X-Keys, P.I. Engineering Inc., Williamston, MI) placed in their right hand, with each key/finger corresponding to a specific column (left most column: thumb). Players had to select a target column, and the token would drop to the bottom of the column automatically after 2000 ms had elapsed. During scanning, stimuli were presented via a computer connected to a video projector and reflected into a mirror positioned in front of subjects’ eyes.

Study design and procedure

Subjects were told that they would play a game online with other individuals who were in separate remote location. The game

was designed such that it was very challenging to complete the patterns in the allotted time, and subjects were made aware of this to make sure that they were motivated to exert similar effort in all trials. To ensure that subjects were motivated to adopt the requested mental stance (i.e., cooperation or competition), they were also told that they would be evaluated during the game based on how close they came to completing a given pattern, or how well they did at blocking a pattern.

Before scanning, subjects received training on the tasks in a mock scanner. They each completed a minimum of 10 trials of each type of condition to ensure that they understood the game and that they could manipulate the response box efficiently enough to be able to play the game within the allotted time.

Once in the magnet, subjects were first shown 5-s video clips of the players that they would be interacting with. The players introduced themselves and specified the role they would have in the game (i.e., competitor or cooperator). This experimental setup was designed to create an ecologically valid setting in which subjects were engaged in real social interactions with peers. Subjects were told that the video clip method was chosen to minimize interaction between players. Three females and three male confederates were selected as actors and were age-matched with the study participants. Female actors were used for female participants and male actors for male participants to minimize cross-gender effects that could influence social interaction. In fact, unknown to the participants, the same experimenter played as both the competitor and the cooperator. None of the study participants expressed any doubt about who they actually played with in postscanning debriefing.

The study consisted of four scanning sessions of approximately 10 min each. Each session began with an instruction screen of 10 s followed by 14 blocks of 38 s. Each block started with a 3-s screen displaying the picture of the opponent as well as the type of trials subjects were about to perform (Fig. 2). For instance, in the cooperation condition, the instruction reads, “On these trials, you will *cooperate* with Melanie”; or in the competition condition, the instruction reads, “On these trials, you will *compete* against Jason.” In the baseline trials, subjects were asked to stare at a white cross displayed centrally on a black background. The screen

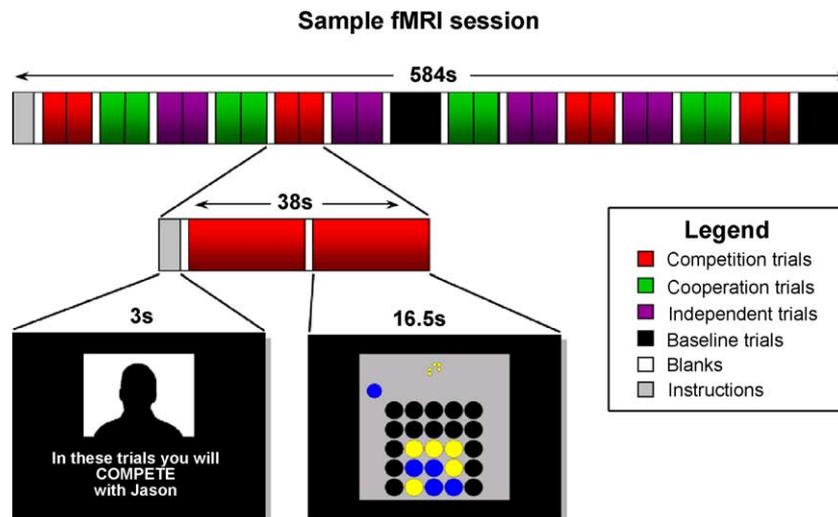


Fig. 2. Time course of an fMRI sample session. Each of the four sessions comprised 14 blocks of two trials each. Every trial started with an instruction screen with the picture of the other player. Blank screens lasted 3 s between blocks of trials and 1 s between trials.

prompt was followed by two trials of the same type, each lasted 16.5 s. All trials were preceded by a 1-s blank screen, and all the blocks were separated by a blank screen of 3 s. The order of the blocks was pseudorandomized so that no two blocks of same type were presented in succession, and each type was presented twice within half a session. The baseline trials were presented on blocks 7 and 14 of each session.

Behavioral measures

To verify that participants' performance reflected the different mental sets that each condition was designed to elicit, two behavioral indices were computed.

1. An error was recorded if, during a trial, a player made two or more consecutive moves which are inconsistent with the goal of that trial, that is, moves that helped the opponent in the competition trials or moves that impeded the confederate in the cooperation trials.
2. The success rate at achieving the goal of each trial in the cooperation and competition conditions was assessed by comparing the final token configuration with its target pattern.

Data acquisition and analyses

MRI data were acquired on a 3-T head-only Siemens Magnetom Allegra System equipped with a standard quadrature head coil. Changes in blood oxygenation level-dependent (BOLD) T2*-weighted MR signal were measured using a gradient echo-planar imaging (EPI) sequence (repetition time TR = 2000 ms, echo time TE = 30 ms, FoV = 192 mm, flip angle 80°, 64 × 64 matrix, 32 slices per slab, slice thickness 4.5 mm, no gap, voxel size = 3.0 × 3.0 × 4.5 mm). For each run, a total of 300 EPI volume images were acquired along the AC–PC plane. Structural MR images were acquired with a MPRAGE sequence (TR = 2500, TE = 4.38, FoV = 256 mm, flip angle = 8°, 256 × 256 matrix, 160 slices per slab, thickness = 1 mm, no gap).

Image processing was carried out using SPM2 (Wellcome Department of Imaging Neuroscience, London, UK), implemented in MATLAB 6.1 (Mathworks Inc., Sherborn, MA). Images were realigned and normalized using standard SPM procedures. The normalized images of 2 × 2 × 2 mm were smoothed by a FWHM 4.5 × 4.5 × 6 Gaussian kernel. A first fixed level of analysis was computed subjectwise using the general linear model with hemodynamic response function modeled as a boxcar function which length covers the two trials (games) of each block. First-level contrasts were introduced in second-level random-effect analysis to allow for population inferences. Main effects were computed using one-sample *t* test, including all subjects for each of the contrasts of interest, which yielded a statistical parametric map of the *t* statistic (SPM *t*), subsequently transformed to the unit normal distribution (SPM *z*). A voxel-level threshold of $P < 0.001$ uncorrected for multiple comparisons ($t=4.02$; $z = 3.10$) was used for regions about which we had a priori hypotheses. A conventional subtraction method was used with this mixed-effect analysis to contrast the brain activity associated with each of the two target conditions (cooperation and competition) versus the control state (independent) and the two target conditions between them.

Results

Behavioral measures

There were very few errors during the cooperation trials (4.4%) or the competition trials (1.5%). This demonstrates that participants understood the directions and performed the task efficiently.

To evaluate the difference in participants' success rate at completing the target patterns, a two-way Condition (2) × Session (4) within-subjects analysis of variance (ANOVA) was computed (Fig. 3). As expected, this ANOVA revealed a significant effect of Condition [$F(1,11) = 1530$, $P < 0.0001$]: cooperation trials led to greater pattern completion. No significant difference was found between the different fMRI sessions ($P > 0.05$). The Condition × Session interaction was not significant. These results show that there is no learning effect across the fMRI scanning and that goal achievement was considerably better in cooperation trials.

Functional imaging data

The overall effect of cooperating towards a common goal compared to playing the game independently showed activation in a number of regions, including the superior and inferior parietal cortices, as well as the superior frontal gyrus bilaterally (Table 1). Activation was also detected in the anterior insula, as well as in the left supplementary motor area. When the competition condition was contrasted with the independent condition, hemodynamic increases were found bilaterally in the anterior insula and in the precuneus. In the right hemisphere, activation was detected in the medial prefrontal cortex/anterior cingulate, superior and inferior parietal cortices, and the superior frontal gyrus.

Direct comparison of the two conditions of interest (cooperation vs. competition, and the reverse comparison) highlighted differences in the cerebral regions specifically recruited by those very distinct social interaction states (Table 2). The contrast examining cooperation versus competition yielded significant activation in the insula and the posterior cingulate bilaterally, as well as in the right anterior frontal cortex. In the left hemisphere, differences were found in the medial orbitofrontal and superior parietal cortices. When competition was contrasted with cooperation, hemodynamic changes were detected in the right superior

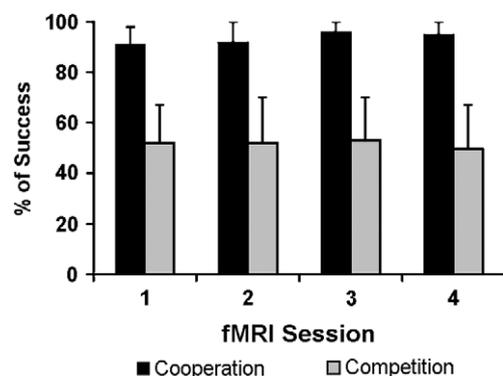


Fig. 3. Histograms showing the mean percentage of success and standard deviations of participants at achieving the target pattern in cooperation and competition trials across the four fMRI sessions.

Table 1

Regions of significant activation resulting from mean group results for the cooperation and competition tasks

Region	Voxel coordinates			z Score
	x	y	z	
<i>Cooperation versus independent</i>				
R superior frontal gyrus	30	2	66	4.00
L superior frontal gyrus	–28	–2	56	3.88
R superior parietal lobe*	32	–66	56	5.61
L superior parietal lobe*	–24	–66	46	5.13
R inferior parietal cortex	46	–34	42	3.96
L inferior parietal cortex	–42	–36	42	4.20
R anterior insula	38	20	2	4.45
L medial cerebellum*	–4	–80	–22	5.47
<i>Competition versus independent</i>				
L superior parietal lobe	–16	–66	64	4.69
R superior parietal lobe	22	–74	58	4.51
R inferior parietal cortex	50	–36	56	4.26
L superior frontal gyrus	–28	4	56	3.87
R superior frontal gyrus	26	4	52	3.95
L medial prefrontal cortex	–8	36	40	3.87
R medial prefrontal cortex	10	30	36	4.45
R middle frontal gyrus	40	52	24	4.20
L anterior insula	–32	18	4	4.22
R anterior insula	42	24	–12	4.21

$P < 0.001$ uncorrected; $k > 20$. Brain regions that were found to be involved in both cooperation and competition are highlighted in bold.

* $P < 0.05$, corrected.

frontal gyrus, in the right inferior parietal lobule, and in the medial prefrontal cortex bilaterally.

Discussion

On the basis of the difference in success rate (i.e., the completion of a given pattern) between cooperation and competition, we

Table 2

Regions of significant activation specific to cooperation and to competition ($k > 50$)

Region	Voxel coordinates			z Score
	x	y	z	
<i>Cooperation versus competition</i>				
L superior parietal cortex	–18	–46	70	4.25
L posterior cingulate	–4	–4	52	4.50
R posterior cingulate	6	–20	48	4.54
L/R posterior cingulate	0	–56	36	4.33
R posterior cingulate	6	–50	24	4.31
L insula	–44	–2	14	4.20
R insula	32	–4	4	4.38
R anterior frontal cortex	10	58	4	4.73
L medial orbitofrontal cortex	–12	36	–12	4.98
<i>Competition versus cooperation</i>				
R superior frontal gyrus	20	10	70	4.17
R inferior parietal lobule ^a	52	–48	46	3.11
R/L medial frontal gyrus	–2	36	40	5.27
L inferior parietal cortex	–42	–58	40	4.14
R superior frontal gyrus	28	60	22	3.97

^a Does not reach the voxel extent threshold.

are confident that participants were actually adopting the appropriate mental set required by the game. In the context of our game, a large number of patterns could only be built with tokens placed in a specific supporting position (see Fig. 1 for an illustration). Thus, given the short allotted time for each trial, it would not have been possible to reach close to 100% success in the cooperation condition unless both players were actively monitoring each other's move in relation to a common goal. In contrast, the low success rate in the competition trials reflects the intentional effort by the opponent to prevent the pattern from being completed.

The functional imaging data show that both the cooperation and the competition states, as compared with independent playing, were associated with a common set of neural regions. Specifically, the right superior parietal cortex and superior frontal gyrus were involved in both mental sets. Note that these hemodynamic changes are unlikely to be related with the motor demand of the tasks, because all conditions involved the exact same number of game moves. In addition, the condition in which participants played independently was designed to comprise similar number of moves (and thus motor demands) towards a goal (building a given pattern), visual elements on the play-grid (e.g., number of tokens, color, motion), but no strategic interpersonal thinking. We thus believe that changes in the two social interaction conditions are likely due to greater attentional and executive demands required during conditions that necessitate monitoring of one's own moves in relation to those of another individual. However, the activation in the superior frontal gyrus, which lies within the frontal eye fields, may be due to there being fewer eye movements in the independent condition.

More interestingly, both conditions that included social interaction led to increased activation in the anterior insula (see Fig. 4). The insula has been characterized as a paralimbic structure due to its connections and associations with the neocortex and limbic structures (Augustine, 1996; Mesulam and Mufson, 1985). Recent evidence from neuroimaging studies point out that this region is an important neural component for the sense of agency, and its activation is related to the attribution of actions to the self (e.g., see Farrer and Frith, 2002; Farrer et al., 2003). Moreover, activation of the anterior insula may also be consistent with its involvement in autonomic arousal (e.g., see Critchley et al., 2000; Oppenheimer et al., 1992). Indeed, as compared to independent play, the two target conditions are likely to elicit social and motivational states of the participants that draw into arousal mechanisms.

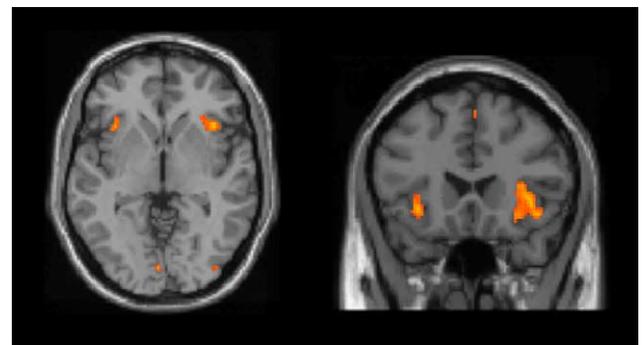


Fig. 4. Bilateral activation of the anterior insula found when participants played the computer game to cooperate or to compete with another individual versus playing independently. Clusters are superimposed on a horizontal ($z = -8$) and coronal ($y = 24$) MRI sections.

The finding of left anterior frontal cortex and orbitofrontal cortex activation, related specifically to cooperation and, resulting from direct comparison with the competitive stance (Fig. 5), is compatible with a previous fMRI study that investigated social interactions by means of the iterated Prisoner's Dilemma Game (Rilling et al., 2002). It has been suggested that, like the rest of the prefrontal cortex, the orbitofrontal cortex has a fundamental role in making behavioral choices, particularly in incompletely specified or unpredictable situations (Elliott et al., 2000). Although both competition and cooperation imply social interactions, we found that the medial orbitofrontal area is specifically activated when participants cooperate with another person. There is ample evidence from evolutionary psychology as well as from developmental psychology to argue that cooperating is more socially rewarding than competing—a source of positive feedback from the other on the performance of the self towards the goal to be accomplished (Barron, 2003). At the neural level, the orbitofrontal cortex is acknowledged to be crucially involved in the motivational control of goal-directed behavior (Tremblay and Schultz, 1999). The role of the medial orbitofrontal cortex and anterior frontal cortex in processing positive feedback information has been suggested by Elliott et al. (1997) from a neuroimaging study that manipulated the presence of performance feedback in planning and guessing tasks. Another fMRI experiment has shown that the orbitofrontal cortex appears to code relative rather than absolute values of rewards (Elliott et al., 2003). In addition, the left-sided medial region of the orbitofrontal appears particularly responsive to reward, and this fits well with the approach-withdrawal theory (see Davidson, 2003, for a review). We suggest that, in our experiment, the reward value stems from the psychological satisfaction of reaching a common goal through interaction with a conspecific. This would be compatible with the idea that the reward value of a response could be related to its familiarity or rightness (Elliott et al., 2000).

The opposite contrast (competition vs. cooperation) revealed activation in the right inferior parietal cortex as well as a number of regions in the frontal lobes including medial frontal gyrus and left superior frontal gyrus. We suggest that competing with another person involves less merging of the self and other, whereas cooperating with another person involves greater self–other merging (DeCremer and Stouten, 2003). The right inferior parietal activation may arise because the distinction between the self and other is more highlighted during competition than cooperation. Such an idea would be consistent with the accumulating evidence

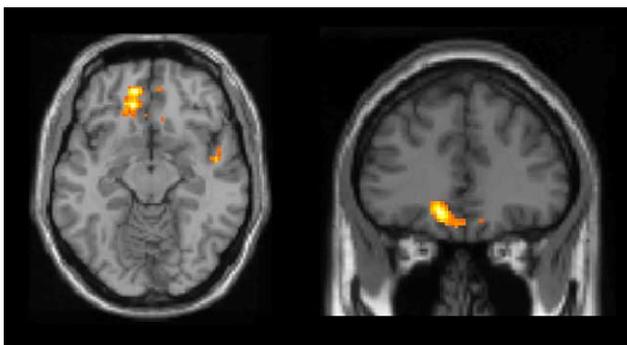


Fig. 5. Left medial orbitofrontal cortex activation cooperation. Clusters are superimposed on horizontal ($z = -12$) and coronal ($y = 36$) MRI sections.

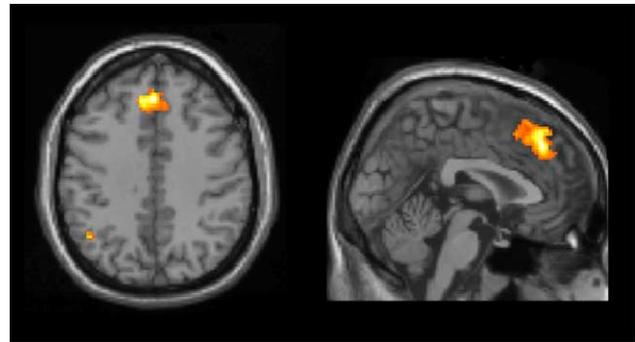


Fig. 6. Medial prefrontal cortex activation found in the competition. Clusters are superimposed on horizontal ($z = 40$) and sagittal ($y = -2$) MRI sections.

indicating that the right inferior parietal cortex plays a role in the distinction between self-produced actions and actions generated by others (e.g., Farrer and Frith, 2002; Meltzoff and Decety, 2003). Notably, this region is activated when subjects observe their own actions being imitated by someone else and hence driven to monitor who is doing what (Berlucchi and Aglioti, 1997; Chaminade and Decety, 2002; Decety et al., 2002), or when confusion may potentially occur between one's own action and its visual consequences (Farrer et al., 2003). Moreover, lesions of the right inferior parietal cortex may lead to confusion between the self and the other (see Blakemore and Frith, 2003; Jackson and Decety, 2004, for recent reviews).

The involvement of the medial prefrontal cortex specifically in competition is also of great interest (see Fig. 6). There is hard evidence that this region around the paracingulate sulcus in the medial prefrontal cortex plays a specific role in mentalizing. It contains spindle cells, a class of large projection neurons found only in great apes and humans, which are thought to be involved in coordinating widely distributed neural activity involving emotion and cognition (Allman et al., 2001). This region is generally considered to play a crucial role in theory of mind (ToM), since its activation is systematically found in neuroimaging studies of attribution of intentions in a variety of settings and tasks (see Frith and Frith, 2003, for a review). In addition, patients with lesion of this region are seriously impaired in understanding materials requiring attribution of mental states to others (Happé et al., 1999; Stuss et al., 2001). Adopting a competitive stance requires a mentalizing component to maintain both self and other perspectives of the game and therefore, we hypothesize, requires the computing resources of the medial prefrontal cortex.

Moreover, there are theoretical reasons to suppose that mentalizing demands of cooperation and competition differ in some aspects. In case of competition, the opponent's upcoming behavior is less predictable than in the case of cooperation in which there is a clear expectation for the behavior of the other agent. Research by Sebanz et al. (2003), as well as Knoblich and Jordan (2003), demonstrated that one's own actions are facilitated when actions of the other are at the disposal of the self. This is the case in the cooperation trials, but exactly the opposite during the competition trials. Thus, the strong increase in the medial prefrontal cortex during competition may in part reflect higher executive processing demands. Further support for our interpretation is provided a study of Elliott and Dolan (1998) who report that this region is activated even when volunteers performed a hypothesis-testing task that

does not involve social interactions. This view argues for a more general function and domain-independent functionality related to the initiation and maintenance of nonautomatic cognitive processing (Ferstl and von Cramon, 2002). Such a function in cognitive control, which has limited capacity, is subserved by the prefrontal cortex (Cohen et al., 2000). In addition, developmental research shows that executive control is an enabling factor for children succeeding on various theory of mind tasks (Carlson et al., 2002; Cole and Mitchell, 2000; Ozonoff et al., 1991).

More generally, these two distinct views as to what ToM or other forms of social cognition actually involve may not be incompatible. One view posits that social cognition consists of one or more specialized modules that are explicitly dedicated to handling mind reading, particularly a region in the anterior paracingulate cortex (see Frith and Frith, 2003). The other view argues that ToM itself is an emergent property of other more fundamental cognitive processes associated with executive functions (e.g., see Barrett et al., 2003; Moses, 2001; Russell, 1996). Future research is needed to elucidate the functional relation between executive functions and mentalizing process and how they can be fragmented into subcomponents with their respective neural implementation. However, it is clear that the two views may not be mutually exclusive. For instance, Gallagher and Frith (2003) suggested that the activity in the medial prefrontal cortex occurs when cues are used to determine an agent's mental state that is decoupled from reality and to handle simultaneously these two perspectives on the world (see Leslie, 1987). This decoupling mechanism is likely to require some aspects of executive functions, in particular, executive inhibition, that is, the deliberate suppression of a salient cognition or response to achieve an internally represented goal (Nigg, 2001). Together, these arguments are consistent with the hypothesis that executive functions evolved to serve social planning in primates and, in humans, are applied to both physical world and the social realm (Humphrey, 1988).

In conclusion, the present study demonstrates that, in addition to a system involved in self/other processing, distinct neural regions are recruited depending on the nature and the reward value of social interaction. We find that cooperation provides a social incentive and is associated with right orbitofrontal involvement, and competition requires additional mentalizing resources and is associated with an increase in medial prefrontal activity. In everyday life, our interaction with others involves both cooperative and competitive states of mind that elicit different motivational goals.

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