

Published in final edited form as:

*Neuroimage*. 2004 October ; 23(2): 744–751. doi:10.1016/j.neuroimage.2004.05.025.

## The neural bases of cooperation and competition: an fMRI investigation

Jean Decety<sup>\*</sup>, Philip L. Jackson, Jessica A. Sommerville, Thierry Chaminade, and Andrew N. Meltzoff

Social Cognitive Neuroscience Laboratory, Institute for Learning and Brain Sciences, University of Washington, Seattle, WA 98195-7988, USA

### Abstract

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.

### Keywords

Social interaction; Executive functions; Theory of mind; fMRI; Agency; Cognitive neuroscience; Cooperation; Competition

### 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.

Lesions of the frontal lobe, especially the ventromedial regions, produce a wide range of cognitive and emotional deficits including many aspects, such as decision making, which are at play in social interactions (Bechara et al., 2000; Damasio et al., 2003). Only a few neuroimaging studies have investigated cooperation and competition in humans. In one functional magnetic resonance imaging (fMRI) study, participants played an economic trust game with another person following a fixed probabilistic strategy (McCabe et al., 2001). The results showed a significant activation of the right medial prefrontal cortex during the interaction. Another study examined cerebral activity during a cooperative game, the Prisoner's Dilemma (Rilling et al., 2002). Ventromedial frontal cortex activation was detected when participants engaged in mutual cooperation. In addition, the anterior cingulate cortex was found to be involved in this game. However, this latter region was also found to be activated in a positron emission tomography study where participants were asked to adopt "an intentional stance" when playing against an opponent in a competitive manner (Gallagher et al., 2002).

Thus, the available evidence indicates that social interactions involve a specific set of cortical regions, but further investigation is needed to elucidate the respective contribution of these neural structures in the different mind sets of the agent when they cooperate toward a common goal or when they compete for this goal. The aim of the present study was to investigate the neural basis of these two social cognitive processes in the same individuals

while they engage in well-controlled social interactions. We designed a computer game to provide fMRI-compatible, controlled bouts of cooperation and competition (see Fig. 1).

We predicted that neural activation while playing this computer game will reflect both mentalizing and executive functions because they are key processes in cooperation and competition. Since different regions of the prefrontal cortex mediate different aspects of executive functions (Elliott, 2003), it is reasonable to expect both common as well as distinct components of the prefrontal cortex depending on the particular mental state (i.e., cooperation vs. competition) adopted by the subject during game play. Mentalizing tasks are systematically associated with medial prefrontal cortex activation (Frith and Frith, 2003), and we thus anticipate response in this part of the brain, especially during competition when partners have different goals/intentions.

Because there is converging evidence from evolutionary psychology and developmental science to argue that cooperation is psychologically rewarding for the individual as well as for the group, we expected that frontal regions involved in reward processing would be specifically activated during cooperation trials. Furthermore, we predicted that regions implicated in the sense of agency, that is, the feeling that we are the cause of our actions and their consequences, specifically the inferior parietal cortex (Blakemore and Frith, 2003; Farrer and Frith, 2002; Farrer et al., 2003; Ruby and Decety, 2001), would be activated during both cooperative and competitive states.

## Material and methods

### Participants

Twelve right-handed healthy volunteers (six females, six males) aged between 21 and 28 years participated in the study. They gave written informed consent and were paid for their participation. No subject had any history of neurological, major medical, or psychiatric disorder. The 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  $5 \times 5$  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  $3 \times 3$  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 cooperater). 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 cooperater. 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 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 competitions 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 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 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.

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 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.

## Acknowledgments

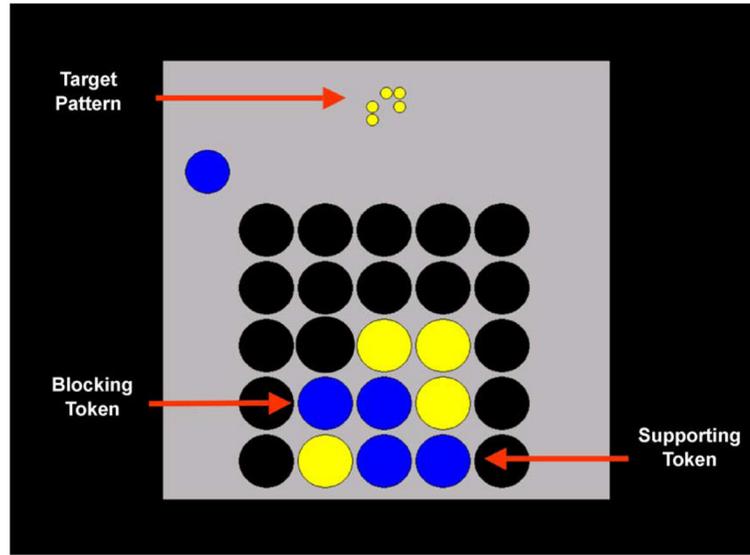
This research was supported by the Institute for Learning and Brain Sciences and also, in part, by a grant from NIH (HD-22514). The fMRI scanning was conducted at the Lewis Center for Neuroimaging, University of Oregon, Eugene, OR. We thank Scott Watrous for technical assistance with fMRI data acquisition and all the staff for their collaboration.

## References

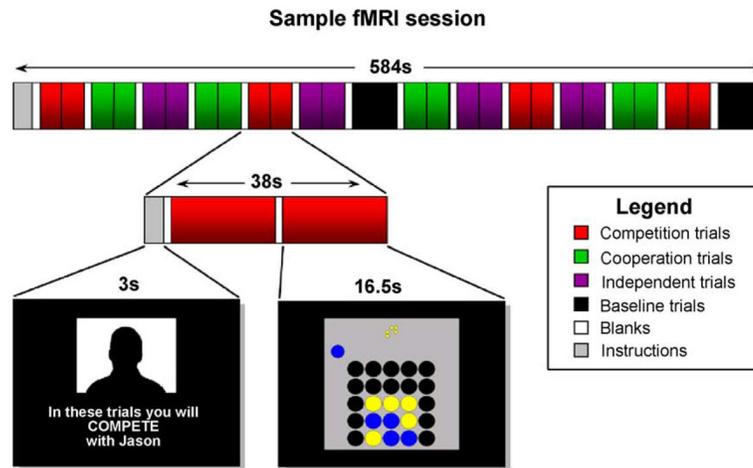
- Adolphs R. Social cognition and the human brain. *Trends Cogn Sci.* 1999; 3:469–479. [PubMed: 10562726]
- Allman JM, Hakeem A, Erwin JM, Nimchinsky E, Hof P. The anterior cingulate cortex: the evolution of an interface between cognition and emotion. *Ann NY Acad Sci.* 2001; 935:107–117. [PubMed: 11411161]
- Augustine JR. Circuitry and functional aspects of the insular lobe in primates including humans. *Brain Res Rev.* 1996; 22:229–244. [PubMed: 8957561]
- Barrett L, Henzi P, Dunbar RIM. Primate cognition: from what now to what if. *Trends Cogn Sci.* 2003; 7:494–497. [PubMed: 14585446]
- Barron B. When smart groups fail. *J Learn Sci.* 2003; 12:307–359.
- Bechara A, Tranel D, Damasio H. Characterization of the decision-making deficit of patients with ventromedial prefrontal cortex lesions. *Brain.* 2000; 123:2198–2202.
- Berlucchi G, Aglioti S. The body in the brain: neural bases of corporeal awareness. *Trends Neurosci.* 1997; 20:560–564. [PubMed: 9416668]
- Blakemore SJ, Frith CD. Self-awareness and action. *Curr Opin Neurobiol.* 2003; 13:219–224. [PubMed: 12744977]
- Byrne, RW.; Whiten, A. *Machiavellian Intelligence.* Oxford Univ. Press; Oxford: 1988.
- Carlson SM, Moses LJ, Breton C. How specific is the relation between executive function and theory of mind? Contributions of inhibitory control and working memory. *Infant Child Dev.* 2002; 11:73–92.
- Chaminade T, Decety J. Leader or follower? Involvement of the inferior parietal lobule in agency. *NeuroReport.* 2002; 13:1975–1978. [PubMed: 12395103]
- Cohen JD, Botvinick M, Carter CS. Anterior cingulate and prefrontal cortex: who's in control? *Nat Neurosci.* 2000; 3:421–423. [PubMed: 10769376]
- Cole K, Mitchell P. Siblings in the development of executive control and theory of mind. *Br J Dev Psychol.* 2000; 18:279–295.
- Critchley HD, Elliott R, Mathias CJ, Dolan RJ. Neural activity related to generation and representation of galvanic skin conductance responses: an fMRI study. *J Neurosci.* 2000; 20:3033–3040. [PubMed: 10751455]
- Damasio, AR.; Adolphs, R.; Damasio, H. The contribution the lesion method to functional neuroanatomy of emotion. In: Davidson, RJ.; Scherer, KR.; Godsmith, HH., editors. *Handbook of Affective Neuroscience.* Oxford University Press; New York: 2003. p. 66-92.
- Davidson RJ. Darwin and the neural bases of emotion and affective style. *Ann NY Acad Sci.* 2003; 1000:316–336. [PubMed: 14766646]
- Decety J, Sommerville JA. Shared representations between self and others: a social cognitive neuroscience view. *Trends Cogn Sci.* 2003; 7:527–533. [PubMed: 14643368]
- Decety J, Chaminade T, Grèzes J, Meltzoff AN. A PET exploration of the neural mechanisms involved in reciprocal imitation. *NeuroImage.* 2002; 15:265–272. [PubMed: 11771994]
- DeCremer D, Stouten J. When do people find cooperation most justified? The effect of trust and self–other merging in social dilemmas. *Soc Justice Res.* 2003; 16:41–52.
- Dunbar RIM. The social brain: mind, language, and society in evolutionary perspective. *Annu Rev Anthropol.* 2003; 32:163–181.
- Eisler R, Levine DS. Nurture, nature, and caring: we are not prisoners of our genes. *Brain Mind.* 2002; 3:9–52.
- Elliott R. Executive functions and their disorders. *Br Med Bull.* 2003; 65:49–59. [PubMed: 12697616]

- Elliott R, Dolan RJ. Activation of different anterior cingulate foci in association with hypothesis testing and response selection. *Neuro-Image*. 1998; 8:17–29. [PubMed: 9698572]
- Elliott R, Frith CD, Dolan RJ. Differential neural response to positive and negative feedback in planning and guessing tasks. *Neuropsychologia*. 1997; 35:1395–1404. [PubMed: 9347486]
- Elliott R, Dolan RJ, Frith CD. Dissociable functions in the medial and lateral orbitofrontal cortex: evidence from human neuroimaging studies. *Cereb Cortex*. 2000; 10:308–317. [PubMed: 10731225]
- Elliott R, Newman JL, Longe OA, Deakin JFW. Differential response patterns in the striatum and orbitofrontal cortex to financial reward in humans: a parametric functional magnetic resonance imaging study. *J Neurosci*. 2003; 23:303–307. [PubMed: 12514228]
- Farrer C, Frith CD. Experiencing oneself vs. another person as being the cause of an action: the neural correlates of the experience of agency. *NeuroImage*. 2002; 15:596–603. [PubMed: 11848702]
- Farrer C, Franck N, Georgieff N, Frith CD, Decety J, Jeannerod M. Modulating the experience of agency: a positron emission tomography study. *NeuroImage*. 2003; 18:324–333. [PubMed: 12595186]
- Ferstl EC, von Cramon DY. What does the frontomedian cortex contribute to language processing: coherence or theory of mind? *Neuro-Image*. 2002; 17:1599–1612. [PubMed: 12414298]
- Flavell JH. Cognitive development: children's knowledge about the mind. *Annu Rev Psychol*. 1999; 50:21–45. [PubMed: 10074674]
- Frith U, Frith CD. Development and neurophysiology of mentalizing. *Philos Trans R Soc Lond, B*. 2003; 358:459–473. [PubMed: 12689373]
- Gallagher HL, Frith CD. Functional imaging of 'theory of mind'. *Trends Cogn Sci*. 2003; 7:77–83. [PubMed: 12584026]
- Gallagher HL, Jack AI, Roepstorff A, Frith CD. Imaging the intentional stance in a competitive game. *NeuroImage*. 2002; 16:814–821. [PubMed: 12169265]
- Happé F, Brownell H, Winner E. Acquired 'theory of mind' impairments following stroke. *Cognition*. 1999; 70:211–240. [PubMed: 10384736]
- Humphrey, NK. The social function of intellect. In: Byrne, RW.; Whiten, A., editors. *Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes, and Humans*. Clarendon; Oxford: 1988. p. 13-26.
- Jackson PL, Decety J. Motor cognition: a new paradigm to study self other interactions. *Curr Opin Neurobiol*. 2004; 14:259–263. [PubMed: 15082334]
- Knoblich G, Jordan JS. Action coordination in groups and individuals: learning anticipatory control. *J Exper Psychol, Learn, Mem, Cogn*. 2003; 29:1006–1016. [PubMed: 14516231]
- Leslie A. Pretense and representation: the origins of "Theory of Mind". *Psychol Rev*. 1987; 94:412–426.
- McCabe K, Houser D, Ryan L, Smith V, Trouard T. A functional imaging study of cooperation in two-person reciprocal exchange. *Proc Natl Acad Sci USA*. 2001; 98:11832–11835. [PubMed: 11562505]
- Meltzoff AN, Decety J. What imitation tells us about social cognition: a rapprochement between developmental psychology and cognitive neuroscience. *Philos Trans R Soc Lond, B*. 2003; 358:491–500. [PubMed: 12689375]
- Mesulam, MM.; Mufson, EJ. The insula of Reil in man and monkey. In: Peters, A.; Jones, E., editors. *Cerebral Cortex*. Plenum Press; New York: 1985. p. 179-226.
- Moses LJ. Executive accounts of theory of mind development. *Child Dev*. 2001; 8:1–25.
- Nigg JT. Is ADHD a disinhibitory disorder? *Psychol Bull*. 2001; 127:571–598. [PubMed: 11548968]
- Oppenheimer SM, Gelb A, Girvin JP, Hachinski VC. Cardiovascular effects of human insular cortex stimulation. *Neurology*. 1992; 42:1727–1732. [PubMed: 1513461]
- Ozonoff S, Pennington BF, Rogers S. Executive functions in high-functioning autistic individuals: relationship to theory of mind. *J Child Psychol Psychiatry*. 1991; 32:1081–1105. [PubMed: 1787138]
- Rilling JK, Gutman DA, Zeh TR, Pagnoni G, Berns GS, Kitts CD. A neural basis for social cooperation. *Neuron*. 2002; 35:395–405. [PubMed: 12160756]

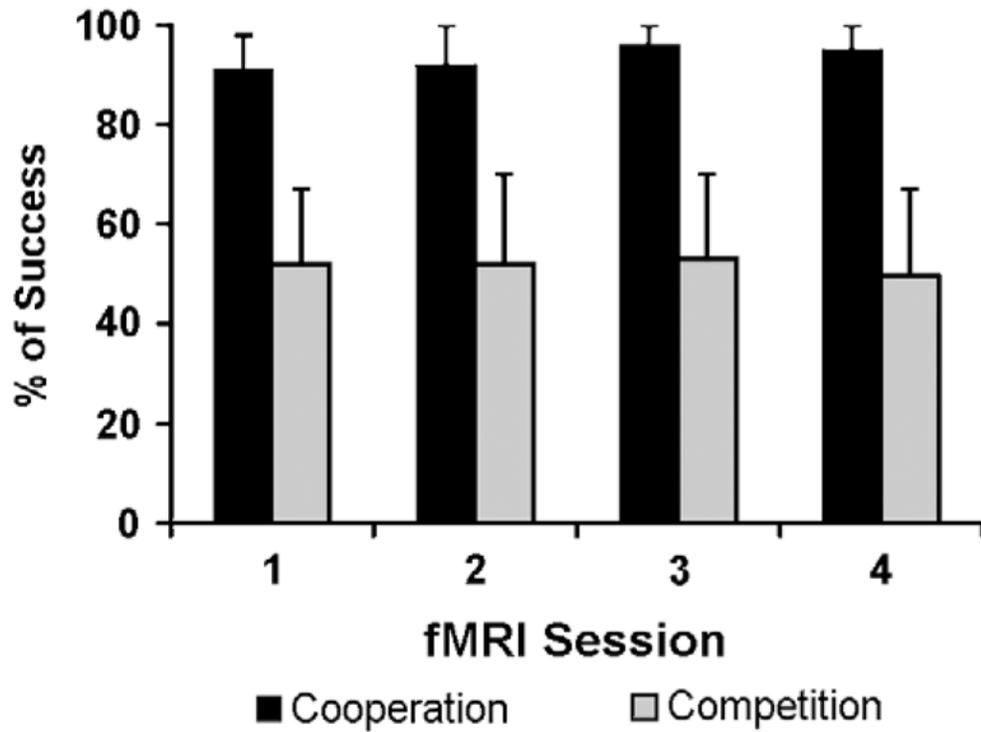
- Ruby P, Decety J. Effect of subjective perspective taking during simulation of action: a PET investigation of agency. *Nat Neurosci.* 2001; 4:546–550. [PubMed: 11319565]
- Russell, J. *Agency and its Role in Mental Development.* Psychology Press; Hove: 1996.
- Sebanz N, Knoblich G, Prinz W. Representing others' actions: just like one's own? *Cognition.* 2003; 88:B11–B21. [PubMed: 12804818]
- Shallice, T. *From Neuropsychology to Mental Structure.* Cambridge University Press; Cambridge: 1998.
- Sommerville, JA.; Hammond, AJ. "I did it all by myself": exploring preschool children's source-monitoring errors. Poster presented at the Biennial Meeting of the Society for Research in Child Development; Tampa, FL. April; 2003.
- Spencer, H. *Principles of Psychology.* Williams and Norgate; London: 1870.
- Stevens JR, Hauser MD. Why be nice? Psychological constraints on the evolution of cooperation. *Trends Cogn Sci.* 2004; 8:60–65. [PubMed: 15588809]
- Stuss DT, Gallup GG, Alexander MP. The frontal lobes are necessary for theory of mind. *Brain.* 2001; 124:279–286. [PubMed: 11157555]
- Tremblay L, Schultz W. Relative reward preference in primate orbitofrontal cortex. *Nature.* 1999; 398:704–708. [PubMed: 10227292]
- Trivers R. The evolution of reciprocal altruism. *Q Rev Biol.* 1972; 46:35–57.
- Vonk R. Effects of cooperative and competitive outcome dependency on attention and impression preferences. *J Exp Soc Psychol.* 1998; 34:265–288.



**Fig. 1.** Illustration of one trial of the game. The color of the target displayed above the vertical grid indicates which player is building the pattern during this trial, in this case, the yellow player. Black circles correspond to empty slots. The tokens appear automatically every 2000 ms on top of the grid, on the side of the player whose turn it is to play (in this example, the blue player is next). Players have to move the token horizontally until it reaches the desired column, where the token will drop (as if subjected to gravity). Blocking tokens prevent an opponent from completing a pattern (competition); supporting tokens are required to build patterns (cooperation). Note that both cooperative and competitive moves are shown on the same board for illustrative purposes. In the fMRI experiment, each game is played in turn, depending on the instructions given. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



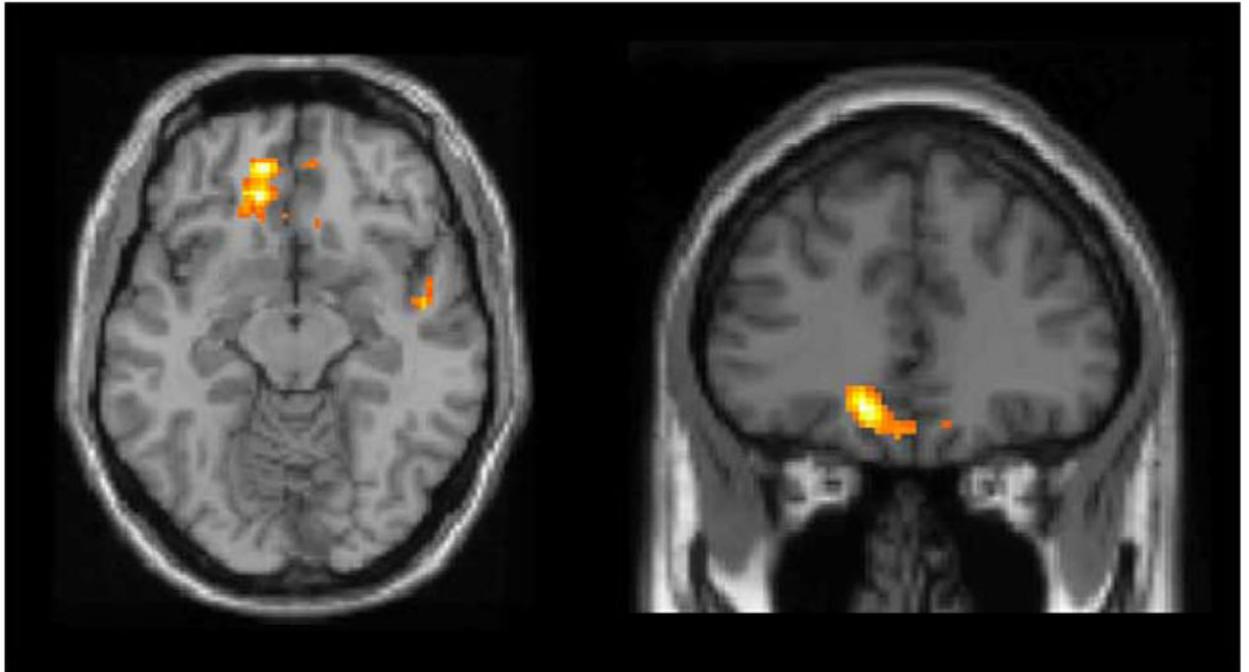
**Fig. 2.** Time course of an fMRI sample session. Each of the four sessions comprised 14 blocks of two trials each. Every trial started with an instruction screen with the picture of the other player. Blank screens lasted 3 s between blocks of trials and 1 s between trials.



**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.



**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.



**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.

**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>				
<b>R superior frontal gyrus</b>	30	2	66	4.00
<b>L superior frontal gyrus</b>	-28	-2	56	3.88
<b>R superior parietal lobe *</b>	32	-66	56	5.61
<b>L superior parietal lobe *</b>	-24	-66	46	5.13
<b>R inferior parietal cortex</b>	46	-34	42	3.96
L inferior parietal cortex	-42	-36	42	4.20
<b>R anterior insula</b>	38	20	2	4.45
L medial cerebellum *	-4	-80	-22	5.47
<i>Competition versus independent</i>				
<b>L superior parietal lobe</b>	-16	-66	64	4.69
<b>R superior parietal lobe</b>	22	-74	58	4.51
<b>R inferior parietal cortex</b>	50	-36	56	4.26
<b>L superior frontal gyrus</b>	-28	4	56	3.87
<b>R superior frontal gyrus</b>	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
<b>R anterior insula</b>	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.

**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 <sup>a</sup>	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

<sup>a</sup>Does not reach the voxel extent threshold.