Brain and Cognition 77 (2011) 401–411

Contents lists available at SciVerse ScienceDirect

Brain and Cognition

journal homepage: www.elsevier.com/locate/b&c

An fMRI study of the social competition in healthy subjects

M. Polosan [a], M. Baciu [b,*], E. Cousin [b], M. Perrone [b], C. Pichat [b], T. Bougerol [b]

[a] Pôle de Psychiatrie et Neurologie, CHU Grenoble, France
[b] Laboratoire de Psychologie et Neurocognition, UMR CNRS 5105, Université Pierre Mendès-France, Grenoble, France

ARTICLE INFO

Article history:
Accepted 25 August 2011
Available online 28 September 2011

Keywords:
Theory of Mind
Social
Executive
Stroop
Competition
Human
Machine
fMRI
Healthy

ABSTRACT

Social interaction requires the ability to infer another person's mental state (Theory of Mind, ToM) and also executive functions. This fMRI study aimed to identify the cerebral correlates activated by ToM during a specific social interaction, the human–human competition. In this framework, we tested a conflict resolution task (Stroop) adapted to a virtual situation of competition. The participants were instructed to play in order to win either against a human-like competitor (human–human competition) or against a non-human competitor (human–machine competition). Only the human–human competition requires ToM as this type of competition is performed under social interaction. We identified first the classical network of executive regions activated by Stroop. Secondly, we identified the social (human–human) competition regions, represented by the bilateral superior and inferior frontal gyri, the anterior cingulate, the insula, the superior and anterior temporal, the hippocampus, the fusiform gyrus, the cuneus and the precuneus. Finally, we identified the executive regions that were modulated by the human–human competition, i.e., the executive control regions additionally activated when mentalizing in the context of social competition. They constituted a network predominant to the right and composed of the superior and middle frontal, anterior cingulate, insula and fusiform gyrus. We suggest that our experimental paradigm may be useful in exploration of the cerebral correlates of social adjustments in several situations such as psychiatric disorders presenting executive and social dysfunctions.

1. Introduction

Human interactions are based on various cognitive and emotional abilities unified within the concept of social cognition. Social interactions include various processes such as social perception (facial expressions, gaze processing), social cognition (ToM, empathy) and executive functions (Hari & Kujala, 2009). The executive functions are specifically involved in the adaptation to new situations that require the overcoming of a habitual response by shifting mental sets, reasoning and planning or maintaining goals. Overall, all these processes are required during social interactions (Suchy, 2009). Moreover, the executive functions modulate the social interactions because people have to constantly integrate feedbacks from the social environmental and elaborate adapted responses. The concept of social cognition relies mainly on the ability to imagine what others think, feel or intend to do in social situations and interactions (Adolphs, 2001). In other words, this concept defines the ability to make inferences about the mental state of other people, a function called Theory of Mind (ToM) (Premack & Woodruff, 1978). Although many neuroimaging studies have explored the cerebral substrate of ToM in various social situations, very few approached this ability during specific social interactions such as competition and cooperation. The social behavior in between -human interactions requires executive control functions but also ToM ability – crucial for the interaction between people.

According to the evolutionary theory, the social competition would be essential to natural selection and social organization (Bowles, 2006; Nowak, 2006). Social competition operates in synergy with another essential social interaction mode, which is cooperation, for shaping the human social behavior. Thus, it has been shown that between-group competition increases the within-group cooperation (Puurtinen & Mappes, 2009), while the within-group competition reduces the cooperation between non-relatives (West et al., 2006).

The competition interactions imply different executive and control mental processes, such as the following: *mental flexibility*, which is the rapid mental adaptation to environmental changes; *decision making* in order to make the appropriate response choice; *inhibition* of pre-potent and non-relevant responses; and *ongoing action monitoring* in order to target the strategies of the opponent competitor (Shallice, 1998). Alongside this executive processing during between-humans competition interaction, each competitor should imagine and anticipate the other's mind state and behavior and thus engage, in other words, the ToM. Moreover, the social competitive behavior includes self-to-other comparison that influences the

* Corresponding author. Address: Laboratoire de Psychologie et Neurocognition, UMR CNRS 5105, 1251 Avenue Centrale, BSHM, BP 47, 38040 Grenoble Cedex 09, France.

E-mail address: mbaciu@upmf-grenoble.fr (M. Baciu).

0278-2626/$ - see front matter © 2011 Elsevier Inc. All rights reserved.
doi:10.1016/j.bandc.2011.08.018

decision making and induces specific social emotions like envy and schadenfreude (gloating) (Dvash, Gilam, Ben-Ze'ev, Hendler, & Shamay-Tsoory, 2010; Fliessbach et al., 2007). These emotions interfere with an evaluation process of people during the social interaction; the evaluation is mostly based on comparison reasoning rather than their intrinsic value (Takahashi et al., 2009).

A large number of studies explored the cerebral substrate of social interactions (Assaf et al., 2009; Baron-Cohen et al., 1994; Baron-Cohen et al., 1999; Brunet, Sarfati, Hardy-Bayle, & Decety, 2000; Castelli, Happe, Frith, & Frith, 2000; Ciaramidaro et al., 2007; Gallagher, Jack, Roepstorff, & Frith, 2002; Gallagher et al., 2000; Goel, Grafman, Sadato, & Hallett, 1995; Hampton, Bossaerts, & O'Doherty, 2008; McCabe, Houser, Ryan, Smith, & Trouard, 2001; Vogeley et al., 2001; Zaki, Hennigan, Weber, & Ochsner, 2010). Nevertheless, only a few studies focused on social competition's neural correlates. For instance, Gallagher et al. (2002) studied social competition by using PET in healthy subjects involved in a competition video game. They highlighted the role of the anterior cingulate gyrus, the medial frontal cortex and the inferior parietal lobule, regions also mentioned by other authors for the same topic and question (Decety, Jackson, Sommerville, Chaminade, & Meltzoff, 2004). During a decision-making task in social competition, Halko, Hlushchuk, Hari, and Schurmann (2009) reported the activation of temporo-parietal junction and the inferior frontal gyrus, both related to the ability to make inferences about the other partner's intentions (Rilling, Sanfey, Aronson, Nystrom, & Cohen, 2004). During social interactions like competition, the medial prefrontal cortex and temporal pole play a more specific role in "on-line" (implicit) ToM process (Assaf et al., 2009). Other areas such as posterior cingulate gyrus, precuneus, superior temporal sulcus, hippocampus, hypothalamus and thalamus have also been reported during social interaction tasks and were particularly related to ToM. Social emotions like envy and schadenfreude related to social comparison may also activate the ToM network (Shamay-Tsoory, Tibi-Elhanany, & Aharon-Peretz, 2007; Takahashi et al., 2009). The number of regions belonging to this large network was often reported as related to executive inhibition control processes (Carter, Botvinick, & Cohen, 1999; Langenecker, Nielson, & Rao, 2004; Mead et al., 2002). Within this framework and given that acting under social competition needs a large panel of executive control abilities, it is difficult to distinguish the regions specifically activated by the executive control functions from those related to the competition situation by itself and to ToM.

ToM is a complex cognitive function, incompletely understood and probably related to executive and control operations (Goukon et al., 2006; Perner, Lang, & Kloo, 2002), and thus involved in harmonious social interactions. A significant correlation between ToM and the inhibitory control has been suggested by different studies of an early (preschooler) age (Carlson, Mandell, Williams, & 2004; Carlson, Moses, & Claxton, 2004; Hughes & Ensor, 2005; Rasmussen, Wyper, & Talwar, 2009; Yang, Zhou, Yao, Su, & McWhinnie, 2009). This correlation is robust and independent of the subject's culture (Sabbagh, Xu, Carlson, Moses, & Lee, 2006). At adulthood, the relationship between executive/control functions and ToM is more controversial. Several neuropsychological observations in patients with frontal lobe lesions did not report correlation between executive function and performances of ToM (Rowe, Bullock, Polkey, & Morris, 2001), while other studies found such a correlation (Charlton, Barrick, Markus, & Morris, 2009; Saltzman, Strauss, Hunter, & Archibald, 2000). Nevertheless, as performances decrease with aging for both ToM and executive control functions, it has been accepted that in some way, they should be correlated (Langenecker et al., 2004; Maylor, Moulson, Muncer, & Taylor, 2002).

Social competition is experimentally simulated by using interactive video games such as *Ultimatum Game* (Rilling et al., 2004; Sanfey, Rilling, Aronson, Nystrom, & Cohen, 2003) or *Prisoner's Dilemma game* (Babiloni et al., 2007; Hauert & Stenull, 2002; Kiesler, Sproull, & Waters, 1996). Given that these games simulate cooperation rather than competition interactions, in this study we used a paradigm focused on the competition behavior evaluation. Our experimental paradigm was based on a cognitive color-naming Stroop test (Stroop, 1935) modified by adding a virtual context of social competition. To test the competition, the participants were asked to perform the color-naming interference test by competing against an adversary who was presented either as a human or as a machine adversary. Instructions about the test and the "adversary" were given in order to induce an "on-line" implicit mentalizing process while performing the task. A visual feedback was sent after each response in order to inform participants about their performance relative to the opponent's. ToM was evaluated by comparing human-to-human vs. human-to-machine interactions. The human–human competition under social interaction can be simulated by a human–computer interaction, a paradigm that was already used in other studies (Assaf et al., 2009; Gallagher et al., 2002; McCabe et al., 2001; Rilling et al., 2004).

By using this paradigm, the aim of our fMRI study performed in healthy subjects was to highlight the cerebral correlates of social (human–human) interaction in a situation of competition, while participants performed a modified version of the Stroop test. After the identification of regions activated by the executive functions and by competition, we were interested to know which of the executive regions were specifically recruited by human–human competition, which involved according to the paradigm's construction, a mentalizing (ToM) process.

2. Materials and methods

2.1. Participants

We examined 14 right-handed healthy volunteers (10 females), with mean age of 35.9y (SD = 7.2y). The handedness was determined by means of a modified version of Edinburgh Handedness Inventory (Oldfield, 1971). Participants were recruited from the university and hospital staff and had no history of psychiatric, neurological or other major medical disorder. All of them provided written informed consent, and the study was approved by the local Ethics Committee of Grenoble Hospital.

2.2. Task and stimuli

The participants were instructed to perform a classical Stroop test that was adapted to a virtual situation of competition. Specifically, the subjects were told to perform a classical color-naming task by competing against an adversary, human or machine.

In order to induce a real competition climate, a scenario was played before the participant entered the MRI scanner. The "human" opponent was presented to the participant: a real person who was in front of a computer screen on which the test was ready to start. Another computer connected to the first one was presented as the "machine" opponent. None of the participants realized that was only a "scenario" and not a real situation. Actually, the participant was always playing against a computer. The participants were instructed to play to win by responding as quickly and correctly as possible. Moreover, they were told to be aware of the opponent's intentions and strategies of response. They were informed that the computer's strategy of competition "depend only on some initial parameters of the participant's competition style" (number of errors, reaction time, etc.); they were told that these parameters helped the computer to "guess" the participant's intentions/strategies. In addition, the participants were told that the computer was programmed to further follow a fixed responding strategy, which was not changing according to the participant's responses, in contrast to the human adversary, described as able to change his intentions and constantly adapt his strategies, depending on each trial's outcome/feedback and on the participant's playing style.

Besides the basic responding strategies, based on the imbalance between the response accuracy (more time consuming) and the response speed (quicker but more hazardous), the participant was told that the "human" opponent might possibly try to cheat/deceit by varying his response strategy (i.e., slowing "his" response speed in order to let the participant win several trials and make the participant more confident in his own performances/playing style and thus decreasing his attention to the following trials, and then speed up the responses in order to surprise and win the next trials, etc.). Thus, the participants were aware of the interest in understanding the "human" adversary's strategy, while understanding the computer's strategy was not considered as worthy, since they could not influence its behavior.

Each response was followed by a visual feedback in order to inform the participant about his/her performance with respect to the adversary's. At the end of the experiment, all participants were debriefed and asked to provide information about their specific feelings while performing the task. Overall, they were asked about their attitudes and feelings toward the adversary according to its type, "human" or "machine," as well as the amount of effort and motivation and the possible strategies they developed for each condition. The stimuli were French written color words usually used in the cognitive Stroop interference test, according to two conditions: Congruent and Incongruent. In the "Congruent" (control color naming) condition (C), the ink's color and the color's name word were the same (e.g., the word "blue" was written in blue ink). In the "Incongruent" (Stroop) condition (I), the word's ink color and the color's name word were different (e.g., the word "red" was written in green). For both conditions, Congruent and Incongruent, the stimuli colors were « red », « blue » and « green ».

Four experimental conditions were tested: Human Congruent (HC), Human Incongruent (HI), Machine Congruent (MC) and Machine Incongruent (MI). Each condition was presented once during the experimental paradigm illustrated in Fig. 1. The condition included 21 stimuli, pseudo-randomly presented. Each stimulus (word) was centered on the middle of a black screen and written in "Courier New" font, size 24. The stimulus presentation time was 1500 ms, with 500 ms fixation point between items. A 500 ms visual feedback was sent after each stimulus in order to emphasize the competition and motivation feelings of subjects. Participants were told that the feedback depends on both accuracy (% correct responses, CR) and speed (RT, response time). Thus, compared to the adversary partner, correct and faster responses generated a positive feedback (« happy » emoticon), while false and/or slower responses generated a negative feedback (« sad » emoticon). Furthermore, in order to remind of the type of competition, human or machine, the emoticon was associated in a peripheral corner of the screen with a standing person or computer picture, respectively.

All visual stimuli were displayed on a computer monitor by using the E-prime software (E-prime Psychology Software Tools Inc., Pittsburgh, USA). The monitor was connected to a video projector (Epson EMP 8200) permitting the transmission of visual stimuli into the magnet. The subject was able to visualize the stimuli by means of a projection screen situated behind the magnet and a mirror centered above the participant's eyes. The participants were instructed to give manual instead of vocal responses, in order to avoid movement artifacts generated articulation (Zysset, Muller, Lohmann, & von Cramon, 2001). The responses were generated by means of three response keys (three types of responses were possible according to three colors). In order to reduce memory demands, a written instruction (c.f., Fig. 2) for reminding responses was permanently displayed on the screen, below the stimuli. Participants were required to respond to the color of the word, by pressing a response button. The manual responses were recorded, analyzed and the task performance was evaluated according to conditions (Control and Stroop conditions) and the type of social interaction (Human, Machine).

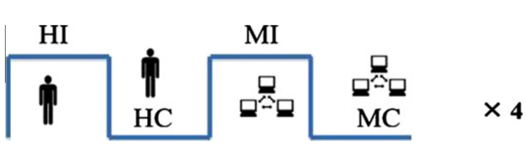

Fig. 1. The experimental paradigm alternated four experimental conditions: HI – Human Incongruent, HC – Human Congruent, MI – Machine Incongruent, MC – Machine Congruent. The paradigm was presented during the fMRI scan, and four fMRI scans have been acquired during fMRI session.

2.3. Functional MRI paradigm

A "block" design was used during the fMRI session. Four runs were measured during the fMRI session. Each run was composed of four periods, one for each experimental condition. During each period, after 3 s instruction screen presentation, the 21 events were shown. Each event was composed of 1500 ms stimulus (Congruent or Incongruent), 500 ms visual feedback and 500 ms fixation. Each event lasted 2.5 s. An event example is presented in Fig. 2. The periods were randomly presented across runs and subjects. The total duration of each run was 4 min 30. During each run, we measured the whole brain volume 86 times. The functional MRI acquisition lasted 18 min. Before entering into the magnet, the participants were trained to perform the task. In order to reinforce the task learning, the participants underwent a second short training period inside the magnet, just before the MR acquisition.

2.4. MR acquisition

The experiment was performed in a whole-body 3T MR scanner (Bruker MedSpec S300) with 40 mT/m gradient strength. For runs, the manufacturer-provided gradient-echo/T2* weighted EPI method was used. Thirty-nine adjacent axial slices parallel to the bi-commissural plane were acquired in interleaved mode. Slice thickness was 3.5 mm. The in-plane voxel size was 3×3 mm (216×216 mm field of view acquired with a 72×72 pixels data matrix; reconstructed with zero filling to 128×128 pixels). The main sequence parameters were TR = 3 s, TE = 30 ms and flip angle = 77°. To correct images for geometric distortions induced by local B0-inhomogeneity, a B0 fieldmap was obtained from two gradient echo data sets acquired with a standard 3D FLASH sequence (ΔTE = 9.1 ms). The fieldmap was subsequently used during data processing. Finally, a T1-weighted high-resolution three-dimensional anatomical volume was acquired, by using a 3D Modified Driven Equilibrium Fourier Transform (MDEFT) sequence (field of view = $256 \times 224 \times 176$ mm; resolution: $1.333 \times 1.750 \times 1.375$ mm; acquisition matrix: $192 \times 128 \times 128$ pixels; reconstruction matrix: $256 \times 128 \times 128$ pixels).

2.5. Data analysis

2.5.1. Spatial pre-processing

Data analysis was performed by using the general linear model as implemented in SPM5 (Welcome Department of Imaging Neuroscience, London, UK, www.fil.ion.ucl.ac.uk/spm) where each event is modeled using a hemodynamic function model. Data analysis started with several spatial pre-processing steps. First, the functional volumes were time-corrected (slice timing) with the 19th

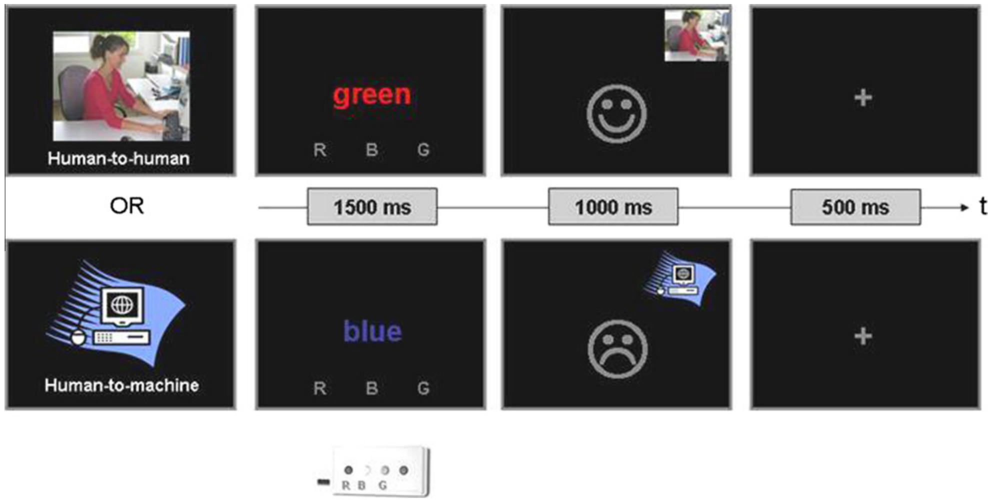

Fig. 2. Example of the experimental paradigm: each epoch included 21 events. An event was composed of 1500 ms stimulus (Congruent or Incongruent) presentation, 500 ms visual feedback and 500 ms fixation. Each event lasted 2.5 s. The 3 s instruction screen was presented only once at the beginning of each epoch and illustrated the type of interaction (human–human or machine–human). The visual feedback informed the volunteer about the task performance.

slice as reference, in order to correct effects induced by the different acquisition time of each slice within the functional volume. Subsequently, all volumes were realigned to correct head motion using rigid body transformations. After discarding the four first slices allowing the scanner to reach equilibrium, the first volume of the first ER-fMRI session was taken as reference volume (i.e., this volume was originally the fifth volume). Unwrapping was performed by using the individually acquired fieldmaps, to correct for interaction between head movements and EPI distortions (Andersson, Hutton, Ashburner, Turner, & Friston, 2001) – weighted anatomical volume was co-registered to mean images created by the realignment procedure and was normalized to the MNI space using a trilinear interpolation. The anatomical normalization parameters were subsequently used for the normalization of functional volumes. Finally, each functional volume was smoothed by an 8-mm Full Width at Half Maximum (FWHM) Gaussian kernel to ameliorate differences in intersubject localization. Time series for each voxel were high-pass filtered (1/128 Hz cutoff) to remove low-frequency noise and signal drift.

2.5.2. Statistical analysis

Considering the type of competition (Human, Machine) and the congruence word – ink color of each stimulus (Congruent, Incongruent), we defined four experimental conditions: HI, HC, MI and MC. These conditions were modeled as four regressors and convolved with the canonical form of the hemodynamic response function (HRF). Moreover, movement parameters derived from realignment corrections (three translations and three rotations) were also taken into account in the design matrix, as additional factors.

We performed first a statistical analysis at individual level, and in this respect, the general linear model was used to generate the parameter estimates of activity at each voxel, for each condition, and each subject.

Secondly, we performed a random-effect group analysis of the contrast images derived from individual analyses (Friston et al., 1995). All linear contrasts of interest calculated for each subject were entered into one-sample t-tests. Clusters of activated voxels were then identified, by using an empirically defined threshold ($P < 0.001$ uncorrected, $T > 3.95$, cluster size $\geqslant 5$ voxels). Specifically, the following contrasts have been calculated:

2.5.2.1. Main effects. *Main effect of Stroop*: The contrast [I(H + M) > C(H + M)] was calculated in order to identify the executive regions required by Stroop. The opposite contrast [C(H + M) vs. I(H + M)] was also calculated.

Main effect of competition: The contrast [H(I + C) > M(I + C)] was calculated in order to explore the cerebral regions required by the social (human–human) competition. The opposite contrast [M(I + C) > H(I + C)] was calculated to identify regions activated by the machine–human competition.

2.5.2.2. Interaction. To identify executive regions (during Stroop execution) recruited specifically in social (human–human) competition, we calculated the interaction [H(I > C)] > [M(I > C)]. The opposite contrast [M(I > C)] vs. [H(I > C)] revealed the executive regions modulated by human–machine interaction.

The anatomical location of the activated regions was determined with Talairach and Tournoux (1988) atlas and the AAL correspondences (Tzourio-Mazoyer et al., 2002). An in-house modification of the "spm_list.m" file including non-linear transformation of MNI to Talairach (http://imaging.mrccbu.cam.ac.uk/imaging/MniTalairach) allowed visualization of both MNI and Talairach coordinates of SPM results.

3. Results

3.1. Behavioral results

Behavioral data from one subject was lost due to technical problems. We finally took into account 13 subjects for performing this analysis. We checked first that Correct Responses Rates (% CR) for the main condition (Incongruent vs. Congruent) were above the chance level. The results are reported in Table 1. Response accuracy did not differ according to opponent or according to task condition ($p > .05$). Then, the Reaction Times (RTs) for correct responses were collapsed over the four experimental conditions and submitted to a repeated-measure analysis of variance (ANOVA) with Type of competition (Human, Machine) and Word congruence (Congruent – Control condition, Incongruent – Stroop condition) as within-subject factors. The analysis revealed significant congruence effect (Incongruence: 795.47 ms, Congruence: 682.24 ms; $F_{1,12} = 32.08$, $P < 0.0005$; Fig. 3), suggesting a significant interference Stroop (conflict resolution) effect. We did not obtain a significant effect of the type of interaction (Human: 751.65 ms, Machine: 726.06 ms; $F < 1$) meaning that both types of competition were equivalent in terms of difficulty. No statistical interaction was

Table 1
Resumes the mean correct responses rates (% CR) for Control (Congruent stimuli) and Stroop (Incongruent stimuli) conditions ($n = 13$) for each Type of interaction (human, H or machine, M) during the Stroop interference task. The p values corresponding to t-test against the chance level are reported.

Word congruence	Congruent		Incongruent	
Type of interaction	H	M	H	M
n Participants	13	13	13	13
Mean correct response (%)	85.1%	85.3%	78.2%	80.4%
Standard error (%)	6%	9.3%	9.1%	11%
t-Value (*against chance level*)	21.13	13.7	11.11	9.98
p Value	<0.0005	<0.0005	<0.0005	<0.0005

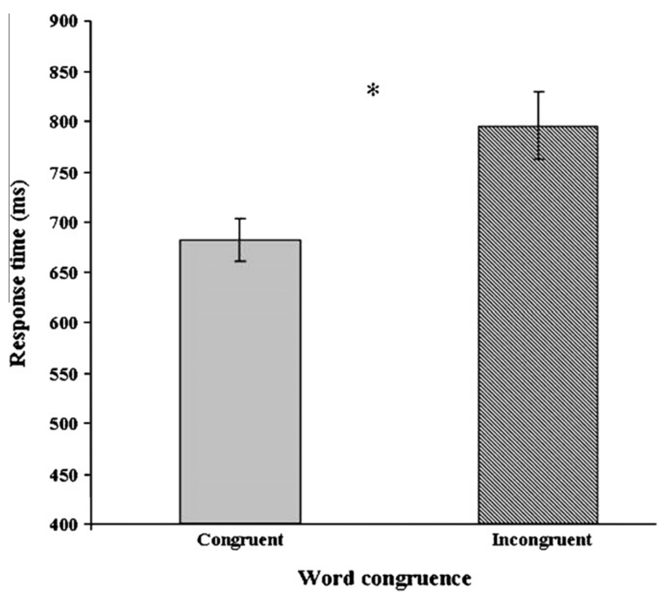

Fig. 3. Illustrates word congruence effect in terms of mean reaction time (mRT, ms) of $n = 13$ subjects. The subjects provided significantly faster responses for Congruent than for Incongruent condition. The gray bar indicates the Congruent condition, and the crossed bar indicates the Incongruent condition.

obtained between Congruence and Type of competition ($F < 1$). Thus, we considered that interference effect was similar for two types of competitive interaction, human or machine. During the post-experiment debriefing phase, all participants confirmed their high motivation to perform the task. They felt equally engaged and motivated to perform the task, whatever the condition (H or M). However, they reported more difficulties to respond to Incongruent than to Congruent items. All participants confirmed that during H condition, they tried to "guess" the "opponent's" state of mind and they needed to understand which was the strategy of the adversary and detect possible switches from one strategy to another. During M condition, the participants rather focused on their own responses instead of the computer's behavior as they were told that the computer always follows a fixed strategy. Thus, the participants thought the computer would behave the same regardless of what they did, so they chose to ignore its behavior. They felt motivated and incited to win by the feedback emoticons.

3.2. Functional MRI results

3.2.1. Main effect of Stroop

The cerebral regions revealed by the contrast Incongruent (Stroop condition) vs. Congruent (control condition), independently of the type of competition, are summarized in Table 2 and showed in Fig. 4 Panels A and B. The activated regions provided by the contrast [I(H + M) vs. C(H + M)] constitute the "Stroop inhibition network" and were represented by the right anterior cingulate (BA 24, 32), right superior frontal (BA 10), bilateral middle frontal (BA 6), right inferior frontal (BA 44, 45), right insula, right inferior parietal (BA 39, 40), left precuneus (BA 7), bilateral cuneus (BA 19) and right fusiform gyrus (BA 37). The opposite contrast [C(H + M) vs. I(H + M)] did not reveal suprathreshold voxels.

3.2.2. Main effect of competition

Human–human competition recruited several regions mentioned in Table 3. They were the left prefrontal (BA 10), right inferior frontal (BA 45), left anterior cingulate (BA 32), bilateral superior temporal (BA 38, 41, 22), right hippocampus, bilateral fusiform (BA 37) and bilateral cuneus and precuneus (BA 5, 7). These regions are illustrated in Fig. 4 Panel A and C. No suprathreshold voxels were detected by the opposite contrast, suggesting that there were no regions that were significantly more active in the machine condition than the human condition (see Table 4).

3.2.3. Interactions

The focus of the statistical interaction was on areas of activity during the Stroop interference condition (Incongruent) that were more active when engaged in competition with another human than with a machine. They were identified by the contrast [H(I > C)] > [M(I > C)] and were located bilaterally but predominant to the right. The activation was represented by the left superior (BA 10) and right middle frontal (BA 46), frontal, right anterior cingulate (BA 32), right insula, right fusiform, right superior (BA 20) and inferior temporal (BA 37). All these regions are illustrated in Fig. 5. The contrast [M(I > C)] > [H(I > C)] did not reveal suprathreshold voxels.

4. Discussion

Various social interactions involve executive mental processes such as decision making, the mental flexibility, the suppression of irrelevant responses, but also the ability to make inferences about the other person's mental state, cognitive function known as Theory of Mind (ToM) (Premack & Woodruff, 1978). It has been shown that this function is crucial for between-humans interactions (Adolphs, 2001). A specific type of social interaction, the competition, requires not only the permanent optimization of performances by a rapid mental shifting and suppression of irrelevant responses, in order to win the competition, but also the capacity to understand and predict the adversary intentions. There is a permanent interaction and interdependence between cognitive executive control operations on one side and ToM on the other, suggesting common regions for both executive functions and ToM, as mentioned by other studies (Bull, Phillips, & Conway, 2008; Carlson, Moses, et al., 2004; Langdon, Coltheart, Ward, & Catts, 2001). Indeed, among executive functions, the inhibition (suppression) of the tendency of pre-potent response is required for both normal "mentalization" and cognitive inhibition during a Stroop test. The Stroop test assesses the inhibition of automatic pre-potent processes such as reading in order to follow a voluntary instruction. Based on the assumptions that executive functions and ToM are intimately related (Champagne-Lavau & Joanette, 2009), we consider that cognitive inhibition ability is related to the inhibition required for mentalization. This ability is necessary to suppress the spontaneous pre-potent *first-person perspective* (egocentric relation) and adopt a more appropriate *third-person perspective* (allocentric relation), essential for understanding the other's mind (Langdon & Coltheart, 2001; Langdon et al., 2001). As an executive function, the inhibition appears to be the most related to ToM abilities (Bull et al., 2008). Even if the neural

Table 2
Resumes the activated regions for Stroop interference (conflict resolution) in social competition, provided by the contrast [I(H + M) > C(H + M)] and the contrast [C(H + M) > I(H + M)]. The anatomical location, the number of voxels, the statistical values of the peak of activation and the Talairach coordinates (*x*, *y*, *z*) are mentioned for each region.

Contrast	Region	H	BA	*k*	*x*	*y*	*z*	*T*
I(H + M) > C(H + M)	*Frontal cortex*							
	Middle frontal	R	6	65	12	6	67	6.65
	Superior frontal	R	10	25	33	53	20	5.29
	Anterior cingulate	R	32	9	6	8	45	4.22
	Middle frontal	L	6	13	−39	−0	48	4.58
	Inferior frontal	R	45	7	48	18	6	4.21
	Anterior cingulate	R	32	12	15	30	18	4.02
	Insula	R	13	10	33	27	12	5.09
	Parietal cortex							
	Inferior parietal	R	40	7	36	−59	45	4.58
	Superior parietal	L	7	7	−27	−49	61	4.99
	Occipito-temporal cortex							
	Fusiform	R	37	526	45	−65	−11	5.60
	Cuneus/Precuneus	L	7/19	201	−12	−73	49	6.31
	Precuneus	L	7	14	−3	−53	51	5.11
	Cuneus	R	17	17	12	−96	8	4.66
C(H + M) > I(H + M)	*No suprathreshold voxels*							

Abbreviations: H = hemisphere; R = right hemisphere; L = left hemisphere; BA = Brodmann area; k = number of voxels/cluster; H = human–human interaction; M = machine–human interaction, I = Stroop (Incongruent stimuli) condition, C = control (Congruent stimuli) condition.

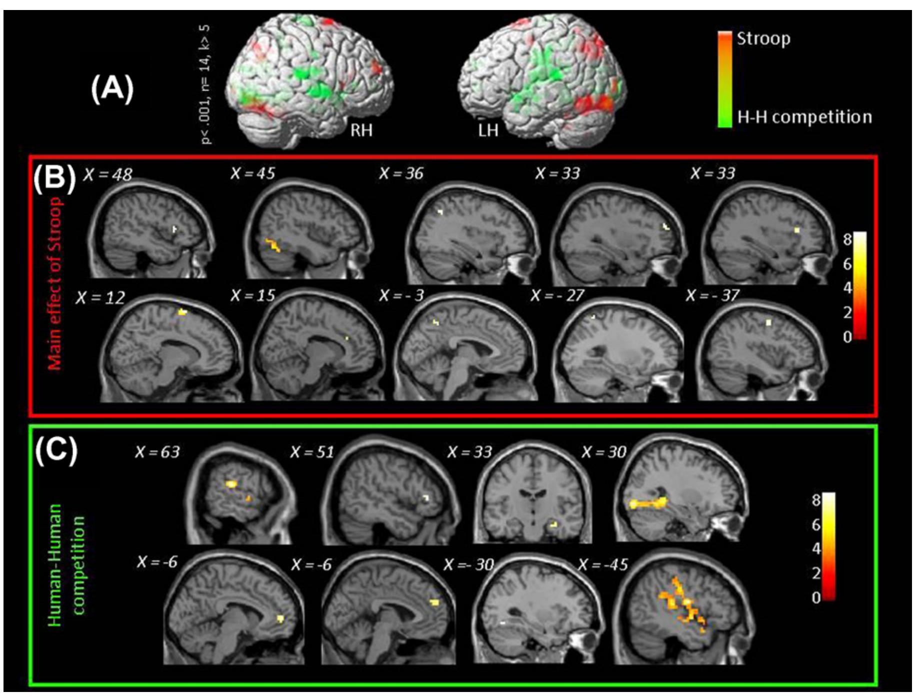

Fig. 4. Panel A shows the cerebral regions (in red) activated during Stroop provided by the contrast [I(H + M) > C(H + M)] and the cerebral regions (in green) activated during human–human competition (in green) provided by the contrast [H(I + C) > M(I + C)]. The activation is projected onto 3D-anatomical templates in lateral view. Panel B shows the same Stroop regions illustrated in red in the Panel A, but which are projected onto 2D anatomical slices in saggital view. Panel C shows the same human–human competition regions illustrated in green in the Panel A, but projected onto 2D anatomical saggital slices. *Abbreviations*: RH = right hemisphere; LH = left hemisphere; H–H = human–human competition. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

substrates of executive functions and ToM are not strictly identical (Pickup, 2008), some overlapping of regions cannot be excluded [(i.e., the medial prefrontal cortex is involved in self-related and self-regulation/monitoring processes required by both Stroop inhibition and ToM (Abu-Akel, 2003; Carter, MacDonald, Ross, & Stenger, 2001; Stuss, Gallup, & Alexander, 2001); the precuneus is required not only by attention but also by a specific ToM component, the perspective-taking (Ruby & Decety, 2001)]. Therefore, based on these arguments and previous studies (Carlson et al., 2004), we may consider that several inhibition regions support inhibitory processes for both executive functions and ToM.

In the present fMRI study performed in healthy subjects, we asked participants to perform a classical color-naming Stroop interference test, modified by inducing a virtual situation of competition. Participants were instructed to play to win either against a human or a machine adversary partner, and the participant instructions reinforced ToM involvement, as they had to be aware of the opponent's play strategy/intentions. By using this original

Table 3
Resumes the activated regions resulted from the main effect of human–human competition, provided by the contrast [H(I + C) > M(I + C)]. The machine–human competition explored with the contrast [M(I + C) > H(I + C)] did not reveal significant activation. The anatomical location, the number of voxels, the statistical values of the peak of activation and the Talairach coordinates (*x*, *y*, *z*) are mentioned for each region.

Contrast	Region	H	BA	*k*	*x*	*y*	*z*	*T*
H(I + C) > M(I + C)	*Frontal cortex*							
	Superior frontal	L	10	18	−6	51	4	7.57
	Superior frontal	L	10	19	−6	51	28	5.74
	Frontal inferior	R	45	14	51	33	4	4.77
	Anterior cingulate	L	32	10	−6	51	8	6.54
	Temporal cortex							
	Superior and anterior temporal gyrus	L	22/38	52	−45	9	18	5.05
	Superior temporal	R	22/41	297	63	−27	18	8.47
	Hippocampus	R	–	26	33	−15	−21	6.15
	Occipito-temporal cortex							
	Fusiform	R	23/37	93	30	−84	−7	8.27
	Fusiform	L	37	32	−30	−69	−10	4.78
	Cuneus/precuneus	R/L	5/7	258	−27	−42	−7	6.56
M(I + C) > H(I + C)	*No suprathreshold voxels*							

Abbreviations: H = hemisphere; R = right hemisphere; L = left hemisphere; BA = Brodmann area; k = number of voxels/cluster; H = human–human competition; M = machine–human competition, I = Stroop (Incongruent stimuli) condition, C = control (Congruent stimuli) condition.

Table 4
Resumes the activated regions provided by human–human competition in situation of Stroop, provided by the interaction [H(I > C)] vs. [M(I > C)]. The interaction [M(I > C)] vs. [H(I > C)] did not reveal significant activation. The anatomical location, the number of voxels, the statistical values of the peak of activation and the Talairach coordinates (*x*, *y*, *z*) are mentioned for each region.

Contrast	Region	H	BA	*k*	*x*	*y*	*z*	*T*
[H(I > C)] > [M(I > C)]	*Frontal cortex*							
	Superior frontal	L	6	43	54	−9	52	6.36
	Middle frontal	R	46	10	27	57	24	6.97
	Anterior cingulate	R	32	5	12	30	24	5.86
	Insula	R	13	30	36	18	−4	6.88
	Temporal cortex							
	Inferior temporal	L	37	72	−54	−57	−14	6.33
	Superior temporal	R	20	32	66	−48	−6	5.19
	Occipito-temporal cortex							
	Fusiform	R	37	373	30	−42	−18	6.96
[M(I > C)] > [H(I > C)]	*No suprathreshold voxels*							

Abbreviations: H = hemisphere; R = right hemisphere; L = left hemisphere; BA = Brodmann area; k = number of voxels/cluster; H = human–human competition; M = machine–human competition, I = Stroop (Incongruent stimuli) condition, C = control (Congruent stimuli) condition.

experimental paradigm, we focused on two aspects: the Stroop interference effect (conflict resolution, i.e., Incongruent vs. Congruent) in competition and the ToM (Human vs. Machine).

4.1. Stroop regions

Our results showed that Stroop interference (conflict resolution) in a situation of competition activated the anterior cingulate gyrus (BA 24/32), superior (BA 10), middle (BA 6) and inferior (BA 44, 45) frontal gyri, the insula, the inferior parietal lobule (BA 39, 40), the precuneus (BA 7), cuneus (BA 19) and the fusiform gyrus (BA 37). These results are in agreement with other studies reporting results for the cognitive Stroop test (Roberts & Hall, 2008). The anterior cingulate gyrus (BA 24, 32) can be related to conflict monitoring (Botvinick, Braver, Barch, Carter, & Cohen, 2001; Botvinick, Nystrom, Fissell, Carter, & Cohen, 1999; Carter et al., 1999, 2000; Cohen et al., 2002; Kerns et al., 2004), error detection (see review by Bush, Luu, and Posner (2000)) and response selection (Erickson et al., 2004; Milham, Banich, & Barad, 2003; Milham, Banich, Claus, & Cohen, 2003; Paus, 2001). The activation of superior (BA 6), medial (BA 10) middle (BA 46) frontal gyri and insula could be related to interference processes (Harrison et al., 2005). Overall, the interference-related activity (Incongruent – Stroop vs. Congruent – Control condition) reflects the executive inhibition control network ("Stroop inhibition network"). We did not obtain the activation of the premotor cortex, as reported by previous cognitive Stroop studies (Melcher & Gruber, 2009). The premotor cortex can be related to the participants effort to overcome the interference and to ensure an adequate task performance. In our study, the performance (response accuracy) of Congruent and Incongruent conditions was similar, meaning that the effort need to perform the task was relatively the same for both conditions and it may explain the lack of a premotor activation.

Overall, the regions activated by the executive functions reported in our study can be grouped in two systems (a) anterior including the dorsolateral prefrontal cortex and anterior cingulate gyrus, particularly involved in conflict resolution (processing relevant vs. irrelevant information) and (b) posterior system including the inferior parietal regions and the precuneus, particularly related to selective attention processes (Banich et al., 2000; Casey et al., 2000; Roberts & Hall, 2008) in competitive interaction. These results are in agreement with those reported by Decety et al. (2004). Additionally, toward the Decety et al. results, we reported the activation of temporo-occipital regions such as right fusiform gyrus (BA 37) and right cuneus (BA 17/19) probably due to differences of the experimental paradigms used in these two studies.

The right inferior parietal lobule (BA 40) is specifically related to the identification of action and its visual consequences (Farrer et al., 2003) as well as in error detection (Rubia, Smith, Brammer, & Taylor, 2003). The right inferior frontal gyrus (BA 45) is required

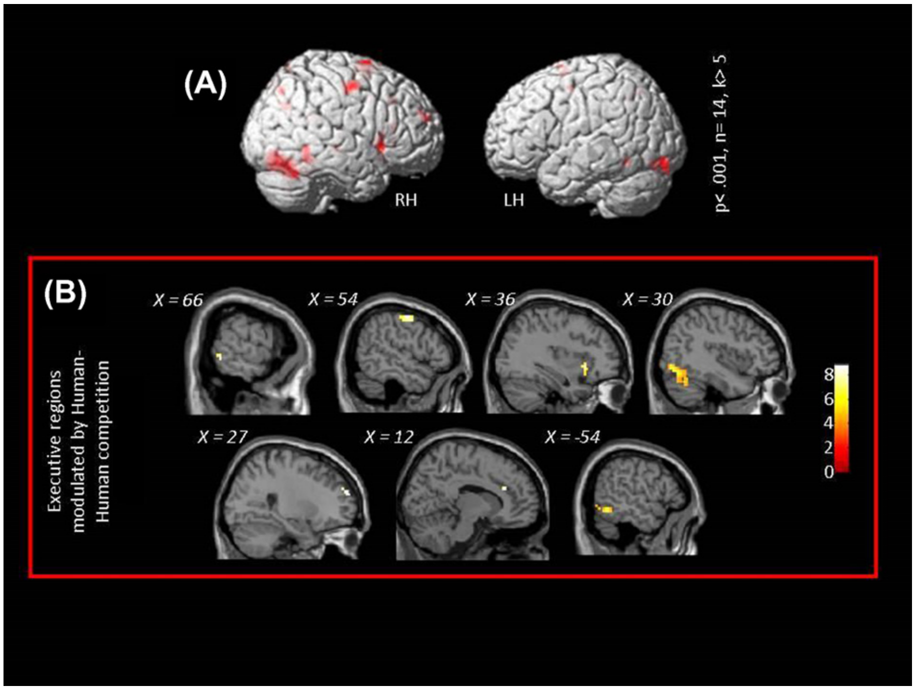

Fig. 5. Illustrates the executive regions modulated by human–human competition (considered ToM-like regions) as revealed by the interaction [H(I > C)] > [M(I > C)] and projected either onto 3D-anatomical template in lateral view (Panel A) or onto 2D-anatomical saggital slices (Panel B). *Abbreviations:* RH = right hemisphere; LH = left hemisphere.

during successful inhibitory control (Chambers et al., 2007; Langenecker et al., 2004; Rubia et al., 2003). The insula may be related to executive control (Melcher & Gruber, 2009; Roberts & Hall, 2008) and emotional processing (Levens & Phelps, 2010).

4.2. Competition regions

Social interaction (human–human) of competition activated the left prefrontal (BA 10), right inferior frontal (BA 45), left anterior cingulate (BA 32), bilateral superior temporal (BA 38, 41, 22), right middle temporal (BA 21), right hippocampus, bilateral fusiform (BA 37) and bilateral precuneus (BA 5, 7). Their activation reflects various processes occurring during social competition, and their role is detailed in the following paragraphs.

The right inferior frontal activation may be related to reward-expectancy required in social competition as the participant played in order to win. The role of this region during competition was already shown especially when the subject's behavior potentially leads to a profit (Halko et al., 2009). Additionally, the activation of the inferior frontal gyrus might reflect the participant's effort to observe the competition (observation of actions) as well as the pursuit of goals while playing against a "human" opponent (Iacoboni et al., 1999; Johnson-Frey et al., 2003).

The medial prefrontal cortex, the left anterior cingulate and the superior temporal regions are considered "ToM regions" (Gallagher & Frith, 2003). The anterior cingulate gyrus, especially the BA 32, seems particularly involved in understanding the opponent intentions; in this framework, this region would operate in coordination with the left temporo-parietal cortex (Amodio & Frith, 2006; Ciaramidaro et al., 2007). Ciaramidaro et al. (2007) showed that precuneus is related to both types of intentions: private and social. Moreover, the precuneus is involved in processing of "self" and particularly of self-related evaluation and distinction from others (Legrand & Ruby, 2009). Additionally, this region is involved in the perspective-taking required by the social interaction and ToM processing (first-person and third-person perspectives; both of them are necessary during competition) (Ruby & Decety, 2001).

Compared to human–machine, human–human competition potentially required more cognitive resources, such as memory and reasoning, reflected by the activation of hippocampus and dorsolateral prefrontal cortex (BA10). Indeed, participants were aware that the "human" opponent might change the strategy, and this awareness required a supplementary cognitive effort. This supplementary effort may explain the activation (a) of precuneus reflecting higher attentional demands (Banich et al., 2000) and (b) of inferior frontal gyrus reflecting higher motor inhibition (Rubia et al., 2003). The activation of fusiform gyrus is in line with its implication in social interactions (Iacoboni et al., 2004).

4.3. Stroop regions modulated by human–human interaction

They were the left superior (BA 10) and right middle (BA 46) frontal gyri, right anterior cingulate (BA 32), right insula, right fusiform, right superior (BA 20) and left inferior temporal (BA 37). These regions suggest that several executive areas are specifically modulated during human–human interaction, thus also involved in ToM, which was induced by the task.

The right hemisphere predominance during human–human social competition regions is supported by earlier neuropsychological observations in patients with right frontal, temporo-parietal and basal ganglia lesions which induced specific deficit in attributing intentional states and particularly, those involving second-order mental states such as the attribution of a mental state related to the representation of another person's mental state (Champagne-Lavau & Joanette, 2009; Griffin et al., 2006). Thereafter, we comment on the possible role of regions modulated by human–human competition.

Right anterior insula belongs to the social cognitive network (Rilling, Dagenais, Goldsmith, Glenn, & Pagnoni, 2008) and would be involved in the agency and attribution of actions to self (Farrer & Frith, 2002; Farrer et al., 2003). The activity of this region is modulated by the social context. This region may be also related to other cognitive processes such as emotional and arousal processing (Craig, 2009) particularly relevant in between-humans competition, unreciprocated cooperation (Rilling, Goldsmith, et al., 2008), decision making under competition (Halko et al., 2009) and decision associated with risk (Xue, Lu, Levin, & Bechara, 2010).

Right fusiform gyrus has been classically reported for face discrimination, face identification processing (Grill-Spector, Knouf, & Kanwisher, 2004; Haxby et al., 1994) and eye-gaze perception (Haxby, Hoffman, & Gobbini, 2000). More recent studies also suggest the implication of this region in social interactions (Iacoboni et al., 2004). In our study, the task does not include any explicit human face processing. Moreover, the picture of the rival is shown only once at the beginning of each block and repeated only in a peripheral corner of the feedback screen; a supplementary argument for this conjecture is that the peak of our activation does not match with the classical face area of the fusiform gyrus (Tsao & Livingstone, 2008). Thus, a mental imagery of the adversary face could have occurred, mainly during human interaction condition. The mental representation of the human face may be crucial for understanding the other's intentions in social context. Nevertheless, as this cue with a social valence has been presented only in the H condition, this might limit our interpretation of this region's activation.

Right anterior cingulate gyrus would be related to empathic interaction (Schulte-Ruther, Markowitsch, Fink, & Piefke, 2007) and to monitoring of actions in conflict situations (Rushworth, Kennerley, & Walton, 2005). With respect to our paradigm, the competition interaction requires permanent detection and processing of errors followed by subsequent adaptation of behavior in order to optimize performance. All these processes may partially depend on the anterior cingulate gyrus (de Bruijn, de Lange, von Cramon, & Ullsperger, 2009; Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004 Ridderinkhof, van den Wildenberg, Segalowitz, & Carter, 2004). Furthermore, between-humans competitive interaction needs the identification of self, which may elicit the activation of the anterior cingulate gyrus (Newman-Norlund, Ganesh, van Schie, De Bruijn, & Bekkering, 2009). The anterior cingulate activation may also be related to the social emotions potentially induced by the competition and comparison of the outcome, mainly envy when the adversary was winning (Dvash, Gilam, Ben-Ze'ev, Hendler, & Shamay-Tsoory, 2010; Takahashi et al., 2009)

The dorsolateral prefrontal cortex (right middle frontal and left superior frontal) activation may be related to ToM as suggested by previous neuroimaging and lesion studies (Kobayashi, Glover, & Temple, 2007). The dysfunction of these regions may lead to difficulties in the use of social cues in order to make interpersonal judgments (Mah, Arnold, & Grafman, 2004) and difficulties in social perception (Geraci, Surian, Ferraro, & Cantagallo, 2010), both required by the competition interaction induced with our paradigm.

The human–human competition modulates the activity of several regions situated bilaterally but predominant to the right. The permanent flexibility and dynamic of social interactions need permanent modulation of the activity of regions composing the executive network. ToM may be required to modulate and adjust the activity of executive regions; the involvement may be specifically important when social interactions take place under the situation of competition. The present study supports the suggested link between executive functioning and theory of mind in social interaction, as highlighted by developmental studies (Carlson, 2009; Sabbagh et al., 2006).

4.4. Limitations of the study

Despite these encouraging results, we are aware of several limitations of this study. First of all, the use of this task in order to explore ToM function should be validated by future experiments. Indeed, performing a Stroop test does not classically require ToM abilities. Moreover, our paradigm did not allow direct objective measure of ToM engagement during the task. Nevertheless, the activation obtained when participants played against the "human" competitor indirectly suggests ToM involvement and confirmed the essential role of the context (instructions and social "scenario") in the social cognitive function, which is ToM. Despite relatively short duration of stimuli presentation imposed by Stroop constraints, all participants declared that during task they tried to "guess" and "find out" the opponent's playing style and strategies.

However, despite the limits, our paradigm is original because it targets the reciprocal interactions between executive functions and "on-line," not retrospective, ToM in social interaction. These interactions may belong to the mechanisms that drive the adaptive behavior in real social life. This aspect has not been considered so far by other studies. Furthermore, the dual tasks classically used to assess alternatively either executive functions or ToM could be only an approximate approach as they do not assess these functions simultaneously (see Bull et al., 2008). Moreover, it may be possible that the difference H vs. M may also reflect higher attentional demands as in human competition the participants had to cope with a double task (attention to task *per se* and attention to human competitor). Future experiments are planned in order to affine the paradigm and make sure that what we depict in terms of activation is clearly related to ToM.

5. Conclusions

The results of this fMRI study show that the activity of several executive network regions revealed by Stroop are modulated by the social (human–human) interactions in a situation of competition. As this situation requires ToM, the modulated regions revealed by this study may be considered as essential for both ToM and executive functions. Supplementary evidence and adjustments of the paradigm are needed in order to confirm these results. Subsequently, this paradigm may be a useful tool for studying cerebral networks involved in social adjustment of patients with psychiatric disorders, such as bipolar disorder and schizophrenia (Green, 2006; Tabares-Seisdedos et al., 2008).

References

Abu-Akel, A. (2003). A neurobiological mapping of theory of mind. *Brain Research. Brain Research Reviews, 43*(1), 29–40.

Adolphs, R. (2001). The neurobiology of social cognition. *Current Opinion in Neurobiology, 11*, 231–239.

Amodio, D. M., & Frith, C. D. (2006). Meeting of minds: The medial frontal cortex and social cognition. *Nature Reviews Neuroscience, 7*, 268–277.

Andersson, J., Hutton, C., Ashburner, J., Turner, R., & Friston, K. (2001). Modeling geometric deformations in EPI time series. *Neuroimage, 13*, 903–919.

Assaf, M., Kahn, I., Pearlson, G. D., Johnson, M. R., Yeshurun, Y., Calhoun, V. D., et al. (2009). Brain activity dissociates mentalization from motivation during an interpersonal competitive game. *Brain Imaging and Behavior, 3*(1), 24–37.

Babiloni, F., Astolfi, L., Cincotti, F., Mattia, D., Tocci, A., Tarantino, A., et al. (2007). Cortical activity and connectivity of human brain during the prisoner's dilemma: An EEG hyperscanning study. In *Conference proceedings, annual international conference of the IEEE Engineering in Medicine and Biology Society*, pp. 4953–4956.

Banich, M. T., Milham, M. P., Atchley, R., Cohen, N. J., Webb, A., Wszalek, T., et al. (2000). FMRI studies of Stroop tasks reveal unique roles of anterior and posterior brain systems in attentional selection. *Journal of Cognitive Neuroscience, 12*(6), 988–1000.

Baron-Cohen, S., Ring, H., Moriarty, J., Schmitz, B., Costa, D., & Ell, P. (1994). Recognition of mental state terms: Clinical findings in children with autism and a functional neuroimaging study of normal adults. *British Journal of Psychiatry, 165*, 640–649.

Baron-Cohen, S., Ring, H. A., Wheelwright, S., Bullmore, E. T., Brammer, M. J., Simmons, A., et al. (1999). Social intelligence in the normal and autistic brain: An fMRI study. *The European Journal of Neuroscience, 11*, 1891–1898.

Botvinick, M. M., Braver, T. S., Barch, D. M., Carter, C. S., & Cohen, J. D. (2001). Conflict monitoring and cognitive control. *Psychological Review, 108*, 624–652.

Botvinick, M., Nystrom, L. E., Fissell, K., Carter, C. S., & Cohen, J. D. (1999). Conflict monitoring versus selection-for-action in anterior cingulate cortex. *Nature, 402*, 179–181.

Bowles, S. (2006). Group competition, reproductive leveling, and the evolution of human altruism. *Science, 314*, 1569–1572.

Brunet, E., Sarfati, Y., Hardy-Bayle, M. C., & Decety, J. (2000). A PET investigation of the attribution of intentions with a nonverbal task. *Neuroimage, 11*, 157–166.

Bull, R., Phillips, L. H., & Conway, C. A. (2008). The role of control functions in mentalizing: Dual-task studies of theory of mind, executive function. *Cognition, 107*, 663–672.

Bush, G., Luu, P., & Posner, M. (2000). Cognitive and emotional influences in anterior cingulate cortex. *Trends in Cognitive Sciences, 4*, 215–222.

Carlson, S. M. (2009). Social origins of executive function development. *New Directions for Child and Adolescent Development, 2009*, 87–98.

Carlson, S. M., Mandell, D. J., & Williams, L. (2004). Executive function and theory of mind: Stability and prediction from ages 2 to 3. *Developmental Psychology, 40*, 1105–1122.

Carlson, S. M., Moses, L. J., & Claxton, L. J. (2004). Individual differences in executive functioning and theory of mind: An investigation of inhibitory control and planning ability. *Journal of Experimental Child Psychology, 87*, 299–319.

Carter, C. S., Botvinick, M. M., & Cohen, J. D. (1999). The contribution of the anterior cingulate cortex to executive processes in cognition. *Reviews in the Neurosciences, 10*, 49–57.

Carter, C. S., Macdonald, A. M., Botvinick, M., Ross, L. L., Stenger, V. A., Noll, D., et al. (2000). Parsing executive processes: Strategic vs. evaluative functions of the anterior cingulate cortex. *Proceedings of the National Academy of Sciences of USA, 97*, 1944–1948.

Carter, C. S., MacDonald, A. W., 3rd, Ross, L. L., & Stenger, V. A. (2001). Anterior cingulate cortex activity and impaired self-monitoring of performance in patients with schizophrenia: An event-related fMRI study. *American Journal of Psychiatry, 158*(9), 1423–1428.

Casey, B. J., Thomas, K. M., Welsh, T. F., Badgaiyan, R. D., Eccard, C. H., Jennings, J. R., et al. (2000). Dissociation of response conflict, attentional selection, and expectancy with functional magnetic resonance imaging. *Proceedings of the National Academy of Sciences of USA, 97*, 8728–8733.

Castelli, F., Happe, F., Frith, U., & Frith, C. (2000). Movement and mind: A functional imaging study of perception and interpretation of complex intentional movement patterns. *Neuroimage, 12*, 314–325.

Chambers, C. D., Bellgrove, M. A., Gould, I. C., English, T., Garavan, H., McNaught, E., et al. (2007). Dissociable mechanisms of cognitive control in prefrontal and premotor cortex. *Journal of Neurophysiology, 98*, 3638–3647.

Champagne-Lavau, M., & Joanette, Y. (2009). Pragmatics, theory of mind and executive functions after a right-hemisphere lesion: Different patterns of deficits. *Journal of Neurolinguistics, 22*, 413–426.

Charlton, R. A., Barrick, T. R., Markus, H. S., & Morris, R. G. (2009). Theory of mind associations with other cognitive functions and brain imaging in normal aging. *Psychology and Aging, 24*, 338–348.

Ciaramidaro, A., Adenzato, M., Enrici, I., Erk, S., Pia, L., Bara, B. G., et al. (2007). The intentional network: How the brain reads varieties of intentions. *Neuropsychologia, 45*(13), 3105–3113.

Cohen, L., Lehericy, S., Chochon, F., Lemer, C., Rivaud, S., & Dehaene, S. (2002). Language-specific tuning of visual cortex? Functional properties of the Visual Word Form Area. *Brain, 125*, 1054–1069.

Craig, A. D. (2009). How do you feel – now? The anterior insula and human awareness. *Nature Reviews: Neuroscience, 10*, 59–70.

de Bruijn, E. R., de Lange, F. P., von Cramon, D. Y., & Ullsperger, M. (2009). When errors are rewarding. *The Journal of Neuroscience, 29*, 12183–12186.

Decety, J., Jackson, P. L., Sommerville, J. A., Chaminade, T., & Meltzoff, A. N. (2004). The neural bases of cooperation and competition: An fMRI investigation. *Neuroimage, 23*, 744–751.

Dvash, J., Gilam, G., Ben-Ze'ev, A., Hendler, T., & Shamay-Tsoory, S. G. (2010). The envious brain: The neural basis of social comparison. *Human Brain Mapping, 31*(11), 1741–1750.

Erickson, K., Milham, M., Colcombe, S., Kramer, A., Banich, M., Webb, A., et al. (2004). Behavioral conflict, anterior cingulate cortex, and experiment duration: Implications of diverging data. *Human Brain Mapping, 21*, 98–107.

Farrer, C., Franck, N., Georgieff, N., Frith, C. D., Decety, J., & Jeannerod, M. (2003). Modulating the experience of agency: A positron emission tomography study. *Neuroimage, 18*, 324–333.

Farrer, C., & Frith, C. D. (2002). Experiencing oneself vs another person as being the cause of an action: The neural correlates of the experience of agency. *Neuroimage, 15*, 596–603.

Fliessbach, K., Weber, B., Trautner, P., Dohmen, T., Sunde, U., Elger, C. E., et al. (2007). Social comparison affects reward-related brain activity in the human ventral striatum. *Science, 318*(5), 1305–1308.

Friston, K., Holmes, A., Worsley, K., Poline, J., Frith, C., & Frackowiak, R. (1995). Statistical parametric maps in functional imaging: A general linear approach. *Human Brain Mapping, 2*, 189–210.

Gallagher, H. L., & Frith, C. D. (2003). Functional imaging of 'theory of mind'. *Trends in Cognitive Sciences, 7*, 77–83.

Gallagher, H. L., Happe, F., Brunswick, N., Fletcher, P. C., Frith, U., & Frith, C. D. (2000). Reading the mind in cartoons and stories: An fMRI study of 'theory of mind' in verbal and nonverbal tasks. *Neuropsychologia, 38*, 11–21.

Gallagher, H. L., Jack, A. I., Roepstorff, A., & Frith, C. D. (2002). Imaging the intentional stance in a competitive game. *Neuroimage, 16*, 814–821.

Geraci, A., Surian, L., Ferraro, M., & Cantagallo, A. (2010). Theory of Mind in patients with ventromedial or dorsolateral prefrontal lesions following traumatic brain injury. *Brain Injury, 24*(7–8), 978–987.

Goel, V., Grafman, J., Sadato, N., & Hallett, M. (1995). Modeling other minds. *NeuroReport, 6*, 1741–1746.

Goukon, A., Ohuchi, T., Kikuchi, T., Hirano, M., Noguchi, K., & Hosokawa, T. (2006). Developmental order driving the relationship between executive functions and theory of mind: A case study. *Psychological Reports, 98*, 662–670.

Green, M. F. (2006). Cognitive impairment and functional outcome in schizophrenia and bipolar disorder. *Journal of Clinical Psychiatry, 67*(Suppl. 9), 3–8. discussion 36–42.

Griffin, R., Friedman, O., Ween, J., Winner, E., Happe, F., & Brownell, H. (2006). Theory of mind and the right cerebral hemisphere: Refining the scope of impairment. *Laterality, 11*, 195–225.

Grill-Spector, K., Knouf, N., & Kanwisher, N. (2004). The fusiform face area subserves face perception, not generic within-category identification. *Nature Neuroscience, 7*, 555–562.

Halko, M. L., Hlushchuk, Y., Hari, R., & Schurmann, M. (2009). Competing with peers: Mentalizing-related brain activity reflects what is at stake. *Neuroimage, 46*, 542–548.

Hampton, A. N., Bossaerts, P., & O'Doherty, J. P. (2008). Neural correlates of mentalizing-related computations during strategic interactions in humans. *Proceedings of the National Academy of Sciences of USA, 105*(18), 6741–6746.

Hari, R., & Kujala, M. V. (2009). Brain basis of human social interaction: From concepts to brain imaging. *Physiological Reviews, 89*(2), 453–479.

Harrison, B. J., Shaw, M., Yucel, M., Purcell, R., Brewer, W. J., Strother, S. C., et al. (2005). Functional connectivity during Stroop task performance. *Neuroimage, 24*, 181–191.

Hauert, C., & Stenull, O. (2002). Simple adaptive strategy wins the prisoner's dilemma. *Journal of Theoretical Biology, 218*, 261–272.

Haxby, J. V., Hoffman, E. A., & Gobbini, M. I. (2000). The distributed human neural system for face perception. *Trends in Cognitive Sciences, 4*, 223–233.

Haxby, J. V., Horwitz, B., Ungerleider, L. G., Maisog, J. M., Pietrini, P., & Grady, C. L. (1994). The functional organization of human extrastriate cortex: A PET-rCBF study of selective attention to faces and locations. *The Journal of Neuroscience, 14*, 6336–6353.

Hughes, C., & Ensor, R. (2005). Executive function and theory of mind in 2 year olds: A family affair? *Developmental Neuropsychology, 28*, 645–668.

Iacoboni, M., Lieberman, M. D., Knowlton, B. J., Molnar-Szakacs, I., Moritz, M., Throop, C. J., et al. (2004). Watching social interactions produces dorsomedial prefrontal and medial parietal BOLD fMRI signal increases compared to a resting baseline. *NeuroImage, 21*, 1167–1173.

Iacoboni, M., Woods, R. P., Brass, M., Bekkering, H., Mazziotta, J. C., & Rizzolatti, G. (1999). Cortical mechanisms of human imitation. *Science, 286*, 2526–2528.

Johnson-Frey, S. H., Maloof, F. R., Newman-Norlund, R., Farrer, C., Inati, S., & Grafton, S. T. (2003). Actions or hand-object interactions? Human inferior frontal cortex and action observation. *Neuron, 39*, 1053–1058.

Kerns, J., Cohen, J., MacDonald, A., III, Cho, R., Stenger, V., & Carter, C. (2004). Anterior cingulate conflict monitoring and adjustments in control. *Science, 303*, 1023.

Kiesler, S., Sproull, L., & Waters, K. (1996). A prisoner's dilemma experiment on cooperation with people and human-like computers. *Journal of Personality and Social Psychology, 70*.

Kobayashi, C., Glover, G. H., & Temple, E. (2007). Children's and adults' neural bases of verbal and nonverbal 'Theory of Mind'. *Neuropsychologia, 45*(7), 1522–1532.

Langdon, R., & Coltheart, M. (2001). Visual perspective-taking and schizotypy: Évidence for a simulation-based account of mentalizing in normal adults. *Cognition, 82*, 1–26.

Langdon, R., Coltheart, M., Ward, P., & Catts, S. (2001). Mentalising, executive planning and disengagement in schizophrenia. *Cognitive Neuropsychiatry, 6*, 81–108.

Langenecker, S. A., Nielson, K. A., & Rao, S. M. (2004). FMRI of healthy older adults during Stroop interference. *Neuroimage, 21*, 192–200.

Legrand, D., & Ruby, P. (2009). What is self-specific? Theoretical investigation and critical review of neuroimaging results. *Psychological Review, 116*, 252–282.

Levens, S. M., & Phelps, E. A. (2010). Insula and orbital frontal cortex activity underlying emotion interference resolution in working memory. *Journal of Cognitive Neuroscience*. epub.

Mah, L., Arnold, M. C., & Grafman, J. (2004). Impairment of social perception associated with lesions of the prefrontal cortex. *American Journal of Psychiatry, 161*(7), 1247–1255.

Maylor, E. A., Moulson, J. M., Muncer, A. M., & Taylor, L. A. (2002). Does performance on theory of mind tasks decline in old age? *British Journal of Psychology, 93*, 465–485.

McCabe, K., Houser, D., Ryan, L., Smith, V., & Trouard, T. (2001). A functional imaging study of cooperation in two-person reciprocal exchange. *Proceedings of the National Academy of Sciences of USA, 98*, 11832–11835.

Mead, L. A., Mayer, A. R., Bobholz, J. A., Woodley, S. J., Cunningham, J. M., Hammeke, T. A., et al. (2002). Neural basis of the Stroop interference task: Response competition or selective attention? *Journal of the International Neuropsychological Society, 8*, 735–742.

Melcher, T., & Gruber, O. (2009). Decomposing interference during Stroop performance into different conflict factors: An event-related fMRI study. *Cortex, 45*, 189–200.

Milham, M., Banich, M., & Barad, V. (2003). Competition for priority in processing increases prefrontal cortexís involvement in top-down control: An event-related fMRI study of the Stroop task. *Cognitive Brain Research, 17*, 212–222.

Milham, M., Banich, M., Claus, E., & Cohen, N. (2003). Practice-related effects demonstrate complementary roles of anterior cingulate and prefrontal cortices in attentional control. *Neuroimage, 18*, 483–493.

Newman-Norlund, R. D., Ganesh, S., van Schie, H. T., De Bruijn, E. R., & Bekkering, H. (2009). Self-identification and empathy modulate error-related brain activity during the observation of penalty shots between friend and foe. *Social Cognitive and Affective Neuroscience, 4*, 10–22.

Nowak, M. A. (2006). Five rules for the evolution of cooperation. *Science, 314*, 1560–1563.

Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia, 9*, 97–113.

Paus, T. (2001). Primate anterior cingulate cortex: Where motor control, drive and cognition interface. *Nature Reviews Neuroscience, 2*, 417–424.

Perner, J., Lang, B., & Kloo, D. (2002). Theory of mind and self-control: More than a common problem of inhibition. *Child Development, 73*, 752–767.

Pickup, G. J. (2008). Relationship between Theory of Mind and executive function in schizophrenia: A systematic review. *Psychopathology, 41*(4), 206–213.

Premack, D., & Woodruff, G. (1978). Chimpanzee problem-solving: A test for comprehension. *Science, 202*, 532–535.

Puurtinen, M., & Mappes, T. (2009). Between-group competition and human cooperation. *Proceedings. Biological Sciences/ The Royal Society, 276*, 355–360.

Rasmussen, C., Wyper, K., & Talwar, V. (2009). The relation between theory of mind and executive functions in children with fetal alcohol spectrum disorders. *Canadian Journal of Clinical Pharmacology, 16*, 370–380.

Ridderinkhof, K. R., Ullsperger, M., Crone, E. A., & Nieuwenhuis, S. (2004). The role of the medial frontal cortex in cognitive control. *Science, 306*, 443–447.

Ridderinkhof, K. R., van den Wildenberg, W. P., Segalowitz, S. J., & Carter, C. S. (2004). Neurocognitive mechanisms of cognitive control: The role of prefrontal cortex in action selection, response inhibition, performance monitoring, and reward-based learning. *Brain and Cognition, 56*, 129–140.

Rilling, J. K., Dagenais, J. E., Goldsmith, D. R., Glenn, A. L., & Pagnoni, G. (2008a). Social cognitive neural networks during in-group and out-group interactions. *Neuroimage, 41*, 1447–1461.

Rilling, J. K., Goldsmith, D. R., Glenn, A. L., Jairam, M. R., Elfenbein, H. A., Dagenais, J. E., et al. (2008b). The neural correlates of the affective response to unreciprocated cooperation. *Neuropsychologia, 46*, 1256–1266.

Rilling, J. K., Sanfey, A. G., Aronson, J. A., Nystrom, L. E., & Cohen, J. D. (2004). The neural correlates of theory of mind within interpersonal interactions. *Neuroimage, 22*, 1694–1703.

Roberts, K. L., & Hall, D. A. (2008). Examining a supramodal network for conflict processing: A systematic review and novel functional magnetic resonance imaging data for related visual and auditory stroop tasks. *Journal of Cognitive Neuroscience, 20*, 1063–1078.

Rowe, A. D., Bullock, P. R., Polkey, C. E., & Morris, R. G. (2001). "Theory of mind" impairments and their relationship to executive functioning following frontal lobe excisions. *Brain, 124*, 600–616.

Rubia, K., Smith, A. B., Brammer, M. J., & Taylor, E. (2003). Right inferior prefrontal cortex mediates response inhibition while mesial prefrontal cortex is responsible for error detection. *Neuroimage, 20*, 351–358.

Ruby, P., & Decety, J. (2001). Effect of subjective perspective taking during simulation of action: A PET investigation of agency. *Nature Neuroscience, 4*, 546–550.

Rushworth, M. F., Kennerley, S. W., & Walton, M. E. (2005). Cognitive neuroscience: Resolving conflict in and over the medial frontal cortex. *Current Biology, 15*, R54–R56.

Sabbagh, M. A., Xu, F., Carlson, S. M., Moses, L. J., & Lee, K. (2006). The development of executive functioning and theory of mind: A comparison of Chinese and U.S. preschoolers. *Psychological Science, 17*, 74–81.

Saltzman, J., Strauss, E., Hunter, M., & Archibald, S. (2000). Theory of mind and executive functions in normal human aging and Parkinson's disease. *Journal of the International Neuropsychological Society, 6*, 781–788.

Sanfey, A. G., Rilling, J. K., Aronson, J. A., Nystrom, L. E., & Cohen, J. D. (2003). The neural basis of economic decision-making in the Ultimatum Game. *Science, 300*, 1755–1758.

Schulte-Ruther, M., Markowitsch, H. J., Fink, G. R., & Piefke, M. (2007). Mirror neuron and theory of mind mechanisms involved in face-to-face interactions: A functional magnetic resonance imaging approach to empathy. *Journal of Cognitive Neuroscience, 19*, 1354–1372.

Shallice, T. (1998). *From neuropsychology to mental structure*. Cambridge: Cambridge University Press.

Shamay-Tsoory, S. G., Tibi-Elhanany, Y., & Aharon-Peretz, J. (2007). The green-eyed monster and malicious joy: The neuroanatomical bases of envy and gloating (schadenfreude). *Brain, 130*(Pt 6), 1663–1678.

Stroop, J. (1935). Studies of interference in serial verbal reactions. *Journal of Experimental Psychology: General, 18*, 643–662.

Stuss, D. T., Gallup, G. G., Jr., & Alexander, M. P. (2001). The frontal lobes are necessary for 'theory of mind'. *Brain, 124*, 279–286.

Suchy, Y. (2009). Executive functioning: Overview, assessment, and research issues for non-neuropsychologists. *Annals of Behavioral Medicine, 37*(2), 106–116.

Tabares-Seisdedos, R., Balanza-Martinez, V., Sanchez-Moreno, J., Martinez-Aran, A., Salazar-Fraile, J., Selva-Vera, G., et al. (2008). Neurocognitive and clinical predictors of functional outcome in patients with schizophrenia and bipolar I disorder at one-year follow-up. *Journal of Affective Disorders, 109*, 286–299.

Takahashi, H., Kato, M., Matsuura, M., Mobbs, D., Suhara, T., & Okubo, Y. (2009). When your gain is my pain and your pain is my gain: Neural correlates of envy and schadenfreude. *Science, 323*(5916), 937–939.

Talairach, J., & Tournoux, P. (1988). *Co-planar stereotaxic atlas of the human brain*. New York: Thieme.

Tsao, D. Y., & Livingstone, M. S. (2008). Mechanisms of face perception. *Annual Review of Neuroscience, 31*, 411–437.

Tzourio-Mazoyer, N., Landeau, B., Papathanassiou, D., Crivello, F., Etard, O., Delcroix, N., et al. (2002). Automated anatomical labelling of activations in spm using a macroscopic anatomical parcellation of the MNI MRI single subject brain. *Neuroimage, 15*, 273–289.

Vogeley, K., Bussfeld, P., Newen, A., Herrmann, S., Happe, F., Falkai, P., et al. (2001). Mind reading: Neural mechanisms of theory of mind and self-perspective. *Neuroimage, 14*, 170–181.

West, S. A., Gardner, A., Shuker, D. M., Reynolds, T., Burton-Chellow, M., Sykes, E. M., et al. (2006). Cooperation and the scale of competition in humans. *Current Biology, 16*, 1103–1106.

Xue, G., Lu, Z., Levin, I. P., & Bechara, A. (2010). The impact of prior risk experiences on subsequent risky decision-making: The role of the insula. *Neuroimage*. epub.

Yang, J., Zhou, S., Yao, S., Su, L., & McWhinnie, C. (2009). The relationship between theory of mind and executive function in a sample of children from mainland China. *Child Psychiatry and Human Development, 40*, 169–182.

Zaki, J., Hennigan, K., Weber, J., & Ochsner, K. N. (2010). Social cognitive conflict resolution: Contributions of domain-general and domain-specific neural systems. *Journal of Neuroscience, 30*(25), 8481–8488.

Zysset, S., Muller, K., Lohmann, G., & von Cramon, D. Y. (2001). Color-word matching stroop task: Separating interference and response conflict. *Neuroimage, 13*, 29–36.