RESEARCH ARTICLE

The role of the right temporo-parietal junction in social decision-making

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Abstract

Identifying someone else's noncooperative intentions can prevent exploitation in social interactions. Hence, the inference of another person's mental state might be most pronounced in order to improve social decision-making. Here, we tested the hypothesis that brain regions associated with Theory of Mind (ToM), particularly the right temporo-parietal junction (rTPJ), show higher neural responses when interacting with a selfish person and that the rTPJ-activity as well as cooperative tendencies will change over time. We used functional magnetic resonance imaging (fMRI) and a modified prisoner's dilemma game in which 20 participants interacted with three fictive playing partners who behaved according to stable strategies either competitively, cooperatively or randomly during seven interaction blocks. The rTPJ and the posterior-medial prefrontal cortex showed higher activity during the interaction with a competitive compared with a cooperative playing partner. Only the rTPJ showed a high response during an early interaction phase, which preceded participants' increase in defective decisions. Enhanced functional connectivity between the rTPJ and the left hippocampus suggests that social cognition and learning processes co-occur when behavioral adaptation seems beneficial.

KEYWORDS

competition, cooperation, fMRI, justice sensitivity, mental model, social exchange, social cognition, social learning, Theory of Mind

1 | INTRODUCTION

The ability to infer the goals or intentions of another person is essential to guide behavior in social situations. From an evolutionary perspective, mental-state inferences might have evolved in order to avoid exploitation in social exchange situations and thereby reinforce cooperation (Brüne & Brüne-Cohrs, 2006). In support of this notion, empirical evidence indicates that memory processes (Buchner, Bell, Mehl, & Musch, 2009; Chiappe, Brown, & Dow, 2004; Suzuki, Honma, & Suga, 2013) and logical reasoning are enhanced when someone cheats in an interaction (Cosmides, Barrett, & Tooby, 2010; Stone, Cosmides, Tooby, Kroll, & Knight, 2002). This cognitive benefit has been found in subjects from developed nations and hunter-horticultures, pointing to the relevance of this specific mechanism for our species (Sugiyama, Tooby, & Cosmides, 2002). Importantly, the specialization for identifying a person who cheated, is only noticeable when a person behaved intentionally, but not accidentally (Cosmides et al., 2010). Consequently,

brain regions underlying the inference of other persons' mental states, might show enhanced neural responses during the evaluation and identification of someone's detrimental behavior, which we tested in this study.

Previous studies using fMRI to examine these Theory of Mind processes (ToM, Premack & Woodruff, 1978) suggest that mental state inferences are processed by a neural circuit comprising the temporo-parietal junction (TPJ), the medial prefrontal cortex (mPFC), and the posterior cingulate cortex (PCC) (Saxe & Powell, 2006; Schurz, Radua, Aichhorn, Richlan, & Perner, 2014). In several fMRI studies, the rTPJ has been repeatedly found to be relevant for reasoning about and understanding other persons' mental states, pointing to its outstanding role for ToM processes (Saxe & Kanwisher, 2003; Saxe & Wexler, 2005). Besides its general significance for mental states inferences, implications of rTPJ functioning for real-life interactions have been tested in previous studies. For example, during moral decision-making, the temporary inhibition of the rTPJ with transcranial magnetic

stimulation (TMS) leads to less consideration of someone else's beliefs during moral judgments (Young, Camprodon, Hauser, Pascual-Leone, & Saxe, 2010). This finding points out that the rTPJ integrates beliefs in the decision-making process, particularly when someone else's actions are perceived as more relevant (Carter, Bowling, Reeck, & Huettel, 2012). Furthermore, it has been shown that the rTPJ processes deviations between the own expectations about another person's intentions and their real intentions (Cloutier, Gabrieli, O'Young, & Ambady, 2011; Saxe & Wexler, 2005). The mentioned characteristics are supposedly important in strategic interactions when assumptions about cooperative or competitive goals differ between the interaction partners. In order to protect from exploitation it is highly beneficial to detect selfish persons in social exchanges early (Trivers, 1971). We, therefore, hypothesized that the rTPJ has a specific relevance during an initial interaction phase with a defective person, because people may expect fairness and reciprocity in exchange situations (Gintis, Bowles, Boyd, & Fehr, 2003; Trivers 1971) and will punish those who deviate from these expectations (Fehr & Gächter, 2002; Fehr, Fischbacher, & Gächter, 2002; Spitzer, Fischbacher, Herrnberger, Grön, & Fehr, 2007).

Interestingly, however, only a few studies have investigated whether different intentions influence the brain responses in the ToM network differently. These findings indicate that the right inferior parietal cortex, which comprises the rTPJ (Decety, Jackson, Sommerville, Chaminade, & Meltzoff, 2004; Liu, Saito, Lin, & Saito, 2017) and the medial prefrontal cortex (Decety et al., 2004) are stronger implicated in a competitive than a cooperative interaction. Yet, in these studies the participants were informed about the interaction context, that is, whether they will interact competitively or cooperatively with someone else. In real-life, however, the brain has to infer if the other person pursues a selfish or a cooperative goal, based on behavioral cues during an interaction. In this study we therefore examine how the brain processes and learns about previously unknown persons who behave cooperatively or competitively to oneself.

In order to examine mentalizing processes on-line during an interaction, game theory can provide an ecological and valid way, because subjects engage directly in social situations in the course of the decision-making process (Frith & Singer, 2008; Sanfey, 2007). Accordingly, enhanced neural activity in regions associated with ToM processes, that is, the rTPJ, the mPFC, and the PCC/precuneus, can be found during the interaction with another player in strategic games (Kircher et al., 2009; Schurz et al., 2014). Furthermore, a specific advantage of social decision-making games for the investigation of ToM is the possibility to investigate social learning mechanisms in repeated interactions. This aspect is particularly important, because recent evidence suggests that the activity in the TPJ is attenuated, once a person's intentions are predictable or expected (Brown & Brüne, 2012; Koster-Hale & Saxe, 2013). This assumption paves a way for the idea that mentalizing processes stimulate learning about someone's intentions in repeated interactions. The TPJ is a candidate brain region to process and share information with memory regions, since attention and memory streams converge in it (Carter & Huettel, 2013). Accordingly, it has been suggested that the TPJ receives and shares semantic information with memory regions such as the hippocampus and the temporal poles during ToM (Binder & Desai, 2011; Cabeza,

Ciaramelli, & Moscovitch, 2012). However, whether a coupling between the rTPJ with memory brain regions is a neural underpinning of beneficial social decision-making is yet unknown.

In this study, we conducted a paradigm grounded in game theory, a modified prisoner's dilemma game, to assess brain responses during a strategic interaction with persons differing in their cooperativeness. Participants interacted alternately with three fictive playing partners who behaved according to stable strategies either competitively, cooperatively, or randomly during the game. Based on the above considerations, we predicted enhanced neural response in ToM brain regions, such as the rTPJ, the mPFC, and the PCC in all three conditions. However, we expected amplified rTPJ-activity during the interaction with a competitive playing partner, because the playing partner's non-cooperative decisions are of high relevance and may deviate from the own cooperative intentions. In line with this, we expected that participants increase their defective decisions during the course of the competitive interaction which may be associated with increased rTPJ-responses in an early and decreasing responses in later interaction phases. As predicted by a predictive coding framework (Brown & Brüne, 2012; Koster-Hale & Saxe, 2013) higher neural responses are expected by a stronger breach of prior expectations. Accordingly, higher rTPJ-activity can be expected in individuals with a higher alertness to social inequity. Therefore, we predicted that individuals high in trait justice sensitivity (Schmitt, Baumert, Gollwitzer, & Maes, 2010) show a higher rTPJ-activity during an early competitive interaction. Furthermore, we expected a functional coupling between the rTPJ and brain regions that are necessary for memory formation, which could be a neural basis of beneficial social decision-making.

2 | MATERIALS AND METHODS

2.1 | Participants

Twenty right-handed participants (10 females) between 23 and 38 years of age ($M \pm STD = 28.79 \pm 4.93$) participated in the study. All participants were native German speakers, had normal or corrected-to-normal vision, and reported no history of psychiatric or neurological disorders. The study was approved by the local Ethics Committee at Philipps-University Marburg and all participants gave written informed consent prior to the experiment. Participants were paid for the participation in the study.

2.2 | Stimuli

Faces of 12 (6 female and 6 male) fictional playing partners were selected from the Chicago Face Database (Ma, Correll, & Wittenbrink, 2015). Two different faces were used per condition and presented in counterbalanced order between participants. The faces were selected on the basis of nearly identical ratings in categories that might influence social decision-making. Hence, the faces did not differ significantly in trustworthiness (Female: $M \pm STD = 3.66 \pm 0.19$, Male: $M \pm STD = 3.65 \pm 0.14$), attractiveness (F: $M \pm STD = 3.69 \pm 0.32$, M: $M \pm STD = 3.52 \pm 0.48$), or

FIGURE 1 fMRI-task: Examples of an interaction sequence with the competitive (upper interaction partner) and the cooperative playing partner (lower interaction partner). Each interaction block started with a picture of the counterpart. After that, a fixation cross indicated that the participant had to decide between the defective (D, right button) and the cooperative (C, left button) choice, which was followed by the presentation of a table depicting the outcome for both players. In the upper row of the table, the decision of the playing partner was presented, in the lower row the participant's choice. In the middle column of the table the button press of each player was depicted. The left column showed the payoff for the current trial, whereas the right column showed the accumulated outcome of all payoffs within one block. After the interaction block with one player finished, another playing partner was presented in pseudorandomized order. The accumulated payoff started by zero in each new block. The participants interacted with each counterpart in seven interaction blocks and each block contained six decisions (only three are shown). The upper part of the figure shows the exemplary interaction with the competitive partner, who defected (D) in five out of six decisions, whereas the participant cooperated (C) in the first two trials and defected in the third [Color figure can be viewed at wileyonlinelibrary.com]

age (F : $M \pm STD = 25.56 \pm 1.19$, M : $M \pm STD = 25.82 \pm 2.22$). The ratings are based on data of the Chicago Face Database.

2.3 | Experimental task

Participants were told that they will interact with three real playing partners in a social decision-making game (prisoner's dilemma game). In fact, each participant interacted with a computer algorithm representing three fictive playing partners who behaved according to one stable strategy either competitively (defecting in 83.3% of trials), cooperatively (cooperating in 83.3% of trials), or randomly (cooperating/defecting in 50% of trials, respectively) during the entire experiment. The interaction blocks started with the presentation of a picture and a name of the current playing partner, so participants were aware with whom they will interact in the current block (Figure 1). The participants then had to decide in six times per block to press the left (cooperate) or the right (defect) button which was indicated by a fixation cross. After the decision phase the outcome for both players was presented. In the case that both partners cooperated, both obtained a high score (20 points each), but when one partner defected and the other one cooperated, the defective partner received a higher outcome than the cooperative one (20 vs. 10). If both partners defected, both obtained zero points (see Supporting Information). The intentional playing partners (competitive, cooperative) defected or cooperated in 5 out of 6 decisions per block, respectively. The random playing partner cooperated and defected three times per block. After interacting with one playing partner the next interaction block began with a new playing partner. The participants interacted with each playing partner in seven blocks in total, leading to 42 decisions with each partner. The interaction sequences and the playing partners' decisions were pseudorandomized.

After interacting with all counterparts once, a control condition in which the picture of the playing partner was replaced by a red cross

and the hint that due to technical reasons no playing partner is connected was displayed. During the control condition participants were instructed to alternately press the right and the left button in seven blocks with six decisions and no outcomes were presented. Due to the within-subjects design the participants were able to accumulate evidence about the playing partners' goals during the experiment and change their strategy for their own benefit.

Prior the experiment, the participants practiced the game in a training session, to make sure that the game procedure had been understood. Furthermore, pictures of the participants were taken during the introduction phase and they were asked to wear a gray shirt, as the fictive playing partners did to make the experimental story more credible (see Supporting Information).

2.4 | Behavioral data analysis

Behavioral data were analyzed with SPSS 19 (IBM Corp., NY). Repeated measurement ANOVAs (rmANOVA) were conducted to test our behavioral hypothesis. Once a significant Mauchly's test indicated that the assumptions of sphericity had been violated, we corrected the degrees of freedom with a Huynh-Feldt correction. Following a significant omnibus test, we conducted paired t -tests in order to analyze the direction of effect of participants' choices in the different time phases (early vs. middle/late interaction phase, middle vs. late interaction phase). Tests are reported at an alpha level of $p \leq .05$. The hypothesis for which we had specified the direction of effect a-priori was tested one-tailed. This applies to the hypothesis concerning the behavioral time-course analysis (early vs. middle/late COMP interaction phase) in which we expected that participants will increase their defective choices during the time-course in the competitive interaction in order to avoid exploitation. Our hypothesis is based on ample empirical evidence that humans react with behavioral adaptation to unequal

outcomes in social exchanges (e.g., Fehr & Gächter, 2002; Sanfey, Rilling, Aronson, Nystrom, & Cohen, 2003). The reported effect sizes are partial eta square for the ANOVAs and Cohen's *d* for the paired *t*-tests.

2.5 | Social learning during the competitive interaction—identification value

In order to model individual differences in social learning during the competitive interaction, we calculated a value representing each participant's changes in cooperative choices with increasing interaction phases. For this analysis, we added the differences between the cooperative decisions from the second to the last block, relative to the first block according to the following equation: Identification value = $\sum_{i=2}^7 (x_i - x_1)$. The *x* indicates the sum of cooperative choices (range: 0–6) during a specific block *i* (range: 2–7) in the competitive interaction in relation to the cooperative choices in the first block (*x*₁). Hence, we chose the value as an estimate of the decrease in cooperative decisions over the blocks of the experiment in relation to the first block in which participants probably had not formed a mental model of the playing partner's behavior yet, indicating their default choices.

A negative value indicates that the participant decreased the cooperative choices during the experiment, indicating enhanced learning of the playing partner's strategy and thus adaptive behavior over the time course. A positive value indicates that the participant increased the cooperative choices during the experiment, indicating unfavorable adaptive behavior. A value of zero shows that a participant played the same strategy from the first block onwards.

2.6 | Adaption between the playing partners—dynamic ToM

We examined individual differences in the behavioral adaption to the two playing partners' strategy with intentional behavior (competitive and cooperative). Therefore, we calculated the difference between the defective choices against the competitive and the defective choices against the cooperative playing partner for each participant. A positive dynamic ToM value indicates a higher adaption to both partners' strategy as participants behaved more competitively against the competitive playing partner but less competitively to the cooperative playing partner. Hence, the value can be interpreted as each participant's understanding of the social environment, that is, the simultaneous consideration of multiple playing partners' intentions. We use this term to conceptualize an individual's capability to adapt and represent intentionally different playing partners on a behavioral level. We expected that this value is associated with brain regions relevant for memory processes or updating of social knowledge.

2.7 | Personality assessment

Justice sensitivity can be seen as an individual's readiness to perceive injustice in social situations (Baumert, Rothmund, Thomas, Gollwitzer, & Schmitt, 2013; Schmitt et al., 2010). The trait was assessed with the justice sensitivity inventory (Schmitt et al., 2010) consisting of 40 items in total which measure four different facets (10 items for each facet).

The construct can be theoretically distinguished by four perspectives: observer, beneficiary, perpetrator, and victim sensitivity. All facets have in common that they reflect an individual's concern for justice, as correlations among them suggest (Schmitt, Gollwitzer, Maes, & Arbach, 2005; Schmitt et al., 2010). However, observer, beneficiary, and perpetrator sensitivity reflect a genuine concern for justice, whereas victim sensitivity reflects a rather selfish concern (Gollwitzer, Schmitt, Schalke, Maes, & Baer, 2005; Schmitt et al., 2005). Given these findings we used a global measure for an individual's genuine justice concerns (consisting of beneficiary, perpetrator, and victim sensitivity). One participant did not complete the questionnaire, which is why we report data for the trait analysis for 19 participants.

2.8 | Imaging procedure

2.8.1 | fMRI data acquisition

All images were acquired using a Siemens 3-Tesla Trio, A Tim scanner with a 12 channel head matrix receive coil. Functional images were acquired using a T2* weighted single shot echo planar imaging (EPI) sequence (parallel imaging factor of 2 (GRAPPA), TE = 30 ms, TR = 2,000 ms, flip angle 90°, slice thickness 3.6 mm, matrix 64 × 64, in-plane resolution 3 × 3 mm², bandwidth 2,232 Hz/pixel, EPI factor of 64, and an echo spacing of 0.51 ms). Data from 33 transversal slices oriented to the AC–PC line were gathered in descending order.

2.8.2 | fMRI data preprocessing

Data preprocessing and analysis were performed using SPM8 (<http://www.fil.ion.ucl.ac.uk/spm>) implemented in MATLAB 13a (MathWorks, MA). The first five volumes of each functional run were discarded from the analysis to account for T1 equilibration effects. Functional data were realigned and unwrapped, corrected for slice timing, spatially normalized onto a common brain space (Montreal Neurological Institute, MNI) and spatially smoothed using a Gaussian filter with a 8-mm full-width half maximum (FWHM) Gaussian kernel.

2.9 | Whole-brain analysis

For each condition, (competitive, cooperative, random, control) the onset of the decision and the subsequent feedback phase (4 s) was convolved with a canonical hemodynamic response function (HRF) leading to one regressor per condition. Besides the task regressors, the presentation phase of the playing partner's pictures was modeled as a single regressor and included with the realignment parameters as nuisance regressors in a general linear model (GLM). The high-pass filter was adapted to the experimental design and set to 284 Hz. Contrast maps for comparisons between the different task conditions (competitive, cooperative, and random) and between the task conditions and the control condition were calculated in a first-level analysis in each subject and then submitted to a second-level random effects analysis. For the conjunction (null) analysis the contrast maps between the control and task conditions were entered in a full factorial design. Comparisons between the task conditions were conducted on the second-level with one-sample *t*-tests. To control for multiple comparisons, a cluster

FIGURE 2 (a) Behavioral data: Conditions (RAND = random, COMP = competitive, and COOP = cooperative) and participants defective (D) or cooperative (C) choices. (b) Defective choices in the early (2–3 Block), middle (4–5 Block), and late (6–7 Block) interaction phase in the COMP and COOP condition. (c) Linear changes of decisions over the seven time blocks. Abbr. condition:choice. Error bars indicate SEM [Color figure can be viewed at wileyonlinelibrary.com]

extent threshold was used via Monte–Carlo simulation (Slotnick, Moo, Segal, & Hart, 2003). The whole-brain activation was simulated assuming a type I error voxel activation of $p = .001$, this revealed a cluster extent of 47 contiguous resampled voxels as sufficient to correct for multiple comparisons at $p < .05$. Percent signal change was extracted from the significant clusters using rfxplot (Gläscher, 2009).

2.10 | Time course analysis

In order to test the hypothesis that the activity in ToM regions would decrease with increasing interaction phases, we specified a second GLM with one regressor for the early (2 and 3 block), middle (4 and 5 block), and late (6 and 7 block) interaction phase, respectively. The first interaction block per condition, the presentation of the playing partners and the realignment parameters were included in the GLM as regressors of no interest. Analyses were conducted between the competitive and cooperative condition and within conditions to analyze activation differences between the different experimental time phases. The time course analysis was conducted one-tailed, because we predicted decreasing responses based on theoretical assumptions about brain regions responses during ToM (Koster-Hale & Saxe, 2013). Given that our predictions are based on a directional ground, one-tailed testing seems to be appropriate for hypothesis testing (Cho & Abe, 2013).

2.11 | Functional connectivity

In order to assess how the functional connectivity between the rTPJ and other brain regions changed during the interaction with a competitive versus cooperative partner, we conducted a generalized psychophysiological interaction (gPPI; McLaren, Ries, Xu, & Johnson, 2012).

This method has been shown to be more sensitive and specific as the standard form of PPI, by including the entire experimental space in the model (McLaren et al., 2012). The seed region was functionally defined by the entire cluster ($k = 59$, peak coordinates: $x = 66$, $y = -44$, $z = 30$) resulting from the whole brain analysis of the second-level contrast $\text{COMP} > \text{COOP}$. For the further analysis the regions eigenvariate was extracted. Contrast maps were calculated in the first-level and submitted to a second-level random effects analysis with one sample t -tests. The dynamic ToM value was used as covariate of interest in a multiple regression second-level analysis. Functional connectivity values were extracted with MarsBar (<http://marsbar.sourceforge.net/>).

3 | RESULTS

3.1 | Analysis of choice data

A $3 \times 2 \times 7$ (Condition $\times$ Decision $\times$ Time) rmANOVA revealed a significant main effect of decision ($F(1, 19) = 10.02$, $p = .005$, $\eta_p^2 = .35$) indicating that the participants more often defected than cooperated (Figure 2a). A significant condition $\times$ decision interaction ($F(2, 38) = 11.92$, $p < .001$, $\eta_p^2 = .39$) shows that the participants interacted with the competitive (COMP) playing partner more competitively than cooperatively than with the cooperative (COOP) ($F(1,19) = 15.31$, $p = .001$, $\eta_p^2 = .45$) or the random (RAND) playing partner ($F(1,19) = 19.25$, $p < .001$, $\eta_p^2 = .50$) (Figure 2a).

A significant decision $\times$ time interaction shows that the participants reduced their cooperative (and increased their defective) choices during the course of the experiment ($F(6, 114) = 2.20$, $p = .048$, $\eta_p^2 = .10$). Furthermore, they adapted their decisions between the conditions over the time course differentially, as a marginal significant

TABLE 1 Results of the conjunction analysis

Cluster	Anatomical region	x	y	z	t-value
Cluster 1 (Voxel: 30468)	R inferior parietal lobule	32	-54	46	11.08
	R angular gyrus	30	-60	46	10.82
	R supramarginal gyrus	50	-46	42	9.16
	L cerebellum	-34	-68	-30	8.73
	L inferior parietal lobule	-32	-56	50	8.07
Cluster 2 (Voxel: 24328)	R middle frontal gyrus	44	36	28	10.86
	R precentral gyrus	42	6	32	10.16
	R insula lobe	32	22	-2	9.22
	R superior frontal gyrus	32	58	16	8.23
	R middle orbital gyrus	38	50	-8	8.21
	R middle frontal gyrus	44	24	32	7.89
	R posterior-medial frontal	6	24	50	7.71
	R superior medial gyrus	6	32	42	7.64
Cluster 3 (Voxel: 2687)	L precentral gyrus	-46	2	34	9.27
	L inferior frontal gyrus	-44	30	28	6.31
	L middle frontal gyrus	-28	0	50	4.31
Cluster 4 (Voxel: 1270)	L superior frontal gyrus	-32	52	0	5.80
	L middle frontal gyrus	-36	54	10	5.19
	L middle orbital gyrus	-26	48	-12	4.67
Cluster5 (Voxel: 301)	R MCC	-6	-28	39	6.02

All reported regions were corrected for multiple comparisons on a cluster-level ($p < .05$, cluster height threshold of $p = .001$). Coordinates are reported in MNI space.

condition $\times$ decision $\times$ time interaction indicates ($F(11,15, 211.76) = 1.74$, $p = .066$, $\eta_p^2 = .084$). This effect was driven by a stronger increase in the defective (and decrease in the cooperative) choices in the COMP versus COOP condition over the experimental blocks ($F(6,114) = 2.40$, $p = .032$, $\eta_p^2 = .11$) and a marginally significant difference between the COMP versus RAND condition ($F(6,114) = 1.94$, $p = .080$, $\eta_p^2 = .09$). Further analysis showed that the participants reduced their cooperative choices and increased their defective choices linearly over time while interacting with the COMP playing partner ($F(1,19) = 5.37$, $p = .032$, $\eta_p^2 = .22$; $F(1,19) = 4.39$, $p = .050$, $\eta_p^2 = .19$) indicating beneficial adaptive behavior over the time course (Figure 2c). This trend was only present in the COMP condition.

3.2 | Behavioral changes between the early, middle, and late interaction phase

The increase of defective choices over the early, middle, and late interaction phases differed significantly between the COMP and the COOP condition ($F(2,38) = 3.56$, $p = .038$, $\eta_p^2 = .16$) (Figure 2b). As hypothesized, in the COMP condition participants increased their defective choices significantly from the early to the middle phase ($t(19) = 2.01$, $p = .030$, $d = .45$, 1-tailed) and marginally significant from the early to the late interaction phase ($t(19) = 1.53$, $p = .071$, $d = .33$, 1-tailed). No significant changes occurred from the middle to the late phase in the COMP condition and no significant differences were found in the COOP condition.

3.3 | Reaction times

A 3×7 (Condition $\times$ Time) rmANOVA showed that the reaction times decreased linearly in the course of the experiment indicated by a

significant linear contrast of time ($F(1,19) = 7.10$, $p = .015$, $\eta_p^2 = .27$). No significant differences in reaction times existed between the conditions ($F(2,38) = 1.43$, $p > .05$) nor between the factors ($F(7.85,149.13) = .52$, $p > .05$).

3.4 | fMRI results

3.4.1 | Conjunction analysis

A conjunction (null) analysis between the contrasts of the task conditions versus control condition revealed that the ToM network showed consistently higher neural responses in all task conditions compared with the control condition (Table 1, Figure 3). We found activation in large clusters comprising the rTPJ, the medial prefrontal cortex, and the PCC/precuneus indicating that the task conditions strongly activated the ToM network.

3.4.2 | Competitive versus cooperative interaction

The contrast COMP $>$ COOP interaction revealed higher activity in the right temporo-parietal junction (rTPJ) and the right posterior-medial frontal gyrus (pMPFC; Figure 4a; Table 2). The higher activity of the rTPJ and the pMPFC underlines our prediction that ToM processes are amplified during the interaction with a defective other.

The reverse contrast (COOP $>$ COMP interaction) showed activation in a large cluster with main peaks in the bilateral basal forebrain and the rectal gyrus (Table 2) and extending activity in the ACC (BA 33 and s24), subgenual area (BA 25), bilateral caudate, bilateral putamen, and medial orbitofrontal regions.

FIGURE 3 Conjunction (null) analysis: [(random vs. control) $\cap$ (competitive vs. control) $\cap$ (cooperative vs. control)]. The SPM is corrected for multiple comparison on a cluster-level ($p < .05$) [Color figure can be viewed at wileyonlinelibrary.com]

3.5 | Neural activity changes in ToM regions during different time phases

The rTPJ-activity decreased stronger linearly over the interaction phases in the COMP than in the COOP condition as a significant interaction (Time $\times$ Condition) of a linear trend analysis revealed ($F(1,19) = 3.03$, $p = .049$, $\eta_p^2 = .14$, 1-tailed). As hypothesized, the rTPJ-BOLD response showed a significant decrease from the early to the middle ($t(19) = 2.57$, $p = .01$, $d = 0.57$, 1-tailed), and a marginally significant decrease from the early to the late interaction phase during the COMP condition ($t(19) = 1.51$, $p = .074$, $d = 0.34$, 1-tailed) (Figure 4d). No activation differences were found between the middle and the late phase ($t(19) = 0.43$, $p > .05$). In the COOP condition the rTPJ-activity did not differ significantly between the time phases (Figure 4d).

The pMPFC-activity did not differ significantly in different time phases between the COMP and the COOP condition ($F(2,38) = 1.37$, $p > .05$) (Figure 4e). Further tests for activity changes between the time phases in the pMPFC during the COMP interaction revealed no significant differences as well (early vs. middle phase: $t(19) = -.64$, $p > .05$; middle vs. late phase: $t(19) = -.01$, $p > .05$).

3.6 | Justice sensitivity and rTPJ-activity

We examined whether the rTPJ-activity during the early COMP interaction is associated with personality differences in justice concerns. Persons high in justice sensitivity showed a significantly higher rTPJ-activity during the early COMP interaction ($r_s = .519$, $p = .023$, two-tailed) indicating that they undergo a higher breach of prior fairness concerns. Importantly, the amount of defective choices was not significantly associated with trait justice sensitivity ($r_s = -.223$, $p = .360$, two-tailed).

3.7 | rTPJ-connectivity: competitive versus cooperative interaction

A gPPI-analysis of the entire competitive interaction revealed higher functional connectivity of the rTPJ with the bilateral medial temporal poles during the COMP compared with the COOP condition (Figure 5b, Table 3).

3.8 | rTPJ-hippocampus connectivity is associated with social learning

The analysis of the rTPJ connectivity during the early phase showed an enhanced coupling between the rTPJ and the left hippocampus and the right cerebellum in the COMP compared with the COOP condition (Table 3). Due to the high relevance of the hippocampus for learning, we compared the changes in functional connectivity between the different time phases between the COMP and the COOP condition. A 3×2 -rmANOVA revealed a significant time $\times$ condition interaction ($F(2,38) = 7.04$, $p = .003$, $\eta_p^2 = .27$). This indicated a higher connectivity in the early versus the middle ($F(1,19) = 12.66$, $p = .002$, $\eta_p^2 = .40$) and in the early versus the late phase ($F(1,19) = 12.47$, $p = .002$, $\eta_p^2 = .40$) in the COMP versus the COOP condition (Figure 5i). No significant differences were found between the middle and the late phase between the conditions ($F(1,19) = .23$, $p > .05$). Within the COMP condition we found a marginally significant decrease in the functional connectivity between the early and the middle ($t(19) = 2.04$, $p = .055$, $d = 0.46$) and a significant decrease from the early to the late phase ($t(19) = 2.21$, $p = .040$, $d = 0.49$). No significant differences existed between the middle and the late phase ($t(19) = -.17$, $p > .05$). In the COOP condition we found a connectivity increase from the early to the middle ($t(19) = -2.16$, $p = .044$, $d = .50$) and from the early to the late phase ($t(19) = -3.06$, $p = .006$, $d = 0.56$) which reached significance. No significant differences existed between the middle and the late phase ($t(19) = -.059$, $p > .05$).

A significant linear regression showed that higher functional connectivity between the rTPJ and the hippocampus during the early compared with the late COMP interaction phase was significantly associated with the identification value and thus with beneficial social learning over the experimental time course ($t(19) = -2.56$, $\beta = -.52$, $p = .02$).

3.9 | rTPJ-connectivity: dynamic ToM

The dynamic ToM analysis, which represents the behavioral adaptation between the two playing partners, revealed a significant functional connectivity between the rTPJ and the left thalamus in the COMP compared with the COOP interaction at a more liberal threshold of $p = .001$ at 20 subsequent activated voxels (Figure 5a, Table 3). Furthermore, the cluster activation extended in the left hippocampus.

FIGURE 4 (a) SPM of the contrast COMP > COOP interaction. The SPM is corrected for multiple comparison on a cluster-level ($p < .05$). (b) % signal change of the rTPJ-activity in the COMP and COOP condition. (c) % signal change of the pMPFC in the COMP and COOP condition. (d) rTPJ-activity in different time phases in the COMP and the COOP condition. (e) rTPJ-activity in different time phases in the COMP and the COOP condition. Error bars indicate SEM [Color figure can be viewed at wileyonlinelibrary.com]

4 | DISCUSSION

Theoretical assumptions indicate that ToM processes encourage the identification of competitive persons in social interactions (Brüne & Brüne-Cohrs, 2006). Our data provide empirical evidence to support this hypothesis, as the rTPJ and pMPFC showed enhanced neural responses during the interaction with a repeatedly defecting person in an iterated prisoner's dilemma game. The rTPJ showed a significant time-dependent signal change, with higher activity during an early and reduced activity in subsequent interaction phases. Hence, the rTPJ seems to have a high relevance when another person's goals and intentions require behavioral adaptation. Furthermore, the rTPJ was functionally connected with the left hippocampus and the medial temporal

poles during the competitive interaction, brain regions that are relevant for memory encoding and retrieval (Binder & Desai, 2011; Dolan, Lane, Chua, & Fletcher, 2000). Our data therefore indicate that the rTPJ has a distinct role in forming social knowledge during decision-making.

Previous studies reported a consistent activation of the ToM network when people interact with others in social decision-making tasks (Decety et al., 2004; Elliott et al., 2006; Gallagher, Jack, Roepstorff, & Frith, 2002; Rilling, Sanfey, Aronson, Nystrom, & Cohen, 2004; Schneider-Hassloff, Straube, Nuscheler, Wemken, & Kircher, 2015; Schneider-Hassloff et al., 2016; Schurz et al., 2014). In line with these findings our participants showed activation in brain regions underlying ToM processes such as the rTPJ (Saxe & Kanwisher, 2003; Saxe & Wexler, 2005), the mPFC (Kircher et al., 2009; Schurz et al., 2014),

TABLE 2 Results of the whole-brain analysis

Cluster	Anatomical region	x	y	z	t-value
Competitive > Cooperative					
Cluster 1 (Voxel: 102)	R posterior-medial frontal	16	18	64	5.42
Cluster 2 (Voxel: 59)	R temporo-parietal junction				
	R supramarginal gyrus	66	-44	30	5.14
	R superior temporal gyrus	66	-52	22	4.68
Cooperative > Competitive					
Cluster 1 (Voxel: 481)	Basal forebrain (Ch 4)	10	4	-16	5.81
	R rectal gyrus	20	14	-7	3.98

All reported regions were corrected for multiple comparisons on a cluster-level ($p < .05$, cluster height threshold of $p = .001$). Coordinates are reported in MNI space.

FIGURE 5 (a) Results of the functional connectivity analysis with the dynamic ToM values (see in c) revealed a connection between the rTPJ (seed region) and the left thalamus (extending to the left hippocampus) in the competitive versus cooperative contrast. (b) Functional connectivity between the rTPJ and the thalamus in both conditions. (c) Distribution of dynamic ToM values between participants, calculated as the difference in the competitive behavior against the competitive and the cooperative playing partner. A black line indicates that the participant interacted more competitively with the COMP and less competitively with the COOP person, grey vice versa. (d) Results of the gPPI analysis of the rTPJ (seed region) revealed enhanced functional connectivity with the bilateral medial temporal poles in the COMP > COOP contrast. (e) Functional connectivity in both conditions between the rTPJ and the bilateral medial temporal poles. (f) Functional connectivity differences between the rTPJ and the hippocampus during the experiment (early-late) is correlated with decreasing cooperative behavior in the competitive condition. (g) Results of the gPPI analysis in the early competitive phase revealed significant functional connectivity between the rTPJ (seed region) and the left hippocampus. (h) Functional connectivity in the early competitive phase between the rTPJ and the hippocampus. (i) Functional connectivity between the rTPJ and the hippocampus between the different time phases. Error bars indicate SEM [Color figure can be viewed at wileyonlinelibrary.com]

TABLE 3 Results of the functional connectivity analysis

Cluster	Anatomical region	x	y	z	t-value
Competitive > Cooperative					
Cluster 1 (Voxel: 85)	R medial temporal pole	32	16	-42	4.67
Cluster 2 (Voxel: 50)	L medial temporal pole	-36	4	-44	4.78
Early phase Competitive > Cooperative					
Cluster 1 (Voxel: 104)	R cerebellum	18	-76	-22	4.57
Cluster 2 (Voxel: 57)	L hippocampus	-38	-20	-14	5.41
Dynamic ToM-Value Competitive > Cooperative					
Cluster 1 (Voxel: 34)	L thalamus	-28	-22	-6	4.66

Reported regions were corrected for multiple comparisons on a cluster-level ($p < .05$, cluster height threshold of $p = .001$) except the analysis of the dynamic ToM-value which is reported at $p = .001$ (uncorrected) and an extent threshold of 20 activated voxels. Coordinates are reported in MNI space.

and the PCC (Bzdok et al., 2015; Mar, 2011) in all task conditions (competitive, cooperative, and random playing partner).

However, our data point out that specific regions within the ToM network, the rTPJ and the pMPFC, are sensitive when someone behaves competitively and hence awkwardly for oneself. Previous findings indicate that humans react sensitively to unequal distributions of limited goods in social exchange situations (Fehr et al., 2002; Fehr & Gächter, 2002), which is why the detection of someone's defective intents could be a privileged cognitive process (Brüne & Brüne-Cohrs, 2006; Trivers, 1971). In line with this assumption, brain regions that underlie ToM, like the pMPFC (Schuwerk et al., 2014) and the rTPJ (Cloutier et al., 2011; Saxe & Wexler, 2005), are involved in the processing of discrepancies between one's own beliefs and the beliefs of others. In the current study, the participants changed their strategy during the competitive interaction, indicating that they detected deviations between the own and the playing partner's goals. For a region relevant for social learning we expected to find increased neural activity particularly when behavioral differences are most strongly. We predicted that the rTPJ might code the deviations between the interacting partners' different behavioral goals. Therefore, we examined the activity changes in the rTPJ and the pMPFC in different time phases. Only the rTPJ but not the pMPFC showed higher activity during the early competitive interaction phase in which the behavioral differences were most strongly. This finding indicates that computations within the rTPJ represent a functional processing mechanism of a person's selfish intents and the related negative outcome. These findings are in line with previous research showing that the rTPJ is relevant for considering another person's belief during decision-making (Young et al., 2010) particularly when actions have a high self-relevance (Carter et al., 2012). However, our data point out that the relevance of the rTPJ decreases with increasing evidence about others in repeated interactions, which might indicate a revised mental model of the interacting partners' intentions. Alternatively, lower monetary outcome as well as violations of reward expectations could explain such an activation pattern. However, as such processes are usually not related to the rTPJ and would rather be related to brain regions such as the anterior cingulate cortex (Bush et al., 2002; Gehring & Willoughby, 2002), the ventral tegmental area, substantia nigra (Schultz, Dayan, & Montague, 1997), or the nucleus caudate and the lateral prefrontal cortex (Asaad & Eskandar, 2011), it is unlikely that outcome of the decisions per se explain the rTPJ activation pattern.

The rTPJ is a heterogeneous region (Carter & Huettel, 2013), accordingly recent findings support a functional separation of the rTPJ in an anterior and a posterior part (aRTPJ/pRTPJ) based on connectivity-based parcellation studies (Bzdok et al., 2013; Mars et al., 2011). Meta-analytical findings suggest that particularly the aRTPJ is implicated in strategic games (Schurz et al., 2014) which is in line with the location of the rTPJ main peak in the current study. The aRTPJ has been found to be relevant in processing functional different tasks such as attention-reorienting and false-belief tasks (Krall et al., 2015, 2016). Consequently, the idea has been raised about an "overarching" function of the aRTPJ, which explains the regions involvement in both processes with one common mechanism (Krall et al., 2015; Schuwerk, Schurz,

Müller, Rupprecht, & Sommer, 2017). Such a mechanism might be neural predictive coding (Bzdok et al., 2013; Krall et al., 2015). In this framework the neural system is expected to perform forward predictions about upcoming events, leading to higher neural responses to unexpected stimuli (Brown & Brüne, 2012; Koster-Hale & Saxe, 2013). This assumption is in line with a previous hypothesis that the rTPJ allocates attentional resources to behaviorally relevant stimuli indicating that the region is critically involved in processing breaches of prior expectations (Corbetta, Patel, & Shulman, 2008; Krall et al., 2015).

In this sense, our novel finding of a specific rTPJ response pattern, which is enhanced neural responses during an early and attenuated response in subsequent competitive interaction phases can be parsimoniously explained by a predictive coding process. During the early interaction phase participants showed significantly more cooperative tendencies leading to a higher personal loss and probably a breach of prior expectations about the other person's goals and intentions. We suggest that these expectations arise from personal beliefs about own and others' social behavior and might be further shaped by higher-order social norms. Our data shows that individuals high in justice sensitivity (Schmitt et al., 2010) show higher neural responses in the rTPJ during the early competitive interaction phase, which suggests a higher error response, probably due to initial justice concerns in social interactions. This finding points out that stable personal concepts shape social interactions a-priori. However, once the experience suggests that the model in the current environment is incorrect and an adaptation seems beneficial, the rTPJ might process these deviations and rearrange the model by novel information.

Importantly, the observed neural processes are consistent with concepts in personality psychology. These assume that traits constitute a sensitivity for environmental stimuli (Blum, Rauthmann, Göllner, Lischetzke, & Schmitt, 2018; Marshall & Brown, 2006). In this sense, a person high in one trait (e.g., justice sensitivity) detect and react earlier and stronger to even moderate trait-congruent stimuli in the environment (e.g., injustice), indicating an amplified perception of these situations. In this sense, the rTPJ can be seen as a brain region relevant for amplifying responses to environmental stimuli when they have a high relevance for oneself. However, further studies have yet to show whether the interaction between person and situation provides novel evidence about the rTPJ function. This may be tested with a design in which the stimuli strength (i.e., the situation) is graded parametrically (Blum et al., 2018; Schmitt et al., 2013).

Findings of our and previous studies suggest a potential right-hemisphere lateralization of the TPJ in ToM processes (Saxe & Wexler, 2005). Conflicting results come from a prominent lesion study that suggests that the left TPJ (ITPJ) has a causal impact on the ability to infer others' beliefs (Samson, Apperly, Chiavarino, & Humphreys, 2004). In this sense meta-analytical evidence indicates that the bilateral TPJ is part of a core ToM network (Schurz et al., 2014). In line with these findings, our results suggest that the bilateral TPJ is implicated in all mentalizing conditions (compared with a control condition). However, during the competitive interaction we found a higher relevance of the rTPJ, indicating that especially the right hemisphere is implicated in the processing of important social interactions.

A recent study suggests that the relevance of the rTPJ arises from a global mechanism which is relevant for performing different cognitive tasks (Lee & McCarthy, 2016). The authors used a within-subjects design to search for a common neural substrate in Theory of Mind, attention-reorienting and biological motion processing tasks. The results indicate that the rTPJ (but not the lTPJ) showed regional overlapping activity in all three tasks, pointing out that the region provides a domain-spanning mechanism relevant for the processing of all tasks (Lee & McCarthy, 2016). Such a mechanism might be an updating process of an internal model of the environment, thereby changing expectations of upcoming events which is fundamental to initiate an appropriate action in the current context (Geng & Vossel, 2013; Lee & McCarthy, 2016). It might be that such a process is lateralized in the right hemisphere, which might explain the relevance of the rTPJ in interactions with selfish others.

Furthermore, recent findings suggest that the functional relevance of the rTPJ partly arises from its connectivity profile with other brain regions (Bzdok et al., 2013; Poepl et al., 2016; Schuwerk et al., 2017). Accordingly, Schurz et al. (2014) proposed the idea that the nature and location of rTPJ-activity varies by its functional coupling with other brain regions. Similarly, it has been suggested that activity changes in the rTPJ indicate a processing change from a stimulus-dependent to a stimulus-independent network and hence a switch between external and internal/memory-informed processes (Bzdok et al., 2013). Our new findings point out that relevance of the rTPJ in social decision-making partially arises due to its temporal dynamic coupling with the left hippocampus.

The rTPJ was functionally connected with the left hippocampus (CA2 region) during the early competitive interaction phase. Previous studies have shown that the hippocampus is implicated in the encoding, updating, and modulation of memory representations that underlies flexible behavior (Rubin, Watson, Duff, & Cohen, 2014; Wimmer & Shohamy, 2012). Especially, the hippocampus' CA2 subregion, has been causally linked with social memory processes in an animal model (Hitti & Siegelbaum, 2014), underlining its relevance in social learning (Mou, 2016). Given these findings we suggest that the rTPJ-hippocampus connectivity indicates that mentalizing and memory formation processes co-occur and underlie individual social learning during the game as further analyses showed. Individuals with higher social learning curves had a higher rTPJ-hippocampus coupling during an early and a lower coupling during a late competitive interaction phase. This finding suggests that the rTPJ and the hippocampus are implicated in learning about another person's goals and intentions at an early stage in a relevant context. Learning-dependent changes in the hippocampus have been shown previously. Several studies point out that the responses in the hippocampus are high during initial learning and decrease with learning increase (Iglói, Doeller, Berthoz, Rondi-Reig, & Burgess, 2010; Schendan, Searl, Melrose, & Stern, 2003; Wolbers & Büchel, 2005). Similar changes in the metabolic activity can be expected for the rTPJ, when mental states of another person become predictable (Bzdok et al., 2013; Brown & Brüne, 2012; Koster-Hale & Saxe, 2013) indicating that learning processes are associated with decreasing neural activity in both areas. Our results therefore extend previous findings that emphasize the role of the rTPJ in reasoning

about the contents of another person's mind (Saxe & Kanwisher, 2003) and the relevance of the hippocampus in beneficial decision-making (Gupta et al., 2009) by showing that connectivity changes between both regions are associated with favorable social learning. From a theoretical perspective, we suggest that the rTPJ and the left hippocampus are involved in generating a mental model of another person's goals and intentions, which seems to be the foundation for adaptive behavior, probably until obvious changes in the environment occur.

Additional evidence for this hypothesis comes from our analysis of individual differences in adaptive behavior against multiple partners. We calculated a score representing a participants understanding of the social environment, as a higher ratio of defective choices against the competitive than against the cooperative partner indicates. We found that the higher behavioral adaptation correlated with a higher connectivity between the rTPJ and the left thalamus with extending activation in the hippocampus, pointing again to the relevance of the rTPJ-hippocampus coupling in social learning.

Additionally, we found that the rTPJ was functionally connected with the cerebellum during the early phase in the competitive interaction. Patients with cerebellar lesions show deficits in ToM which suggests its involvement in social cognitive processes (Hoche, Guell, Sherman, Vangel, & Schmahmann, 2016; Parente et al., 2013). Accordingly, the cerebellum is a reliable finding in social cognitive tasks that require abstract social thinking, such as trait inferences (Van Overwalle, Baetens, Mariën, & Vandekerckhove, 2014). A similar interpretation comes from Ito (2008) who suggested that the cerebellum is associated with building mental representations. Taken together, our results strengthen the argument that the rTPJ is functionally connected with regions that facilitate the learning about others' mental states, when behavioral adaptation is beneficial.

Besides the relevance of the hippocampus and the cerebellum during the task, the medial temporal poles, another area that is associated with memory (Olson, Plotzker, & Ezzyat, 2007) and social cognitive processes (Gobbini, Koralek, Bryan, Montgomery, & Haxby, 2007; Kircher et al., 2009; Schurz et al., 2014; Völlm et al., 2006) was connected with the rTPJ during the competitive interaction. Their reliable activation during social cognitive tasks has been interpreted as a retrieval of social semantic knowledge (Ross & Olson, 2010) probably to utilize personal experiences to comprehend the mental states of others (Frith & Frith, 2003; Moriguchi et al., 2006). Our data support this interpretation, since we found the largest strategy changes during the competitive interaction.

Further studies have yet to show whether the rTPJ-connectivity or an imbalance in its subregional connectivity (Poepl et al., 2016) with brain regions relevant for memory formation are associated with social cognitive deficits in specific psychiatric disorders. Impairments in ToM abilities have been found in patients with autism spectrum disorder (Baron-Cohen, Wheelwright, Hill, Raste, & Plumb, 2001) and schizophrenia (Bora, Yucel, & Pantelis, 2009; Sprong, Schothorst, Vos, Hox, & Van Engeland, 2007). Patients with schizophrenia show biased processing of other peoples' intentions during psychotic episodes, i.e., they feel pursued or believe others hold malevolent intentions (American Psychiatric Association, 2013). These symptoms could be linked with

dysfunction in brain regions that shape mental states of others. Accordingly, it has been speculated that an altered connectivity between the TPJ and the hippocampus is associated with specific psychotic symptoms in schizophrenia (Wible, 2012). Our findings suggest that the connectivity between both regions is fundamental for social predictive processes. Therefore, the rTPJ-hippocampus connectivity might be a target for further studies examining the pathophysiology of schizophrenia.

4.1 | Limitations

Findings should be interpreted in light of the study limitations. We have modeled the decision and outcome phase in the fMRI analysis as one event, which is why cognitive processes and brain activity cannot be exclusively attributed to one of the phases. However, meta-analytical evidence indicates that the rTPJ is a reliable finding in strategic decision-making (Schurz et al., 2014) and previous findings suggest that the rTPJ is implicated in relevant social decisions (Carter et al., 2012) which is clearly in line with our results and interpretations. Nevertheless, further studies may pinpoint the cognitive processes underlying the changes in rTPJ-activity. For example, further research might examine this processes by stimuli highly self-relevant but not monetary in nature. Additionally, it might be worth to examine whether the reduction of rTPJ-activity is driven, as suggested, by a general process like predictive coding. Accordingly, the nature of a person's predictions should be further considered, ideally in a person x situation interaction framework (Blum et al., 2018).

Our data points out that individuals high in trait justice sensitivity show higher rTPJ-activity during the early COMP interaction phase. Therefore, we suggest that individual factors and social norms frame social interactions a-priori which may be grounded in an abstract mental model of the self, the other and interaction rules which then translate into behavioral decisions. A fine-grained account how and to what extend such models are modulated by the environment and hence produce an error response could be highly profitable for further research.

5 | CONCLUSION

In summary, we found that the rTPJ has a distinct role during the interaction with a noncooperative person, indicating its significance in processing others' mental states during fundamental social exchange situations. The connectivity of the rTPJ with regions underlying memory formation and retrieval suggests that ToM processes and social learning are closely linked when behavioral adaptation seems beneficial.

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest with the content of this article.

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SUPPORTING INFORMATION

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