Processing of Prediction Errors in Mentalizing Areas

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Abstract

■ When seeing people perform actions, we are able to quickly predict the action's outcomes. These predictions are not solely based on the observed actions themselves but utilize our prior knowledge of others. It has been suggested that observed outcomes that are not in line with these predictions result in prediction errors, which require additional processing to be integrated or updated. However, there is no consensus on whether this is indeed the case for the kind of high-level social–cognitive processes involved in action observation. In this fMRI study, we investigated whether observation of unexpected outcomes causes additional activation in line with the processing of prediction errors and, if so, whether this activation overlaps with activation in brain areas typically associated with social–cognitive processes. In the first part of the experiment, participants watched animated movies of two people playing a bowling game, one experienced and one novice player. In cases where the player's score was higher or lower than expected based on their skill level, there was increased BOLD activity in areas that were also activated during a theory of mind task that participants performed in the second part of the experiment. These findings are discussed in the light of different theoretical accounts of human social–cognitive processing. ■

INTRODUCTION

In our day-to-day social interactions, we collect information about people around us. For instance, we might remember that one person is very knowledgeable, whereas another person is good at playing tennis. We use this information to build up expectations of the behavior of other people and the outcomes of their behavior given a certain context. We will therefore be more likely to ask our knowledgeable friend to join our pub quiz team, as this person will probably answer more questions correctly. This way, prior knowledge about others helps us understand the world and correctly respond to events.

This importance of prior knowledge is in line with the idea that predictions play a key role in cognitive processing. For instance, it has been suggested that predictions aid efficient processing as expected events are perceptually facilitated whereas unexpected events result in prediction errors, which require additional processing to be integrated (or updated) into the brain's model of the world (Summerfield & de Lange, 2014; Clark, 2013; Friston, 2010; Rao & Ballard, 1999). That is, when the unexpected events might be explained by a priori unlikely causes, then the prediction error can be minimized by assuming that such an unlikely cause indeed is in place, as this best explains the unlikely event. For rather low-level cognitive processes, such as visual perception, unexpected events have indeed been found to result in additional processing as indexed, for instance, by increased RTs (O'Reilly et al., 2013; Berti & Schröger, 2004) and brain activity (Kok, Jehee, & de Lange, 2012; Summerfield, Trittschuh, Monti, Mesulam, & Egner, 2008).

Although there is no consensus that prediction errors also arise when people process more abstract, social information, several findings do suggest that this is the case. Koster-Hale and Saxe (2013) review evidence that both neural and behavioral responses to observed actions depend on whether this action is expected or unexpected given the available contextual information. For instance, RTs slow down when people observe another person holding an object with an incorrect grip (Bach, Knoblich, Gunter, Friederici, & Prinz, 2005; Van Elk, Van Schie, & Bekkering, 2009). In addition, areas that are part of the brain's mentalizing network show increased activity in response to unexpected actions. The mentalizing network includes the TPJ, the STS, and the medial pFC) and is assumed be involved in mental state inference (Frith & Frith, 2006). Top–down and bottom–up signals in both TPJ and medial pFC are modulated by the probability of an agent-caused event (Van Pelt et al., 2016), and brain activity in these and related areas increases when observed actions are not in line with a person's facial expression (Vander Wyk, Hudac, Carter, Sobel, & Pelphrey, 2009), with the properties of the object on which the action is performed (Bach, Gunter, Knoblich, Prinz, & Friederici, 2009; de Lange, Spronk, Willems, Toni, & Bekkering, 2008), with the request to

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cooperate (Shibata, Inui, & Ogawa, 2011), or when observed actions are implausible given the context (Brass, Schmitt, Spengler, & Gergely, 2007).

In most of these studies, actions and their outcomes were expected or unexpected based on general world knowledge about the characteristics of objects and constraints imposed by certain contexts rather than information about specific persons. However, similar effects were found in studies focusing on situations in which people build up expectations based on their prior experiences with a specific person. For example, in studies in which participants read descriptions of another person's behavior that were consistent (e.g., "Tolvan gave her sister a hug") or inconsistent (e.g., "Tolvan gave her mother a slap") with a trait suggested by a previous description (e.g., "Tolvan gave her brother a compliment"), inconsistent descriptions resulted in increased brain activity compared with consistent descriptions (Dungan, Stepanovic, & Young, 2016; Mende-Siedlecki, Cai, & Todorov, 2012; Ma et al., 2011). In these studies, however, participants did not observe unexpected actions online but could imagine them based on stories describing the actions. It is unknown whether the same effects also arise in case people observe an outcome that is unexpected given the knowledge about the actor's earlier performance.

The studies described so far suggest that there might be a general mechanism for the processing of behavior that is unexpected given prior knowledge of a specific person, involving the integration of prediction errors with current beliefs. In case there is indeed such a general mechanism, then we might expect that the processing of outcomes that are unexpected given our prior experiences with the person performing the action would also result in increased processing. Indeed, in a previous study, we found that responses to questions slow down when people see that the outcome of another person's action is not as would be expected based on prior experiences, suggesting that prediction errors play a role in the processing of these events (Heil, Kwisthout, van Pelt, van Rooij, & Bekkering, 2018). As this was a behavioral study, we could not determine in which brain areas this additional processing takes place.

Therefore, we set out to test whether the processing of outcomes that are expected or unexpected based on our knowledge about a person also causes additional activation in line with the processing of prediction errors. Furthermore, we investigated whether such additional activity would arise in brain areas encompassing the mentalizing network, which is associated with higher social–cognitive processes. In case brain activation related to unexpected outcomes would be found to overlap with activation in brain areas typically associated with social–cognitive processes, this would support the idea that the processing of prediction errors related to action outcomes and social–cognitive processes have a common neural substrate. Furthermore, if activation patterns for unexpected action outcomes are found to be similar to activation patterns for false (social–cognitive) beliefs, similar underlying neural computations are likely being performed within both contexts.

In this fMRI study, participants watched animated movies of two people playing a bowling game, one experienced and one novice player. Assuming that unexpected events would result in prediction errors that require additional processing to be integrated into current beliefs, we hypothesized that, in cases where the player's score was higher or lower than expected based on their skill level, BOLD activity would increase. Moreover, based on the idea that prediction errors do not only drive low-level, but also more high-level, social–cognitive processing, it was expected that this additional activity would also arise in brain areas traditionally associated with social–cognitive processes.

METHODS

Participants

Thirty-five healthy, right-handed individuals with normal or corrected-to-normal vision participated in this study. All but one participant scored below the cutoff of 32 on the Dutch translation of the Autism Spectrum Quotient Questionnaire (AQ; Hoekstra, Bartels, Cath, & Boomsma, 2008; Baron-Cohen, Wheelwright, Skinner, Martin, & Clubley, 2001). Head motion greater than 3.5 mm in any direction (greater than the voxel size) was used as a threshold for exclusion. Furthermore, as the novice (experienced) player got a low (high) score in 75% of all trials showing this player, participants who only attended to either the agent or the outcome could still reach an accuracy of 75% for the question about the unattended factor (the outcome or the agent, respectively). Therefore, an accuracy below 85% for each question, based on all trials in which participants responded with a button press (i.e., all nonmissing trials), was used as a threshold for exclusion. Data from 13 participants were excluded in total (Table 1) because of (i) low accuracy (< 85%), (ii) missing responses (> 20%), (iii) high AQ score (> 32), (iv) early discontinuation of the experiment, (v) excessive head motion, and (vi) technical failure. This resulted in a final data set of 22 participants (13 women, 9 men) aged between 18 and 28 years (M = 22.05 years, SD = 2.44 years). Written informed consent was obtained from each participant, and participants received course credits or 20 euros for participation. The study was approved by the local ethics committee (CMO Regio Arnhem-Nijmegen).

Stimuli

For the bowling task, 24 animated movies were created using Autodesk's 3ds Max 2014 and MotionBuilder 2014. Each movie showed one of two possible bowling players (selected from WorldViz Vizard Complete Characters) on

Table 1. Summary of Excluded Participants

Excluded Participants	*Reason for Exclusion*
1	Missing = 22.6%
2	Incomplete data
3	Head motion
4	Incomplete data
5	Head motion
6	Accuracy = 80%
7	Technical error scanner
8	Head motion
9	Head motion
10	Incomplete data
11	Head motion
12	Head motion
13	AQ score = 44

Criteria for exclusion were the following: (i) low accuracy (< 85%), (ii) missing responses (> 20%), (iii) high AQ score (AQ > 32), (iv) early discontinuation of the experiment (incomplete data), (v) excessive head motion (> 3.5 mm in x, y, or z direction), and (vi) technical failure.

a bowling lane, throwing a ball directed at the pins at the end of the lane. The ball rolled either slightly left or slightly right of the center, and upon hitting the pins, one, two, three, six, seven, or eight pins fell down. The kinematics of the ball movement was not related to a specific player or outcome. Each movie lasted 5 sec, and the player disappeared after 1.2 sec, to keep the visual display of the action outcomes the same for the two players. Examples of the bowling task stimuli are publicly available at: https://figshare.com/s/33125be1ac5d7d80819a.

For the theory of mind (ToM) task, we used the localizer task described by Dodell-Feder, Koster-Hale, Bedny, and Saxe (2011; saxelab.mit.edu/superloc.php), based on the initial task by Saxe and Kanwisher (2003). This task used 20 short stories either about a person holding a false belief or about an outdated representation, such as a map or photograph showing something that no longer exists. These stories were translated to Dutch, as all participants were native or fluent speakers of Dutch.

All stimuli were presented using Presentation software (Version 17.2, www.neurobs.com).

Bowling Task

For the bowling task, we used a within-subject design that was similar to the one in our previous study (Heil et al., 2018). As in that study, participants read instructions on the screen, explaining that they would be watching movies of two people playing a bowling game and answering questions about these movies. They were told that there was one novice and one experienced player, who usually obtained scores matching their skill levels. To allow them to associate appearance of the agent with his skill level, participants performed four practice trials, in which they received information about which agent they would see before each movie was presented.

In the main task, there were 288 trials in total, all following the procedure shown in Figure 1. In 75% of all trials, movies showed the novice or experienced player obtaining an expected score, and in 25% of all trials, they showed the player obtaining an unexpected score of at least 4 points higher or lower than their average

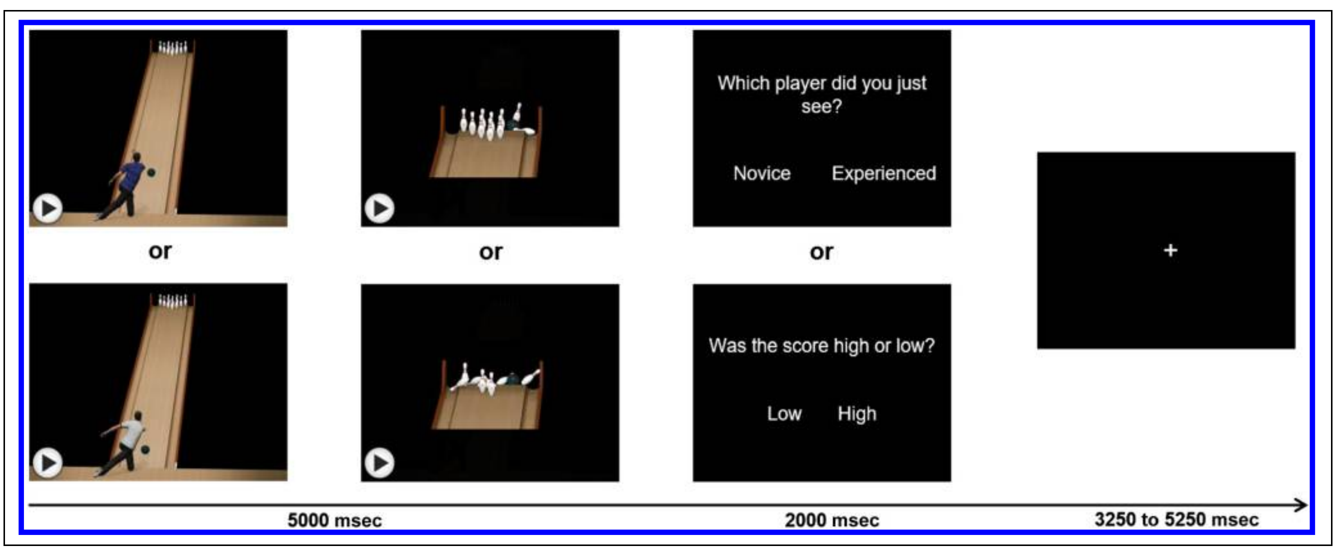

Figure 1. Schematic representation of the procedure in the bowling task. Each trial started with a 5000-msec bowling movie showing either the novice or experienced player who scored either high or low. This movie was followed by one of two possible questions concerning the player or the score. The question was presented for 2000 msec, even if participants required less time to answer it. Each trial ended with a fixation cross. Example videos of the bowling task stimuli are publicly available (see Methods).

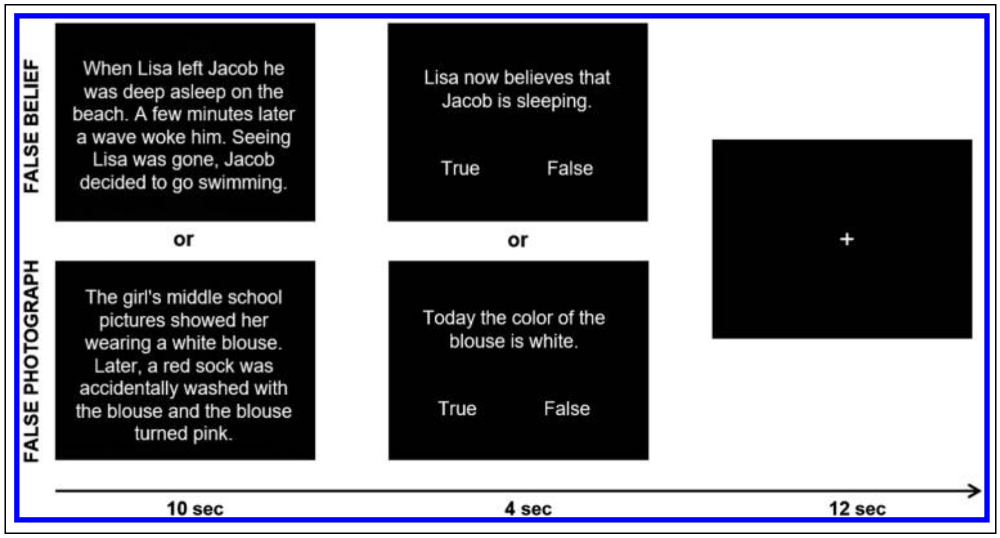

Figure 2. Schematic representation of the procedure in the ToM task, with examples from the original version of the task in English. Each trial started with a short story that was followed by a statement. Participants indicated whether the statement was true or false. Each trial ended with a fixation cross.

score. More specifically, the novice player received a low score (1, 2, or 3) in 108 of 144 trials, whereas the experienced player received a high score (6, 7, or 8) in 108 of 144 trials. Within the category of low scores, a score of 2 was most frequent (96 of 144 trials), as was a score of 7 in the category of high scores. The other scores (i.e., 1, 3, 6, and 8) appeared very infrequently (a total of 32 of 288 trials) and were included as fillers that provided variability in scores to make the experiment more naturalistic.

After each movie, participants answered one of two questions. These questions were written in Dutch, and either asked whether they saw the experienced or the novice player or whether a small or a large number of pins fell down. These questions were presented in random order, and participants were not aware which question they would be asked in each trial. Each question was presented on the screen for 2 sec. Participants were instructed to answer as quickly as possible by pressing a left or a right button on a button box. These buttons corresponded to two answer options presented underneath the question, the order of which was randomized to prevent motor preparation. Unlike in the practice trials, participants did not receive feedback on the accuracy of their answer. Each trial was followed by a fixation cross, presented for a duration randomized between 3250 and 5250 msec. Data were collected in one run, and participants could take a short break in the scanner after the first 144 trials, while data collection continued.

Theory of Mind Task

We used an adapted version of the ToM task that is commonly used to identify brain areas specific for mentalizing (Dodell-Feder et al., 2011; Saxe & Kanwisher, 2003). In this task, participants read a total of 20 short stories, describing either a false belief or a false photograph. Following the procedures used by Dodell-Feder and colleagues, each story was presented for 10 sec and followed by a question about the story. Participants were given 4 sec to answer the question before the trial ended. The order of the stories was randomized for each participant. After each question, a fixation cross was shown for 12 sec (see Figure 2).

fMRI Data Acquisition

Functional images were acquired using a 3-T MRI scanner (Siemens Magnetom Skyra, located in Nijmegen, The Netherlands) with a 32-channel head coil. A multiecho EPI sequence sensitive to the BOLD signal contrast was used (34 transversal slices with a voxel resolution of $3.5 \times 3.5 \times 3.0$ mm, acquired in ascending order, repetition time = 2.07 sec, echo times = 9, 19.25, 29.5, and 39.75 msec, distance factor = 17%, 90° flip angle, 224 mm field of view). The first 30 volumes were used for calculation of the echo-weighting parameters and were discarded in data anal- ysis. During the break between the bowling task and the ToM task, high-resolution anatomical images (voxel size $1 \times 1 \times 1$ mm) were acquired using a T1-weighted magnetization prepared rapid gradient echo sequence (repetition time = 2.3 sec, echo time = 3.03 msec, flip angle 8°, 256 mm field of view).

Preprocessing

A custom MATLAB (Version R2012b; The MathWorks) script was used to combine the multiecho image acquisitions with the SPM8 toolbox (https://www.fil.ion.ucl.ac.uk/spm; Wellcome Trust Centre for Neuroimaging, London, United Kingdom). Before combining the four echoes, the first echo volumes were realigned (motion correction) to the first volume of the first echo, and the volumes of the remaining echoes were realigned to the first volume of the first echo and resliced. In this process, six rigid body head movement parameters were created.

To combine the echoes within each volume, the echo-weighting parameters derived from the first 30 volumes were applied to the echoes of all remaining volumes.

The combined multiecho images for both the bowling task and the ToM task were further preprocessed using FMRIB Software Library (FSL; https://fsl.fmrib.ox.ac.uk/fsl/; Wellcome Centre Integrative Neuroimaging, Analysis Group, FMRIB, Oxford, United Kingdom; Jenkinson, Beckmann, Behrens, Woolrich, & Smith, 2012; Woolrich et al., 2009; Smith et al., 2004) Version 5.0.2.1. Preprocessing steps, carried out using FEAT (fMRI Expert Analysis Tool; Woolrich, Behrens, Beckmann, Jenkinson, & Smith, 2004; Beckmann, Jenkinson, & Smith, 2003; Woolrich, Ripley, Brady, & Smith, 2001) Version 6.00, included slice-timing correction (using Fourier space time-series phase-shifting), high-pass temporal filtering (using Gaussian-weighted least-squares straight line fitting, with $\sigma = 50$ sec), spatial smoothing for the univariate analysis only (using a Gaussian kernel of FWHM = 8 mm), and grand mean intensity normalization of the entire 4D data set by a single multiplicative factor. Voxels belonging to brain tissue were extracted from nonbrain tissue voxels using the Brain Extraction Tool (Smith, 2002).

fMRI Analyses

Statistical analyses of the preprocessed data were conducted using a general linear model implemented in FEAT Version 6.00. For all first-level analyses, the time course of each regressor was convolved with the double gamma hemodynamic response function. Time-series statistical analysis was carried out using FILM (Woolrich et al., 2001) with local autocorrelation correction (prewhitening). Resulting contrast images were linearly registered to the high-resolution T1-weighted image using the BBR method of FLIRT (Jenkinson, Bannister, Brady, & Smith, 2002; Jenkinson & Smith, 2001) within the normal search space, then spatially normalized to the T1-weighted MNI-152 stereotaxic space template (2 mm) with 12 degrees of freedom within the normal search space.

For the bowling task, we distinguished two conditions: two levels of expectancy (expected vs. unexpected outcome). The trials related to the agent and outcome questions were combined and not analyzed separately. The onset of the events of interest in the bowling task corresponded to the end of the bowling animation, when the question appeared on the screen. Regressors of interest consisted of the "expected" and "unexpected" time courses. Nuisance regressors consisted of the filler trials, error trials, RTs (modeled as event duration relative to each trial's onset), the self-paced break during scanning, the six rigid body motion parameters, and the temporal derivatives of the convolved time courses for the filler trials, error trials, RT durations, and break. Contrasts of interest were "expected > unexpected" and "unexpected > expected," the latter contrast was named the effect of "expectancy." The higher level analysis (group mean) of the bowling task was carried out using FLAME (FMRIB's local analysis of mixed effects) Stages 1 and 2. Only voxels within the standard MNI-152 2-mm brain were included in the analysis. *Z*-statistic (Gaussianized T/F) images were initially thresholded using clusters determined by $Z > 3.1$ and a corrected cluster significance threshold of $p < .05$, controlling the family-wise error rate (Eklund, Nichols, & Knutsson, 2016; Worsley, 2002).

For the ToM task, we distinguished two conditions: false belief and false photograph. The onset of the events of interest was set to the moment the question appeared on the screen. Regressors of interest consisted of the "false belief" and "false photograph" time courses. Nuisance regressors consisted of the six rigid body motion parameters at the first level. One contrast of interest was analyzed "false belief > false photograph" and was named the effect of "theory of mind" (ToM). In the higher level analysis, the difference in RTs between the false belief and false photograph conditions (demeaned) was included as a nuisance regressor. The higher level analysis (group mean) of the ToM task was carried out using FLAME Stages 1 and 2. Only voxels within the standard MNI-152 2-mm brain were included in the analysis. *Z*-statistic (Gaussianized T/F) images were initially thresholded using clusters determined by $Z > 3.1$ and a corrected cluster significance threshold of $p < .05$, controlling the family-wise error rate.

Upon inspection of the first higher level results of both the bowling and ToM tasks, cluster sizes were deemed too large in extent at the cost of specificity. Therefore, to reduce the extent and increase the specificity of significant clusters, the thresholding was increased post hoc to be determined by $Z > 4.0$ and a corrected cluster significance threshold of $p < .05$, the results of which were used in all subsequent analyses.

In a follow-up analysis, we created a mask of the false belief > false photograph contrast from the ToM task and investigated a significant effect of the unexpected > expected contrast from the bowling task within this ToM mask. This higher level analysis was carried out using FLAME Stages 1 and 2. *Z*-statistic (Gaussianized T/F) images were thresholded using clusters determined by $Z > 4.0$ and a corrected cluster significance threshold of $p < .05$, controlling the family-wise error rate. Brain regions are based on the Harvard–Oxford Structural Atlas and the Mars TPJ connectivity-based parcellation atlas as part of FSL.

Single-subject and group-level unthresholded statistical maps of the conditions of interest and single-subject readouts of the overlapping ROIs of the bowling and ToM tasks are publicly available here: https://figshare.com/s/33125be1ac5d7d80819a.

Behavioral Analyses

For the bowling task, RTs to the questions that followed movies in which the outcome was 2 or 7 were analyzed using 2 (expected vs. unexpected) × 2 (agent question vs. outcome question) repeated-measures ANOVAs on accuracy and RTs as dependent variables of interest for the main analysis. Questions following movies with scores 1, 3, 6, and 8 were excluded from the analysis. Additionally, missing trials were excluded from both analyses, and incorrect answers were excluded from the RT analysis. Following our previous study (Heil et al., 2018), the three-way interaction between agent (novice vs. experienced), outcome (2 vs. 7 pins), and question (agent vs. outcome question) was additionally analyzed.

For the ToM task, the difference between the false belief and false photograph conditions was tested using repeated-measures ANOVAs (one factor with two levels) for accuracy and RTs as dependent variables of interest.

RESULTS

Behavioral Data Bowling Task

Based on the assumption that unexpected events result in prediction errors that require additional processing, RTs to questions following unexpected events (i.e., a novice player obtaining a high score or an experienced player obtaining a low score) were anticipated to be higher than those to questions following expected events (i.e., a novice player obtaining a low score or an experienced player obtaining a high score). The results of the bowling task show that this is indeed the case: Seen in the main effect of Expectancy, participants needed more time to answer questions that followed an unexpected outcome (M = 940.78 msec, SD = 166.52), compared with questions that followed an expected outcome (M = 917.17 msec, SD = 163.42), $F(1, 21) = 5.33$, $p = .031$, $\eta^2_G = .005$. In addition, there was a significant effect of Question, $F(1, 21) = 23.14$, $p < .001$, $\eta^2_G = .004$, with longer RTs for the agent question (M = 939.63 msec, SD = 163.90) than for the outcome question (M = 918.32 msec, SD = 166.21) but no significant interaction effect between Question and Expectancy, $F(1, 21) = 3.38$, $p = .080$, $\eta^2_G < .001$ (see Figure 3A).

The average accuracy was 96.1% over all nonmissing trials. On average, only 1.4% of trials was not answered within the time limit and thus counted as missing. The main effect of Expectancy was marginally significant with

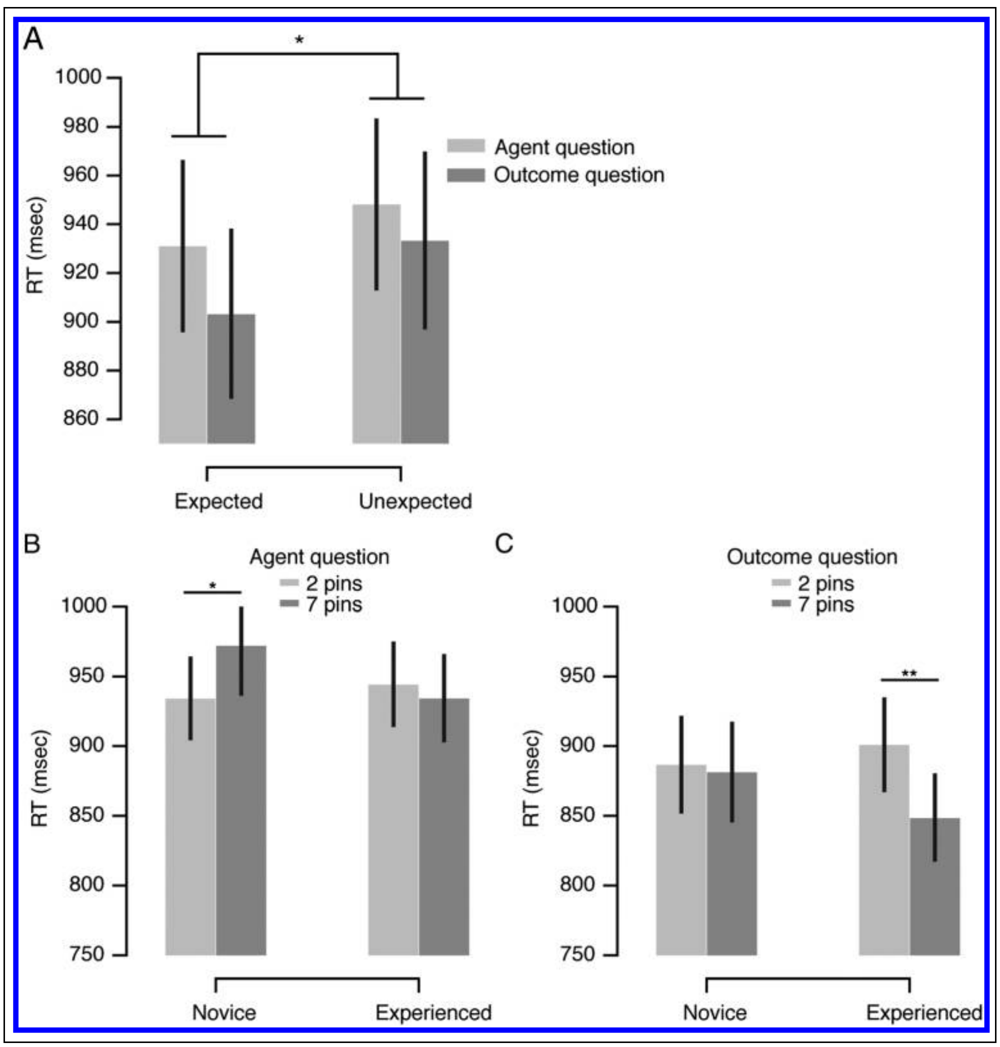

Figure 3. RT results for the bowling task. (A) RTs (mean ± SEM) to questions about the agent or the outcome following scores that were expected or unexpected given the agent's skill level. RTs for (B) the agent question and (C) outcome question, separately for bowler expertise level and outcome (scores 2 and 7). *$p < .05$, **$p < .01$.

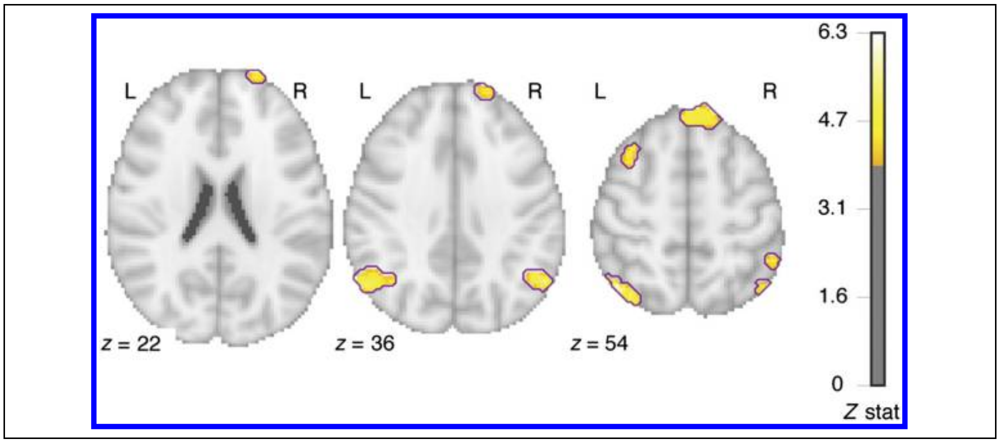

Figure 4. Significant clusters of BOLD activation for the unexpected > expected contrast of the bowling task. Results are cluster-level corrected using a family-wise error (FWE) rate of 0.05. Coordinates are in MNI space. Statistical maps with lower thresholds are publicly available (see Methods).

higher accuracy for expected trials (*M* = 96.8%, *SD* = 0.04) as compared with unexpected trials (*M* = 95.3%, *SD* = 0.06), $F(1, 21) = 4.17$, $p = .054$, $\eta^2_G = .022$. There was no difference between participants' accuracy for the agent question (*M* = 95.9%, *SD* = 0.05) as compared with the outcome question (*M* = 96.1%, *SD* = 0.05), $F(1, 21) = 1.20$, $p = .285$, $\eta^2_G < .001$. There was no interaction between the factors of Expectancy and Question for accuracy, $F(1, 21) = 0.06$, $p = .815$, $\eta^2_G < .001$.

Following our previous study (Heil et al., 2018), we additionally investigated the full three-way interaction between Agent, Outcome, and Question type for the RT data. The three-way interaction between Agent, Outcome, and Question was not significant in this data set, $F(1, 21) = 0.001$, $p = .975$, $\eta^2_G < .001$. Follow-up analyses showed that, for the agent question (Figure 3B), there was an interaction between Agent and Outcome, $F(1, 21) = 6.94$, $p = .016$, $\eta^2_G = .007$, as was previously obtained. Paired-samples *t* tests showed that, for the agent question, unexpected events resulted in higher RTs for the novice player, $t(1, 21) = 2.28$, $p = .033$; however, this was not the case for the experienced player, $t(1, 21) = 0.86$, $p = .399$. For the outcome question (Figure 3C), a trend toward an interaction between Agent and Outcome was present, $F(1, 21) = 3{,}77$, $p = .066$, $\eta^2_G = .006$. Paired-samples *t* tests showed that, for the outcome question, unexpected events resulted in higher RTs for the experienced player, $t(1, 21) = 3.18$, $p = .005$; however, this was not the case for the novice player, $t(1, 21) = 0.31$, $p = .762$.

Behavioral Data ToM Task

For the ToM task, accuracy data suggest that the task was sufficiently difficult. Participants scored on average 70.2% correct over all trials. Participants' accuracy scores were equal for the false belief (*M* = 70.4%, *SD* = 0.26) as compared with the false photograph condition (*M* = 70.0%, *SD* = 0.27), $F(1, 21) = 0.01$, $p = .907$, $\eta^2_G < .001$. Participants were slower to respond to the false belief trials (*M* = 2824.78 msec, *SD* = 229.94) as compared with the false photograph trials (*M* = 2683.91 msec, *SD* = 289.27), $F(1, 21) = 11.96$, $p = .002$, $\eta^2_G < .076$. Note the difference in RTs between the conditions on the ToM task was included as a (higher level) nuisance regressor in the fMRI analysis of the ToM data. Behavioral data for this task were not further analyzed, as there were no relevant questions related to these data.

fMRI Data Bowling and ToM Task

In the fMRI analyses of the bowling task, we tested whether the observation of unexpected outcomes causes additional activation as compared with expected outcomes, in line with the processing of prediction errors. In this whole-brain analysis, data for the question about the outcome and the question about the player were combined as the questions mostly served to ensure that participants would attend to all aspects of the scene and

Table 2. Significant Clusters of BOLD Activation for the Unexpected > Expected Contrast of the Bowling Task

Brain Region	*x*	*y*	*z*	*k*	*Z-stat*
Left inferior parietal lobe	−44	−64	54	729	6.30
Right inferior parietal lobe	54	−60	36	340	5.52
Right superior frontal lobe	10	38	58	196	5.19
Left middle frontal gyrus	−36	16	54	97	4.89
Right frontal pole	24	64	22	77	4.63
Right frontal pole	20	54	36	60	4.56
Left middle frontal gyrus	−48	16	46	40	4.81
Right inferior frontal lobe	50	−46	56	39	4.70

Results are cluster-level corrected using an FWE rate of 0.05. MNI coordinates (x, y, z) of local maxima for each cluster are given, including the cluster voxel extent (k) and the Z-statistic (Z-stat) at those coordinates.

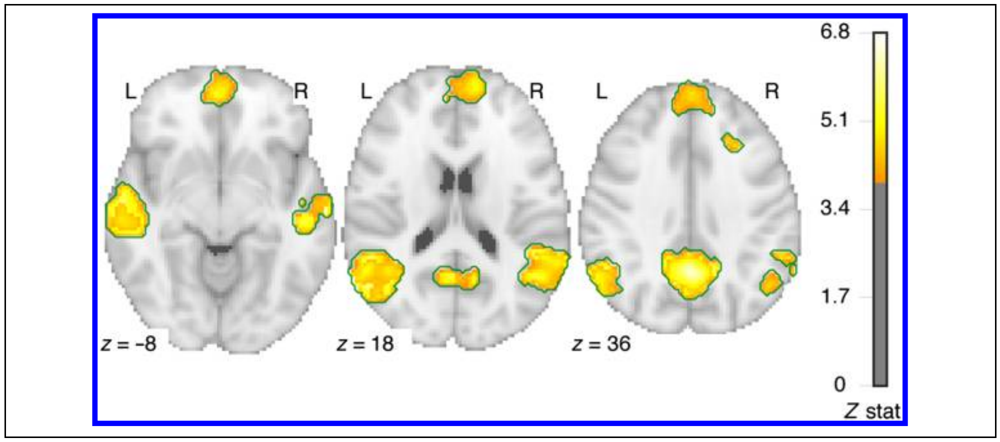

Figure 5. Significant clusters of BOLD activation for the false belief > false photograph contrast of the ToM task. Results are cluster-level corrected using an FWE rate of 0.05. Coordinates are in MNI space. Statistical maps with lower thresholds are publicly available (see Methods).

no interaction effect between question and expectancy was found in the behavioral analysis. Our main interest was in the unexpected > expected contrast, which revealed significant activation in the bilateral inferior parietal lobes, along the lateral occipital cortex and extending into the angular gyri, bilateral middle frontal gyri, the right superior frontal lobe, and the right frontal pole (see Figure 4 and Table 2). No significant clusters were obtained for the contrast expected > unexpected.

In the analyses of the ToM task, activation arising when participants read a story describing a false photograph was subtracted from the activation arising when they read a story describing a person holding a false belief. This false belief > false photograph contrast showed significant activation in the bilateral inferior parietal lobes, along the angular gyrus and extending into lateral occipital cortex, the bilateral middle temporal gyri extending into the temporal poles, the medial precuneus cortex, the medial paracingulate cortex, and the right inferior and superior frontal lobe (see Figure 5 and Table 3).

Furthermore, we analyzed whether activation related to unexpected events in the bowling task partly overlaps with activation in brain areas typically associated with social–cognitive processes, using the inclusive mask based on the functional data from the ToM task. This mask, based on the false belief > false photograph contrast, was assumed to reflect activity associated with social–cognitive processing. Using an inclusive masking approach, we investigated whether there were voxels within this ToM mask that were also significantly more active during the observation of unexpected as compared with expected events in the bowling task. The results (presented in Table 4 and Figure 6A–C) showed significant clusters in the bilateral angular gyri, including the TPJ, and the left middle temporal gyrus.

Effects of interest within ROIs (see Table 4) were investigated further at the single-subject level. Readouts of parameter estimates for the bowling task and the ToM task at the single-subject level are publicly available (see Methods). The conjunction between the expectancy and ToM effects was furthermore investigated at the single-subject level with contrasts thresholded at $p < .05$ and uncorrected for multiple comparisons. The number of conjunctive voxels ranged from 0 to 15,547 in MNI space (M = 2094.32, SD = 3525.16). Most participants (20/22) showed nonzero overlap between the expectancy and ToM effects.

Multivariate Analyses of the Expectancy and ToM Effects

The inclusive masking analysis of the expectancy effect within ToM ROIs resulted in the bilateral inferior parietal lobes and left middle temporal gyrus. It is possible that the information contained within these regions is content specific—in other words, the two contrasts of interest may share similar activation patterns. We hypothesized that the pattern of the multivariate response within the ROIs for the unexpected condition of the bowling task

Table 3. Activations for the False Belief > False Photograph Contrast

Brain Region	*x*	*y*	*z*	*k*	*Z-stat*
Right middle temporal gyrus	64	−18	−8	3839	6.54
Left precuneus cortex	−2	−66	40	2442	6.84
Left paracingulate gyrus	−6	54	−4	2054	5.74
Left middle temporal gyrus	−60	−12	−8	2043	6.06
Left inferior parietal lobe	−54	−64	18	1775	6.19
Right superior frontal lobe	24	24	40	196	5.59
Right inferior frontal gyrus	56	30	12	154	5.37

All results are cluster-level corrected using an FWE rate of 0.05. MNI coordinates (x, y, z) of local maxima for each cluster are given, including the cluster voxel extent (k) and the Z-statistic (Z-stat) at those coordinates.

Table 4. Activations for the Unexpected > Expected Contrast of the Bowling Task within the ToM Task Significant ROIs (False Belief > False Photograph Contrast)

Brain Region	*x*	*y*	*z*	*k*	*Z-stat*
Left inferior parietal lobe	−54	−62	40	191	5.63
Right inferior parietal lobe	54	−62	36	63	5.33
Left middle temporal gyrus	−62	−28	−12	15	4.21

All results are cluster-level corrected using an FWE rate of 0.05. MNI coordinates (x, y, z) of local maxima for each cluster are given, including the cluster voxel extent (k) and the Z-statistic (Z-stat) at those coordinates.

would be more similar to the false belief condition of the ToM task as compared with the expected condition.

First, the magnitude of the correlation of responses (parameter estimates) between the unexpected condition and the false belief condition was compared with that of the correlation of responses between the expected condition and the false belief condition across all voxels within significant clusters (see Table 4). The difference between correlations (normalized Pearson's coefficient) was significant (p = .003; nonparametric permutation test; Figure 7A). The pattern of results was in the hypothesized direction, namely with more similar responses for the unexpected condition versus the false belief condition as compared with the expected condition versus the false belief condition. Following this result, we repeated the same correlation analysis for each of the separate clusters (Figure 7B–D). The difference between correlations was significant within the left and right inferior parietal lobe clusters (p = .001 and p = .012 respectively), but not within the middle temporal gyrus cluster (p = .189). Notably, the left inferior parietal lobe cluster showed a negative correlation between the expected and the false belief condition (Figure 7B), whereas the right inferior parietal lobe cluster showed a positive correlation between the unexpected and the false belief condition (Figure 7C).

No Relationship between Brain Activation and AQ Scores

A correlation between the self-reported social experience of the participants, as measured by the AQ (M = 12.36, SD = 4.77, range = 3–21), and brain activation for the contrasts of interest would provide evidence for a direct link between social processing and region-specific brain activation. The AQ score has previously been linked to brain activation and structure in a nonclinical sample (Von dem Hagen et al., 2010).

Activation within the voxels defined by the expectancy effect within the ToM ROIs (parameter estimates) was averaged for the false belief > false photograph contrast (M = 38.78, SD = 33.34, range = −60.99 to 104.69) and the unexpected > expected contrast (M = 17.84, SD = 15.58, range = −16.06 to 49.38). Multiple linear regression (ordinary least squares) was used to predict AQ score based on the normalized expectancy and ToM activation. The regression model was not significant, $F(2, 19) = 0.40$, p = .677, with an R^2 of .040.

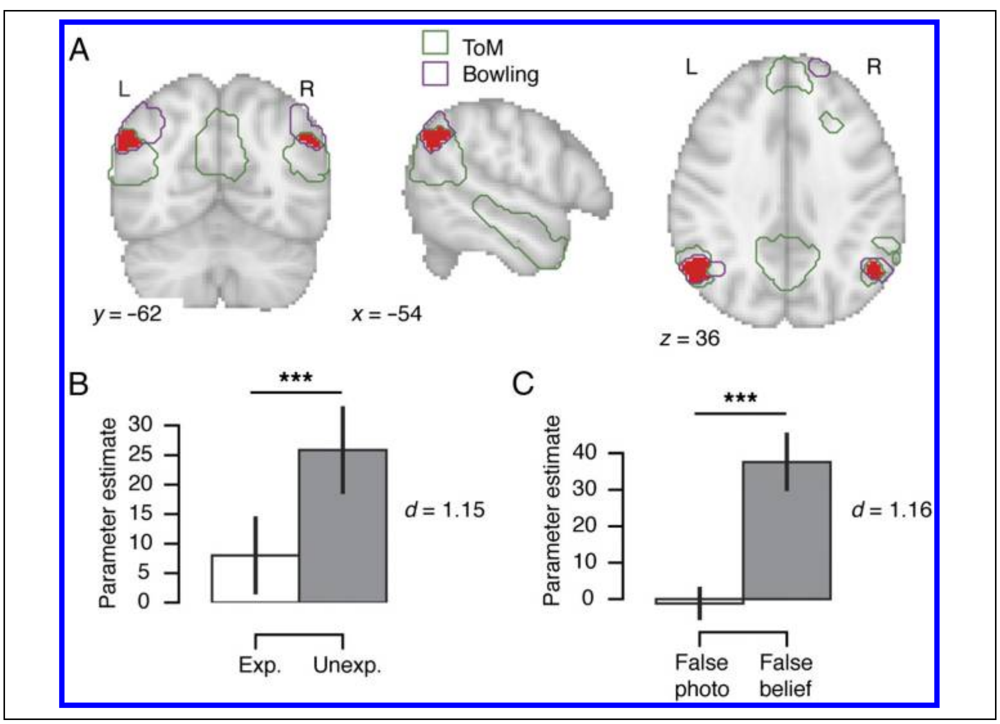

Figure 6. Conjunction of BOLD responses for bowling and ToM tasks. (A) Significant clusters for the unexpected > expected contrast of the bowling task (purple) and the false belief > false photograph contrast of the ToM task (green). The significant clusters from the inclusive masking analysis of the unexpected > expected contrast of the bowling task within the ToM ROIs are indicated in red, and within these clusters the readouts of parameter estimates for (B) the bowling task and (C) the ToM task. Cohen's d indicates effect size for the difference between conditions. Coordinates are in MNI space. ***p < .001.

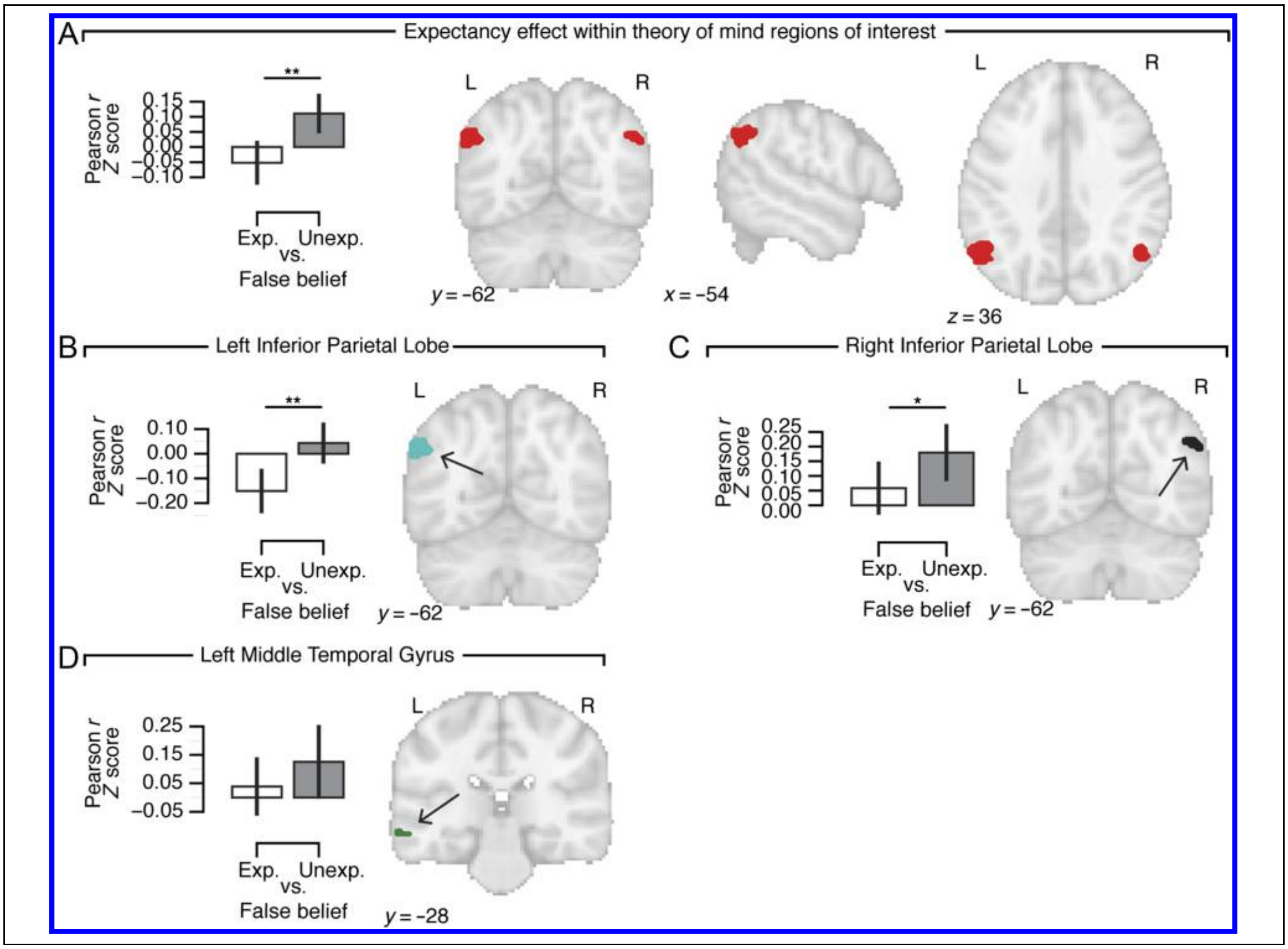

Figure 7. Multivariate analysis of similarity within ROIs. Conditions of interest were expected (Exp.) versus false belief and unexpected (Unexp.) versus false belief responses (parameter estimates of activity). (A) Similarity analysis across all voxels within the significant clusters of the inclusive masking analysis (expectancy effect within ToM ROIs) and within each separate cluster as a post hoc ROI, (B) left inferior parietal lobe, (C) right inferior parietal lobe, (D) left middle temporal gyrus. *p < .05, **p < .01.

DISCUSSION

In this study, we investigated the processing of outcomes that are unexpected given prior knowledge about the person performing the action. There are two main findings. First, the results of this experiment show increased neural activity in a network of regions when participants saw an animated bowling player obtaining a higher or lower score than expected: the bilateral inferior parietal lobes, along the lateral occipital cortex and extending into the angular gyri, bilateral middle frontal gyri, the right superior frontal lobe, and the right frontal pole. Second, comparing the activity arising during this bowling task with that arising during a ToM task, we found that several brain regions were implicated: the bilateral angular gyri including the TPJ, and the left middle temporal gyrus. Within these regions, neural activity increased not only when participants considered the false beliefs of another person, but also when they observed unexpected outcomes.

The finding that the TPJ shows increased activity during the processing of unexpected outcomes as well as during the processing of other people's false beliefs suggests that observation of outcomes that are expected or unexpected given previous experiences with the person performing the action involves higher level social–cognitive processes. The TPJ has been pinpointed as one of the core areas in the mentalizing network, a network of areas involved in the processing of social information (Frith & Frith, 2006; Saxe & Kanwisher, 2003). As this area is not only recruited when people read stories about the thoughts or behavior of other people but also during the bowling task used in this experiment, it seems that online observation of agent's actions and their consequences activates knowledge or processes also engaged when mentalizing about imagined scenarios.

Some have suggested that the TPJ is specifically involved in thinking about another person's thoughts (Saxe & Powell, 2006), although the area has also been found to be active during more general attention-related tasks, which has inspired alternative theories about its functions. For instance, it has been suggested that there are different clusters within the TPJ—one involved in attention and the other in social processing (Krall et al., 2015; Mars et al., 2011). It has also been suggested that the area may be primarily involved in reorienting attention and that it is also active during tasks requiring social cognition, because such tasks involve reorienting of attention and other more domain-general processes (Van Overwalle & Baetens, 2009; Corbetta, Patel, & Shulman, 2008; Decety & Lamm, 2007; Mitchell, 2007). Our findings do not distinguish between these different theories and do therefore not imply that the processes involved are necessarily uniquely social. It is well known that the angular gyrus is considered a multisensory hub (Seghier, 2013). Furthermore, the lack of correlation obtained here between the AQ scores and brain activation (for the effects of ToM and expectancy) might further support the notion that processing in this TPJ region is not specific to social processing but more generally related to expectancy, which depending on context may include expectations about social agents and actions (Von dem Hagen et al., 2010).

Importantly, however, the outcomes are only unexpected based on participants' prior experiences with the bowling player: Knowing that a player is experienced makes a low score unexpected. The outcomes themselves are equally frequent, and our results can therefore not be explained by an overall difference in frequency. One possibility is that participants predict the score based on the association between the player and his identifying color. As we have shown in a previous study, the expectancy effect found in the bowling task seems to not only require associating a color and a score but also the causal relation between the two (Heil et al., 2018). In that study, we found that when participants see a player throw a bowling ball toward the pins and the causality of the score is attributed solely to a color (i.e., there is no association between the player and the color), there is no effect of expectancy. Knowing that the "player" causes the ball to move toward the pins and knock them over is necessary for people to predict the score based on which person is currently playing. This suggests that the areas activated are involved in more abstract, higher order processes that support predictions about outcomes based on knowledge about a person. However, in the current study, we did not perform a strict control for the proposed hierarchical prediction order between agent and performance as in the discussed the article by Heil et al. (2018). Thus, alternatively, the found activity could be related to a more contextual cue such as the player–color association.

The finding that observation of outcomes that are unexpected given previous experiences with the person performing the action causes increased neural activity is in line with the idea that prediction errors play a key role in cognitive processing. As such, it is also in agreement with previous studies showing that the processing of unexpected events requires more resources in terms of time (e.g., O'Reilly et al., 2013) and neural activation (Summerfield et al., 2008). A potential interpretation of these findings is that there is a common mechanism involving the integration of prediction errors that underlies not only the processing of observed behavior that is unexpected given prior knowledge about that specific person but also the processing of unexpected events in general. This hypothesis is supported by the fact that the multivariate response during the unexpected condition of the bowling task was more similar to the false belief condition of the ToM task, as compared with the expected condition. We suggest that a more in-depth investigation into the similarity of the Expectancy to ToM patterns, and their spatial distribution, is an interesting avenue for follow-up studies using representational similarity analysis or decoding of unexpected versus expected events related to social processing.

The idea of a general prediction error integration mechanism is a central assumption of the predictive processing framework, which has been posed as a unifying framework for brain functioning (Clark, 2013; Friston, 2005). In this framework, it is assumed that incoming information is compared with predictions and that potential prediction errors arising from this comparison are then used to update the generative models underlying these predictions. In this sense, cognitive processing is primarily focused on this integration of prediction errors. Although the idea that this framework can explain perceptual inference is gaining acceptance, there is no consensus on whether it can also explain more abstract, social processing (e.g., Koster-Hale & Saxe, 2013). Our findings are in line with this last idea, but they do not distinguish between the predictive processing and other frameworks. For instance, based on an account in which probabilistic inference takes place after rather than before the observation of the events, one could assume that inference of a less probable event requires more processing resources than inference of a more probable event, resulting in increased activity in trials that we labeled as "unexpected." Based on such an account, we would indeed predict similar results, but whereas the predictive processing framework assumes that this additional processing is required to explain away prediction error, it is unclear which mechanism requires additional processing in case of such nonpredictive type of probabilistic inference. Because the posterior probability of the causes is conditioned on the observed event, it is computationally no longer relevant whether the event was likely or unlikely.

Furthermore, it seems that the predictive processing framework could actually be seen as complementary to several other accounts of human cognition. Especially associative theories are sometimes suggested to compete with the predictive processing framework, but they might not necessarily oppose it. As Press, Heyes, and Kilner

(2011) suggest, for example, the associative sequence learning model and the predictive processing framework seem to address related but different questions. Associative sequence learning, on the one hand, explains how relations are learned, whereas predictive processing, on the other hand, explains how learned relations support inferences about other people's actions and their outcomes. Moreover, associative sequence learning assumes that events are associated when their occurrence follows the principles of the Rescorla–Wagner model (Cooper, Cook, Dickinson, & Heyes, 2013). According to this model, learning does not take place because two events simply co-occur, but because this co-occurrence is unexpected and thus results in a prediction error (Rescorla & Wagner, 1972).

Finally, we address some limitations of the current study. First, although action outcomes are often unexpected given the observed kinematics, we did not consider kinematic differences in this study. The movies showed both players moving in similar ways, so that we could control for the effect of kinematics and investigate whether differences in behavior and brain activity were really the result of differences in knowledge about the skill level of the players. This is a relatively high-level process, whereas the prediction of action outcomes given kinematics is a more low-level process (Kilner, 2011). Future studies could match the kinematics of players with their skill levels and investigate the role of kinematics in the processing of unexpected action outcomes. A second, related limitation is that the prior knowledge that participants could use to predict the outcome was based on "stories" about the agent in the sense that they were told whether the agent was a novice or an experienced player. This is similar to previous studies (e.g., Dungan et al., 2016; Mende-Siedlecki et al., 2012; Ma et al., 2011) in which an increase in brain activity was found in response to descriptions of a person's behavior that did not match previous descriptions of that person. Although participants in this study also built up experience with the two players and their average scores, it was not investigated whether people also build up expectations about another person's future actions (and the outcomes of these actions) based solely on previously observed behavior. The current study provides evidence that a more sophisticated multivariate pattern analysis approach would be fruitful in future studies specifically designed (e.g., condition-rich designs; Kriegeskorte, Mur, & Bandettini, 2008) to investigate the type of information being encoded during the processing of prediction errors in mentalizing regions.

To conclude, the findings of the current study are in line with the idea that prediction errors play a key role in the processing of outcomes that are unexpected given prior knowledge about a person and that part of these prediction errors is integrated in brain areas typically associated with social–cognitive processes, although lower-level associative mechanisms cannot be ruled out. Future research will need to determine whether context-specific social–cognitive processes are indeed built upon general predictive principles that have been attributed to more low-level processing.

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