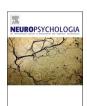
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The effect of incorrect prior information on trust behavior in adolescents

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ABSTRACT

During adolescence, social cognition and the brain undergo major developments. Social interactions become more important, and adolescents must learn that not everyone can be trusted equally. Prior knowledge about the trustworthiness of an interaction partner may affect adolescents' expectations about the partner. However, the expectations based on prior knowledge can turn out to be incorrect, causing the need to respond adaptively during the interaction. In the current fMRI study, we investigated the effect of incorrect prior knowledge on adolescent trust behavior and on the neural processes of trust. Thirty-three adolescents ($M_{age} = 17.2$ years, SD_{age} = 0.5 years) played two trust games with partners whose behavior was preprogrammed using an algorithm that modeled trustworthy behavior. Prior to the start of both games, participants received information suggesting that the partner in one game was untrustworthy (raising incorrect expectations) and the partner in the other game trustworthy (raising correct expectations). Results indicated that participants adapted their trust behavior following incorrect prior expectations. No evidence for a change in trust behavior was shown when prior expectations were correct. fMRI analyses revealed that when receiving the partner's response, activity in the dorsolateral prefrontal cortex and in the superior parietal gyrus were increased when participants had incorrect expectations about the partner compared to when participants had correct expectations. When making trust decisions, no significant differences in neural activity were found when comparing the two games. This study provides insight into how adolescent trust behavior and neural mechanisms are affected by expectations and provides an increased understanding of the factors that influence adolescent social interactions.

1. Introduction

During adolescence, major changes in socio-cognitive processes take place and these developments are associated with functional and structural changes in the brain (Kilford et al., 2016). At the same time, social interactions and peer relationships become more important (Brown and Larson, 2009; Erdley and Day, 2017). Socio-cognitive processes, such as learning to trust and responding adaptively to the intentions and feedback of others, are essential for successful social interactions and social relationships (Lewicki and Wiethoff, 2000). The initial trust we place in others at the start of an interaction may be affected by prior knowledge about the other person. Sometimes, the prior knowledge may be incorrect, causing the need to adapt trust behavior during the interaction. The neural processes underlying the

effect of expectations on trust have only been investigated in adults (Delgado et al., 2005; Fareri et al., 2012; Fouragnan et al., 2013; Phan et al., 2010), whereas adaptive trust behavior may be particularly important during adolescence as many new relationships are formed during this period. To gain more insight into the effects of expectations on trust during social interactions in adolescents, we examined the effect of incorrect prior information about a partner's trustworthiness on trust behavior and on the related neural processes in a group of adolescents.

A well-known experimental paradigm to examine trust behavior during social interactions is the trust game (Berg et al., 1995). This game simulates a social interaction in which two players share money across one or multiple rounds on the basis of trust. In each round, the participant (the trustor) allocates an amount of money between themselves and the partner (the trustee) during the investment phase. The amount of

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money that is shared with the partner is called the investment and tripled before the partner receives it. The investment is indicative of trust behavior. Next, during the feedback phase of the game, the partner decides on the amount of money to return to the trustor and keeps the remainder for themselves. The return is indicative of reciprocal behavior, and this is expected to influence the trustor's trust decision (i. e., investment) in the next round. Using this game, several studies have shown that adolescence is an important period for the development of trust behavior. Results of some of these studies indicate that with age, adolescents show more initial trust at the start of the trust game and adolescents are increasingly more able to fine-tune their trust behavior in response to the trustworthiness of their interaction partner (Lee et al., 2016 [ages 12–18]; Sutter and Kocher, 2007 [ages 8–68]; Van den Bos et al., 2012 [ages 11–21]; Van den Bos et al., 2010 [ages 9–22]).

The neural mechanisms of trust in adults and (late) adolescents have been investigated in multiple studies and results have shown the contribution of brain areas that are generally known for their involvement in mentalizing, social reward and learning processes, and cognitive control processes (Alós-Ferrer and Farolfi, 2019; Krueger and Meyer-Lindenberg, 2019). Mentalizing processes play a role during the trust game, as it is essential to understand the thoughts and intentions of the other player in order to anticipate their behavior (Krueger and Meyer-Lindenberg, 2019). Previous studies in young adults and adolescents that used the trust game have demonstrated the engagement of brain areas such as the medial prefrontal cortex (mPFC) and the temporoparietal junction (TPJ), which have both been related to mentalizing (Fareri et al., 2020 [ages 21-32]; Fett et al., 2014 [ages 13-49]; Fujino et al., 2020 [mean age 27]; Lemmers-Jansen et al., 2019 [ages 13-19]; Lemmers-Jansen et al., 2017 [ages 16-27]), and have found age-related changes in TPJ activity (Fett et al., 2014 [ages 13-49]; Lemmers-Jansen et al., 2017 [ages 16–27]). Furthermore, other studies investigating socio-cognitive processes indicated that activity levels in the TPJ are increased in adults (>18 years) compared to adolescents (10-17 years), while the mPFC is more activated in adolescents (9-18 years) than in adults (>18 years) (Blakemore, 2008). Differential behavior and mPFC activity between adolescents and adults was also indicated in a study by Somerville et al. (2013) in which the results revealed an inverted-U shape pattern where adolescents (13-19 years) showed increased self-reported self-embarrassment and increased mPFC activity (the peak was around 17.2 years) compared to children (7-12 years) and adults (20-24 years).

Additional to mentalizing processes, reward and learning processes are also involved in the trust game, as the feedback behavior of the partner is integrated with available and relevant information about the partner to ultimately learn what the partner is like (Krueger and Meyer-Lindenberg, 2019). Meta-analytic evidence on the trust game showed increased ventral striatum activity during decisions to trust, while activity in the caudate was increased when receiving the partner's response (Bellucci et al., 2017). Both areas have been related to (associative) learning and reward processes in social settings and show developmental changes in activity levels across adolescence into young adulthood (Cox and Witten, 2019; Joiner et al., 2017; Knutson and Cooper, 2005; Lutz and Widmer, 2014; Suzuki and O'Doherty, 2020). Also, age-related changes in caudate activity during adolescence into adulthood have been found in studies using the trust game (Fett et al., 2014 [ages 13-49]; Lemmers-Jansen et al., 2017 [ages 16-27]). Using a different task, focused on prediction error signaling, it was found that activity in the ventral striatum was higher in adolescents (14–19 years) compared to children (8-12 years) and adults (25-30 years) (Cohen et al., 2010).

Furthermore, cognitive control processes are necessary to store and retrieve information about the partner during the trust game, and to keep track of conflicting information in order to flexibly adapt one's own goal-directed behavior (Krueger and Meyer-Lindenberg, 2019; Megías et al., 2017). Multiple studies have shown the engagement of the dlPFC during the trust game, which is an important brain area that is part of the

cognitive control system (Feng et al., 2021 [mean age 26]; Krueger and Meyer-Lindenberg, 2019; Lemmers-Jansen et al., 2017 [mean age 21]; Menon and D'Esposito, 2022). Age-related increases in dlPFC activity have been found when using the trust game (Lemmers-Jansen et al., 2017 [ages 16–27]). Using a different task, a quadratic pattern of feedback learning performance and dlPFC activity was found across adolescence into early adulthood (8–27 years, leveling off around 18–20 years), indicating that complex cognitive control processes and related brain areas show developmental changes across adolescence into young adulthood (Peters et al., 2016). Activity within the regions engaged in the trust game (such as the mPFC, TPJ, ventral striatum, caudate, and dlPFC) has also been reported in various other social decision-making paradigms than the trust game, underscoring their involvement in socio-cognitive processes (Joiner et al., 2017; Suzuki and O'Doherty, 2020).

The design of the trust game enables the implementation of experimental manipulations. This allows the investigation of the nuances of social interactions, such as the relative influence of prior information about the partner's trustworthiness versus the influence of the partner's actual reciprocal behavior during the game on the behavior of the trustor. The use of prior information to manipulate the partner's reputation has been successfully operationalized in previous studies in adults, which showed that the presence and content (trustworthy, untrustworthy, neutral) of prior information elicited differential neural activity (Delgado et al., 2005 [mean age 26]; Fareri et al., 2012 [mean age 22]; Fouragnan et al., 2013 [mean age 29]; Phan et al., 2010 [mean age 30]). Providing prior information about the partner's trustworthiness may result in a discrepancy between the trustor's expectations about the partner and the actual partner behavior during the game, for example, when the prior information is incorrect. When such discrepancy is recognized, the trustor needs to adapt their trust behavior accordingly. Detecting such a discrepancy and responding accordingly requires socio-cognitive processes and cognitive control processes, such as mentalizing and the adjustment of thoughts and actions, which undergo major development throughout adolescence (Blakemore, 2012; Crone and Dahl, 2012; Kilford et al., 2016; Luna et al., 2015). This makes adolescence a phase of life during which it is of particular interest to examine the ability to adaptively deal with complex social interactions. Limited research has been done in adolescents on the effect of incorrect prior information about the partner's trustworthiness on trust behavior. A behavioral study by Lee et al. (2016) showed that late adolescents (16-18 years) and mid-adolescents (14-15 years) were more flexible in changing their trust behavior in response to incorrect prior information compared to young adolescents (12-13 years). The question of the effect of incorrect prior information on trust-related neural processes in adolescents remains to be investigated.

In the current study, we used two trust games to investigate the effect of incorrect prior information on trust behavior and on the related neural activity in adolescents. In both games, unbeknownst to the participants, the interaction partner's behavior was determined by the same algorithm that modeled trustworthy behavior. Prior to the start of each game, participants were provided with information about how the partner behaved during previous trust game rounds. We expected that this information would influence the adolescents' expectations about how the partner would behave during the subsequent trust games rounds. In one game, the prior information and the actual partner behavior were consistent, as the information described the partner's behavior as trustworthy, and the algorithm that determined the partner's behavior over the course of the game modeled trustworthy behavior (this was called the consistent condition). In the other game, the prior information and the actual partner behavior were inconsistent, as the information suggested the partner was untrustworthy, while the preprogrammed partner's behavior was trustworthy (this was called the inconsistent condition). Due to the inconsistency between the prior information and the actual behavior in the inconsistent condition, we hypothesized that, compared to the consistent condition, the

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inconsistent condition would elicit lower initial trust behavior (indicated by a lower starting investment during the first trust game trial) and greater adaptation of trust behavior over the course of the game (indicated by a stronger increase of investments across trials). Furthermore, using a region-of-interest approach, we investigated neural activity within a priori defined regions based on previous studies that used the trust game and examined the involvement of cognitive processes (mentalizing processes, reward and learning processes, and cognitive control processes) and the related brain areas (Bellucci et al., 2017; Krueger and Meyer-Lindenberg, 2019). We tested the hypothesis that the investment phase and the feedback phase of the inconsistent condition, in comparison to the investment phase and the feedback phase of the consistent condition, would result in increased activity in areas related to social learning and cognitive control (ventral striatum, caudate, dlPFC). This was hypothesized because the partner's behavior in the inconsistent condition can be experienced as unexpected, requiring more learning and cognitive control processes to adapt one's own behavior accordingly. Furthermore, we hypothesized that the investment phase and the feedback phase of the inconsistent condition, compared to the investment phase and the feedback phase of the consistent condition, would result in increased activity in areas related to mentalizing (mPFC, TPJ), as the inconsistency between the prior information and the actual behavior may result in greater uncertainty to understand the partner's intentions and mental states. We expected similar brain areas to be involved in the investment phase and the feedback phase of the game because findings of previous studies indicated that cognitive processes and related brain areas overlap between both phases of the game (King-Casas et al., 2005; Redcay and Schilbach, 2019).

2. Methods

2.1. Participants

The participants were recruited from the fifth-year level at a high school in The Netherlands (N=38). Participants received £15.00 for participation and an additional monetary payout. Based on the algorithms used, the minimum amount of the payout that could be earned was £7.00 and the maximum amount was £20.00. In the trust game,

participants were playing with euros so the payout, which was based on the earnings of an arbitrary trust game trial, was directly added to the €15.00 that participants already received for participation. Of the 38 participants, two participants were excluded due to too much head movement during fMRI scanning (>3 mm), two participants were excluded because they erroneously did the same condition twice, and one participant was excluded because the participant did not seem to be aware that the returned amount of money was supposed to be from a collaborating peer and related to their own investment. Instead, the participant stated after scanning and reported on the post-scanning questionnaire, that the investments were based on telephone numbers and postal codes. As a result, 33 participants ($M_{age} = 17.2$ years, $SD_{age} =$ 0.5 years, age range = 16.1-18.3, 25 female) were included in the analyses. The study was approved by the Scientific and Ethical Review Board of the Faculty of Behavioral and Movement Sciences of the Vrije Universiteit Amsterdam.

2.2. Materials

2.2.1. Trust game

Participants played two conditions of the trust game (in counterbalanced order). They were told that they would play games with sameaged peers that were being scanned at another scanning location. In reality, the behavior of both interaction partners was modeled by a preprogrammed algorithm. Each game consisted of twenty experimental trials and twelve control trials in randomized order (see Fig. 1). An experimental trial started with a cue to invest (3 s). Next, the participant made an investment between zero and ten euros by using their index finger to move the cursor and to select a number (maximum duration of 4 s). Once the investment was made, the next screen was shown that presented the investment (2 s). The investment was tripled before it was received by the partner. A waiting period followed (2-4 s) and, next, a fixation cross was presented (0.5 s). Next, the partner's return was shown (3 s), followed by a screen that showed the total earnings for each player for the specific trial (3-5 s). A fixation cross was inserted (0.5 s) before the next trial started. During control trials, the participant was instructed to select a specified number (this number was between zero and ten and randomly selected). A control trial started with a cue (3 s). Next, similarly to making an investment during the experimental trial,

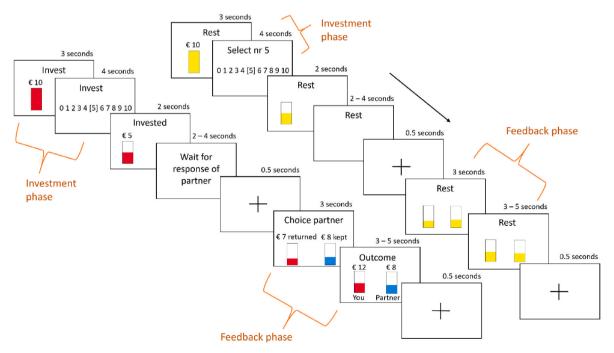


Fig. 1. The trust game. An experimental trial (left) and a control trial (right). The seconds above the screens indicate the durations of the screens.

the participant moved the cursor to the specified number (maximum duration of 4 s). After pressing, a screen was shown that presented the selection (2 s). A waiting period followed (2–4 s) and a fixation cross was presented (0.5 s). Similar to the experimental trials, this was followed by a screen that showed colored bars that displayed the selected number (3 s), and this was followed by another screen that displayed colored bars in which the colored part was increased compared the previous screen (3–5 s). The control trial ended with a fixation cross (0.5 s). Experimental trials targeted a social interaction, while control trials were not based on any type of social interaction nor contained any information related to a social interaction. This design is comparable to the trust game used in previous fMRI studies (Fett et al., 2014; Hanssen et al., 2021; Lemmers-Jansen et al., 2017, 2019). The task was presented in Presentation® software (NeurobehavioralSystems).

Participants were told that they would play two games with peers that were being scanned at another scanning location. The behavior of both partners was determined by the same algorithm that modeled trustworthy behavior. So, the same algorithm was used in both conditions. The specifics of the algorithm is detailed below.

For each experimental trial, the return of the partner was based on the participant's investment multiplied by a predefined factor. The factor for the first trial was 1.0, 1.1, 1.2, 1.3, 1.4, or 1.5, where each factor had a chance of 1/6th to be selected. For the remaining nineteen trials, the value of the factor changed based on whether the trustor increased or decreased their investment compared to the previous trial. In case of an increase in the investment, the value of the factor increased with 0.05. In case of a decrease in the investment, the value of the factor decreased with 0.05. The value of the factor for these nineteen trials could not go below 1.0 and not go above 1.6. In other words, the partner's return was at least as high as the participant's investment.

2.2.2. Trust game questionnaire

Participants completed a trust game questionnaire after scanning. They rated the trustworthiness of both partners (on a scale from one to seven) and were asked about what they thought the goal of the study was and if they noticed anything remarkable about the partners.

2.3. Procedure

Participants visited the MRI scanning location together with their parent(s)/caregiver(s) and provided active written informed consent. Participants were informed that they would play games with same-aged peers that were being scanned at a different scanning location and that they would receive €15.00 for participation and an additional monetary payout. Then, participants laid down in a mock scanner to become familiarized with the scanning environment. Next, using a computer, three acquaintance rounds with each partner were played in a separate testing room. In these rounds, the participant made an investment between zero and ten euros but the partner's return was not yet revealed. After these acquaintance rounds, the participant laid down in the MRI scanner and was told a connection was going to be made to the other scanning location. During this time, the participant saw a screen with the text 'connecting'. After a few seconds, the participant was informed that the connection had been established successfully. They were then shown the information about the first partner's returns during the acquaintance rounds. In the consistent condition, this information was formulated as 'the partner always returned more than the investments you made'. This is the consistent condition because the prior information suggested a trustworthy partner and the actual behavior during the trust game was also trustworthy (see 2.2 Materials). In the inconsistent condition, the information was formulated as 'the partner never returned more than the investments you made'. This information gave the impression that the partner was untrustworthy while the actual behavior throughout the trust game was trustworthy (see 2.2 Materials), hence the name inconsistent condition. We will refer to this information as the 'prior information' about the partner's trustworthiness. After

showing the prior information about the first partner, the first trust game was played. When the first trust game was finished, the prior information about the second partner was shown and the second trust game was played. The order of the conditions was counterbalanced. Participants completed a trust game questionnaire (see 2.2 *Materials*) outside the scanner after finishing the task and were debriefed via e-mail about the research aims after all data collection for the study had been completed.

2.4. Behavioral data analyses

2.4.1. Manipulation checks

A multi-level model was used to verify that the prior information presented between the acquaintance rounds and the start of the trust game had the intended effect. Trial served as the predictor variable (4 levels: acquaintance round 1, acquaintance round 2, acquaintance round 3, and the first trust game trial) and the investments as the dependent variable. A Helmert contrast was used to test whether the investment during the first trust game trial in the consistent condition was higher compared to the investments made during the acquaintance rounds. A similar model was set up for the inconsistent condition to test whether the investment during the first trust game trial was lower than the investments made during the acquaintance rounds. Additionally, a dependent t-test was used to examine whether the investment during the first trial in the inconsistent condition was lower compared to the investment during the first trial in the consistent condition. Furthermore, differences in the trustworthiness of both partners reported on the trust game questionnaire were tested using a dependent t-test.

2.4.2. Behavioral analyses

A multi-level model was used to examine the effect of incorrect prior information on trust behavior throughout the game (performed in R version 4.1.1 using the *lme4* and *lmerTest* packages) (Bates et al., 2015; Kuznetsova et al., 2017; RCoreTeam, 2020). Using multi-level models, the mean starting point in investments can be captured by a fixed intercept, while individual differences in starting points can be accounted for by a random intercept. Similarly, the mean trajectory of change in investments is modeled by a fixed slope, while a random slope accounts for individual differences in the change in investments.

The model fitting procedure included multiple steps in which fixed or random effects were added. The effects were kept in the consecutive model only when the model fit improved as a result of adding the effects. The current design included repeated measurements of the same participant over trials in two conditions. The investments served as outcome variable. The maximum likelihood estimation method was used to fit the models. Model comparison was done using the likelihood ratio test. Models were regarded significantly better if the p-value of the log likelihood ratio test was lower than .05 (p < .05). Akaike Information Criterion (AIC) values and Bayesian Information Criterion (BIC) values were provided for completeness (lower values indicate a better model fit).

First, a null model consisting of a random intercept for the level condition and the level participant was fitted (without fixed effects). The first level of the model is the level of time (i.e., trials), the second level is the level of condition, and the third level is the level of participant. In model 1, the linear main effect of time, the main effect of condition, and the interaction between the linear effect of time and condition were added as fixed effects. When the fit of model 1 was significantly better than the fit of the null model, we continued fitting model 2. In model 2, the quadratic main effect of time, the main effect of condition, and the interaction between the quadratic effect of time and condition were added as fixed effects. When the fit of model 2 was significantly better than the fit of the model 1, we continued fitting model 3. In model 3, a random slope for time at the level of condition and the level of participant were added.

2.5. MRI data acquisition

MRI scans were acquired using a Philips 3 T Achieva MRI scanner. For each participant, fMRI data were collected during two experimental runs of T2*-weighted EPI. The runs consisted of a minimum of 317 and a maximum of 350 scans, depending on the task duration (repetition time (TR) = 2 s, echo time (TE) = 54 msec, ascending sequential acquisition, 37 slices, gap thickness = 0.3 mm, field of view (FOV) = 240 \times 240 \times 122 mm, voxel size = 3 \times 3 \times 3 mm). A T1-weighted 3D multishot TFE anatomical scan was acquired (TR = 8 msec, TE = 3.9 msec, 220 slices, FOV = 240 \times 188 \times 220 mm, voxel size = 1 \times 1 \times 1 mm).

2.6. Preprocessing fMRI data

fMRI analyses were done using Statistical Parametric Mapping 12. For preprocessing, all functional images were realigned using a rigid body transformation with a least squared difference method between consecutive images. Then, the structural image was co-registered to a realigned mean functional image. Next, the structural image was segmented, and normalization parameters were estimated using unified segmentation. These parameters were used to transform the functional images and the structural image into Montreal Neurological Institute (MNI) space. Last, smoothing was applied on normalized functional images using an 8 mm Gaussian kernel full width at half maximum.

2.7. ROI definition

Regions of interest (ROIs) were based on review studies and a meta-analysis of the trust game literature and on an individual trust game studies carried out in adolescents. The left ventral striatum (x, y, z = -2, 2, -6) and right caudate (x, y, z = 12, 18, -4) were included based on the results of a meta-analysis by Bellucci et al. (2017). Furthermore, the mPFC, TPJ, and dlPFC were included based on two recent review studies on trust games (Alós-Ferrer and Farolfi, 2019; Krueger and Meyer-Lindenberg, 2019). The specific coordinates of these regions were based on trust game studies in adolescents (mPFC: x, y, z = 0, 42, 6; right TPJ: x, y, z = 45, -43, 32; right dlPFC: x, y, z = 51, 18, 30) (Lemmers-Jansen et al., 2017, 2019). An 8 mm sphere was created around the coordinates of the mPFC, TPJ, and dlPFC. A 5 mm sphere was created around the coordinates of the ventral striatum and the caudate because of their small size and their position near the ventricles. Coordinates of the ROIs are presented in MNI space (see Fig. 3B).

2.8. MRI data analyses

We carried out two types of MRI analyses. The first type of analysis was based on average neural activity during the experimental trials relative to the control trials (detailed in the next paragraphs). In line with the behavioral analyses that examined changes in investments during the task, a second type of analysis was set up to examine time-related changes in neural activity. For this, the trials of the task were modeled in two blocks (that is, the first half of the trials and the second half of the trials) and the average neural activity per block was analyzed and compared to each other. Details on this additional analysis can be found in the supplementary materials A.

For the first type of analysis, a general linear model (GLM) was set up for each individual. The GLM consisted of two runs, one for each condition, and both runs included four task regressors of interest, a regressor modeling the task periods of no interest, and six motion parameters (a high-pass filter was included to remove low frequencies not of interest, cut-off 128 s). The first task regressor of interest modeled the 'investment phase' of the experimental trials and covered the period from the start of the experimental trials until an investment was made (3–7 s, depending on how fast the investment was made, see Fig. 1). The second task regressor of interest modeled the 'investment phase' of the control trials and covered the period from the start of the control trials

until a selection was made (3–7 s, depending on how fast the selection was made, see Fig. 1). The third task regressor of interest modeled the 'feedback phase' of the experimental trials and was defined as the time that the participant viewed the return of the partner and the earnings of the experimental trials (6–8 s, see Fig. 1). The fourth task regressor of interest modeled the 'feedback phase' of the control trials and contained the period that the participant viewed the two screens that displayed the colored bars of the selected number (6–8 s, see Fig. 1). The task regressor of no interest consisted of the period before the start of the experiment, i. e., when the prior information was shown (4 s), and of the period when the investment was shown (2 s). The waiting screen and the fixation crosses were not modeled. Next, for each participant and each condition, an investment contrast and a feedback contrast were created that contrasted the investment phase and the feedback phase of the experimental trials to the equivalent phase of the control trials.

ROI analyses were performed on second level to examine the effect of incorrect prior information on neural activity within the ROIs. Using the MarsBar version 0.44 toolbox (http://marsbar.sourceforge.net), average contrast values were extracted for each participant, condition, and ROI. These contrast values were submitted into second level analyses. We tested for differences in neural activity between the investment phase of the inconsistent condition and the investment phase of the consistent condition as well as between the feedback phase of the inconsistent condition and the feedback phase of the consistent condition. First, for each phase (i.e., investment phase and feedback phase), a dependent ttest was performed per ROI (so, five t-tests per phase). Per phase, a Bonferroni correction was used to correct for multiple comparisons (the adjusted significance cut-off was 0.05/5 t-tests = .01). Second, additional whole-brain analyses were done to explore activity outside the ROIs by using a dependent t-test separately for the investment phase and the feedback phase. Whole-brain analyses were cluster-corrected using a cluster defining threshold of p < .001, and a cluster-probability of p < .001.05, family-wise error corrected.

Additionally, we verified whether the neural activity patterns elicited during the task, irrespective of the prior information manipulation, are in accordance with previous trust game studies. To this end, we examined task-related activity during the investment and feedback phase within the two conditions (relative to the control trials). First, separately for each condition and each phase (i.e., investment phase and feedback phase), one sample t-tests per ROI were performed (so, five ttests per phase). Per phase, the results were corrected for multiple comparisons using a Bonferroni correction (the adjusted significance cut-off was 0.05/5 t-tests = 0.01). Second, whole-brain analyses were performed by using a one-sample t-test separately for the investment phase of the inconsistent condition, the investment phase of the consistent condition, the feedback phase of the inconsistent condition, and for the feedback phase of the consistent condition (all relative to the equivalent phase of the control trials). Again, whole-brain analyses were cluster-corrected using a cluster defining threshold of p < .001, and a cluster-probability of p < .05, family-wise error corrected.

3. Results

3.1. Behavioral results

3.1.1. Manipulation checks

The investment during the first trial in the inconsistent condition was significantly lower than the investments during the acquaintance rounds (t(96) = -4.413, p < .001). The investment during the first trial in the consistent condition was significantly higher compared to the investments during the acquaintance rounds (t(96) = 3.371, p = .001). Furthermore, results showed that the investment during the first trial in the inconsistent condition was significantly lower than the investment during the first trial in the consistent condition (t(32) = 5.588, p < .001, mean investment inconsistent condition: 4.55, mean investment consistent condition: 6.76). The mean and standard deviation of the

investments per trial can be found in the supplementary materials B. The rating of the partner's trustworthiness did not significantly differ between the inconsistent partner and the consistent partner (t(32) = 1.291, p = .206).

3.1.2. Behavioral analyses

The multi-level model building procedure showed the best fit for model 3, which included the linear and quadratic main effect of time, the main effect of condition, the interaction between the linear effect of time and condition, and the interaction between the quadratic effect of time and condition as fixed effects, and a random slope for time at the level of condition and the level of participant (the results of the log likelihood test when model 3 was compared to model 2 were: χ 2(4) = 57.161, p < .001). Results of the model building procedure are shown in Table 1 and a full description of model 3 is shown in Table 2. Results of model 3 showed a significant interaction between the quadratic effect of time and condition indicating that the effect of time is different in the two conditions. Follow-up analyses indicated a signficiant quadratic effect of time in the inconsistent condition (t(594) = -3.167, p = .001) (see Fig. 2). No evidence for a quadratic effect of time (t(594) = 0.545, p= .586) nor for a linear effect of time (t(33) = 0.204, p = .839) was found in the consistent condition (see Fig. 2).

3.2. fMRI results

Results of the dependent t-tests showed no significant differences in activity in the ROIs when comparing the investment phase of the inconsistent condition (relative to the control trials) and the investment phase of the consistent condition (relative to the control trials) (ventral striatum: t(32) = -1.118, p = .272; caudate: t(32) = -0.674, p = .505; mPFC: t(32) = 1.317, p = .197; TPJ: t(32) = 0.615, p = .543; dlPFC: t(32) = -0.554, p = .583, see Fig. 3A). During the feedback phase, a significant difference in dlPFC activity between the inconsistent condition (relative to the control trials) and the consistent condition (relative to the control trials) was found (t(32) = -3.105, p = .004, mean inconsistent condition: 0.795, mean consistent condition: 0.605, see Fig. 3A). Furthermore, a difference in caudate activity during the feedback phase was found when comparing both conditions but did not reach the Bonferroni corrected significance level (t(32) = -2.577, p =.015, mean inconsistent condition: 0.145, mean consistent condition: 0.061, see Fig. 3A). No evidence for significant differences were found in the ventral striatum, mPFC, and TPJ during the feedback phase when comparing both conditions (ventral striatum: t(32) = 0.233, p = .817; mPFC: t(32) = -0.744, p = .463; TPJ: t(32) = -1.311, p = .199, see Fig. 3A). Whole-brain analyses did not reveal significant differences in activity when comparing the investment phase of the inconsistent condition (relative to the control trials) and the investment phase of the consistent condition (relative to the control trials). However, increased activity in the right superior parietal gyrus (number of voxels: 373; MNI coordinates: 28, -68, 46; Z-value: 4.73) was found when comparing the feedback phase of the inconsistent condition (relative to the control trials) to the feedback phase of the consistent condition (relative to the control trials). Whole-brain analyses were cluster-corrected using a cluster defining threshold of p < .001, and a cluster-probability of p < .001.05, family-wise error corrected.

The analyses to examine task-related neural activity within the conditions within the ROIs revealed significant increased activity in the ventral striatum and the caudate during the investment phase of the

Table 1Akaike Information Criterion (AIC) and Bayesian Information Criterion (BIC) values of the model building procedure. The final model is printed in bold.

| Null model | Model 1 | Model 2 | Model 3 |
|------------|-----------|-----------|-----------|
| AIC BIC | AIC BIC | AIC BIC | AIC BIC |
| 5614 5635 | 5574 5610 | 5568 5615 | 5519 5586 |

inconsistent condition (relative to the control trials) and significant increased activity in the caudate and the mPFC during the investment phase of the consistent condition (relative to the control trials) (see Table 3). Furthermore, significant increased activity was found in the caudate, TPJ, and dlPFC during the feedback phase of the inconsistent condition (relative to the control trials) and in the TPJ and dlPFC during the feedback phase of the consistent condition (relative to the control trials) (see Table 3). The results of the whole-brain analyses to examine neural activity within both conditions (separately for the investment phase and the feedback phase) are shown in the supplementary materials C.

4. Discussion

In the current study, we examined the effect of incorrect prior information about the interaction partner's trustworthiness on adolescent trust behavior and related neural activity. Results showed that when participants initially had incorrect expectations about the trustworthiness of their interaction partner, they adapted their trust behavior in response to the partner's actual trustworthiness that was shown during the game. Furthermore, results of the ROI analyses revealed that during the feedback phase of the trust game, activity in the dIPFC was increased when participants had incorrect expectations about the partner compared to when they had correct expectations. Furthermore, results of the whole-brain analyses revealed increased superior parietal gyrus activity during the feedback phase when participants had incorrect expectations about the partner compared to when they had correct expectations. During the investment phase of the trust game, no evidence was found for differences in neural activity as a result of incorrect expectations compared to correct expectations.

Results indicated that the interaction partner's reputation could be manipulated by providing prior information. This was shown by the adjustments that participants made to their first investment compared to their investments during the acquaintance rounds (i.e., a lower first investment during the inconsistent condition relative to the investments made during the acquaintance rounds and a higher first investment during the consistent condition relative to the investments made during the acquaintance rounds). Additionally, in line with the hypotheses, results showed that the first investment during the inconsistent condition was lower compared to the first investment during the consistent condition, indicating that initial trust behavior can be manipulated by prior information. The effect of prior information on initial trust was also found in ealier studies in adults (Delgado et al., 2005; Fouragnan et al., 2013) and adolescents (Lee et al., 2016). Furthermore, in line with the hypotheses, the results revealed that the effect of time on investments was different in the two conditions. Specifically, the results indicated that when the partner behaved more trustworthily than would be expected based on prior information (i.e., the inconsistent condition), adolescents changed their trust behavior by increasing their investments during the initial trials, while this increase flattened toward the end of the game. This means the adolescents were able to understand this rather complex social interaction by signaling the inconsistency between the prior information and the partner's actual behavior during the game, and then incorporate the partner's feedback when making their own decisions regarding the amount they wished to invest. The results further indicated there was variability between participants in the rate of change in the investments (i.e., a random slope). Future research may build upon this to examine possible predictors that could explain the variability in the rates of change (e.g., personality traits or characteristics of one's social life, such as the number of social interactions one has daily). Furthermore, when the partner's behavior matched the participant's initial expectations (i.e., the consistent condition), results revealed no evidence that adolescents showed a trial-related increase or decrease in their trust behavior. Overall, these results indicate that the change in trust behavior during the games was influenced by the social context (i.e., the partner's behavior). These results extend previous

Table 2
Results fit model 3.

| | Beta coefficient | Standard deviation/Standard error ^a | t-value (p-value) | 95% CI ^b | |
|--------------------------|------------------|--|-------------------|---------------------|--------|
| | | | | Lower | Upper |
| Random effects | | | | | |
| Intercept within-person | | 1 | | 0.654 | 1.429 |
| Slope within-person | | 0.091 | | 0.06 | 0.125 |
| Intercept between-person | | 1.556 | | 1.08 | 2.158 |
| Slope between-person | | 0.038 | | 0.00 | 0.086 |
| Residual | | 1.772 | | 1.703 | 1.845 |
| Fixed effects | | | | | |
| Intercept | 6.767 | 0.31 | 21.833 (<.001) | 6.144 | 7.389 |
| Time linear | 0.802 | 4.393 | 0.183 (.86) | -7.936 | 9.540 |
| Time quadratic | 1.342 | 2.506 | 0.535 (.59) | -3.574 | 6.257 |
| Condition | -0.629 | 0.194 | -3.249 (.003) | -1.019 | -0.238 |
| Time linear*condition | 15.413 | 5.899 | 2.613 (.01) | 3.505 | 27.32 |
| Time quadratic*condition | -9.411 | 3.544 | -2.655 (<.01) | -16.362 | -2.459 |

^a Standard deviation reported of the random effects, standard error reported of the fixed effects.

^b The 95% CI for the random effects is on the standard deviation of the effect as the *lmerTest* package does not report beta coefficients and *p*-values for random effects. The 95% CI for the fixed effects is on the beta coefficient.

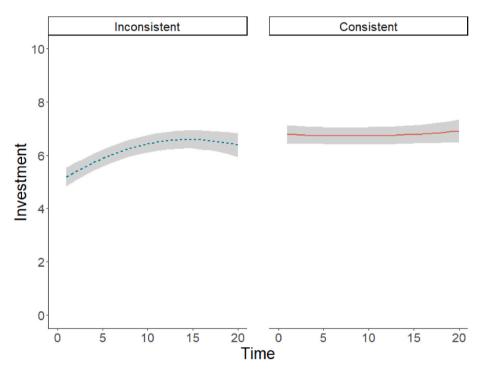


Fig. 2. A significant interaction between time and condition. Time (i.e., trials during the trust game) is displayed on the x-axis. Investments are displayed on the y-axis. Left panel: Post-hoc analyses showed a significant quadratic effect of time on the investments in the inconsistent condition. Right panel: No evidence was found for a significant effect of time on the investments in the consistent condition.

findings by Lee et al. (2016) by showing that adolescents are able to overcome incorrect prior information and adapt their trust behavior accordingly.

ROI findings revealed that during the feedback phase of the game, activity within the dlPFC in the inconsistent condition was significantly higher compared to the consistent condition. In line with our hypothesis, the increased dlPFC activity found in the inconsistent condition may be related to the conflict that arose between the prior information and the actual partner behavior, and the ability of the participants to use the relevant information to update their thoughts, responses, and strategy (as shown, for example, by the significant increase of trust behavior in the inconsistent condition). Relatedly, in another trust game study, dlPFC activity increased when participants changed their trust behavior following unexpected partner behavior compared to when participants did not (Smith-Collins et al., 2013). This study suggests dlPFC activity might be related to expectancy violation and strategic thinking during

social situations (Smith-Collins et al., 2013). In the same line, results of other studies have also pointed toward the role of the dlPFC in cognitive control processes (Declerck et al., 2013; Friedman and Robbins, 2022; Menon and D'Esposito, 2022; Niendam et al., 2012; Suzuki and O'Doherty, 2020). In another study, the dlPFC was shown to encode the value of the reputational prior (Fouragnan et al., 2013). That is, dlPFC activity was more increased during interactions with partners when the prior information suggested a cooperative partner compared to interactions with partners where prior information suggested an individualistic partner (Fouragnan et al., 2013). These results were also found for the mPFC (Fouragnan et al., 2013). Results of the current study suggest that in addition to encoding the value of the prior, dlPFC activity may also encode how prior information relates to the actual behavior of the partner during the game.

In addition to dIPFC activity responding differently in the inconsistent versus the consistent condition, results of the whole-brain analyses

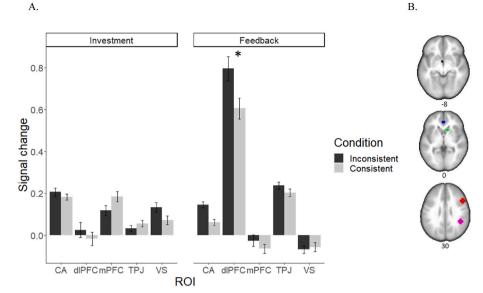


Fig. 3. (A) Signal changes in the ROIs during the investment phase and feedback phase. ROIs are displayed on the x-axis. CA = caudate, dlPFC = dorsolateral prefrontal cortex, mPFC = medial prefrontal cortex, TPJ = temporoparietal junction, VS = ventral striatum. Mean activity (in arbitrary units) is displayed on the y-axis. Error bars depict the standard error of the mean. Left panel: Signal changes in the ROIs during the investment phase of the inconsistent condition (black) and during the investment phase of the consistent condition (grey), both relative to the equivalent phase of the control trials. Right panel: Signal changes in the ROIs during the feedback phase of the inconsistent condition (black) and the feedback phase of the consistent condition (grey), both relative to the equivalent phase of the control trials. Analyses showed a significant difference in dIPFC activity between the inconsistent condition and the consistent condition during the feedback phase. (B) Regions of interest. Black = ventral striatum, blue = mPFC, green = caudate, red = dlPFC, pink = TPJ. The numbers in the figure represent z-coordinates. To view this figure in color, please see the online version of this article.

Table 3

Results of neural activity within the conditions within the ROIs. The first column describes the results of the task-related analyses of the investment phase of the inconsistent condition (relative to control trials), the second column describes the results of the task-related analyses of the investment phase of the consistent condition (relative to control trials), the third column describes the results of the task-related analyses of the feedback phase of the inconsistent condition (relative to control trials), and the fourth column describes the results of the task-related analyses of the feedback phase of the consistent condition (relative to control trials). In all columns, the *t*-value is shown, and the *p*-value is indicated in brackets. The asterisk indicates significance at a Bonferroni corrected cut-off of .01.

| ROI | Investment Inconsistent condition | Investment Consistent condition | Feedback Inconsistent condition | Feedback Consistent condition |
|---------------------|---|---------------------------------------|---------------------------------------|-------------------------------------|
| Caudate | 5.286 (<.001)* | 6.32 (<.001)* | 5.057 (<.001)* | 2.124 (.042) |
| dlPFC | 0.362 (.72) | -0.255 (.801) | 6.842 (<.001)* | 5.991 (<.001)* |
| mPFC | 2.451 (.02) | 3.77 (<.001)* | -0.452 (.654) | -1.518 (.139) |
| TPJ | 1.1 (.28) | 1.859 (.072) | 6.788 (<.001)* | 5.284 (<.001)* |
| Ventral striatum | 2.899 (.007)* | 1.725 (.094) | -1.889 (.068) | -1.293 (.205) |

revealed that the right superior parietal gyrus showed increased activity in the inconsistent condition compared to the consistent condition. Previous research has related the superior parietal gyrus to cognitive control and selective attention processes (Corbetta and Shulman, 2002; Esterman et al., 2009; Menon and D'Esposito, 2022). So, as hypothesized and discussed earlier, these cognitive processes may have been more engaged during the inconsistent condition compared to the consistent condition. Furthermore, in line with our results in which the partner in the inconsistent condition behaved unexpectedly, and thereby elicited adaptive behavior from the trustor, Smith-Collins et al. (2013) found that left superior parietal gyrus activity was increased during successful adaptation behavior compared to unsuccessful adaptation behavior during a trust game with a partner who showed unexpected behavior.

Furthermore, neuroimaging results revealed a difference in caudate activity, indicating higher caudate activity in the inconsistent condition compared to the consistent condition, however, this result did not survive the Bonferroni correction. This could be due to the modest sample

size used in the current study. Previous studies using prior information have suggested that caudate activity is related to feedback and learning processes (Delgado et al., 2005; Fouragnan et al., 2013; Smith-Collins et al., 2013). As we hypothesized beforehand, it is plausible that the inconsistent condition appealed to social learning and reward signaling processes more so than the consistent condition. However, because this finding was not significant, future research is needed to replicate these findings before conclusions can be drawn. Furthermore, we hypothesized ventral striatum activity to be increased in the inconsistent compared to consistent condition but no significant difference in ventral striatum activity was revealed between the two conditions. We also assumed that, compared to the consistent condition, the inconsistent condition would result in greater uncertainty with regards to the partner's intentions and mental states, and therefore result in increased activity in the mPFC and TPJ (which are areas related to mentalizing processes). However, the analyses did not reveal evidence of significant differences in mPFC and TPJ activity between the two conditions. Results of the within-condition analysis (i.e., to examine task-related activity within both conditions relative to the control trials) did reveal TPJ activity during both conditions. This might suggest that processes involved in understanding the partner's intentions and goals were engaged within both conditions. Activity within the mPFC was only significant during investments in the consistent condition (where the prior information suggested a trustworthy partner). In line with this, Fouragnan et al. (2013) showed increased mPFC activity during decisions to share money with a partner when prior information was available about a cooperative partner. These findings may suggest that the mPFC is more engaged when uncertainty is reduced due to prior information and this information suggests trustworthy behavior from the partner (similar to the consistent condition in the current study). Last, exploratory neural time-analyses did not show evidence that, when comparing both conditions, the prior information affected neural activity differently in the first half of the game than in the second half of the game (for details see the supplementary materials A).

The results discussed above should be viewed in light of several limitations. First, a modest sample size was used which reduces the statistical power to correctly reject the null hypothesis. A second limitation of the current study is that deception was used, as participants were told they were going to play games with same-aged peers, while in fact we used a computer algorithm to model the partner's behavior. This deception was essential to the experimental design to ensure that both partners displayed equally trustworthy behavior during the game, and

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that this behavior was consistent with the prior information in one condition and inconsistent with the prior information in the other condition. Participants were fully debriefed following the study. That is, after data collection for the study had finished, participants were sent an e-mail about the study aims and the reason for using deception in the study design. With regards to the validity of the manipulation, there were no signs that participants did not believe the manipulation or thought there was anything unusual about the interaction partners based on their answers on the questionnaire directly after scanning. We did not ask the participants directly about their beliefs regarding the interaction partner as directly asking could elicit doubts about the nature of the partners. A third limitation of the study was that control trials of the trust game did not tap into (non-social) risk-taking and reward processes, meaning that based on the current design, we cannot conclude that the results are solely related to social processes, instead, the findings may also be influenced by other processes such as risk taking based on monetary rewards. Also, the number of trials per condition is somewhat low which may have reduced the statistical power. However, a higher number of trials might have resulted in habituation and, therefore, we used a comparable design to other trust game studies in which significant neural activity related to the trust game was found (Fett et al., 2014; Lemmers-Jansen et al., 2019).

The results of the current study provide insight into adolescent adaptive social behavior during social interactions. Multiple behavioral and neuroimaging studies have shown that development still occurs between late adolescence and young adulthood, for example, there are major changes in behavior but also in the neural activity and functional connectivity between and within brain areas (Crone and Dahl, 2012; Grayson and Fair, 2017; Gu et al., 2015; Marek et al., 2015; Somerville et al., 2013; Stevens, 2016; Váša et al., 2020). Perhaps late adolescents may still be finetuning their learning processes regarding who can be trusted and who cannot. For future research, we suggest using a longitudinal sample (as this design is best suited to study within-person change) to examine how the skills required to fine-tune trust behavior and the related neural processes develop during (late) adolescence into early adulthood. Another suggestion for future studies is to investigate whether there are individual differences related to the neural and behavioral processes of trust behavior and examine possible predictors of these individual differences, for example, indicators of social interactions or indicators of social relationships in daily life which are based on trust.

To conclude, the novel results provide insight into the effect of incorrect prior information about a partner's trustworthiness on trust behavior and related neural processes in adolescents. Results revealed that when incorrect prior information is provided, adolescents integrated the feedback of the partner into their own decision-making process and increased their trust behavior. Furthermore, participants showed increased activity in the dlPFC and in the superior parietal gyrus, which are related to cognitive control and attention processes. The results of the current study help us understand how adolescents deal with social interactions, for example, how they respond when others behave unexpectedly or when others cannot be trusted. These skills are important as adaptive social behavior fosters social relationships through successful social interactions. An increased understanding of the factors that influence adolescent social relationships are crucial to enable the promotion of healthy social development, in which peer relationships play a crucial role and can increase wellbeing, for example, through providing companionship and social support.

Author contributions

Conceptualization: H.S., N.L., N.A., and L.K.; Methodology: H.S., M. K., B.B., M.B.; Software; N.L.; Formal analysis: H.S., M.K., B.B., M.B.; Investigation: H.S., N.L., and N.A.; Data curation: H.S., N.L., and M.B.; writing—original draft preparation: H.S. and N.L.; writing—review and editing: M.K., B.B., N.A., L.K., M.B.; Supervision: N.L., L.K., and M.B.;

Project administration: N.L., and N.A.; Funding acquisition: M.K., N.A., and L.K.; All authors have read and agreed to the published version of the manuscript.

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Ethics statement

The study was approved by the Scientific and Ethical Review Board of the Faculty of Behavioral and Movement Sciences of the Vrije Universiteit Amsterdam. All participants and parent(s)/caregiver(s) signed informed consent.

Declaration of competing interest

None.

Data availability

Data will be made available on request.

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Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.neuropsychologia.2022.108423.

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