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Neural processing of observed performance-based errors and rewards in the context of friends and unfamiliar peers across adolescence

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ABSTRACT

Adolescence is characterized by changes in performance monitoring, whereby action outcomes are monitored to subsequently adapt behavior and optimize performance. Observation of performance-based outcomes (i.e., errors and rewards) received by others forms the basis of observational learning. Adolescence is also a period of increasing importance of peers, especially friends, and observing peers forms a crucial aspect of learning in the social context of the classroom. However, to our knowledge, no developmental fMRI studies have examined the neural mechanisms underlying observed performance monitoring of errors and rewards in the context of peers. The current fMRI study investigated the neural correlates of observing performance-based errors and rewards of peers in adolescents aged 9–16 years ($N = 80$). In the scanner, participants observed either their best friend or an unfamiliar peer play a shooting game resulting in performance-dependent rewards (based on hits) or losses (based on misses, i. e, errors), where outcomes affected both the player and the observing participant. Findings showed higher activation in the bilateral striatum and bilateral anterior insula when adolescents observed peers (i.e., best friend and unfamiliar peer) receive performance-based rewards compared to losses. This might reflect the heightened salience of observed reward processing in the peer context in adolescence. Our results further revealed lower activation in the left temporoparietal junction (TPJ) while adolescents observed the performance-based outcomes (rewards and losses) for their best friend than for an unfamiliar peer. Considering that observation of others' performance-based errors and rewards forms the basis of observational learning, this study provides a crucial first step in understanding and potentially improving adolescent observational learning in the peer context.

1. Introduction

Adolescence is a period characterized by changes in performance monitoring of goal-directed behavior (Davidow et al., 2018). Performance monitoring entails detecting deviations of own and observed outcomes (e.g., rewards and errors) compared to the expected outcomes, after which adaptive behavior is issued and optimized to improve performance (Ullsperger et al., 2014). Thus, for optimal adjustment of behavior and improvement of performance is it important to assess performance-based errors and rewards. On a behavioral level, an age-related increase has been found in performance monitoring across childhood and adolescence (e.g., decreases in error rates) (Fitzgerald et al., 2010; Tamnes et al., 2013), suggesting an improvement of monitoring of outcomes and subsequent adjustment of behavior across adolescence.

On a neural level, the posterior medial frontal cortex (pMFC) and anterior insula (AI) have been found to be activated during own performance-based error processing (de Bruijn et al., 2009; Koban and Pourtois, 2014; Radke et al., 2011; Ullsperger et al., 2010). In line with the age-related increases in behavioral performance, activity in the pMFC increases with age across adolescence, also suggesting improvement of performance monitoring with age (Fitzgerald et al., 2010). The pMFC and AI are part of the so-called salience network, involved in processing information that is highly relevant for the person, such as errors (Seeley et al., 2007; Ullsperger et al., 2010) or relevant infrequent events (Harsay et al., 2012; Ullsperger et al., 2010). Besides errors it is also important to monitor performance-based rewards for optimal adjustment of goal-directed behavior. The ventral striatum has been

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found to be activated during own performance-based reward processing (de Bruijn et al., 2009; Overgaauw et al., 2020; Simon et al., 2014). Activation to rewards in the striatum further increases with age across adolescence and peaks around mid-adolescence, signaling increased reward sensitivity at this age (Braams et al., 2014; Peters and Crone, 2017; Schreuders et al., 2018a; van Leijenhorst et al., 2010).

Besides changes in performance monitoring, adolescence is also a period of social re-orientation that is characterized by heightened social motivation and a focus on peer relationships (Crone and Dahl, 2012; Güroğlu, 2021; Güroğlu and Veenstra, 2021; Nelson et al., 2005). The increasing salience of peers across adolescence is also reflected in heightened neural sensitivity to social contexts, such as those including peer presence (Somerville, 2013; van Hoorn et al., 2016). Peers have also been shown to influence the neural responses to errors and rewards. That is, previous work shows heightened reward-related activity in adolescents in the peer context compared to alone (Chein et al., 2011), and heightened error-related neural activity in young adolescent girls in the peer context compared to a nonsocial context (Barker et al., 2018). These results attest the impact of the peer context on the neural processing of errors and rewards, which are crucial processes for complex goal-directed behavior, especially during adolescence. Importantly, heightened neural responses observed in the peer context are even stronger in contexts that involve personally familiar peers, compared with unfamiliar peers (Güroğlu et al., 2008). Friends play an increasingly important role in the lives of adolescents as they gradually become adolescents' primary source of social support (Furman and Buhrmester, 1992). Supporting the significant role of friends on neural processing, higher neural activation in reward regions has been found during social interactions with friends and social decision-making involving friends compared to other peers in adolescents and young adults (Güroğlu et al., 2008; Schreuders et al., 2019).

When own errors and rewards have consequences for others, social cognition is involved, especially mentalizing, which can be described as the ability to interpret and understand others' feelings, mental states, beliefs, and actions (Andrews et al., 2020; Blakemore, 2008). On the neural level, mentalizing is associated with the social brain network, which consists of brain regions such as the medial prefrontal cortex (mPFC), temporoparietal junction (TPJ) and the precuneus (Andrews et al., 2020; Blakemore and Mills, 2014; Braams and Crone, 2016; Pfeifer et al., 2013). In adults, increased activity in the mPFC and precuneus is implied when processing own errors that have consequences for others (Koban et al., 2013; Radke et al., 2011). The mPFC, precuneus and TPJ are also more active while adolescents obtained rewards for others compared to for oneself (Braams et al., 2014). Neural activity in the social brain during reward processing is also modulated by friendship. For example, activation in the precuneus and mPFC during obtaining rewards for friends compared to for oneself is higher for adolescents who reported that their friend deserved to win (Braams and Crone, 2016). Studies in adolescents and young adults have demonstrated that the ventral striatum is also activated during rewards obtained for others, and this activation is stronger for rewards obtained for close others (such as friends or parents) than for strangers or disliked others (Braams et al., 2014; Brandner et al., 2020). Similarly, research in adults has demonstrated higher ventral striatal activation when they shared monetary rewards with a close friend compared to an unfamiliar person or a computer (Fareri et al., 2012).

Observing the errors and rewards received by others can also be advantageous to the observer as it can inform which behavioral adjustments should be made to avoid making the same errors as the person observed. A few studies in adults have examined observed error and reward processing, where one observes the errors or rewards obtained by others. Prior research has shown activation in the mPFC, precuneus and TPJ while adults observed errors of others, and specifically precuneus activation for observed errors in cooperative contexts (i.e., with aligned goals of self and other) (Jääskeläinen et al., 2016; Koban et al., 2010). Research in adults has found activation in the pMFC and AI for observed errors compared to observed performance-based rewards, whereas activation in the ventral striatum has been found for observed performance-based rewards compared to observed errors (de Bruijn et al., 2009). In adults, friendship has been found to modulate the neural activation underlying observed error processing. Prior studies in adults found stronger activation in the pMFC for observing errors of friends compared to observing errors of others (e.g., strangers or disliked others) (Kang et al., 2010; Newman-Norlund et al., 2009). However, to our knowledge, there are no developmental studies examining the neural activation patterns underlying the observation of performance-based errors and rewards in the context of friends. The goal of the current study was to examine the role of friends and unfamiliar peers in the neural mechanisms of observed performance-based error and reward processing (i.e., performance monitoring) across adolescence.

1.1. *Present study*

Although prior research in adolescents has shown that the presence of peers influences neural outcome processing, it is not clear to what extent these effects can be generalized to all peers or are specific for best friends. In the current study, we examined neural activation underlying observed performance-based error and reward processing in the social context of best friends and unfamiliar peers across adolescence (aged 9–16) with a unique design where best friends and unfamiliar peers were actually present during data collection. To examine our research question, participants played a game that included observing a peer (best friend or unfamiliar peer) play, where hits based on performance resulted in monetary reward and errors resulted in monetary loss (Cannonball task; de Bruijn et al., 2009). As is common in everyday life, the monetary consequence of performance affected both players equally. This design enabled us to examine whether neural processing of errors and rewards based on observed behavior was modified by the relationship with the peer performing the task (i.e., best friend vs unfamiliar peer).

Considering that the majority of learning takes place in the social context of the classroom where there are ample opportunities for observational learning, an increased understanding of the processes underlying observation of outcomes (i.e., errors and rewards) received by friends and peers is crucial for improving social learning contexts. That is, observation of performance-based outcomes (i.e., errors and rewards) received by others forms the basis of observational learning (Bellebaum and Colosio, 2014), as observed outcomes can inform future behavioral adjustment to avoid making the same errors as the person observed. Thus, examining observed performance monitoring across adolescence in the context of friends and peers could ultimately inform optimal social learning conditions in the classroom in the future.

Based on prior literature in adults, we expected that the AI and the pMFC would be more strongly activated during observed performance-based errors compared to rewards (de Bruijn et al., 2009). We further expected higher striatum activation during observed performance-based rewards compared to errors (de Bruijn et al., 2009). These effects of rewards and errors on neural activation were expected to be larger for observing a best friend compared to observing an unfamiliar peer (Braams et al., 2014; Brandner et al., 2020; Fareri et al., 2012; Kang et al., 2010; Newman-Norlund et al., 2009). We also expected the involvement of pMFC in observed performance-based error processing to increase with age across adolescence (Fitzgerald et al., 2010), whereas striatum activity during observed performance-based reward processing was expected to peak in mid-adolescence (Braams et al., 2014; Schreuders et al., 2018a). Finally, we examined whether social brain regions were differentially involved during observed performance-based error and reward processing for best friends compared to unfamiliar peers. As the mPFC, TPJ and precuneus are especially responsive to the outcomes of friends, we expected higher activation in these social brain regions during observed outcomes (errors and rewards) for the best friend compared to observed outcomes for an unfamiliar peer (Braams et al., 2014; Braams and Crone, 2016). Based on studies showing that neural activation during reward processing for friends is modulated by individual differences in friendship quality (Braams et al., 2014; Braams and Crone, 2016; Schreuders et al., 2021), we also explored the relation between activation underlying observed outcomes in the friend context and friendship quality.

2. Methods

2.1. Participants

The original sample of this study consisted of 89 participants, of whom 9 were excluded due to excessive movement (>5 mm in any direction, $N = 3$), due to a programming error ($N = 1$) and due to poor task performance ($N = 5$; see below for details on this exclusion criterion). Therefore, the data of 80 participants were used for analyses ($M_{\text{age}} =$ 13.47 years; $SD_{\text{age}} = 2.20$; age range = 9–16 years; 42 males). Out of these 80 participants, 92.5% was born in the Netherlands, 2.5% was born in the United Kingdom; data on the country of birth of four participants was missing.

Participants were recruited via the participant recruitment database of the research lab. The participants were screened on neurological or psychological disorders as reported by the parents and MRI contra indications, which were exclusion criteria for our study. Informed consent was signed by all participants and their parents/caregivers before the start of the study. This study was approved by the university Medical Ethical Testing Committee (METC). The participants received a compensation of €30 for their participation in the study and could earn an additional €5 during the fMRI tasks.

The subscales Similarities and Block Patterns from the Wechsler Intelligence Scale for Children (Wechsler, 1991, Wechsler, 1991) were used to assess IQ in participants under 16 years of age; the same subscales of the Wechsler Intelligence Scale for Adults (WAIS-III; Wechsler, 1997) were used for participants aged 16 years and older. The estimated IQ scores of the participants fell within the normal range ($M = 109.06$; $SD = 12.20$), and IQ was not significantly correlated with age ($r = -0.09$, $p = .42$).

2.2. Procedure

The participants arrived at the scanning session together with at least one parent and their best friend; best friends brought a written consent from their own parents/caregivers for their participation in the study. The best friends received a compensation of €20 for their participation in the study and could earn an additional €3 during the computer tasks. The majority of the best friends were of the same sex as the participant; there were 39 boy-boy, 34 girl-girl, and 4 cross-sex dyads. The mean age difference between the participants and their best friends was small ($M = 0.47$, $SD = 0.40$).

Once at the laboratory, the participants and their best friends met several age-matched unfamiliar peers who were introduced as other study participants, but who were actually confederates. The confederates were youth actors recruited via local theater schools (total $N = 44$). The confederates received a compensation of €5 per session for their participation in the study. These confederates (5 or 6 peers per session) and the accompanying best friend were also part of other studies which are reported elsewhere (Spaans et al., 2018; van Hoorn et al., 2016). The participants shook hands with these unfamiliar peers, and everyone briefly introduced themselves by saying their name. They were explained that the goal of this study was to investigate brain activity during interactive games. The participants were told that they would play online games, while one of them (the participant) would lie in the scanner and all others would play the games on a computer in separate rooms. Subsequently, the confederates and the best friend were all taken to separate testing rooms and the participant was taken to the mock scanner. At this point the confederates actually left the laboratory and the participant and their best friend did not see each other until after the study was completed.

At the mock-scanner the participant was first familiarized with the MRI scanning procedure and received instructions on the fMRI task. The participants were told that they would play the fMRI task in real-time with their best friend and one of the unfamiliar peers (i.e., confederates) they had met previously that day. The MRI scanning session lasted approximately 1 h. Afterwards, the participants filled out a couple of questionnaires. At the end of the session, the participants were debriefed about the larger study setup, and that they played the Cannonball task with a computer and not their best friend and unfamiliar peer. None of the participants expressed doubt about the cover story during the debriefing.

2.3. Materials

2.3.1. Cannonball Task

To examine performance-based error and reward processing, the participants performed an adapted version of the Cannonball task (see Fig. 1; de Bruijn et al., 2009), a task where players take turns in playing and observing another participant play. The other participant could be a best friend or an unfamiliar peer. This paper will only focus on the observe conditions of the task as our research questions were focused on observed performance-based error and reward processing; see Supplements for the results on the play task conditions. The participants performed 160 trials of the task: 80 trials Friend (40 Play; 40 Observe) and 80 trials Unfamiliar (40 Play; 40 Observe). In addition, the participants also played 40 trials of the task by themselves (i.e., Alone), which was used to assess the participants' understanding of the task. Participants who performed very poorly in this Alone condition (i.e., hit rate <40%) were excluded from the analyses, as this condition was the easiest and most straightforward of all conditions ($N = 5$). The order of the three conditions (i.e., playing Alone, with a Friend, and with an Unfamiliar Peer) was counterbalanced across the participants. During the task, performance resulted in equal consequences for both the self and the other player (except for in the Alone condition). The unfamiliar peer (one of the confederates that the participants met previously) was of the same gender as the best friend to keep this constant across the social conditions.

The aim in the Cannonball task is to shoot a target (square) by stopping a horizontally moving cannon (triangle) with a button press when the cannon is precisely lined up with this target. At the start of the task participants received a €3 bonus. On each observation trial, the participants observed a peer hit the target or miss the target, which determined whether they won money (+10 cents for a hit) or lost money (−10 cents for a miss). The performances of the Friend and Unfamiliar players were pre-programmed to result in 50% hit and 50% miss in a randomized fashion.

Each trial started with text presented at the center of the screen, indicating whether the participant observed their best friend or an unfamiliar peer play using the name of the peer (e.g., "Emma plays, you observe"), which was presented for 1500 ms (Fig. 1, screen 1). Subsequently a fixation cross was presented; duration of this screen was jittered for 500, 750, 1000, 1250 or 1500 ms (Fig. 1, screen 2). The next screen presented the cannon and the target. The cannon was always horizontally centered, but the location of the target was randomly determined on every trial (Fig. 1, screen 3). Instantly at onset, the cannon started moving at constant speed in either the left or right direction for a maximum of 3500 ms (2.5 lengths) during which participants observed the peer stop the cannon (Fig. 1, screen 4). The position at which the cannon was stopped was presented for 500 ms before the outcome was provided (Fig. 1, screen 5). The outcome was presented for 750 ms as coloration of the cannon and target (green for hits; red for misses), indicating respectively whether the peer, and thus also the participant, won or lost money (Fig. 1, screen 6). The task was

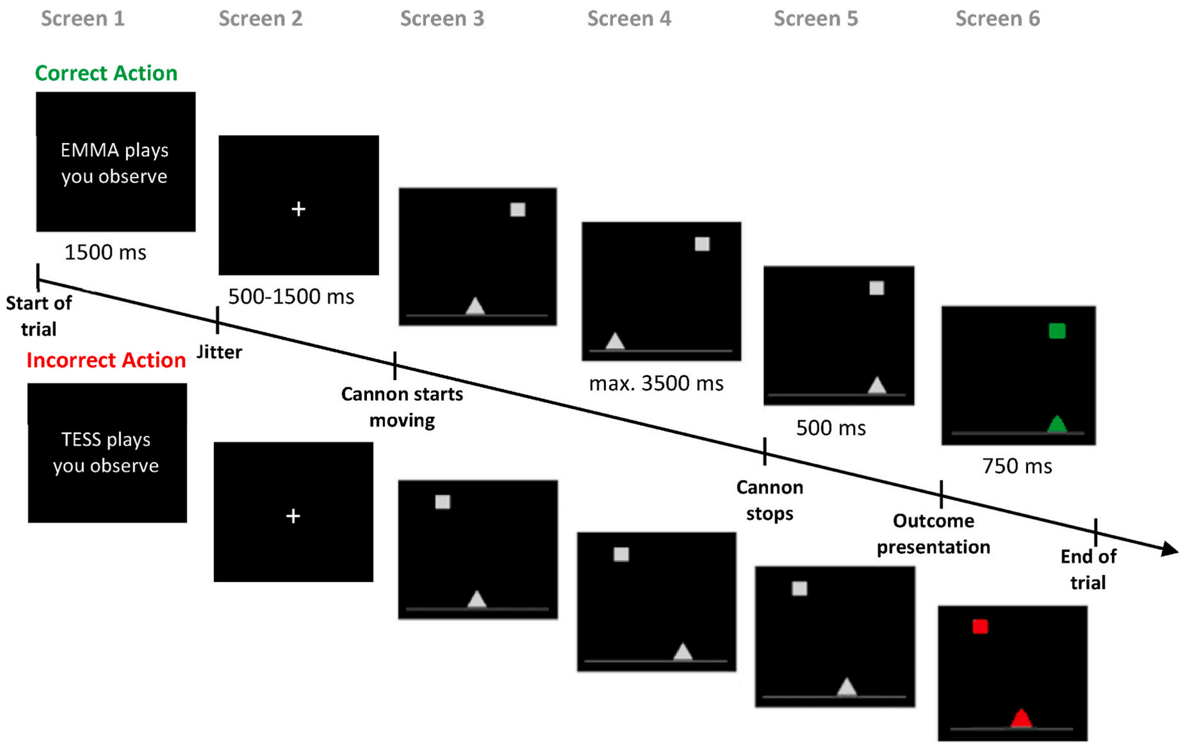

Fig. 1. Trial of Cannonball Task.
Note. A reward trial in the observe Friend condition is presented above the arrow and an error trial in the observe Unfamiliar Peer condition is presented below the arrow.

programmed in E-Prime 2.0.

2.3.2. *Friendship Quality Scale*

Friendship quality was assessed by the adapted short version of the Friendship Quality Scale (FQS; Bukowski et al., 1994). This questionnaire contained 29 items to assess positive and negative friendship quality. The positive friendship quality subscale contained 18 items, and the negative friendship quality subscale contained 11 items. Example items of the subscales are: "*My friend would help me if I needed it*" (positive friendship quality); "*My friend and I can argue a lot*" (negative friendship quality). The participants' responses were rated on a scale ranging from 1 (*not true*) to 5 (*really true*). The negative friendship quality subscale items were reverse coded, so that higher total mean scores on this scale indicated a higher friendship quality. The scale score consisted of the mean of the 29 friendship quality items (including the 11 reverse coded negative friendship quality items, and the 18 positive friendship quality items). The reliability of the FQS is high (Cronbach's alpha was .906 in our study), and it has good criterion validity (Bukowski et al., 1994). The average reported friendship quality was high ($M = 4.19$; $SD = 0.42$); friendship quality was not significantly correlated with age ($r = .07$, $p = .56$), but friendship quality was significantly higher in females ($M = 4.33$) than in males ($M = 4.06$), $t(78) = -3.00$, $p = .004$.

2.4. *MRI data acquisition*

The MRI data was acquired using a Philips 3.0 T MRI scanner with a standard whole-head coil at the University Medical Center. The functional scans were obtained with T2*-weighted echo-planar imaging (EPI) pulse sequence (38 contiguous 2.75 mm oblique axial slices, using sequential acquisition, FOV = 220 mm, 80 × 80 matrix, TR = 2.2s, TE = 30 ms, 2.75 × 2.75 mm in-plane resolution). In order to allow for T1-equilibration effects, the first two volumes of each run were discarded. Furthermore, a high-resolution 3D T1-FFE scan was collected for anatomical reference (TR = 9.76 ms; TE = 4.59 ms, flip angle = 8°, 140 slices, 0.875 × 0.875 × 1.2 mm^3 voxels, FOV = 224 × 168 × 177 mm^3). After the functional scans, a high-resolution 3D T1-weighted anatomical image was acquired (TR = 9.751 ms, TE = 4.59 ms, flip angle = 8°, 140 slices, 0.875 × 0.875 × 1.2 mm^3, FOV = 224.000 × 168.000 × 177.333 mm^3). Stimuli were presented on a screen behind the MRI scanner that could be viewed via a mirror on the head coil. To minimize head movement, foam cushions were placed on both sides of the participants' heads inside the head coil. Besides, the translational movement parameters did not exceed the threshold of >5 mm for all directions and scans for the participants included in the analyses.

2.5. *fMRI preprocessing and analysis*

The imaging data were preprocessed and analyzed with Statistical Parametric Mapping 8 (SPM8; Wellcome Department of Cognitive Neurology, London). The functional scans were slice-time corrected and corrected for differences in rigid body motion. The structural and functional volumes were spatially normalized to T1 templates using a 12-parameter affine transformation together with a nonlinear transformation that involved cosine basis functions. This normalization algorithm also resampled the volumes to 3 mm cubic voxels. The MNI305 stereotaxic space was used to base the aforementioned templates on. Furthermore, the functional volumes were spatially smoothed with a 6 mm FWHM isotropic Gaussian kernel.

The general linear model (GLM) in SPM8 was used to conduct first-level statistical analyses on individual subjects' data. The fMRI time series were modeled as a series of zero duration events convolved with the hemodynamic response function (HRF). We created separate regressors for the conditions (Context: Solo, Friend, Unfamiliar; Action: Play vs Observe; Valence: Reward vs Error), which were included in the full factorial designs. The outcome (monetary reward or loss) onset times of different task conditions were modeled as events of interest. Furthermore, we added an extra parametrically modulated regressor of target size in the model to control for task difficulty, as has been done in previous studies using the Cannonball task (cf. de Bruijn et al., 2009). The text screens indicating whether the participants were playing or observing, and who they were playing the task with were modeled separately (Fig. 1, screen 1). The trials in which the participants failed to respond were modeled as events of no interest, which were used as covariates in a general linear model. A basic set of cosine functions that high-pass filtered the data was also used as covariate in this model. Six motion regressors were added to the model to account for possible motion induced error. The least-squares parameter estimates of height of the best-fitting canonical HRF for each condition were used in pair-wise contrasts. The resulting subject-specific contrast images were submitted to higher-level group analyses.

We performed two separate sets of analyses to examine our two main research questions on i) neural activation patterns involved in observed error and reward processing and ii) the role of social context in observed performance monitoring. In a first set of analyses, we examined valence and social context effects during observed errors and rewards in brain regions involved in error and reward processing. We performed ROI analyses where we selected five ROIs based on previous studies on error and reward processing using the same paradigm in adults (de Bruijn et al., 2009; Overgaauw et al., 2020). Anatomical ROIs of the left AI, right AI, left striatum and right striatum were derived from the Marsbar anatomical toolbox (cf. Overgaauw et al., 2020). Because there is no anatomical ROI of the pMFC in the Marsbar anatomical toolbox, we created a sphere with a diameter of 10 mm around the peak voxel MNI coordinates (4, 32, 38) (de Bruijn et al., 2009; cf. Overgaauw et al., 2020). To investigate valence and context effects on neural activation during observed errors and rewards in error and reward processing regions, we performed five separate 2 (Context: Friend, Unfamiliar) x 2 (Valence: Reward, Error) repeated measures ANOVAs in the five predefined error and reward processing ROIs in the Observe conditions.

Next, to investigate age effects on neural activation during observed errors and rewards in the error and reward processing regions, we performed five separate hierarchical multiple regressions, with the linear effect of mean-centered age as the predictor in the first step, the quadratic effect of mean-centered age as the predictor in the second step, and the cubic effect of mean-centered age as the predictor in the third step. For the three brain regions involved in error processing (left AI, right AI, and pMFC), we focused on neural activation during the ObserveError > ObserveReward contrast (computed as difference score) as the dependent variable. For the two brain regions involved in reward processing (left striatum, right striatum), we focused on neural activation during the ObserveReward > ObserveError contrast (difference score) as the dependent variable.

In a second set of analyses, we examined social context effects during observed outcomes (i.e., monetary reward and loss) in social brain regions. For this purpose, we selected four social brain ROIs based on a study on outcome processing in a social context in adolescence, which guided most of our hypotheses on social context effects: mPFC (MNI 1 57 12), left TPJ (MNI -55 -54 27), right TPJ (MNI 55–54 27), and precuneus (MNI 2–58 46) (Braams and Crone, 2016). These ROIs were originally based on a meta-analysis focusing on mentalizing brain regions (van Overwalle and Baetens, 2009). All ROI analyses were conducted using SPM8’s Marsbar toolbox (Brett et al., 2002). To investigate context effects on neural activation during observed outcomes in social brain regions, we performed four separate repeated measures ANOVAs with Context (Friend, Unfamiliar) as the independent variable in the four predefined social brain ROIs.

Next, to investigate age effects on neural activation during observed outcomes in the social brain regions, we performed four separate hierarchical multiple regressions, with the linear effect of mean-centered age as the first predictor, the quadratic effect of mean-centered age as the second predictor, and the cubic effect of mean-centered age as third predictor. We focused on neural activation across both error and reward processing during the ObserveFriend > ObserveUnfamiliar contrast (computed as difference score) as the dependent variable.

Finally, we explored the relation between neural activation during observed outcomes in the Friend condition with self-reports of friendship quality (mean FQS score). We again focused on the ObserveFriend > ObserveUnfamiliar contrast across both error and reward processing. We conducted separate linear regression analyses within each of the four social brain ROI’s with neural activation during observed outcomes as the dependent variables, and mean FQS as the independent variable.

To control for multiple comparisons, we performed a Bonferroni correction based on the number of ROIs involved in the specific set of analysis. This resulted in a significance level of $\alpha = 0.01$ (number of ROIs = 5) in the first set of analyses on the error and reward processing ROIs and $\alpha = 0.0125$ (number of ROIs = 4) in the second set of analyses on the social brain ROIs.

3. Results

See Table 1 for the demographic characteristics of the participants and friends and participants’ scores the Friendship Quality Scale (Bukowski et al., 1994), friendship duration and friendship interaction frequency with the best friend.

3.1. Task performance

The average hit-rate in the computer-programmed Observe trials was, as intended, around 50% (49.4% for the Friend condition and 49.2% for the Unfamiliar condition). This average hit-rate did not correlate with age ($r = -0.14$, $p = .22$).

3.2. fMRI results

We detected two significant outliers (z-values > |3.29|) in the data, one outlier in the difference score (ObserveError > ObserveReward) of the pMFC, and one outlier in the difference score (ObserveFriend > ObserveUnfamiliar) of the left TPJ. These two outliers were winsorized (Field, 2013).

3.2.1. ROI analyses reward and error processing regions

Firstly, we examined the effects of valence, context, and age on the

Table 1
Demographic characteristics and self-report scales for participants and best friends.

Variable	Participant	Friend
M age	13.47	13.73
SD age	2.20	2.21
Range age	9–16	9–17
Sex (N (%))		
Male	42 (52.5%)	41 (51.2%)
Female	38 (47.5%)	36 (45%)
Missing	0	3 (3.8%)
Friendship Quality Scale		
M	4.19	
SD	0.42	
Min - max	3.34–4.97	
Friendship Duration (N (%))		
(How long do you know each other?)		
<6 months	1 (1.3%)	
6 months - 1 year	13 (16.3%)	
1 year - 2 years	13 (16.3%)	
2 years–3 years	11 (13.8%)	
>3 years	42 (52.5%)	
Friendship Interaction Frequency		
(How many days a week do you see each other?)		
1 day a week	4 (5%)	
2–3 days a week	11 (13.8%)	
4–5 days a week	49 (61.3%)	
6–7 days a week	16 (20%)	

reward and error processing ROIs while adolescents observed peers receive outcomes (monetary reward or loss). A significant effect of valence was found in the left striatum (F (1, 79) $= 13.80$, $p < .001$, η^2p $=$ .15; see Fig. 2A; Supplements Fig. S4A) and the right striatum (F (1, 79) $= 10.87$, $p = .001$, η^2p $= .12$; see Fig. 2B; Supplements Fig. S4B), with higher activation when adolescents observed peers who received rewards based on hits (left striatum: $M = -0.004$, $SE = 0.01$; right striatum: $M = -0.008$, $SE = 0.01$) compared to losses based on errors (left striatum: $M = -0.07$, $SE = 0.02$; right striatum: $M = -0.06$, $SE = 0.02$). There were no significant main effects of context and no significant valence × context interaction effects in the left striatum and in the right striatum (all F's < 0.65; all p's > 0.42). There were no significant effects of age, neither in the left nor right striatum (linear all p's > 0.66; quadratic all *p-change*'s > 0.48; cubic all *p-change*'s > 0.54).

Furthermore, a significant effect of valence was found in the left AI (F (1, 79) $= 8.50$, $p = .005$, η^2p $= .10$; see Fig. 3A; Supplements Fig. S5A) and in the right AI (F (1, 79) $= 7.24$, $p = .009$, η^2p $= .08$; see Fig. 3B; Supplements Fig. S5B), with higher activation when adolescents observed peers who received rewards based on hits (left AI: $M = 0.000$, $SE = 0.02$; right AI: $M = 0.001$, $SE = 0.02$) compared to losses based on errors (left AI: $M = -0.04$, $SE = 0.02$; right AI: $M = -0.05$, $SE = 0.02$). There were no significant main effects of context and no significant valence × context interaction effects in the left AI and in the right AI (all F's < 0.77; all p's > 0.38). There were no significant effects of age, neither in the left nor right AI (linear all p's > 0.50; quadratic all *p-change*'s > 0.23; cubic all *p-change*'s > 0.59).

No significant main effects of valence and context and no significant valence × context interaction effect were found when adolescents observed outcomes in the pMFC (all F's < 0.75; all p's > 0.39). There were no significant effects of age in the pMFC (linear $p = .30$; quadratic *p-change* $= .78$; cubic *p-change* $= .83$).

3.2.2. ROI analyses social brain regions

Secondly, we examined the effects of context and age on the social brain ROIs while adolescents observed peers receive outcomes (monetary reward or loss). A significant main effect of context, F (1, 79) $= 7.53$, $p = .008$, η^2p $= .09$ (see Fig. 4; Supplements Fig. S6), was present in left TPJ, with higher activation when adolescents observed the outcomes received by an unfamiliar peer ($M = 0.03$, $SE = 0.02$) compared to their best friend ($M = -0.05$, $SE = 0.03$). No significant main effects of context were present in mPFC, right TPJ, and precuneus (all F's < 1.49; all p's > 0.22), nor were there significant age effects in any of the social brain ROIs (linear all p's > 0.22; quadratic all *p-change*'s > 0.38; cubic all *p-change*'s > 0.64).

3.2.3. Brain-behavior relations during observed outcomes in friend context

Finally, we conducted a set of exploratory analyses investigating brain-behavior relations between neural activation patterns during observed outcomes in the friend context and friendship quality. To this end, we conducted separate linear regression analyses with the Friend > Unfamiliar contrast in the Observe conditions in each of the four social brain ROIs. We did not find any significant models for the effect of friendship quality on the social brain ROIs (mPFC, left TPJ, right TPJ, and precuneus) in the Friend Observe versus the Unfamiliar Observe condition (all F's < 3.03; all p's > 0.08).

4. Discussion

The aim of the current study was to examine the neural activation patterns underlying observed performance-based error and reward processing in adolescence (9–16 years), using the Cannonball task. We examined these effects in the social context of observing a best friend and an unfamiliar peer, with a unique design where these peers were present during data collection. The adolescents observed the peer lose money (based on errors) or win money (based on hits), and this outcome also had the same consequences for adolescents themselves, thus creating a cooperative context. Our key results showed that the bilateral striatum and bilateral anterior insula (AI) were more active when adolescents observed peers receive hit-based rewards compared to error-based losses, regardless of whether this was a best friend or an unfamiliar peer. We also examined neural activation in social brain regions during observation of outcomes for the best friend and an unfamiliar peer. Our results revealed higher activation in the left TPJ while adolescents observed outcomes for an unfamiliar peer compared to for their best friend. The discussion is structured along these main findings.

4.1. Observed reward processing

Our results showed that adolescents had higher activation in bilateral striatum while observing best friends and unfamiliar peers receive

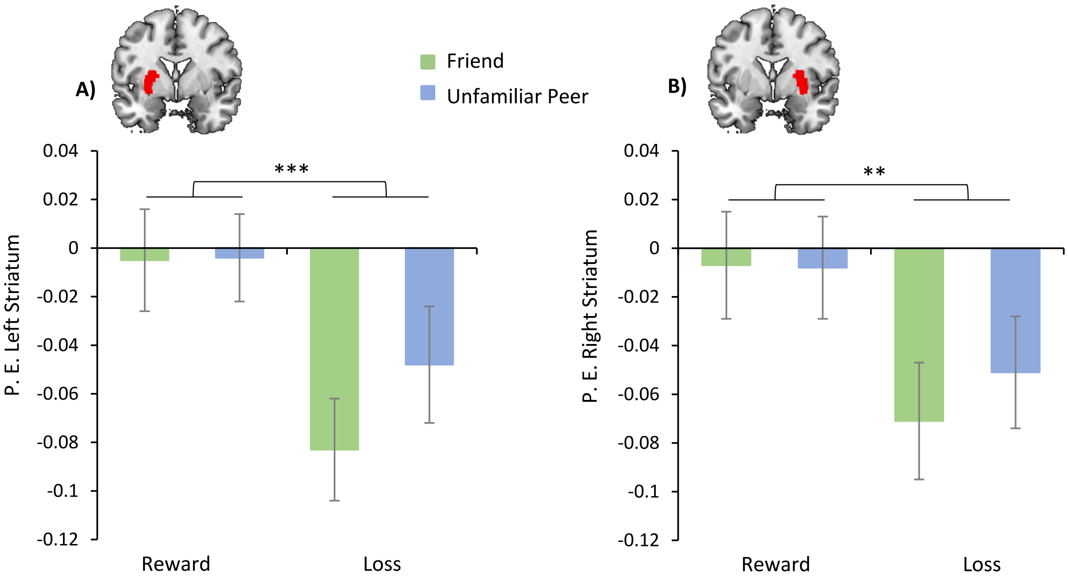

Fig. 2. Effect of valence on left (A) and right (B) striatum activation during observed outcomes (monetary reward or loss)
Note. See Supplements Figs. S4A and S4B for a depiction of the individual datapoints. P. E. = Parameter Estimates. $^{**}p < .01$, $^{***}p < .001$.

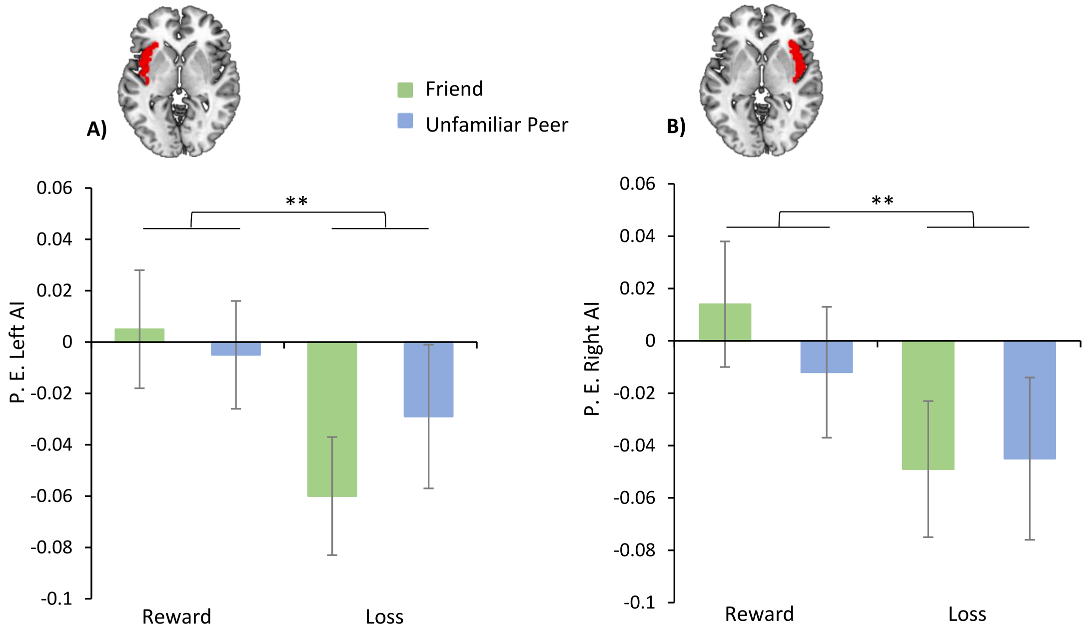

Fig. 3. Effect of valence on left (A) and right (B) AI activation during observed outcomes (monetary reward or loss)
Note. See Supplements Figs. S5A and S5B for a depiction of the individual datapoints. P. E. = Parameter Estimates. **$p < .01$.

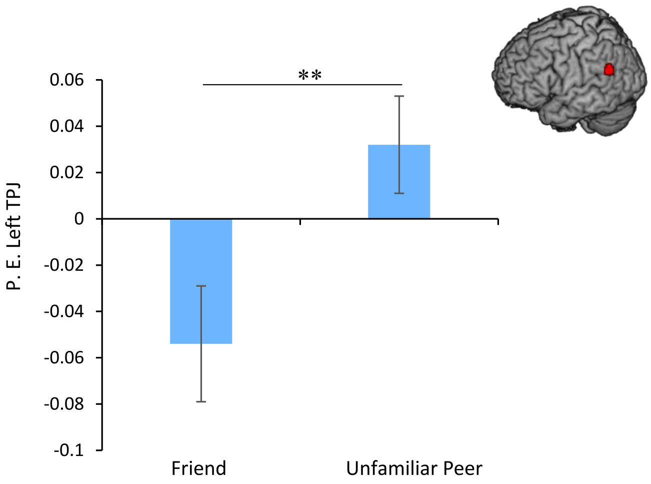

Fig. 4. Effect of context on left TPJ activation during observed outcomes.
Note. See Supplements Fig. S6 for a depiction of the individual datapoints P. E. = Parameter Estimates. **$p < .01$.

performance-based rewards compared to losses. This finding is in line with our hypothesis and previous research in adults demonstrating activation in striatum for observed performance-based rewards (de Bruijn et al., 2009; Overgaauw et al., 2020), and when learning from observing others (Daniel and Pollmann, 2014). However, we did not find a valence by context interaction effect in the striatum, so we did not confirm our hypothesis that activation during reward processing in striatum would be stronger for best friends than for unfamiliar peers.

There is accumulating evidence that striatum activity is sensitive to the social context such that obtaining rewards for close others, e.g., a best friend or a parent, results in higher striatum activation compared to obtaining rewards for an unfamiliar or disliked other (Braams et al., 2014; Brandner et al., 2020, 2021). An important difference with these prior studies is that in our current study participants observed others obtain performance-based rewards that also had consequences for the participants themselves. The absence of an effect of the interaction partner might thus suggest that adolescents in this paradigm are mainly focused on the consequence of the rewards for their own outcomes, i.e., personal gain, which is similar for both interaction partners. This explanation is supported by previous research in adults using the same paradigm in cooperative and competitive contexts, demonstrating the striatum to be specifically sensitive to personal gains, e.g., when observing a competitor miss or when observing a cooperator make a hit (de Bruijn et al., 2009; Overgaauw et al., 2020). Future studies on observed reward processing should further test this in a design where it is possible to dissociate between rewards for self, other, and both, as well as investigating how the social context of cooperation and competition modulates these processes in adolescents.

In the current study, we did not find the expected age effects in striatum activity during observation of rewards. Our expectation was based on previous research showing that activation in the striatum increases with age across adolescence and peaks around mid-adolescence (Braams et al., 2014; Peters and Crone, 2017; Schreuders et al., 2018a; van Leijenhorst et al., 2010). However, these previous studies mainly focused on outcomes for own performance or rewards for the self, whereas the current study focused on observing outcomes for others. Interestingly, in a study by Brandner et al. (2021) where the study design allowed to differentiate between rewards for the self, the other and both, there were no age-related changes between 8 and 19 years in the striatum during obtaining rewards for parents and unfamiliar peers either. One longitudinal study that examined obtaining rewards for best friends (Schreuders et al., 2021) found that the developmental pattern of striatum activity (across ages 8–25) when winning for a best friend showed a quadratic pattern with a mid-adolescent peak only for individuals who had stable best friendships over time. This suggests that there might be friendship characteristics, such as friendship stability, that relate to age-related changes in striatal responses to rewards for others. More extensive research is needed to examine potential developmental differences in processing observed performance-based rewards.

The current findings also revealed that the adolescents had higher activation in bilateral AI while observing peers receive hit-based rewards compared to error-based losses. This finding is at odds with our hypothesis and studies using the same paradigm in adults, where the AI was mainly involved in error processing (de Bruijn et al., 2009; Radke et al., 2011). AI, however, is also a central hub in the so-called salience network, which is involved in processing homeostatically relevant information (Seeley et al., 2007, 2019; Ullsperger et al., 2010). A meta-analysis in adults has shown that the AI is involved in both reward processing for oneself and for others (Morelli et al., 2015), suggesting involvement in processing salient outcomes for others as well. Besides, errors are usually highly salient events, used to steer behavior and optimize performance, and this may explain why increased AI activity has previously been repeatedly demonstrated for error processing. However, another meta-analysis in adults demonstrated that AI responds to salient outcomes, regardless of the valence of these outcomes (Bartra et al., 2013), indicating that saliency depends on more than just the associated reward outcome of an action. The current activation patterns might thus suggest that for adolescents the salience of observed hit-based rewards outweighs that of observed error-based losses. This interpretation is in line with previous studies in adolescents that have demonstrated AI involvement during reward processing (Silverman et al., 2015; Smith et al., 2014). Interestingly, the reverse pattern (i.e., higher AI activation during own error processing compared to reward processing) was currently found when adolescents played themselves (see Supplements), suggesting that salience is relatively increased for *own* performance errors similar to previous findings in adults. Future developmental studies should thus also include an older age group (e.g., young adults) to further our understanding of the developmental patterns of AI and striatum involvement in observed error and reward processing and aim at disentangling salience and valence effects.

4.2. *Observed error processing*

Our results showed no significant effect of valence when adolescents observed outcomes in pMFC. This finding is not in line with our hypothesis and earlier work showing pMFC activation for both own and observed errors in adults (de Bruijn et al., 2009). Although this may indicate that adolescents differ from adults in this regard, we are cautious in drawing developmental-related conclusions based on this finding. Importantly, similar to the AI, the pMFC -specifically anterior cingulate cortex-is also a central hub in the salience network (e.g., Seeley et al., 2007, 2019) and methodological differences between the current study and previous studies using this paradigm should be considered. Previously, the Cannonball task was pre-programmed to result in a mean 60% hit (i.e., rewards) and 40% miss (i.e., losses), thus errors occurred less frequently than hits (e.g., de Bruijn et al., 2009; Overgaauw et al., 2020; Radke et al., 2011). Infrequent events are generally also more salient, and this method thus introduces a possible confound when studying brain areas involved in the salience network. To control for this, the paradigm in the current study was pre-programmed to result in a mean 50% hit (i.e., rewards) and 50% miss (i.e., losses), thus balancing the frequency of observed rewards and errors. In comparison to previous studies, this method may thus have rendered errors less salient for participants, which may at least partly explain the absence of a valence effect in pMFC. Note, however, that this frequency interpretation cannot explain the current presence of the expected valence effect in pMFC when participants played themselves (see Supplements), suggesting that salience might thus indeed better explain the current results. Future dedicated studies on this topic are needed, as research on the neural mechanisms underlying observed error processing in adolescence is to this date scarce.

Finally, we did not find the expected age effects in pMFC activity during observation of errors. Our hypothesis was based on previous work indicating that the pMFC shows higher activation with age (Fitzgerald et al., 2010), which might be suggestive of improved performance monitoring with age. However, age effects on pMFC activation have mainly been reported in studies focusing on own error processing and these effects might be less pronounced or insignificant for observed error processing of peers. Contrary to our hypothesis, we found that pMFC activation for observed error processing was comparable for best friends and unfamiliar peers. Our finding is not in line with prior studies in adults showing increased pMFC activity for observing errors of friends compared to observing errors of others (e.g., strangers or disliked others) (Kang et al., 2010; Newman-Norlund et al., 2009; but see de Bruijn et al., 2009). It could be that this differentiation is not present in younger ages and develops over time into adulthood, which is an interesting hypothesis for future fMRI studies to investigate in both populations.

4.3. *Performance monitoring and the social brain*

Contrary to our hypothesis, our analyses on neural activation in social brain regions (mPFC, precuneus, and bilateral TPJ) showed higher activity in left TPJ when adolescents observed outcomes of an unfamiliar peer compared to those of a best friend. Previous findings in adolescents have been mixed, with some studies showing higher TPJ activation during prosocial decisions for friends compared to unfamiliar and disliked peers and during social interactions with familiar peers in comparison with unfamiliar people (Güroğlu et al., 2008; Schreuders et al., 2018b). However, another study in young adults has found decreased activation in the TPJ for social interactions with unfamiliar interaction partners they care about more (Bault et al., 2015). Other studies have found deactivation in the TPJ while adults viewed pictures of their loved ones (children or romantic partners), so both maternal and romantic love were related to deactivation in the TPJ (Bartels & Zeki, 2000, 2004). Bault et al., 2015 suggested that decreased TPJ activity results from growing closer to somebody, as efforts to infer intentions of others also decreases with closeness. Although TPJ activation patterns for different types of relationships are mixed, our current findings do fit with such an effort-related explanation of closeness.

After exploring brain-behavior relations, we did not find a significant association between friendship quality and neural activation in any of the social brain regions (mPFC, precuneus, and bilateral TPJ). This may suggest that neural activation in the social brain regions (mPFC, precuneus, and bilateral TPJ) during observed error and reward processing of best friends is not modulated by individual differences in friendship quality. However, it is important to note that the average reported friendship quality was high with low variability in the current sample, which may thus explain the absence of a relationship with brain activations.

4.4. *Limitations and future directions*

A few limitations of the current study should be noted. This current study set out to examine our research questions in a sample of adolescents, because this developmental period is characterized by changes in performance monitoring and peer relationships. However, it is crucial for future studies to realize that developmental conclusions can best be reached when including both adolescents and adults in the design, which would also allow for more direct comparison with existing literature which was predominantly performed in adults. Also, the effect of puberty-related changes on neural outcome processing was not one of our research questions, but some adolescents in our sample are undergoing pubertal development, and pubertal development has been shown to be related to activation in the striatum during reward processing in adolescents (op de Macks et al., 2011). Therefore, future fMRI studies should examine and/or control for the possible influence of puberty on observed reward processing in the context of peers. Such future studies that examine the effect of puberty need to carefully consider the age range and sample size taking into consideration that girls enter puberty earlier than boys (e.g., Blakemore et al., 2010).

One strength of the current design is the inclusion of a realistic social context. The current study focused on the neural correlates of observed error and reward processing in which we examined the social context of both best friends and unfamiliar peers, using a unique design where friends and peers were present during data collection. Interpretation of the findings relies on the believability of the experimental manipulation and this physical presence of friends and unfamiliar peers during the data collection session was crucial in ensuring this credibility. As such, the current task closely resembles real life interactions with others, as the adolescents take turn in performing the task or observing the other peer perform, whereby there are always consequences for both the adolescents and peers.

Finally, our work presents one of the first steps in understanding how neural activation in the peer context influences learning, as processing performance-based errors and rewards in the context of friends has implications for adolescent learning in a social context. Performance monitoring of errors and rewards is a crucial component of efficient learning as one can update one's behavior based on the neural signals of errors and rewards. Specifically, observation of performance-based errors and rewards obtained by others can inform one's own behavioral adjustments and thus forms the basis of observational learning (Bellebaum and Colosio, 2014). Considering that observational learning often takes place in the peer context of the classroom, studying the processes underlying the observation of performance-based errors and rewards obtained by friends and peers provides a crucial first step in understanding and potentially improving observational learning in the peer context. In the current study, we found reduced activation in the left TPJ, a brain region involved in mentalizing, while adolescents observed performance-based error and reward processing of their best friend compared to an unfamiliar peer. Future research is needed to further examine whether these results also extend to an observational learning context, which could demonstrate the advantage of this type of learning for adolescents in the social context of peers and friends. Relationship closeness with classmates has previously been shown to promote learning in adolescence (Hartl et al., 2015). Therefore, it is important for future studies to relate neural activation patterns in the social context of (close) peers to paradigms that examine learning behavior across adolescence. Probabilistic observational reinforcement learning paradigms have for example already been used to demonstrate the influence of peers on observational learning in children on a behavioral level (Rodriguez Buritica et al., 2016) and future fMRI studies should use comparable tasks to further unravel the neural mechanisms of peer influence on adolescents' (observational) learning behavior.

Author contributions

Iris Koele: Formal analysis, Writing - Original Draft, Visualization. Jorien van Hoorn: Investigation, Writing - Review & Editing, Funding acquisition. Ellen de Bruijn: Conceptualization, Software, Writing - Review & Editing. Berna Güroğlu: Conceptualization, Writing - Review & Editing, Supervision, Funding acquisition.

Ethics approval statement

The study was approved by the university Medical Ethical Testing Committee (METC), Leiden, the Netherlands and the study conforms to recognized standards of the Declaration of Helsinki.

Declaration of competing interest

The authors declare that they have no known conflict of financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data supporting this study's findings and the experimental paradigm are available on request from the corresponding author (i.j.koele@fsw.leidenuniv.nl).

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.neuropsychologia.2023.108619.

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