Title: Friends and foes: Neural correlates of prosocial decisions with peers in adolescence

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Abstract

Adolescence is a critical period for social orientation to peers and for developing social skills in interactions with peers. In the current study we examined the neural correlates of prosocial decisions for friends and disliked peers, and their links with participants' friendship quality and empathy as indices of social competence. Participants' friends and disliked peers were identified using sociometric nominations. Mid-adolescents (M_{age}=14.6; N=50) distributed coins between themselves and another player in a set of allocation games where they could make prosocial or selfish decisions for their friends and disliked peers, as well as for neutral and unfamiliar peers. Participants made the most prosocial decisions for friends and the least prosocial decisions for disliked peers. Prosocial decisions for friends yielded activity in the putamen and posterior middle temporal gyrus (pMTG) when compared to prosocial decisions for disliked peers, and in the superior parietal lobule (SPL) and precentral gyrus when compared to prosocial decisions for unfamiliar peers. Selfish decisions for friends and decisions for disliked peers did not result in heightened neural activity. Exploratory analyses of the associations between these neural activation patterns and measures of social competence revealed that putamen activity related negatively to negative friendship quality and that empathic personal distress related positively to SPL and precentral gyrus activity. Together, the findings illustrated that the SPL, precentral gyrus, pMTG, and putamen may be involved in promoting the continuation of friendships, and that social competence may modulate these neural mechanisms.

Keywords: peer relationships, social decision-making, fMRI, prosocial behavior, adolescence, friendships

1. Introduction

Adolescence is the transitional period from childhood to adulthood and is marked by significant social changes (Kilford, Garrett, & Blakemore, 2016; Roseth, Johnson, & Johnson, 2008). Compared to children, adolescents spend an increasing amount of their time with peers (Steinberg, 2005) and interactions with peers become increasingly salient for adolescents (Albert, Chein, & Steinberg, 2013; Berndt, 1992; Van Hoorn, Dijk, Meuwese, Rieffe, & Crone, 2014). Interactions that typically involve prosocial behaviors, such as helping, sharing, and giving, contribute to the formation of positive relationships with peers over time (Layous, Nelson, Oberle, Schonert-Reichl, & Lyubomirsky, 2012), whereas selfish behaviors in interactions typically contribute to peer dislike (Carlson, Lahey, & Neeper, 1984). Studies have shown that positive peer relationships based on social preference or likeability, such as friendships, are associated with healthy adolescent development (e.g., Aikins, Bierman, & Parker, 2005; Bukowski, Hoza, & Boivin, 1993; Parker et al., 2015), while involvement in negative peer relationships, that is, relationships based on dislike, is moderately associated with maladaptive functioning (Abecassis, 2003; Card, 2010; Hartup, 2003; Murray-Close & Crick, 2006). Whereas the neural processes underlying interactions with unfamiliar peers have been investigated in numerous studies (for reviews, see Lee & Harris, 2013; Rilling & Sanfey, 2011), few studies have focused on the neural processes underlying interactions with familiar peers, such as friends and disliked peers. In the current study, we aimed to make the first steps in examining how real-life peer relationships may shape the neural mechanism underlying social behavior in interactions with peers in adolescence. Specifically, we examined the neural correlates of prosocial and selfish decisions made toward *familiar* peers, in particular, toward friends and disliked peers, in mid-adolescence. We further explored the links between these neural patterns and social competence as indicated by best friendship quality and empathy.

Prosocial behavior, that is, voluntary actions intended to benefit others (Eisenberg, Fabes, & Spinrad, 2006), is important for forming and maintaining peer relationships (Fehr, Fischbacher, & Gächter, 2002; Markiewicz, Doyle, & Brendgen, 2001; Newcomb & Bagwell, 1995). Prosocial behavior has been shown to involve both self-regulation and mentalizing skills, which allow individuals to inhibit selfish impulses and orient toward others and attempt to understand their perspectives, intentions, and needs (Steinbeis & Crone, 2016; Telzer, Masten, Berkman, Lieberman, & Fuligni, 2011; Van den Bos, Westenberg, Van Dijk, & Crone, 2010). A study examining prosocial decision-making across the ages of eight to 18 years has shown that adolescents become increasingly better at differentiating between their interaction partners with age (Güroğlu, Van den Bos, & Crone, 2014). Specifically, from mid-adolescence onwards, participants made the most prosocial decisions for friends and the fewest prosocial decisions for disliked peers, showing that prosocial decisions become context-dependent with age. As such, mid-adolescence is an important developmental period for examining how prosocial decision-making becomes more differentiated to different types of interaction partners.

Cognitive control and mentalizing brain areas are involved in prosocial decision-making, including the lateral prefontral cortex (lPFC), and the temporoparietal junction (TPJ), the superior temporal sulcus (STS), and the medial prefrontal cortex (mPFC; Masten, Morelli, & Eisenberger, 2011; Steinbeis & Crone, 2016; Telzer et al., 2011; Van Hoorn, Van Dijk, Güroğlu, & Crone, 2016). Developmental fMRI studies have shown an age-related increase in activation of these regulatory and mentalizing brain regions across adolescence (Güroğlu, Van den Bos, & Crone, 2009; Steinbeis, Bernhardt, & Singer, 2012; Van den Bos et al., 2010). The TPJ and STS both are brain regions involved in mentalizing-related processes (Blakemore, 2008; Frith & Frith, 2012) and are suggested to be involved in social tie formation during repeated interactions with unfamiliar peers (Bault, Pelloux, Fahrenfort, Ridderinkhof, & van Winden, 2015). The mPFC, a brain region important for integrating information in order to determine future behavior (Amodio & Frith, 2006; Euston, Gruber, & McNaughton, 2012), is possibly crucial for selecting actions in relation to one's own goals and the goals of others in interactions (Bault, Joffily, Rustichini, & Coricelli, 2011; Bault et al., 2015). Importantly, activation of these brain regions involved in social decision-making has been shown to be modulated by interaction partners. For example, the mPFC and ventral striatum are activated more during interactions with friends relative to other peers, suggesting that interactions with friends might be experienced as more salient and rewarding, thereby contributing to a positive bond (Braams, Peters, Peper, Güroğlu, & Crone, 2014; Fareri & Delgado, 2014; Güroğlu et al., 2008). Interestingly, losing money for *unfamiliar* disliked peers relative to winning money was associated with increased ventral striatum activation (Braams et al., 2014). Such context-related modulation of brain activation patterns during interactions increase our understanding of the processes that are involved in the formation of relationships over time. However, before we can disentangle such developmental patterns, a greater understanding is needed of whether the peer relationship context modulates decision-making and its underlying neural processes in mid-adolescence.

Thus, the aim of the current study was to investigate the neural activation patterns underlying social behaviors toward peers and the ways that relationship **type** modulates brain activity underlying social behavior in a period that is highly significant for forming and continuing friendships, that is, mid-adolescence. To do so, we examined how real-life social contexts affect decision-making and associated neural processes, and how these were related to indices of social competence. This approach aids to understand how the social context affects underlying neural processes that might play a role in the development of peer relationships. We used a set of economic allocation games to examine the neural correlates of prosocial decisions involving real-life friends, disliked and neutral peers, and unfamiliar peers. In these paradigms, participants chose between preset dichotomous sets of coin distributions where one involved a prosocial distribution (i.e., benefiting the interaction partner) and the other involved a selfish distribution (i.e., resulting in a better outcome for the participant either in the form of having more coins than the other player or not allowing the other player have more coins than oneself; (Schreuders, Klapwijk, Will, & Güroğlu, 2018). In line with previous behavioral findings from an adolescent sample, we hypothesized that adolescents would be more prosocial toward friends than neutral or unfamiliar peers and least prosocial toward disliked peers (Güroğlu, et al., 2014). In a recent fMRI study we examined the neural basis of prosocial decision-making in young adults using the same experimental paradigm as in the current study. Our findings in adults showed that posterior regions of the TPJ and the putamen were implicated in prosocial decision-making in interactions with friends and that the STS and putamen were implicated in selfish decision-making in interactions with familiar disliked peers (Schreuders et al., 2018). Based on these prior findings, we expected similar increased activation patterns including the posterior TPJ (pTPJ) and putamen activity during prosocial choices for friends, and STS and putamen activity during selfish choices for disliked peers.

In the current study, we also explored associations between individual differences in best friendship quality and empathy skills, as proxies of social competence, and neural activation patterns during prosocial and selfish decisions for friends and disliked peers. Social competence is expected to promote positive social interactions and relationships. Friendship quality with the best friend (i.e., an indication of the ability to form a positive relationship) and empathy towards others in general are both predictors for social functioning. For example, in prior studies best friendship quality was associated positively with prosocial tendencies (Markiewicz et al., 2001), and higher empathy levels were associated with a better ability to resolve peer relational conflicts (De Wied, Branje, & Meeus, 2007). Furthermore, neuroimaging studies have shown that empathy levels modulated neural responses to observing a peer being excluded and the tendency to send comforting messages to the excluded peer (Masten, Eisenberger, Pfeifer, Colich, & Dapretto, 2013; Masten, Eisenberger, Pfeifer, & Dapretto, 2010). In the current study, we explored whether empathy levels and best friendship quality shaped underlying neural processes during decision-making in peer interactions. Based on prior findings on the role of friendship quality and empathic abilities in social behavior and functioning, we expected that better friendship quality and higher empathic skills would enhance the neural activation patterns that underlie prosocial decision-making with friends.

2. Method

2.1 Participants

The current study was part of the ongoing Nijmegen Longitudinal Study (NLS) on infant and child social development (van Bakel & Riksen-Walraven, 2002). In 1998, we recruited families with a 15-month-old child who lived in a city in the east of The Netherlands. Local health-care centers provided contact information for a subset of 639 families, to whom we sent a letter explaining the study goals. A return card of interest was sent back by 174 families. Out of these families, we randomly selected a subsample of 129 parent-child dyads to participate in the study as we had limited time and financial resources. This resulted in a community sample of 129 children and their parents, which was representative of the Dutch population of families with young children in terms of the number of single parents (5%) and fathers as primary caregiver (2%). The primary caregivers were between 22 and 47 years of age at the time of the recruitment and had an average educational level of 4.95 (*SD* = 1.77) on a 7-point scale ranging from low (elementary school) to high (college degree or higher). For all children, nationality was reported to be Dutch by their parents. This community sample has been followed since the children were 15 months old.

For more detailed information on the prior waves of the longitudinal study, see Niermann et al., 2015; Smeekens, Riksen-Walraven, & van Bakel, 2007; Tyborowska, Volman, Smeekens, Toni, & Roelofs, 2016).

All participants who declared to be willing to continue participation during the 7th wave (n = 108) were approached for participation in the current fMRI study. Healthy and right-handed participants who reported no contra-indications for fMRI and without a history of psychiatric and neurological impairments were considered eligible for participation (n = 58). Seven adolescents who were eligible for participation did not participate due to technical or logistic problems, and one participant was excluded from the analyses due to excessive movement during scanning (> 2.8 mm). This resulted in a sample of 50 mid-adolescents (M_{age} = 14.56, SD = .13, 29 males).

2.2 Procedure

Before scanning, participants and parents gave written informed consent for participation. The participants were familiarized with the scanner environment using a mock scanner and practiced the fMRI task. Participants and parents also filled out a battery of questionnaires. Participants received €30 in gift cards and a small additional endowment of €2 earned with the fMRI task, and their parents received a small gift for participation. The local medical research ethics committee approved the study.

2.3 Measures

2.3.1 Social competence.

2.3.1.1 Friendship quality. Positive and negative best friendship quality was measured with an adapted parent-report version of the friendship quality scale (FQS; adapted from Bukowski, Hoza, & Boivin, 1994). This scale contained 5-point scale items measuring how true each items was for the relationships of the child with their best friend with (1) *not true at all* to (5) *very true*. Parents also had the option to reply with "*I do not know*", considering that they may not have the insights to answer all questions regarding the relationship of their child with their best friend; this response was coded as ‘missing’. Positive friendship quality was measured with 13 questions assessing positive and supportive characteristics of the friendship (*M* = 4.23, *SD* = 0.56), with higher scores indicating higher positive friendship quality. Example items of the positive FQS are “if my friend had to move away, I would miss him/her”, and “My friend and I think of fun things for us to do together”. Negative friendship quality was measured with seven questions assessing negative characteristics of the friendship (*M* = 1.69, *SD* = 0.56), with higher scores indicating higher negative friendship quality. Example items of the negative FQS are “My friend and I can argue a lot”, and “My friend can bug me or annoy me even though I ask him/her not to”.

Here, we report data from participants with at least 75% valid responses (i.e., not including the “*I do not know*” option and a missing response); that is, participants with at least 10 (*n* = 37) and 6 (*n* = 41) valid responses for the positive and negative FQS, respectively, were included. For 43 participants we had valid positive *and/or* negative FQS scores. For 21 participants (48.8%), the best friend for whom the FQS was filled out by the parent was also one of the three friends named in the fMRI task (see below for details). The FQS scales were reliable: mean inter-item correlations within these scales were .362 and .438 for positive and negative FQS, respectively.

2.3.1.2 Empathy. Empathy was assessed with the self-report Interpersonal Reactivity Index (IRI; Davis, 1983). Participants indicated on a 5-point scale whether a statement was (1) *not true* to (5) *true* for them. We used three six-item subscales to measure empathy. Concern for others was measured with the Empathic Concern (EC) subscale (*M* = 3.36, *SD* = 0.56), the tendency to take others’ perspective was assessed with the Perspective Taking (PT) subscale (*M* = 3.40, *SD* = 0.57), and finally, to what extent participants got overwhelmed by others’ emotions was assessed with the Personal Distress (PD) subscale (*M* = 2.29, *SD* =

0.59). We did not include the Fantasy subscale in which empathic responses toward fictional characters is assessed, because we were interested in empathic responses in real-life social settings. The EC, PT, and PD subscales were reliable (Cronbach's alphas were .679, .657, and .741, respectively) and mean inter-item correlations ranged from .235 to .263.

2.3.2 FMRI task description.

2.3.2.1 Peer groups. Prior to the scanning day, participants were asked to provide a list of the names of their current classmates and were asked to rate how much they liked each classmate on a 5-point scale ranging from 1 (*not at all*) to 5 (*very much*). Next, they were asked to fill out a sociometric questionnaire where they were asked to nominate 5 classmates as their friends and indicate which 5 classmates they liked the least. The ratings and nominations obtained were used to determine three types of peers: a) *friends*: classmates who were nominated by the participant as a friend and received a rating of 4 or 5, b) *disliked peers*: classmates who were nominated by the participant as a least liked peer received a rating of 1 or 2, c) *neutral peers*: classmates who received a rating of 3. Participants played the fMRI task with these three groups of familiar peers plus a fourth group of *unfamiliar peers*, who were told to be other same-age participants of the study. The groups of unfamiliar and neutral peers were included in the task as control conditions.

Each of the four groups of peers (i.e., friends, disliked peers, neutral peers, and unfamiliar peers) consisted of two or three players. Overall, we aimed to have three players in each group, but whenever this was not possible we constructed a group with two peers, for example, when participants could name only two disliked peers. Across the four groups of peers, participants either had three peers in each group or two groups with two peer names and two groups with three peer names to keep a balanced distribution across the four groups (also see, Schreuders et al., 2018). There were 43 participants (86%) with three peers in each group and 7 participants (14%) with two peers in two peer groups. Participants were told that they would play each trial of the fMRI task with one person from these four groups of players (i.e., that they would distribute coins between themselves and a peer). Importantly, they were told that three groups of familiar peers consisted of randomly chosen classmates. This was done in order not to give away the purpose of the study and to prevent that participants could use explicit strategies of how to distribute coins. To present the four peer groups in a neutral manner to the participants, the groups were randomly assigned to one of four vehicle symbols named train, bike, car, and boat (Figure 1A). At the end of the experiment, participants were asked to recall the names of all group members and to indicate their attitude toward each group. This was done in order to check whether the manipulation of the group members representing a specific type of relationship was successful and whether participants paid attention to the task (see the Results section for the manipulation checks). In the instructions, it was emphasized that participants' decisions translated to real money and had consequences for themselves as well as for their interaction partners. However, it was not specified how much the coins were worth and how the distribution of coins would be implemented. None of the participants had questions regarding this point during the instructions.

2.3.2.2 Coin distributions. In the scanner, participants played the role of the allocator in a set of three modified dictator games (Fehr, Bernhard, & Rockenbach, 2008; Güroğlu, Will, & Crone, 2014), in which they distributed coins between themselves and another player by choosing one of two preset distributions. Each set of distributions entailed an equity option in which coins were evenly distributed with one coin for the self and one coin for the other player (i.e., 1/1 distribution). The alternative inequity distribution varied across the three games: the alternative distribution for (a) the *advantageous competitive inequity* (ACI) game entailed one coin for the self and zero coins for the other player (i.e., 1/0 distribution); (b) the *self-maximizing inequity* (SMI) game entailed two coins for the self and zero coins for the other player (i.e., 2/0 distribution); and (c) the *disadvantageous prosocial inequity* (DPI) game entailed one coin for the self and two coins for the other player (i.e., 1/2 distribution). The prosocial option was the 1/1 distribution in the ACI (“prosocial giving”) and SMI (“prosocial sharing”) games, and the 1/2 distribution in the DPI game (“disadvantageous prosocial giving”). The selfish option was the 2/0 distribution in the SMI game, the 1/0 distribution in the ACI game, and the 1/1 distribution in the DPI game. Prosocial choices were coded as 1 and selfish choices as 0. The percentage of prosocial choices per interaction partner was calculated across games. We used three different types of games to keep the participants engaged in the task. Prosocial choices always benefited the interaction partner (i.e., the equity option in the ACI and SMI game and the inequity option in the DPI game), whereas selfish choices maximized the outcome for the self (i.e., the inequity option in the ACI and SMI game and the equity option in the DPI game) (Figure 1A).

2.3.2.3 Task duration. The fMRI task included 96 trials presented in a randomized order. Participants engaged in 24 social decisions for members of each of the four groups (i.e., friends, disliked peers, neutral peers, and unfamiliar peers) across three allocation games (i.e., 8 trials per game). Each trial started with a jittered fixation cross (*M* = 1512.5 ms, min = 550 ms, max = 5500 ms: optimized with Opt-Seq2, surfer.nmr.mgh.harvard.edu/optseq/; (Dale, 1999), and was followed by a screen presenting the two sets of coin distributions participants could choose from; this screen also displayed the group symbol along with the names of the group members for that trial. Participants had to respond to the trial within 5000 ms. The option selected by the participants was encircled in red for 1000 ms (Figure 1B). If they failed to respond within 5000 ms, a screen showing “Too late!” was presented for 1000 ms. It was explained that the computer selected a random number of trials to calculate their earnings which would be paid out at the end of the experiment. In reality, all participants were paid €2. See Schreuders et al. (2018) for details on the same experimental paradigm and task design.

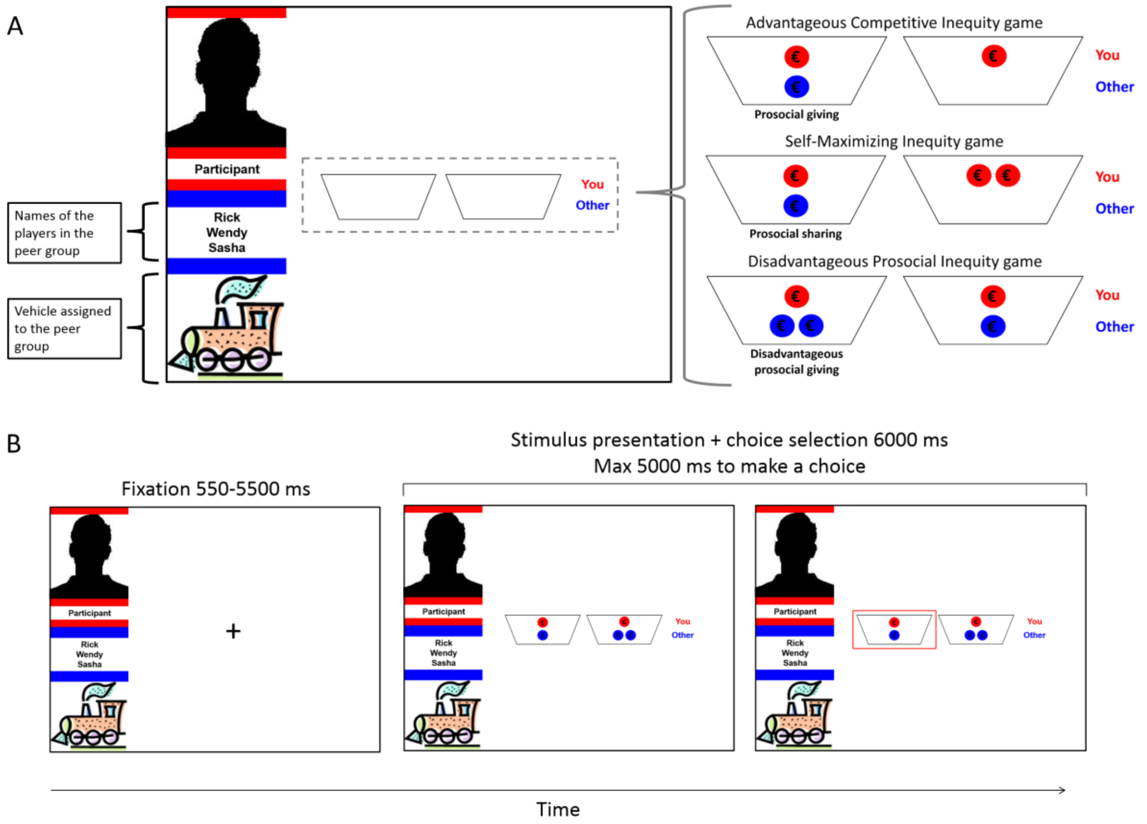

Figure 1. (A) Names of players in each group were displayed in the left bottom panel of the screen (here Rick, Wendy and Sascha). These three group members always belonged to the same peer category (i.e., friend, disliked peer, neutral peer, or unfamiliar peer). The interaction partner was one of these players whose names were displayed. All four peer groups in the task were randomly assigned to a vehicle (i.e., train, bike, car, and boat), which was also displayed in the left bottom panel of the screen (here train). There were three different preset coin distributions, always with a prosocial and a selfish option, depicted here on the left and right, respectively. (B) Example of a trial of the fMRI task. After a fixation cross participants were presented with a screen showing the stimulus and with whom they were playing that trial. At stimulus onset, they could choose between the two options presented on the screen by pressing the corresponding button. A trial ended with selected choice indicated on the screen. Color figure.

2.4 MRI Data Acquisition

MRI scanning was performed with a 3T Siemens Tim Trio scanner. The scanning procedure included (a) a localizer scan, (b) Blood oxygenation level dependent (BOLD) T2* weighted gradient echo planar images (EPI; TR = 2.00 s, TE = 30 ms, 80° flip angle, 38 axial, sequential acquisition, slice thickness = 2.8 mm, field of view (FOV) = 220 mm, and (c) high resolution anatomical T1-weighted MP-RAGE sequence image (TR= 2300 ms, TE= 3.03 ms, 8° flip angle, 192 sagittal slices, FOV= 256 mm, slice thickness = 1.00). Two functional scans were obtained that lasted approximately 6 minutes and 190 dynamics each.

2.5 FMRI Data Analysis

SPM8 software was used for the image preprocessing and analyses (http://www.fil.ion.ucl.ac.uk/spm/). The functional images were preprocessed using slice-time correction (middle slice as reference), realignment, spatial normalization, and smoothing with a Gaussian filter of 8 mm full-width at half maximum. Functional images were spatially normalized to T1 templates, functional images of one participant were spatially normalized to EPI templates. Regressors were modeled as zero-duration events at stimulus onset and convolved with a hemodynamic response function (HRF). Stimulus onset was the moment participants were presented with the two distributions to choose from. Trials on which the participant failed to respond were modeled separately as covariate of no interest and were excluded from further analyses. The modeled events were used as regressors in a general linear model (GLM), along with a basic set of cosine functions that high-pass filtered the data (cutoff 120 seconds) and a covariate for session effects. Autocorrelations were estimated using an autoregressive model order of 1. Additional analyses revealed that participants' response times on stimuli did not affect the results. The results are reported in Montreal Neurological Institute (MNI) 305 stereotactic space. Image pre-processing and analyses were conducted using SPM8 software (http://www.fil.ion.ucl.ac.uk/spm/).

In all neuroimaging analyses, we controlled for the frequency of prosocial choices to minimize its effect as a confounder variable, because the frequency of prosocial choices differed significantly between friends, disliked peers, and unfamiliar peers (see behavioral results). We controlled for the frequency of prosocial choices by calculating a difference score of prosocial choices for each participant (e.g., in the Friend Prosocial > Disliked peer Prosocial contrast: [proportion prosocial choices for friends]$_i$-[proportion prosocial choices for disliked peers]$_{i,}$, where *i* represents a participant), and then we included these values as a covariate in the whole-brain contrasts.

We aimed to examine the neural responses underlying different types of social decisions (i.e., prosocial and selfish) in social interactions with friends and disliked peers. We therefore compared decisions for friends with decisions for disliked peers (as a comparison between the two most “extreme” relationships) and decisions for friends and disliked peers with decisions for unfamiliar peers (who form a similar control condition for all participants). For brevity purposes, we report neuroimaging results involving the neutral peer in the Supplementary Materials (Table S1; Figure S1). We chose to report the results with the unfamiliar peer as comparison condition in these analyses, because the relationship with the unfamiliar peer was homogenous for all participants, as none of the participants was affiliated with the unfamiliar peer in any way, whereas past social interactions with neutral classmates may vary across individuals. Please note that, participants who did not make any prosocial or selfish choices for one of the interaction partners in the contrasts could not be included in the *t*-tests. Therefore, the sample size in these tests occasionally differed from the complete sample size of 50 participants, and ranged from 40 to 48. In addition, we report analyses in the Supplementary Materials where we reran these analyses with a subset of the sample consisting of participants with a minimum number of trials per condition to test the robustness of the results (Table S2 and Table S3).

Finally, in order to examine links between the neural correlates of prosocial and selfish choices and social competence, we extracted parameters of region of interests (ROIs) based on the whole-brain *t*-contrasts using the MarsBaR toolbox (Brett, Anton, Valabregue, & Poline, 2002). In all fMRI analyses, we used an family-wise-error (FWE) cluster-correction at $p < .05$, with a cluster-forming threshold of $p < .001$ (Woo, Krishnan, & Wager, 2014). We explored correlations between neural activation during prosocial choices for friends and disliked peers and indices of social competence. Since sample sizes of these correlation analyses differ from the total sample of 50 participants, we consider these analyses to be exploratory and preliminary.

3. Results

3.1 Manipulation Check

Correct recall of the names was high for friends, disliked peers, and neutral peers (*M* range 87%-99%, *SD* range 6%-32%), with recall – as expected – being lowest for unfamiliar peers (*M* = 43%, *SD* = 37%) and differing significantly from correct name recall for the other three groups, $F(1.99, 87.43) = 42.85$, $p < .001$, Greenhouse-Geisser corrected. Open-ended questions about participants' opinion of the four peer groups were coded into a five-point scale ranging from 1 (*very negative*; e.g., "I do not like these people", or "these kids are arrogant") to 5 (*very positive*; e.g., "These people are my friends", or "I like these people the best"). Participants' opinion of the groups with familiar peers (i.e., friends, neutral peers, and disliked peers) differed significantly from one another, $F(2, 78) = 123.93$, $p < .001$. As expected, participants rated friends more positively (*M* = 4.68, *SE* = .08) than neutral peers (*M* = 3.35, *SE* = .12), who were also rated more positively than disliked peers (*M* = 2.28, *SE* = .14), all *p*s < .001. Regarding the unfamiliar peers, 4 participants (8%) rated this group as neutral (as was indicated by scores of 3 points), 2 participants (4%) as positive (as indicated by scores of 4 and 5 points), and 44 participants (88%) indicated that they could not evaluate this group of peers because they did not know them. Together, these results indicate that participants viewed the relationship with the different group members as intended.

3.2 Behavioral Results

3.2.1 Social competence. Correlation analyses showed that positive and negative friendship quality scores were not significantly correlated, $p = .09$. Scores on the EC subscale were correlated positively with scores on the PT and PD subscales, *Spearman's* $\rho = .32$, $p <$

.05 and $\rho = .59$, $p < .001$, respectively. There was no correlation between PT and PD scores, $p = .09$. Positive FQS scores and PT were positively correlated, *Spearman's* $\rho = .36$, $p < .05$. There were no other significant correlations between the IRI and FQS subscales, *p*s > .240.

3.2.2 FMRI task. Figure 2 depicts for each participant the percentage of prosocial choices made for friends, disliked peers, neutral peers, and unfamiliar peers. As can be seen in Figure 2, participants' changed their individual preferences for prosocial and selfish choices depending on their interaction partner. To examine the participants' number of prosocial choices involving different players, a repeated measures ANOVA was conducted with "player" as the within-subject factor indicating the relationship with the interaction partner (4 levels: friend, disliked peer, neutral peer, and unfamiliar peer) and the percentage of prosocial choices as the dependent variable. Prosocial behavior was significantly modulated by player, $F(1, 49) = 22.89$, $p < .001$. Participants made more prosocial choices for friends (*M* = 78 %, *SE* = 3%) than for disliked peers (*M* = 42%, *SE* = 4%), neutral peers (*M* = 57%, *SE* = 4%), and unfamiliar peers (*M* = 55%, *SE* = 4%), all *p*s < .001. Participants also made more prosocial choices for neutral and unfamiliar peers than for disliked peers, $p < .01$ and $p < .001$, respectively. These behavioral results show that participants made most prosocial decisions for friends and the least prosocial decisions for disliked peers (see Figure 3). Behavioral results showing how the frequency of prosocial choices for friends, disliked peers, unfamiliar peers, and neutral peers differed within the ACI, SMI, and DPI game can be found in the supplementary materials (Figure S1).

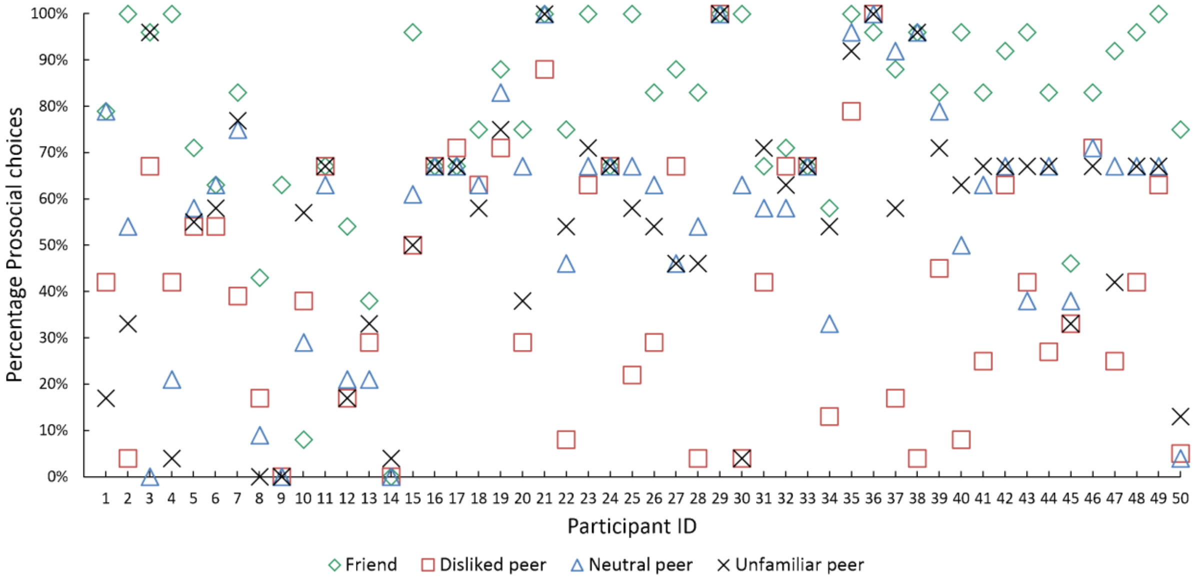

Figure 2. Percentage prosocial choices separately for friends, disliked peers, neutral peers, and unfamiliar peers for each of the 50 participants. Color figure.

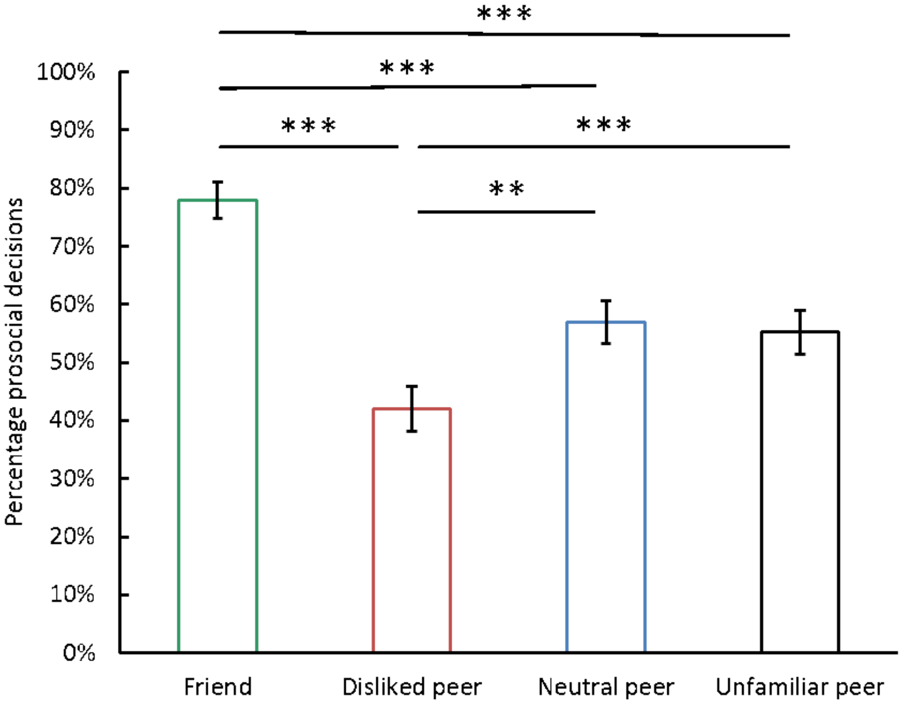

Figure 3. Mean frequency (%) and standard errors of prosocial choices per interaction partner. Significant differences are indicated by an asterisk (*). *$p < .05$, **$p < .01$, ***$p < .001$. Color figure.

3.3 Neuroimaging Results

3.3.1 Prosocial choices for friends. First, we investigated neural activation patterns during prosocial choices for friends versus for disliked peers where we controlled for the frequency of prosocial choices. The whole-brain Friend Prosocial > Disliked Peer Prosocial one sample *t*-test (*n* = 48) yielded activation in brain regions including right putamen, right posterior middle temporal gyrus (pMTG), and scattered clusters of superior parietal lobule (SPL) activity (Figure 4A). Next, we examined the Friend Prosocial > Unfamiliar Peer Prosocial whole brain *t*-test (*n* = 47), which yielded activation in regions including bilateral SPL, and left precentral gyrus (Figure 4B). A complete list of activations can be found in Table 1; activations involved in the *t*-contrast of Unfamiliar Peer Prosocial > Friend Prosocial can be found in the Supplementary Materials.

3.3.2 Selfish choices for friends. In a similar fashion, we examined neural activation patterns during selfish choices for friends. The Friend Selfish > Disliked Peer Selfish (*n* = 40) and Friend Selfish > Unfamiliar Peer Selfish (*n* = 40) *t*-tests did not result in any significant neural responses. Activations involved in the reverse *t*-contrast of Unfamiliar Peer Selfish > Friend Selfish can be found in the Supplementary Materials.

3.3.3 Prosocial choices for disliked peers. The Disliked Peer Prosocial > Friend Prosocial (*n* = 48) and the Disliked Peer Prosocial > Unfamiliar Peer Prosocial (*n* = 47) *t*-tests did not result in significant heightened brain activation. Results for the reverse *t*-contrast Disliked Peer Prosocial > Unfamiliar Peer Prosocial can be found in the Supplementary materials (Table S1).

3.3.4 Selfish choices for disliked peers. The Disliked Peer Selfish > Friend Selfish (*n* = 40), and the Disliked Peer Selfish > Unfamiliar Peer Selfish (*n* = 47) *t*-tests did not yield significant brain activity. The reverse *t*-contrast of Disliked Peer Selfish > Unfamiliar Peer Selfish can be found in the Supplementary materials.

3.3.5 Links with social competence. Finally, we explored Pearson's correlations between neural activation during prosocial choices for friends and social competence as assessed by friendship quality (i.e., positive and negative FQS) and empathy (i.e., IRI subscales EC, PD, and PT). We used the ROI parameter estimates from the putamen and pMTG from the Friend Prosocial > Disliked Peer *t*-contrast and left and right SPL and left precentral gyrus from the Friend Prosocial > Unfamiliar Peer Prosocial *t*-contrast.

For ROIs from the Friend Prosocial > Disliked Peer Prosocial contrast, there was a significant negative correlation between putamen activity and negative FQS (r = -.33, p =.04, n = 40; Figure 4A). There were no other significant correlations between the parameter estimates and positive and negative FQS (ps > .55, ns between 35 and 40) and IRI subscales EC, PD, and PT (ps > .130, n = 39).

For ROIs from the Friend Prosocial > Unfamiliar Peer Prosocial contrast (n = 38), there was a positive correlation between PD in left SPL (r = .40, p =.01), right SPL (r = .44, p < .01), and left precentral gyrus (r = .32, p < .05; Figure 4B). There were no significant correlations between ROI parameters and EC and PT (ps > .21, n = 38) and positive and negative FQS (ps > .17, ns between 34 and 38).

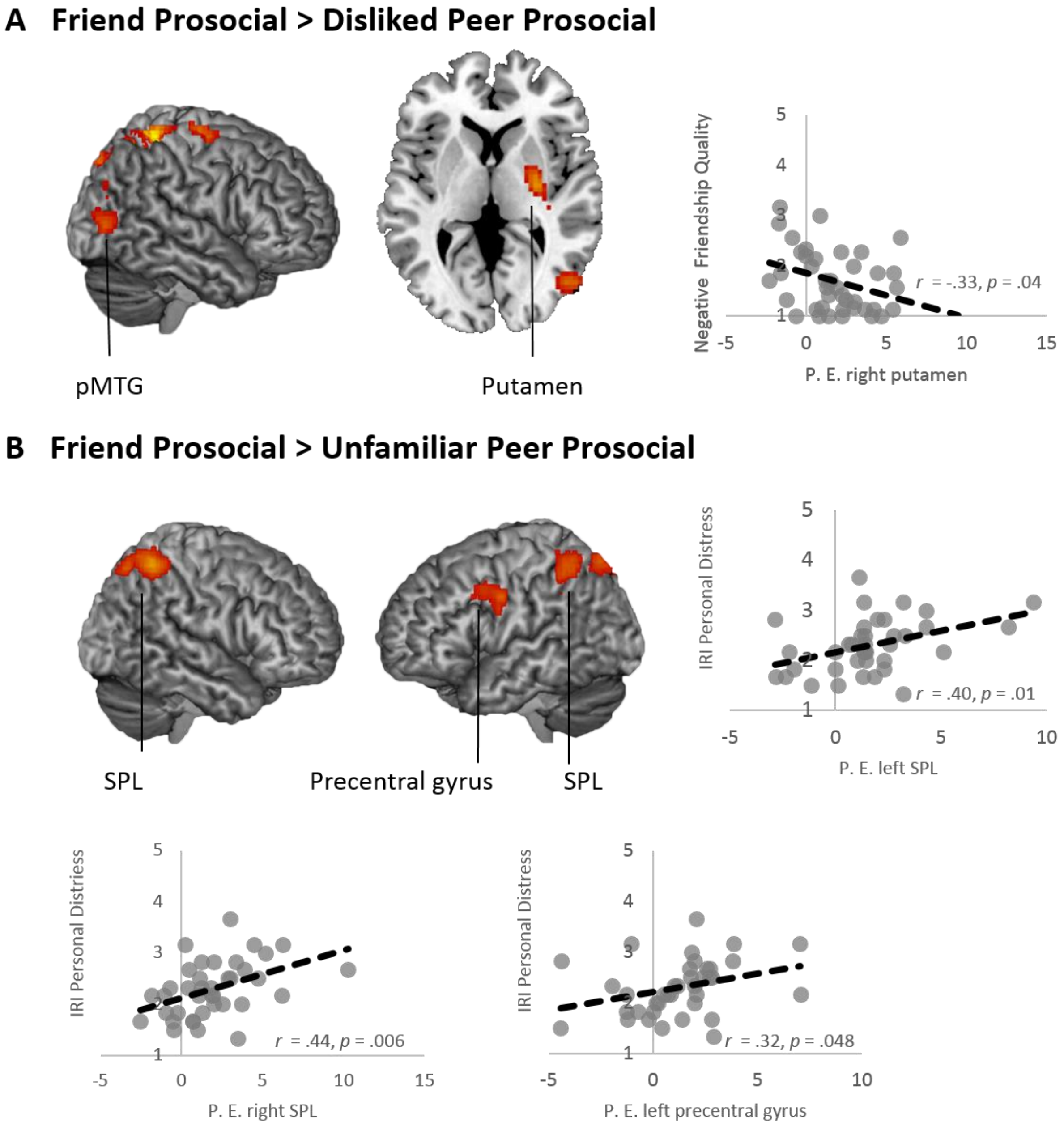

Figure 4. Whole-brain contrasts controlling for the frequency of prosocial behavior for (A) Friend Prosocial > Disliked peer Prosocial with activation in putamen (28, -11, 4) and the pMTG (50, -73, 6), and (B) Friend Prosocial > Unfamiliar peer Prosocial with activation in bilateral SPL (42, -50, 57; -51, -50, 54) and left precentral gyrus (-48, -3, 37). Scatterplots show significant correlations between parameter estimates (P. E.) of regions of interest (ROIs) and social competence measures friendship quality and empathy. pMTG = posterior middle temporal gyrus, SPL = superior parietal lobule. Color figure.

4. Discussion

In this study, we aimed to get a better understanding of how established real-life peer relationships are related to social behavior and their underlying processes in a highly sensitive period for social development, mid-adolescence. More specifically, we examined the neural correlates of prosocial and selfish decisions in interactions with friends and disliked peers in mid-adolescence. The behavioral results confirmed prior findings that participants made most prosocial decisions for their friends and were least prosocial toward disliked peers (Güroğlu, et al., 2014; Schreuders et al., 2018). The neuroimaging results showed that prosocial decisions for friends yielded distinct neural activation patterns when prosocial decisions for friends were contrasted with prosocial decisions for disliked peers (putamen and pMTG) and unfamiliar peers (precentral gyrus and the SPL). Selfish decisions for friends and both prosocial and selfish decisions for disliked peers were not related to any heightened brain activation patterns. We further explored links between social competence measures and brain activity from the regions that were found for prosocial decisions for friends. This revealed that lower parent-reported negative best friendship quality related to greater putamen activity during prosocial decisions for friends relative to prosocial decisions for disliked peers, and that higher levels of self-reported empathic personal distress related to higher levels of bilateral SPL and precentral gyrus for prosocial decisions for friends relative to prosocial decisions for unfamiliar peers.

4.1 Friends

Similar to our findings in Schreuders et al. (2018), although more superior in the current study, activity in the SPL was associated with prosocial decisions for friends when compared to unfamiliar peers, and there was less pronounced scattered SPL activity when compared to disliked peers. Together, these findings suggest that the lateral parietal cortex is involved in social interactions, including prosocial decisions, with others in positive relationship types versus more negative relationship types. It should be noted here that although the same experimental design was employed in the adult sample reported by Schreuders et al. (2018), the studies were conducted in two different scanners of different brands and thus the findings could not be directly compared. Future studies should aim to replicate our current findings by examining the developmental patterns in neural activation patterns underlying social decisions for peers.

Other studies also found parietal regions in the vicinity of the TPJ involved in various social tasks, including adjusting prosocial behavior depending on the social distance of the other (Strombach et al., 2015), attentional processes related to imitating others (Marsh, Bird, & Catmur, 2016), social decision-making in the larger peer group (e.g., Van Hoorn et al., 2016), attentional processes (e.g., Vossel, Geng, & Fink, 2014), and integration of distinct cognitive processes to guide social decision-making (Carter, Bowling, Reeck, & Huettel, 2012). It has also been suggested that these posterior parietal brain regions support neural processes of attention and integration of perspectives (Carter & Huettel, 2013). As such, our findings might suggest that prosocial decisions for liked others might be more readily supported by such spontaneous integration of self and other related perspectives, which might make prosocial behaviors towards liked others easier. Although this interpretation is somewhat speculative, it is important for future studies to investigate the links between the development of these posterior parietal brain regions and the development of prosocial behavior towards liked peers (Güroğlu et al., 2014).

In contrast to our prior study in young adults (Schreuders et al., 2018), the comparison between prosocial choices for friends and for unfamiliar and neutral peers (see Supplementary Materials) revealed precentral gyrus activation. The precentral gyrus is known to be involved in sensorimotor functions (Cooke & Graziano, 2004; Yousry et al., 1997). Although the precentral gyrus is reported in prior studies on social interactions (e.g., Cartmell, Chun, &

Vickery, 2014; Lee & Harris, 2013), its role during social decision-making is still unclear and should be further investigated in future studies of social behavior.

In our prior study with adults, we found enhanced putamen activity during prosocial decisions for friends compared to disliked peers (Schreuders et al., 2018). The current study extends these results by showing that the putamen is also underlying prosocial interactions with friends in mid-adolescence. The putamen is found to be involved in making choices that are most likely to result in a reward or positive outcomes (Balleine, Delgado, & Hikosaka, 2007; Haruno & Kawato, 2006), and in predicting and anticipating on the outcome of prosocial decisions involving peers (Delgado, Frank, & Phelps, 2005). Relatedly, the putamen is shown to be involved in habit formation, such that it is implicated in learning to select an action that is most likely to result in a positive outcome (Brovelli, Nazarian, Meunier, Boussaoud, 2011; Schultz, Tremblay, & Hollerman, 2003). We further found enhanced pMTG activity during prosocial decisions involving friends compared with prosocial decisions with disliked peers. In previous studies on social cognition, activity in the pMTG was linked to lower-order social cognitive functions such as perceiving biological motion, but is hypothesized to play a supporting role in higher order functions involved in mentalizing (Pelphrey, Morris, Michelich, Allison, & McCarthy, 2005). Corroborating prior findings, our results may suggest that the putamen and the pMTG play an important role during the decision-making process in indicating behavior that is consistent with **a (positive) relationship type**, which might have significant implications for promoting the continuation of social relationships such as friendships (Schreuders et al., 2018).

Similar to our findings in young adults, the putamen was also not involved in prosocial decisions for friends when compared to unfamiliar peers in mid-adolescence, suggesting that **the relationship type** might play an important role in putamen activation (Schreuders et al., 2018). Our manipulation check showed that adolescents rated friendships most positive and disliked peer relationships most negative; similarly, our behavioral results showed that adolescents are most prosocial toward friends and least prosocial toward disliked peers. As such, unfamiliar peers are likely to be more similar to friends than relationships based on dislike. The putamen might possibly be also involved in prosocial decisions for unfamiliar peers to a certain extent, whereas it distinguishes most between most positive (i.e., friendships) and most negative (i.e., disliked peers) relationship types.

To summarize, the current study showed involvement of brain regions previously related to social-decision-making in general. More specifically, the current study used an ecologically valid real-life social context and therefore highlights the role of these brain regions in maintaining existing friendships by their involvement in prosocial decisions toward friends. Future developmental studies are crucial to further illuminate the role of these brain regions and their development in the establishment and continuation or dissolution of peer relationships.

4.1.1 Links with social competence. Our preliminary analyses on the role of social competence in decision-making suggest that social competence may modulate activation patterns underlying prosocial decisions for friends. Participants with lower levels of negative friendship quality, that is, friendships that were to a lesser extent characterized **by** conflict and power imbalance, yielded enhanced putamen activity when making prosocial decisions for friends compared with making prosocial decisions for disliked peers. Interestingly, this relation was observed for negative friendship quality in a contrast including disliked peers (i.e., a negative peer relationship), which may suggest that effects of negative friendship characteristics may be particularly salient in this context. Tentatively, positive friendship quality was typically high in all best friendships reported here and thus possibly did not have distinctive power to differentiate between the underlying neural patterns in prosocial decisions. Note also that positive and negative friendship quality were not significantly correlated. It could thus be that the level of negative friendship quality is particularly crucial for illuminating the individual differences related to the underlying neural patterns of prosocial decisions.

Furthermore, greater empathy levels regarding personal distress, which is, getting overwhelmed by others' emotions, were associated with enhanced activity in bilateral SPL and the precentral gyrus during prosocial decisions for friends relative to prosocial decisions for unfamiliar peers. These findings suggest that when compared to prosocial interactions with unaffiliated peers, individual differences in personal distress in response to others' emotional expressions may affect how prosocial decisions for friends are made. Personal distress is often described as a self-oriented reaction to others' emotions (Davis, 1983) that is suggested to relate to maladaptive empathic reactions (Rieffe & Camodeca, 2016). Nevertheless, feelings of empathic personal distress are also found to relate to less bullying (Rieffe & Camodeca, 2016), and to a greater social sensitivity, which is important to interpret social information (Cliffordson, 2002). In this regard, it is also striking that we did not find any links with other dimensions of empathic skills, such as empathic concern and perspective taking, and the neural patterns underlying prosocial decisions for friends. It may be that affective empathy, such as personal distress, differentiates between individuals more strongly than cognitive empathy, such as perspective-taking skills and empathic concern. As the participants from the current study showed relatively low to moderate levels of general personal distress, one could argue that a moderate level of empathic distress may contribute to prosocial tendencies during interactions with friends. The role of different aspects of empathy in decisions for different types of peers should be further investigated in future studies.

Although future studies should further study the role of social competence in decision-making involving friends, our findings support the idea that social competence and positive peer interactions are linked (Hartup, 1996; Wentzel, 1998), and contribute to our understanding of work previously introduced reporting links between best friendship quality and empathy with interactions with peers (De Wied et al., 2007; Markiewicz et al., 2001; Masten et al., 2013; Masten et al., 2010; Twenge, Baumeister, DeWall, Ciarocco, & Bartels, 2007). Although more research is warranted, together, our findings suggest that a greater orientation toward others is associated with greater involvement of neural mechanism underlying decisions that benefit friends.

4.2 Foes

It has been shown that adolescents perceive disliked peers as aggressive and not prosocial (French, Jansen, & Pidada, 2002; LaFontana & Cillessen, 2002), which could explain why adolescents made least prosocial choices in interactions with them in the current study. Individuals might presume that prosocial behavior toward disliked peers is not likely to benefit them later on, which makes prosocial decisions for disliked peers not necessarily worth the investment, especially if they are paired with costs for the self. Despite significant differences in the frequency of prosocial choices for disliked peers compared to friends and unfamiliar peers, prosocial decisions for disliked peers were not associated with any significant heightened neural activation compared to other types of peers. Investigating interactions with disliked peers in an experimental fMRI paradigm is challenging, and studies on this topic are therefore scarce. In our prior study, we employed a similar design where we investigated neural activation patterns of decision-making in interactions with friends and disliked peers in a sample of young adults (Schreuders et al., 2018). In the current study we did not find heightened putamen and STS activity during selfish decisions for disliked peers compared with friends. This discrepancy may suggest developmental differences in the neural underpinnings of decision-making in interactions with disliked peers, but this should be tested explicitly in future studies. Another possible explanation for our lack of heightened neural activation for disliked peers might be that relationships with disliked peers are more diverse than friendships. It has been suggested that negative relationships with disliked peers are based on highly varying reasons and processes that might trigger dislike between individuals (Abecassis, 2003; Abecassis, Hartup, Haselager, Scholte, & Van Lieshout, 2002). Further, it is possible that in the current study not all disliked peers were strongly disliked but that they were relatively least liked compared to other classmates. Although different types and degrees of dislike might elicit similar behavior (i.e., fewer prosocial choices), the underlying reasons and neural mechanisms might be diverse, yielding it difficult to detect consistent neural activation patterns that underlie the same selfish behavior.

4.3 Limitations and Concluding Remarks

Based on the current paradigm, it was challenging to completely dissociate effects of interaction partners and behavior in the neural activation patterns. As our behavioral findings clearly show, prosocial decisions are dependent on the interaction partner. Even though we controlled for frequency of behavior in our contrasts of neuroimaging data, it can be discussed to what extent these results present a full dissociation of the role of interaction partners and behavior, as these are intertwined with each other. This point presents a specific challenge to studying context-dependent social behavior using decision-making tasks. To our knowledge, the current study is the first to examine decision-making in the context of diverse real-life relationships with peers in adolescence. However, the social decisions in the fMRI task could be perceived as being hypothetical because the interaction partners were not present during the scanning session. To make the paradigm more ecologically valid, future studies might consider including the presence of real-life peers in the experiment paradigm. It should be acknowledged that having familiar disliked peers present during testing is a particularly challenging endeavor. Furthermore, to be better able to interpret the functional neural correlates of prosocial decisions involving friends, we report preliminary findings linking individual differences in brain activity to social competence measures. A strength of this study is that we used parent- and self-report measures of social functioning (friendship quality and empathy, respectively). It should also be noted that the participants themselves may be better able to rate the quality of their friendships than their parents. The current study was part of a larger project and we were not able to collect self-reports of friendship quality due to time restraints. Future studies should aim to replicate our findings using self-reports of friendship quality. Future studies should also extend this work by examining relations between social competence and brain activity using active decision-making paradigms that mirror natural peer interactions. Furthermore, future studies should adopt a longitudinal design to examine how adolescents form and maintain (positive) peer relationships, for example by tracking developmental trajectories of the engagement of brain areas during social interactions with peers. Finally, in our study, participants were generally consistent in their behavior, which indicates they did not make random choices in the fMRI task. Although this consistency in choices is desired, it resulted in an imbalanced distribution in our whole brain contrasts, which may have biased the results. Some of our findings may have been driven by adolescents who were inconsistent in their behavior. This issue again relates to the above-mentioned challenge of examining context-dependent social behavior using social decision-making tasks within an fMRI design and needs attention in future studies. Relatedly, we used multiple tests of single effects to test our research questions, because the current design did not allow us to run a more stringent test such as an ANOVA. To get a better understanding of the role of the brain regions mentioned in this study more stringent tests are needed in future studies. We did not exclude participants based on a minimum number of prosocial responses in a specific condition, because participants with few trials in a particular contrast are also those who behave consistently according to their social motivation (e.g., making many prosocial decisions for friends and few prosocial decisions for disliked peers). Additional analyses in which we excluded participants based on their number of prosocial responses confirmed that the neuroimaging results were generally robust (see Supplementary Materials).

In conclusion, this study was the first to examine neural correlates of prosocial decisions in interactions with real-life friends and disliked peers in mid-adolescence. We showed that the relationship with the interaction partner modulates adolescents' prosocial behavior toward peers. Whereas prosocial interactions with friends were related to enhanced activation in brain regions speculatively involved in promoting the continuation friendships, social interactions with disliked peers did not yield enhanced neural activation in any brain regions. Furthermore, we showed that adolescents' social competence further modulate the underlying neural mechanisms of prosocial interactions with friends. Opportunities to develop social skills are particularly important in adolescence, which is a critical period for social reorientation and social learning (Steinberg, 2005; Van den Bos et al., 2010). The current study highlights the significance of prosocial interactions with friends in mid-adolescence, and of including different types of (real-life) interaction partners in experimental designs.

Table 1. *Anatomical labels of regions of neural activation for friends during prosocial choices whole brain contrasts controlled for frequency of prosocial choices. Unindented regions are the peak cluster, and intended regions are subclusters. L = left, R = right.*

Brain Region	L/R	Voxels	*z*	MNI coordinates		
				x	y	z
Friend Prosocial > Disliked Peer Prosocial						
Putamen	R	127	4.35	28	-11	4
Insula			3.89	42	-14	-8
Insula			3.87	36	-17	-2
Postcentral gyrus	L/R	1344	5.20	28	-42	62
Superior parietal lobule			5.07	16	-53	62
Superior parietal lobule			4.75	-20	-59	62
Precentral gyrus	R	118	4.18	28	-14	65
Middle temporal gyrus	R	199	4.04	50	-73	6
Angular gyrus			3.41	47	-73	32
Middle occipital gyrus			3.35	42	-73	23
Friend Prosocial > Unfamiliar Peer Prosocial						
Superior parietal lobule	R	281	4.91	42	-50	57
Superior parietal lobule			3.93	30	-67	57
Inferior parietal lobule			3.34	36	-48	46
Superior parietal lobule	L	154	4.05	-20	-76	57
Middle occipital gyrus			3.70	-28	-73	34
Inferior parietal lobule			3.67	-26	-67	43
Inferior parietal lobule	L	228	4.04	-51	-50	54
-			3.75	-34	-45	29
Inferior parietal lobule			3.48	-42	-39	37
Precentral gyrus	L	152	4.01	-48	-3	37
Precentral gyrus			3.68	-48	8	43
Precentral gyrus			3.65	-45	0	29

Note. Analyses are conducted at the threshold of $p < .001$ FWE cluster-extent based corrected

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