Got a friend in me? Mapping the neural mechanisms underlying social motivations of adolescents and adults

Schreuders, E.

Citation

Schreuders, E. (2019, March 6). *Got a friend in me? Mapping the neural mechanisms underlying social motivations of adolescents and adults*. Retrieved from https://hdl.handle.net/1887/68701

Author: Schreuders, E.
Title: Got a friend in me? Mapping the neural mechanisms underlying social motivations of adolescents and adults
Issue Date: 2019-03-06

CHAPTER FIVE

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

This chapter is under revision as:
Schreuders, E., Smeekens, S., Cillessen, A. H. N., & Güroğlu, B.
Friends and foes:
Neural correlates of prosocial decisions
with peers in adolescence.

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. Explorative analyses to the relations 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, these findings illustrate 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.

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). Studies have shown that positive peer relationships, that is, 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 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 and 18 has shown that adolescents become increasingly better in differentiating between their interaction partners with age (Güroğlu, Van den Bos, & Crone, 2014); from mid-adolescence onwards, participants made most prosocial decisions for friends and least prosocial decisions for disliked peers, showing that prosocial decisions become more context-dependent with age.

The developmental change in social skills across adolescence is reflected in the involvement of cognitive control and mentalizing brain areas in prosocial decisions, 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 showed an age-related increase in activation patterns of these regulatory and mentalizing brain regions across adolescence (Güroğlu, Van den Bos, & Crone, 2009a; Steinbeis, Bernhardt, & Singer, 2012; Van den Bos et al., 2010). The TPJ and STS are both 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 to a greater extent during interactions with friends relative to other peers (Braams, Peters, Peper, Güroğlu, & Crone, 2014; Fareri & Delgado, 2014; Güroğlu et al., 2008). Interestingly, losing money for *unfamiliar* disliked peers relative to winning money is found to be associated with increased ventral striatum activation (Braams et al., 2014b).

The aim of the current study was to make the first steps in understanding the neural activation patterns underlying social behaviors toward peers in a period that is highly significant for social development, that is, adolescence. To do so, we examined how real-life social contexts affect decision-making and associated neural processes, and how these are related to indices of social competence. 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 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., 2018b). Based on these prior findings, we expected similar increased activation patterns including the posterior TPJ (pTPJ)-inferior parietal lobe (IPL) 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 relations 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 posed to promote positive social interactions and relationships. For example, in prior studies it is demonstrated that best friendship quality is associated positively with prosocial tendencies (Markiewicz et al., 2001), and that higher empathy levels are associated with a better ability to resolve peer relational conflicts (De Wied, Branje, & Meeus, 2007). Furthermore, neuroimaging studies showed 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 shape 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 to find that better friendship quality and higher empathic skills would enhance neural activation patterns that underlie prosocial decision-making with friends.

METHOD

Participants

The current study was part of the 8th data collection wave of the Nijmegen Longitudinal Study on Infant and Child Development (NLS; 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).

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.

Measures

Social competence

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 be able to have insights to answer all questions regarding the relationship of their children with their best friend; this response was coded also 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. 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. 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 fMRI task description for details). The FQS scales were reliable: mean inter-item correlations within these scales were .362 and .438 for positive and negative FQS, respectively.

Empathy

Empathy was assessed with the self-report Interpersonal Reactivity Index (IRI; Davis, 1983). Participants indicated on 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 get 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.

FMRI task description

Peer groups

Prior to the scanning day, participants were asked to provide a list of the names of their current classmates and fill out a sociometric questionnaire. Within this questionnaire participants were asked to nominate 5 classmates as their friends and indicate which 5 classmates they liked the least. Participants were also asked to rate how much they liked each classmate on a 5-point scale ranging from 1 (*not at all*) to 5 (*very much*). These ratings and nominations 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 and/or 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 group (i.e., friends, disliked peers, neutral peers, and unfamiliar peers) consisted of two or three players. 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. 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 the 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 had consequences for themselves as well as for their interaction partners. However, it was not specified how this would be implemented. None of the participants had questions regarding this point during the instructions.

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). Prosocial choices in each of the three games, that is, 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"),

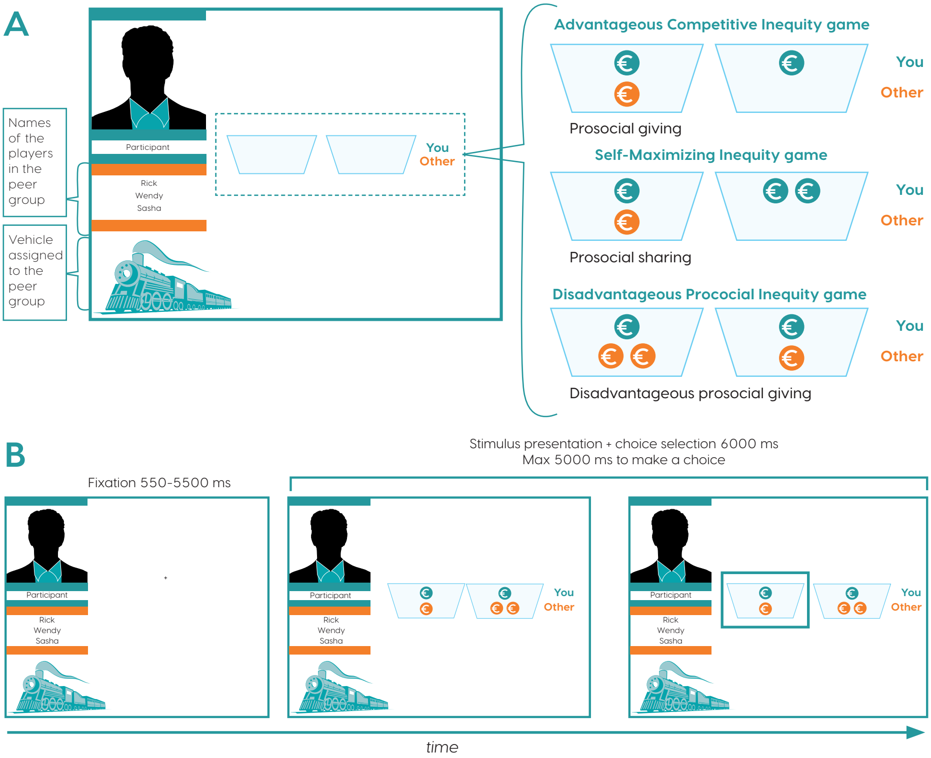

Figure 1. *(A) Names of players in each group were displayed in the left bottom panel of the screen. These three group members always belonged to the same peer category. The interaction partner was one of these players. The peer groups in the task were randomly assigned to a vehicle, which was displayed in the left bottom panel of the screen. There were three different preset coin distributions, always with a prosocial and a selfish option, depicted here on the left and right, respecively. (B) Example 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. A trial ended with selected choice indicated on the screen.*

were coded as 1; selfish choices, that is, 2/0 distribution in the SMI game, the 1/0 distribution in the ACI game, and the 1/1 distribution in the DPI game, were coded 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, whereas selfish choices maximized the outcome for the self (Figure 1A).

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. (2018b) for details on the same experimental paradigm and task design.

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.

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 examined the neural correlates for friends and disliked peers for prosocial and selfish choices by comparing decisions for friends with decisions for disliked peers (as a comparison between the two most "extreme" relationships) and by comparing 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). 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. The whole brain contrasts examining interactions with friends and disliked peers irrespective of choice were not the main focus of this chapter and are therefore also reported in the Supplementary materials (Table S1; Figure S2). 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 explorative and preliminary.

RESULTS

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 5-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.

Behavioral Results

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* ρ = .32, *p* < .05 and ρ = .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* ρ = .36, *p* < .05. There were no other significant correlations between the IRI and FQS subscales, *p*s > .240.

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).

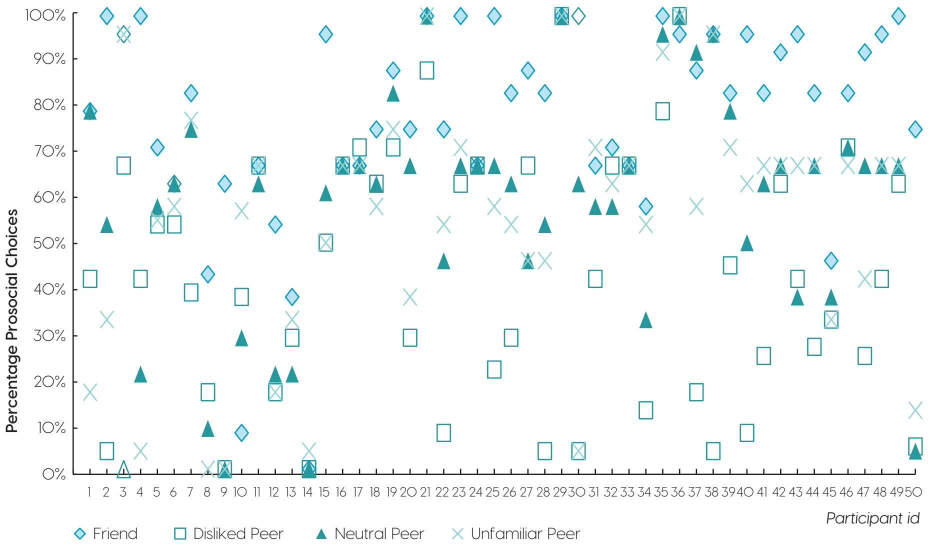

Figure 2. Percentage prosocial choices separately for friends, disliked peers, neutral peers, and unfamiliar peers for each of the 50 participants.

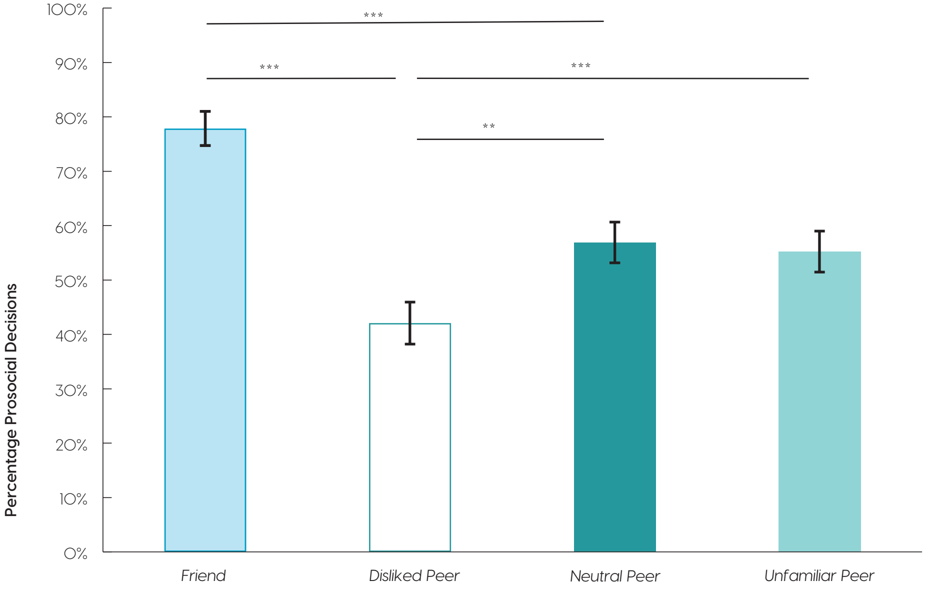

Figure 3. Mean frequency (%) and standard errors of prosocial choices per interaction partner. *Significant differences are indicated by an asterisk (*). *p < .05, **p < .01, ***p < .001.*

Neuroimaging Results

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.

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 Friend Selfish > Unfamiliar Peer Selfish can be found in the Supplementary materials.

Prosocial choices for disliked peers

The Disliked Peer Prosocial > Friend Prosocial (n = 48), and Disliked Peer Prosocial > Unfamiliar Peer Prosocial (n = 47) *t*-tests did not result in significant heightened brain activation. Reverse *t*-contrast of Disliked Peer Prosocial > Unfamiliar Peer Prosocial can be found in the Supplementary materials (Table S1).

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. Reverse *t*-contrast of Disliked Peer Selfish > Unfamiliar Peer Selfish can be found in the Supplementary materials.

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 and activity 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 with EC and PT (*ps* > .21, $n = 38$) and positive and negative FQS (*ps* > .17, *ns* between 34 and 38).

DISCUSSION

In this study, we examined the neural correlates of prosocial and selfish decisions in interactions with friends and disliked peers in mid-adolescents. 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., 2018b). The neuroimaging results showed that prosocial decisions for friends yield distinct neural activation patterns when prosocial decisions for friends are 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.

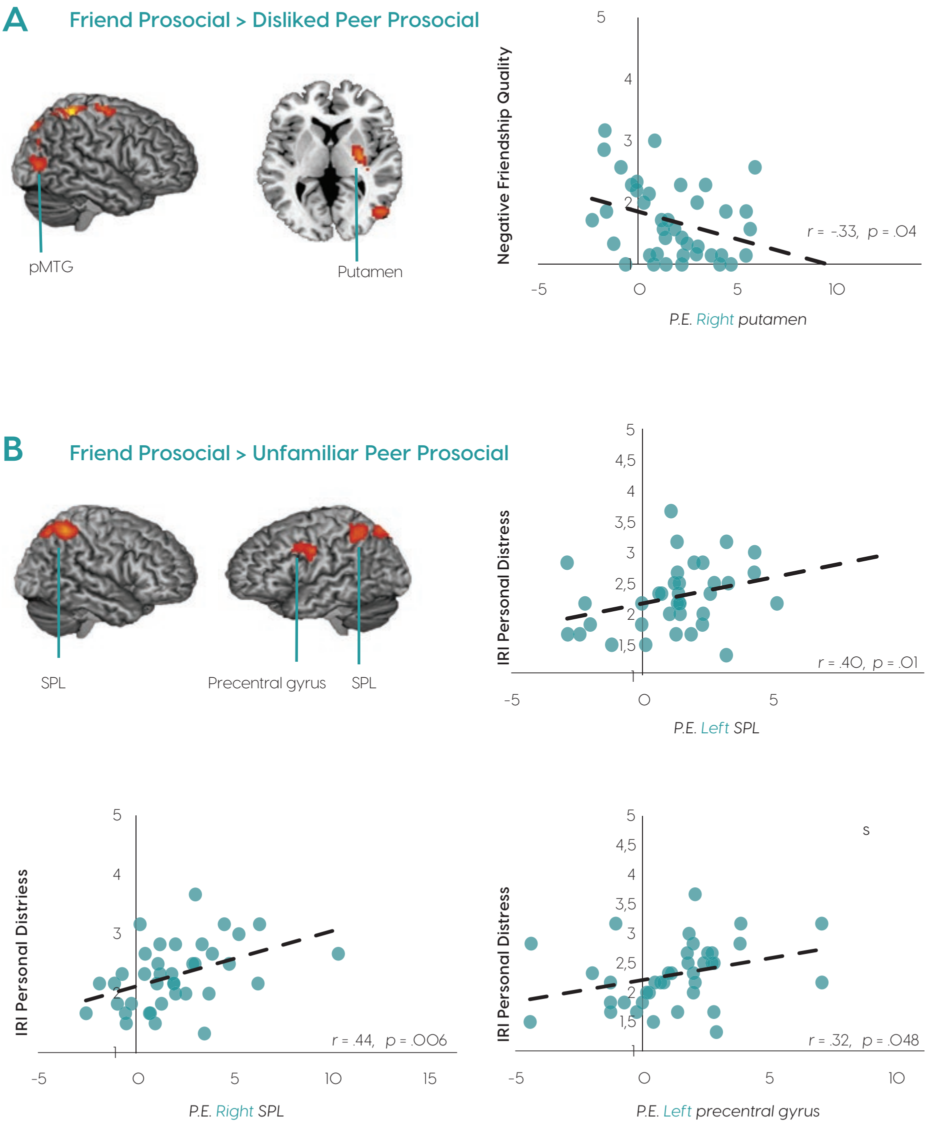

Figure 4. Whole brain contrasts controlling for the frequency of prosocial behavior for (A) Friend Prosocial > Disliked Peer Prosocial with activation in putamen (28, -11, 4) and the pMTG (50, -73, 6), and (B) Friend Prosocial > Unfamiliar Peer Prosocial with activation in bilateral SPL (42, -50, 57; -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.*

Table 1. Anatomical labels of regions of neural activation

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

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 indented regions are subclusters.

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

L = left, R = right.

Friends

Similar to our findings in Schreuders et al. (2018b), 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 prosocial interactions with close others versus more emotionally distant others. 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), 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).

In contrast to our prior study in young adults (Schreuders et al., 2018b), 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.

In our prior study with adults, we found enhanced putamen activity during prosocial decisions for friends compared to disliked peers (Schreuders et al., 2018b). 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). We further found enhanced pMTG activity during prosocial decisions involving friends compared with prosocial decisions with disliked peers. In previous studies on social cognition, acitivity in the pMTG was linked to lower-order social cognitive functions like 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 the (positive) relationship valence, which might have significant implications for promoting the continuation of social relationships like friendships (Schreuders et al., 2018b).

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 difference in relationship valence might play an important role in putamen activation (Schreuders et al., 2018b). 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. Putamen might possibly be also involved in prosocial decisions for unfamiliar peers to a certain extent, whereas it distinguishes most between relationships of most positive (i.e., friendships) and most negative (i.e., disliked peers) valence.

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 with 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.

Furthermore, greater empathy levels regarding personal distress, that 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). As the participants from the current study show relatively low to moderate levels of general personal distress, one could perhaps argue that a moderate level of empathic distress may contribute to prosocial tendencies during interactions with friends.

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). Together, our findings suggest that a greater orientation toward others is associated with greater involvement of neural mechanism underlying decisions that benefit friends.

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., 2018b). 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.

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. 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). To draw more reliable conclusions, future studies should examine relations between social competence and brain activity using active decision-making paradigms that mirror natural peer interactions. 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 is desired, it resulted in an imbalanced distribution in our whole brain contrasts. 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), but 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.