



Research report

Neural responses to social exclusion in adolescents: Effects of peer status



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ABSTRACT

We examined whether adolescents' neural responses to social exclusion and inclusion are influenced by their own popularity and acceptance and by the popularity of their excluders and includers. Accepted adolescents are highly prosocial. In contrast, popular adolescents, who are central and influential, show prosocial as well as antisocial behaviors, such as peer exclusion. Fifty-two 12–16 year-old adolescents underwent a functional magnetic resonance imaging (fMRI) scan while playing the ball-tossing game Cyberball in which they received or did not receive the ball from other virtual players. The other virtual players were described as either highly popular or average in popularity. Participants' own popularity and acceptance were assessed with peer nominations at school ($n = 31$). Participants' acceptance was positively correlated with activity of the dorsal anterior cingulate cortex (ACC) during exclusion. Participants' popularity was positively associated with ventral striatum and medial prefrontal cortex activity during exclusion, but only when the excluders were popular virtual players. Participants showed increased rostral ACC activation to inclusion by players who were average in popularity. These findings indicate that peer status plays an important role in adolescents' neural processing of social exclusion and inclusion. Moreover, these findings underscore that popularity and acceptance are distinct types of high peer status in adolescence, with not only distinct behavioral correlates, but also distinct neural correlates.

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1. Introduction

Adolescents spend a lot of time interacting with peers (Steinberg & Morris, 2001). Not all of these interactions are positive; 41% of adolescents reported exclusion by their peers

in the past two months (Wang, Iannotti, & Nansel, 2009). Frequent exclusion by peers can lead to maladaptive outcomes, including poor academic achievement (DeRosier, Kupersmidt, & Patterson, 1994), depression and anxiety (Ladd & Troop-Gordon, 2003), and aggression (Sturaro, van Lier, Cuijpers, & Koot, 2011).

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1.1. Peer status and social exclusion

Peer status plays a large role in social exclusion in adolescents' daily lives. In adolescence, two moderately correlated types of high status in the peer group are distinguished: acceptance and popularity (Cillessen & Rose, 2005; Parkhurst & Hopmeyer, 1998). Sociometric measures are frequently used to assess peer status in adolescents (Cillessen, 2009). Acceptance is measured by asking adolescents which classmates they like most and least, while popularity is measured by asking which classmates they perceive as most and least popular. Accepted adolescents show high levels of prosocial behaviors and low levels of antisocial behaviors (Sandstrom & Cillessen, 2006). In contrast, popular adolescents, who are central and influential in the peer group, show high levels of both prosocial and antisocial behaviors, such as peer exclusion (Cillessen & Mayeux, 2004; Rose, Swenson, & Waller, 2004).

Examining how peer status is associated with adolescents' responses to social exclusion is highly relevant, given that being popular in the peer group is a priority for many adolescents (LaFontana & Cillessen, 2010). Additionally, socially excluding peers allows adolescents to achieve and maintain popularity (Cillessen & Mayeux, 2004; Rose et al., 2004). While sociometric peer status measures have been widely used to study behavioral correlates of peer status (Cillessen, 2009), few studies have combined sociometric peer status measures with experimental paradigms of social exclusion. This interdisciplinary approach has several advantages. First, combining highly controlled experimental paradigms with well-established sociometric measures of peer status provides both excellent experimental control and high ecological validity, since sociometric peer status measures involve asking adolescents' real life peers (their classmates) about their status in this important peer group. Moreover, experimental paradigms of social exclusion can be combined with neuroimaging methods and sociometric measures of peer status, to investigate whether individual differences in neural responses to exclusion are a function of both the participants' own peer status and the peer status of the excluders.

1.2. Neural responses to social exclusion

The Cyberball paradigm is the most frequently used paradigm to study behavioral and neural responses to social exclusion in adolescents (Bolling et al., 2011; Gunther Moor et al., 2012; Masten et al., 2009; Sebastian et al., 2011; Will, van Lier, Crone, & Güroğlu, 2015). Cyberball is an online ball-tossing game that participants play with virtual players, whose behavior is preprogrammed (Williams & Jarvis, 2006). Participants are first included, and after a while, the virtual players stop throwing them the ball. Exclusion leads to reduced mood and decreased satisfaction of needs, accompanied by activation of the subgenual anterior cingulate cortex (sgACC; located underneath the genu of the corpus callosum; Vogt, 2005), ventral ACC (vACC; located more anterior than the sgACC, extending into the medial prefrontal cortex; Somerville, Kelley, & Heatherton, 2010), dorsal ACC (dACC), medial orbitofrontal cortex (mOFC), anterior insula and ventrolateral prefrontal cortex (VLPFC) (Bolling et al., 2011; Gunther Moor

et al., 2012; Masten et al., 2009; Sebastian et al., 2011; Will, van Lier et al., 2015).

While the neural responses to social exclusion are relatively well-established, little is known about how these neural responses are associated with adolescents' peer status as indexed by sociometric measures (i.e., peer-report). Nevertheless, a handful of studies have explored how neural responses to exclusion are associated with self-reported or parent-reported social functioning or peer status. These prior studies have yielded mixed findings. Some researchers have reported *increased* activation of both emotion-processing regions (dACC, sgACC, insula) and emotion-regulation regions (dACC, VLPFC) in adolescents with more developed interpersonal skills (Masten et al., 2009). In contrast, other researchers observed *reduced* activation of emotion-processing regions (dACC, insula, medial prefrontal cortex; mPFC) in response to exclusion, in adolescents who spent more time with friends (Masten, Telzer, Fuligni, Lieberman, & Eisenberger, 2012), in adolescents who reported to be better able to resist peer influence (Sebastian et al., 2011), and in adolescent girls who reported to be stably accepted compared to adolescent girls who reported to be chronically rejected (Rudolph, Miernicki, Troop-Gordon, Davis, & Telzer, 2016).

1.3. Adolescents' peer status and neural responses to social exclusion

Will, van Lier et al. (2015) were the first to use sociometric measures to examine the association between peer status (i.e., acceptance) and neural responses to social exclusion in adolescents. They used an event-related Cyberball design, which allowed them to not only distinguish between exclusion and inclusion events, but also to focus on a third event: incidental exclusion. This refers to not receiving the ball in an inclusion block, in which participants are overall included but sometimes do not receive the ball, when the other players throw the ball to each other. Will, van Lier et al. (2015) argued that incidental exclusion might serve as a cue for potential rejection. They found that chronically rejected adolescents showed increased dACC activity during both exclusion and incidental exclusion, compared to stably accepted adolescents.

While the findings of Will, van Lier et al. (2015) provide intriguing insights into the association between acceptance and neural responses to exclusion, the association between these neural responses and popularity has remained unexplored, even though popularity is most strongly linked to involvement in social exclusion (Cillessen & Mayeux, 2004). Therefore, the first goal of this study was to examine whether participants' own popularity and acceptance are associated with their behavioral and neural responses to social exclusion. Although popular and accepted adolescents both show high social functioning, they might respond differently to exclusion. Accepted adolescents are highly sensitive to peer relationship problems (Hoglund, Lalonde, & Leadbeater, 2008), and report greater use of emotion-regulation strategies following rejection than less accepted adolescents (Reijntjes, Stegge, Terwogt, Kamphuis, & Telch, 2006). On the basis of these behavioral findings, it may be predicted that participants' acceptance would be positively associated with activation of brain areas implicated in the processing (i.e., dACC, sgACC, insula, mPFC)

and regulation (VLPFC, dACC) of social distress (cf. Masten et al., 2009) in response to exclusion and incidental exclusion. Alternatively, a negative association between acceptance and dACC activity during exclusion and incidental exclusion could also be expected (Will, Crone, & Güroğlu, 2015; Will, van Lier et al., 2015; Rudolph et al., 2016). Popular adolescents, however, are influential and well-connected in the peer group (Dijkstra, Cillessen, Lindenberg, & Veenstra, 2010) and might therefore be less affected by occasional peer exclusion. Thus, we expected that participants' popularity would be negatively associated with activation of brain areas involved in the processing (dACC, sgACC, insula, mPFC) and regulation (VLPFC, dACC) of social distress in response to exclusion and incidental exclusion (cf. Masten et al., 2012; Sebastian et al., 2011).

1.4. Excluders' peer status and neural responses to exclusion

In prior Cyberball studies, no information was provided on the popularity of the virtual players. Adolescents want to affiliate with popular peers (Adler & Adler, 1998; Dijkstra et al., 2010) and place high value on being popular themselves (LaFontana & Cillessen, 2010). Thus, being excluded by popular peers may be more distressing than being excluded by less popular peers. Therefore, the second goal of this study was to examine whether exclusion and incidental exclusion by popular virtual players, compared to virtual players who were average in popularity, elicited increased social distress and increased activation of brain areas involved in the processing and regulation of this distress. Given that popularity, but not acceptance, is positively associated with involvement in peer exclusion (Cillessen & Mayeux, 2004), we compared exclusion and incidental exclusion by virtual players who differed in popularity, but who were similar in acceptance. We expected that participants would show more activation of the sgACC, vACC, dACC, insula, mOFC and VLPFC in response to exclusion and incidental exclusion by popular virtual players than in response to exclusion and incidental exclusion by virtual players who are average in popularity.

Finally, adolescents' behavioral and neural responses to exclusion and incidental exclusion may depend on an interaction between their own popularity and the popularity of those who exclude them. Lansu, Cillessen, and Karremans (2014) found that popular adolescents show increased visual attention to other popular peers, probably because they are competing for the same position in the peer group. Being excluded by popular virtual players might therefore be particularly distressing for participants who are more popular themselves. Thus, the third goal of this study was to investigate whether participants' own popularity interacted with their behavioral and neural responses to exclusion and incidental exclusion by popular virtual players. We anticipated that participants' popularity would be positively associated with activation of emotion-processing regions (dACC, sgACC, vACC, insula, mOFC) and emotion-regulation regions (VLPFC) in response to exclusion and incidental exclusion by popular virtual players, relative to virtual players who were average in popularity (Lansu et al., 2014).

To study neural responses to social exclusion and inclusion, we used an event-related Cyberball design (Gunther

Moor et al., 2012; Will, van Lier et al., 2015) with alternating periods of inclusion and exclusion (Bolling et al., 2011; Sebastian et al., 2011). This design had several advantages over a traditional block design (i.e., one inclusion block followed by one exclusion block): 1) it allowed us to study incidental exclusion; 2) the likelihood of participants becoming fatigued or disengaged was reduced; 3) it provided a more optimal signal-to-noise ratio (Bolling et al., 2011).

2. Material and methods

2.1. Participants

Sixty-one adolescents participated in a functional magnetic resonance imaging (fMRI) session. Nine participants were excluded from the analyses due to head motion >3 mm ($n = 2$), completion of only one run due to feeling ill ($n = 1$), computer software malfunctioning ($n = 2$), limited coverage of the brain ($n = 3$; likely due to moving outside the field of view), or a brain anomaly ($n = 1$). Therefore, 52 adolescents (27 girls) aged 12–16 years ($M = 14.49$, $SD = 1.14$) were included in the analyses. Participants' IQ was estimated based on the vocabulary and block design subtests of the WISC-III (Wechsler, 1991) ($M = 109$, $SD = 13$, range = 80–135). One parent of each participant completed the Child Behavior Checklist (CBCL; Achenbach & Rescorla, 2001). None of the participants scored in the clinical range (T -score ≥ 70) for internalizing or externalizing problems.

All procedures were approved by the medical-ethical committee at the first author's institute. All parents of participants gave informed consent, while all participants gave informed assent.

2.2. Participants' peer status

We approached all participants' schools to collect data on popularity and acceptance using classroom peer nominations (Cillessen, 2009). The mean interval between the fMRI scan and the collection of peer nominations was 4.08 months ($SD = 2.60$ months, range = .23–8.97 months). Popularity and acceptance are highly stable constructs in adolescence (Cillessen & Mayeux, 2004).

On notebook computers, participants and their classmates indicated which classmates they found most and least popular, and which classmates they liked most and least. Nominations received were counted and standardized within classrooms to control for differences in classroom size. Popularity was computed by taking the difference between the standardized numbers of most popular and least popular nominations received. Acceptance was computed as the difference between the standardized numbers of liked most and liked least nominations received. We were able to collect peer nominations data for 38 of the 61 participants. Teachers of the remaining 23 participants did not allow us to collect peer status data in their classroom, because they already participated in other research studies in the school year, or because they did not want the research to interfere with their time spent on teaching and preparing their students for upcoming exams. The 38 participants for whom we collected peer status data came from 28 different classrooms and 10 different

schools. All classmates that were present on the day of testing provided peer nominations. The number of classmates that rated a participant ranged from 16 to 30, due to differences in classroom size. Of these participants, 7 were excluded from the fMRI analyses for various reasons (see above), meaning that we could test the association between adolescents' own peer status and their brain activity for 31 participants (17 girls, 12–16 years, M age = 14.49, SD = 1.06). Popularity and acceptance were not correlated in this sample (r = .25, p = .168).

2.3. Cyberball

All participants completed two runs of the Cyberball task during scanning. Participants read a standard cover story before they were administered the Cyberball task (Williams & Jarvis, 2006). They were told that they would play an online ball-tossing game with two same-gender peers, and that the goal of the game was to study the effects of mental visualization on task performance. We told participants that the other players were at home, and that participants would be connected to them through an online link. To buttress the credibility, the experimenter told participants right before he started the scanner that he was going to text the players to be ready, and that he was starting the online link. The screen displayed: “waiting for the scanner” at that time. Participants were told that they would not meet the other players, but that they were of the same age and gender as participants themselves. Unknown to participants, the behavior of the virtual players was preprogrammed, such that participants either received or did not receive the ball during different periods of the game. The Cyberball task was programmed using Presentation® software (Version 16.2, www.neurobs.com).

Participants played two Cyberball games in a counterbalanced order: once with two popular virtual players, and once with two virtual players who were average in popularity (see below for a detailed description). First, participants played a practice block (consisting of 6 ball tosses) outside of the scanner to get acquainted with the game.

Each Cyberball game in the scanner consisted of eight alternating periods (12 ball tosses) of exclusion (E) and inclusion (I), to increase the signal-to-noise ratio, but reduce participants' fatigue or disengagement (cf. Bolling et al., 2011; Sebastian et al., 2011). Participants received the ball in 33.3% of tosses during inclusion periods, and they never received the ball during exclusion periods. We used an event-related design (cf. Gunther Moor et al., 2012; Will, Crone et al., 2015; Will, van Lier et al., 2015) with three event-types: Exclusion (not receiving the ball within an exclusion period), Inclusion Ball (receiving the ball in an inclusion period), and Inclusion No Ball (not receiving the ball in an inclusion period; i.e., incidental exclusion). In order to have enough Inclusion Ball events to reliably distinguish brain activity related to receiving versus not receiving the ball, there were more inclusion periods than exclusion periods, since participants received or did not receive the ball in only 33.3% of the ball tosses of inclusion periods.

Two different orders (counterbalanced across participants) were administered to minimize potential order effects on neural responses: 1) I-E-E-I-I-E-E-I-I; 2) I-E-I-I-E-E-I-I. Each ball

toss lasted 2 sec, with a jitter of 250–4000 ms between ball tosses.

After participants completed the task, they were debriefed about the deception used in the task. Finally, all participants signed a secrecy contract, in which they promised not to share this information with classmates.

2.4. Manipulation of the popularity of the virtual players

Before playing Cyberball, participants read vignettes of the two players they would be playing with (see Fig. 1). The players of one team were described as popular adolescents; the players of the other team as adolescents who were average in popularity. Specifically, we created descriptions of the hobbies, number of Facebook friends and classmates' opinion of the popularity and acceptance of the virtual players (the “classmates' opinion” was fictitious, as the virtual players obviously did not have classmates). Participants were asked to indicate their number of Facebook friends, hobbies and what they believed their classmates' opinions were of their popularity (“How popular do you think your classmates find you?”) and acceptance (“How much do you think your classmates like you?”) before they played Cyberball. They were told that the other players would get to see these descriptions before the game started as well. Participants were told that they received these descriptions to help them imagine the game more vividly. Virtual players were always of the same gender as the participant. To ensure that participants had thoroughly read the vignettes, they were presented to participants twice: once outside of the scanner, and once inside the scanner, directly before each Cyberball game started. Vignettes were created in two pilot studies (see [supplementary materials](#)). After reading the vignettes (and before playing the game), participants rated the popularity (“How popular do you find these players?”) and acceptance (“How much do you like these players?”) of the players of the popular and average team on a 10-point scale as a manipulation check. In order to control for potential differences between the popular and average players, participants rated on a 10-point scale how similar the players were to them and how often they expected to receive the ball from each team in 12 ball tosses. Finally, participants rated on a 10-point scale how important it was to them to be popular with peers. They then played the game.

2.5. Self-reported social distress

Directly after each of the two Cyberball runs, while still in the scanner, participants answered four questions about their satisfaction of fundamental human needs and two questions about their mood during that game (see [supplementary Table 1](#)). Participants answered these questions separately for the times when they were included and excluded by the other players. Items were rated on a scale from 1 (*do not agree at all*) to 5 (*agree completely*). We created a measure of social distress by taking the mean of the responses to these six items (cf. Bolling et al., 2011; Masten et al., 2009; Sebastian et al., 2011). Answers to positively phrased questions were reversed, so that higher scores indicated more social distress. Internal consistency for the social distress scales was good (Cronbach's α = .67–80).

A

Left Player

Gender: **Boy**
 Number of Facebook friends: **606**
 Hobbies: **Soccer, Basketball**

All classmates of this boy have been asked to indicate how much they like him and how popular they think he is.

His classmates found him to be: **Very popular, and average in terms of likeability**

Right Player

Gender: **Boy**
 Number of Facebook friends: **593**
 Hobbies: **Soccer, Hockey**

All classmates of this boy have been asked to indicate how much they like him and how popular they think he is.

His classmates found him to be: **Very popular, and average in terms of likeability**

Left Player

Gender: **Boy**
 Number of Facebook friends: **90**
 Hobbies: **Soccer, Reading, watching TV**

All classmates of this boy have been asked to indicate how much they like him and how popular they think he is.

His classmates found him to be: **Average in terms of popularity, and average in terms of likeability**

Right Player

Gender: **Boy**
 Number of Facebook friends: **85**
 Hobbies: **Reading, Karate, Watching TV**

All classmates of this boy have been asked to indicate how much they like him and how popular they think he is.

His classmates found him to be: **Average in terms of popularity, and average in terms of likeability**

B

Left Player

Gender: **Girl**
 Number of Facebook friends: **330**
 Hobbies: **Tennis, Partying, Going out with friends**

All classmates of this girl have been asked to indicate how much they like her and how popular they think she is.

Her classmates found her to be: **Very popular, and average in terms of likeability**

Right Player

Gender: **Girl**
 Number of Facebook friends: **353**
 Hobbies: **Hockey, Partying**

All classmates of this girl have been asked to indicate how much they like her and how popular they think she is.

Her classmates found her to be: **Very popular, and average in terms of likeability**

Left Player

Gender: **Girl**
 Number of Facebook friends: **90**
 Hobbies: **Reading, playing the piano, watching TV**

All classmates of this girl have been asked to indicate how much they like her and how popular they think she is.

Her classmates found her to be: **Average in terms of popularity, and average in terms of likeability**

Right Player

Gender: **Girl**
 Number of Facebook friends: **91**
 Hobbies: **Reading, watching TV, singing**

All classmates of this girl have been asked to indicate how much they like her and how popular they think she is.

Her classmates found her to be: **Average in terms of popularity, and average in terms of likeability**

Fig. 1 – Vignettes used to manipulate the popularity of the virtual players in Cyberball, for boys (A) and girls (B). The upper two panels of each figure display the popular virtual players, the lower two panels the virtual players who were average in popularity.

2.6. fMRI data acquisition

Participants were first familiarized with the scanner environment in a mock scanner. Neuroimaging data were collected using a 1.5 T Siemens Avanto scanner. A 32-channel head coil was used, and participants viewed the screen through a mirror mounted on the head coil. To prevent head motion, we placed foam inserts around each participant's head and a piece of paper tape across their forehead and the head coil. We collected the following neuroimaging scans: (1) A multi-echo GRAPPA sequence was used to obtain functional images during the two Cyberball runs of approximately 5 min

each (repetition time = 2010 ms, echo times = 9.4, 20.9, 33, 44, and 56 ms, field of view = 224 mm, 32 slices collected in ascending order, slice thickness = 3 mm, slice gap = .51 mm, flip angle = 90°). Before the first run started, we collected 30 volumes (prescans). The first two volumes of the second run were discarded to allow for a steady state magnetization. (2) In addition, we obtained a T1-weighted anatomical scan (repetition time = 2250 ms, echo time = 2.95 ms, field of view = 256 mm, 176 slices, slice thickness = 1 mm, slice gap = .5 mm, flip angle = 15°, duration = 5 min 14 sec). The two runs of the Cyberball task were always administered in succession.

2.7. Behavioral data analysis

In order to test whether the popularity of the virtual players influenced self-reported social distress during Cyberball, we performed a 2 (Popularity of Virtual Players: Popular vs. Average) \times 2 (Cyberball Period: Exclusion vs. Inclusion) ANOVA with virtual player popularity and Cyberball period as within-subject factors. In order to investigate whether participants' own peer status influenced their self-reported social distress, the analysis was repeated with participants' popularity and acceptance as covariates. Behavioral data analyses were performed using SPSS version 21.

2.8. fMRI data analysis

fMRI data were preprocessed and analyzed in SPM8 (Wellcome Trust Centre for Neuroimaging, London, UK). Based on the 30 prescans, optimal weighting parameters for each of the five echo times were calculated and used to combine the echo times into one image per volume (Poser, Versluis, Hoogduin, & Norris, 2006). Data were realigned using a rigid body transformation, and slice time corrected. The T1-weighted anatomical scan was segmented, and functional images were coregistered to the segmented gray matter image. Finally, data were normalized to an MNI template (ICBM152), and smoothed with a full-width at half maximum Gaussian kernel of 5 mm.

The three event-types (Exclusion, Inclusion Ball, Inclusion No Ball) were modeled in the general linear model implemented in SPM8. We included a total of 36 Exclusion events (3 periods of 12 ball tosses), 20 Inclusion Ball events (5 periods of 12 ball tosses, in which participants received the ball in 33.3% of tosses), and 20 Inclusion No Ball events per run (5 periods of 12 ball tosses, in which participants did not receive the ball in 33.3% of tosses, and in the other 66.7% of tosses, participants either received or threw the ball). Events were modeled at the onset of the ball toss (with a duration of 0 sec), and convolved with a hemodynamic response function and its temporal derivative. Additional regressors were included to model the realignment parameters (18 parameters: 3 translation and 3 rotation parameters, and their square and first-order derivative). We applied a high-pass filter (cutoff = 360 sec, the maximum duration of one Cyberball game/run), to avoid removing any task-induced low-frequency effects.

Pairwise contrast images were first computed at the participant-level, and subsequently entered in group-level one-sample *t*-tests. First, we examined which brain areas were activated by Cyberball events, independent of the effects of peer status. We computed the following pairwise contrasts: Exclusion > Inclusion Ball, Exclusion > Inclusion No Ball, Inclusion No Ball > Inclusion Ball, Inclusion No Ball > Exclusion, Inclusion Ball > Exclusion, Inclusion Ball > Inclusion No Ball. These contrasts were computed for both runs combined, for the full sample ($n = 52$).

Second, to test whether participants' own peer status was associated with their neural responses to exclusion and incidental exclusion, participants' popularity and acceptance scores were added as covariates to one-sample *t*-tests on the following pairwise contrasts (computed for both runs combined): Exclusion > Inclusion Ball and Inclusion No

Ball > Inclusion Ball. Popularity and acceptance scores were included in the same regression analysis, in order to examine the unique association between each type of peer status (controlling for the other type) and brain activation. For each contrast, positive and negative correlations with participants' popularity and acceptance were examined. These analyses included all participants for whom we obtained peer status data ($n = 31$). Third, to test whether participants' neural responses to exclusion and inclusion were affected by the popularity of the virtual players, we computed interaction contrasts at the participant-level, and submitted these to a group-level one-sample *t*-test. Two interaction contrasts were computed: 1) the interaction between the popularity of the virtual players (2 levels: popular and average) and event-type (2 levels: Exclusion and Inclusion Ball); and 2) the interaction between the popularity of the virtual players (2 levels: popular and average) and event-type within an inclusion period (2 levels: Inclusion No Ball and Inclusion Ball). The exact contrast values entered in SPM are specified in the [supplementary materials](#). In order to interpret significant interactions, we extracted parameter estimates from a region of interest (ROI) (spheres with a 6-mm radius) centered on peak voxels identified by the whole-brain analyses using Marsbar 0.43 (Brett, Anton, Valabregue, & Poline, 2002). To interpret the interactions, these parameter estimates were extracted and plotted for each condition that was modeled in the interaction contrast. These analyses were performed on the full sample ($n = 52$).

Finally, we examined whether participants' popularity interacted with the popularity of the virtual players. To this end, participants' popularity score was added as a covariate to one sample-tests on the contrasts Exclusion Popular > Exclusion Average, and Inclusion No Ball Popular > Inclusion No Ball Average. These analyses included all participants for whom we obtained peer status data ($n = 31$).

All whole-brain analyses were corrected for multiple comparisons using FWE-correction ($p < .05$ at the cluster level). We used the Automated Anatomical Labeling (AAL) template as implemented in MRICron to label significant clusters of activation at the whole-brain level. If a region was not included in this atlas (e.g., certain subcortical regions, such as the nucleus accumbens, are not included), we used the Anatomy toolbox implemented in SPM8 to label the activation cluster.

3. Results

3.1. Behavioral results

3.1.1. Manipulation check

Paired *t*-tests indicated that the popularity manipulation of the virtual players was effective. Participants rated the popular team ($M = 8.11$, $SD = 1.08$) as significantly more popular than the team of players that were average in popularity ($M = 5.79$, $SD = 1.24$) [$t(51) = 10.37$, $p < .001$, $d = 2.00$]. Inconsistent with our design plan, participants also rated the popular team ($M = 6.15$, $SD = 1.55$) as less accepted than the team of players that were average in popularity ($M = 6.96$, $SD = 1.05$) [$t(51) = 3.86$, $p < .001$, $d = .60$].

Participants indicated that they felt comparably similar to the popular players and players who were average in popularity [$t(51) = 1.56, p = .126, d = .29$], and expected to receive the ball more often from the players who were average in popularity than from the popular players [$t(51) = 5.68, p < .001, d = .50$]. Participants' popularity and acceptance did not correlate significantly with how similar they felt to the popular players and players who were average in popularity, or to how many balls they expected to receive from them (all p 's $> .13$).

3.1.2. Self-reported social distress

There was a main effect of Cyberball period (see Fig. 2), indicating that participants reported more social distress during exclusion than during inclusion periods ($F(1, 51) = 39.01, p < .001, \eta^2_p = .43$). The popularity of the virtual players, participants' own popularity and acceptance, and participants' self-reported importance of being popular were not significantly associated with participants' self-reported social distress (all p 's $\geq .08$).

3.2. fMRI results

3.2.1. Neural regions involved in the processing of social exclusion and inclusion

Exclusion (compared to Inclusion Ball) elicited activation of the VLPFC, among other regions (see [supplementary Table 2](#) and [Fig. 3](#)). Not receiving the ball in an inclusion period (contrast: Inclusion No Ball > Inclusion Ball) activated similar brain regions as not receiving the ball in an exclusion period (contrast: Exclusion > Inclusion Ball), such as the VLPFC (see [supplementary Tables 2 and 3](#)). Nevertheless, when we directly compared not receiving the ball in an exclusion period to not receiving the ball in an inclusion period (contrast: Exclusion > Inclusion No Ball), several regions were more active during exclusion (see [supplementary Table 2](#)), including the dACC. Brain regions activated by inclusion are reported in [supplementary Table 4](#).

3.2.2. Effects of participants' peer status

We performed t -tests on the contrasts Exclusion > Inclusion Ball and Inclusion No Ball > Inclusion Ball, with participants'

popularity and acceptance as covariates. Participants who were more accepted, showed increased dACC activity (MNI 14 28 28, 62 voxels, $Z = 4.14, df = 28$) during exclusion (contrast: Exclusion > Inclusion Ball), compared to less accepted participants (see [Fig. 4](#)). Participants' acceptance was not associated with brain activity during incidental exclusion (contrast: Inclusion No Ball > Inclusion Ball), and participants' popularity was not associated with brain activity during exclusion or incidental exclusion.

3.2.3. Effects of the virtual players' popularity

To test whether participants' neural responses to exclusion and inclusion were affected by the popularity of the virtual players, we computed interaction contrasts at the participant-level, and submitted these to a group-level one-sample t -test. Two interaction contrasts were computed: 1) the interaction between the popularity of the virtual players (2 levels: popular and average) and event-type (2 levels: Exclusion and Inclusion Ball); and 2) the interaction between the popularity of the virtual players (2 levels: popular and average) and event-type within an inclusion period (2 levels: Inclusion No Ball and Inclusion Ball).

There was a significant interaction between the popularity of the virtual players and event-type in the rostral ACC (rACC) (MNI -4 30 14, 71 voxels, $Z = 4.37, df = 51$). [Fig. 5](#) shows the activation of the rACC for each condition separately: the most pronounced activation was observed for inclusion by the players who were average in popularity, and exclusion by the popular players also activated this region. As can be seen in [Fig. 5](#), being included by the popular players or being excluded by the players who were average in popularity did not activate the rACC.

Exploratory follow-up analyses indicated that the difference in participants' acceptance ratings of the players who were average in popularity and popular players (i.e., acceptance average–acceptance popular) was associated with a stronger response in the rACC to inclusion by the players who were average in popularity ($\rho = .32, p = .023$).

There were no clusters for which the event-type within an inclusion period (e.g., Inclusion No Ball vs. Inclusion Ball) significantly interacted with the popularity of the virtual players.

3.2.4. Interaction between participants' popularity and the virtual players' popularity

In order to examine the interaction between participants' own popularity and the popularity of the virtual players, we performed one-sample t -tests on the contrasts Exclusion Popular > Exclusion Average and Inclusion No Ball Popular > Inclusion No Ball Average, with participants' own popularity score as a covariate. During exclusion (contrast: Exclusion Popular > Exclusion Average), participants' popularity interacted with the players' popularity in two regions: more popular participants showed increased activation, relative to less popular participants, of the VS/basal forebrain (MNI 2 6 8, 56 voxels, $Z = 4.58, df = 28$) and mPFC (MNI -4 62 18, 82 voxels, $Z = 4.18, df = 28$) in response to exclusion by popular players, compared to exclusion by players who were average in popularity (see [Fig. 6](#)). During incidental exclusion (contrast: Inclusion No Ball Popular > Inclusion No Ball Average), there

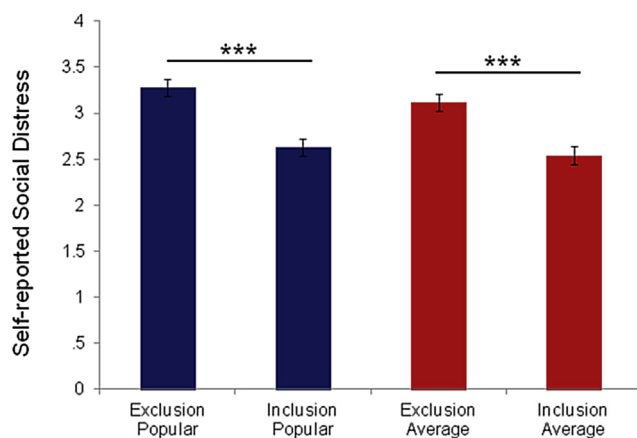


Fig. 2 – Self-reported social distress during exclusion and inclusion by the popular and average teams. * $p < .001$.**

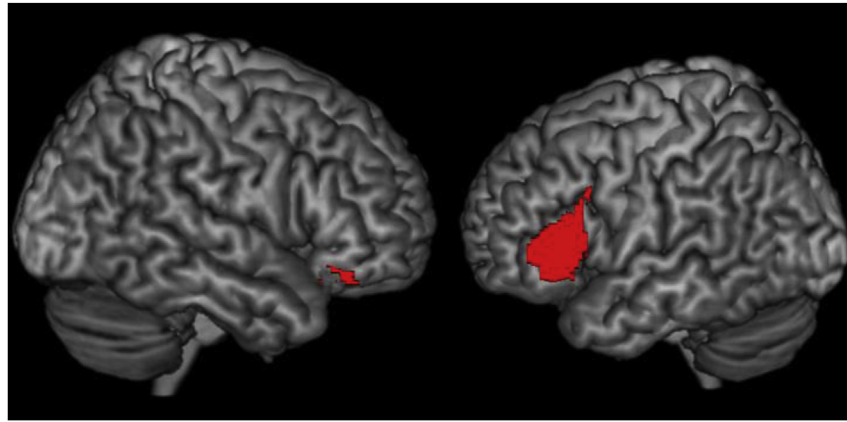


Fig. 3 – Activation of the left VLPFC (MNI -54 32 10) and right VLPFC (MNI 40 34 -14) during exclusion relative to inclusion ball, combined across the popular and average player conditions.

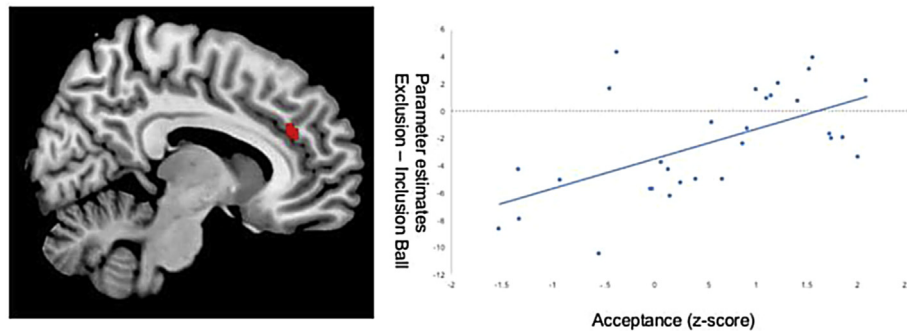


Fig. 4 – Association between participants' acceptance and dACC activity (MNI 14 28 28) during exclusion, compared to inclusion ball ($n = 31$). Note. We used MarsBar 0.43 (Brett et al., 2002) to extract parameter estimates from the clusters identified by the whole-brain analyses.

was no significant interaction between participants' own popularity and the popularity of the virtual players.

4. Discussion

This study had three goals: 1) to investigate whether adolescents' own peer status is associated with their behavioral and

neural responses to social exclusion; 2) to examine whether adolescents' behavioral and neural responses to social exclusion and inclusion in Cyberball are influenced by the popularity of the excluders/includers; 3) to examine whether behavioral and neural responses to exclusion and inclusion show an interaction between adolescents' own popularity and the popularity of the excluders/includers. The main findings were: 1) adolescents' acceptance was positively associated

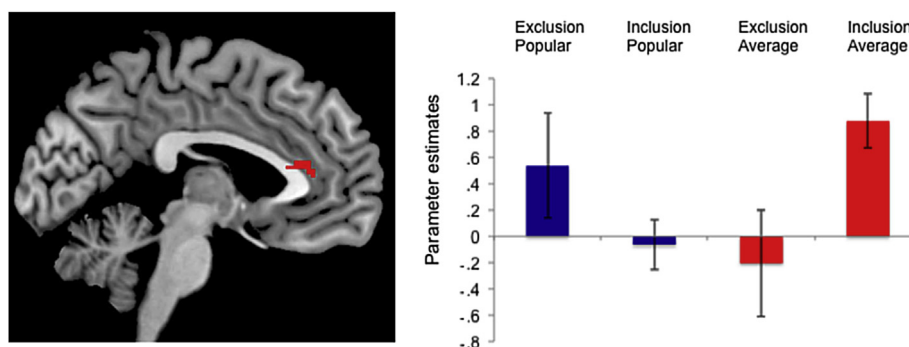


Fig. 5 – Parameter estimates in rostral ACC (MNI -4 30 14) for exclusion and inclusion by the popular virtual players and virtual players who were average in popularity ($n = 52$). Note. We used MarsBar 0.43 (Brett et al., 2002) to extract parameter estimates from the cluster identified by the whole-brain analysis.

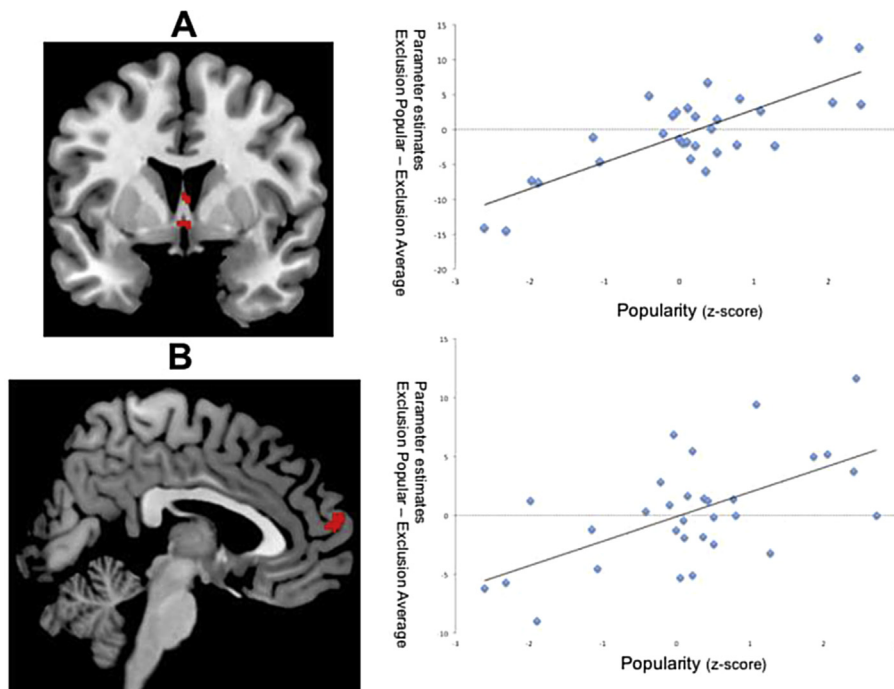


Fig. 6 – A) Association between participants' popularity and VS/basal forebrain activity (MNI 2 6 8) during exclusion by the popular virtual players, relative to exclusion by the virtual players who were average in popularity. **B)** Association between participants' popularity and mPFC activity (MNI -4 62 18) during exclusion by the popular virtual players, relative to exclusion by the virtual players who were average in popularity. *Note.* We used MarsBar 0.43 (Brett et al., 2002) to extract parameter estimates from the clusters identified by the whole-brain analyses.

with dACC activity during exclusion; 2) Participants showed increased activation of the rostral ACC during inclusion by virtual players who were average in popularity, but rated as more accepted than popular players; 3) Participants' popularity was positively associated with activation of the VS and mPFC during exclusion by popular virtual players compared to exclusion by players who were average in popularity.

4.1. Neural regions involved in the processing of social exclusion and inclusion

We used an event-related Cyberball design with alternating periods of inclusion and exclusion. Despite the advantages of his design over a traditional block design (e.g., a reduced likelihood of participants becoming disengaged, a more optimal signal-to-noise ratio), the relatively short periods of exclusion, which were interspersed with periods of inclusion, may have made the exclusion less distressing for participants. Nevertheless, our adaptation of the Cyberball paradigm was effective in eliciting activation of brain areas that have been consistently reported in prior Cyberball studies in adolescents (Bolling et al., 2011; Gunther Moor et al., 2012; Masten et al., 2009, 2012; Sebastian et al., 2011; Will, van Lier et al., 2015). Additionally, and importantly, participants reported increased social distress during exclusion compared to inclusion. Exclusion (relative to Inclusion Ball) activated the VLPFC. Exclusion additionally activated the dACC when it was directly compared to not receiving the ball in an inclusion period. Inclusion (relative to Exclusion) activated the bilateral insula, among other regions, which is consistent with other

studies (Achterberg, van Duijvenvoorde, Bakermans-Kranenburg, & Crone, 2016; Gunther Moor et al., 2012) and might reflect the increased emotional salience of processing socially relevant events (Uddin, 2015).

4.2. Effects of participants' peer status

Consistent with our hypotheses and with prior research (Masten et al., 2009), participants' acceptance was positively associated with activation of the dACC. We used Neurosynth (Yarkoni, Poldrack, Nichols, Van Essen, & Wager, 2011) to support the interpretation of significant activations in this study. Neurosynth is a database that can be used to link terms (e.g., psychological processes, such as *regulation*) to fMRI activations, based on > 11,000 fMRI studies, >400,000 activations and >3000 terms (www.neurosynth.org). The dACC is involved in the processing and regulation of distress (posterior probability = .80 for *reappraisal*, posterior probability = .78 for *painful*). Eisenberger (2012) reviewed the program of research that explored the shared neural correlates of physical and social pain, and found that both types of pain show overlap in the dACC, leading her to argue that dACC activation during social exclusion reflects the experience of social pain. The positive association we observed between dACC activity during exclusion and adolescents' acceptance suggests that adolescents who are accepted by their peers may be more sensitive to negative social experiences (i.e., they may experience more social pain), and are better able to regulate their emotions following these experiences, than less accepted adolescents. Social exclusion elicits aggression and

suppresses pro-social behavior (Gunther Moor et al., 2012; Twenge, Baumeister, DeWall, Ciarocco, & Bartels, 2007; Twenge, Baumeister, Tice, & Stucke, 2001), potentially by reducing the ability to regulate one's emotions (Chester & DeWall, 2014). Importantly, an increased dACC response to social exclusion is associated with increased affiliative behaviors towards the excluders (Chester, DeWall, & Pond, 2016), and decreased aggression in individuals who show high executive functioning (Chester et al., 2014). In order to remain well liked by their peers, accepted adolescents' ability to regulate their emotions and behavior following exclusion may therefore be of key importance. Alternatively, it may be that the increased sensitivity to social exclusion of more accepted adolescents requires greater recruitment of emotion-regulation brain areas. Moreover, accepted adolescents' heightened sensitivity to social exclusion might motivate behaviors that lead to liking by peers.

It must be noted, though, that the increased dACC activity in response to exclusion we observed in more accepted adolescents is inconsistent with two recent studies (Rudolph et al., 2016; Will, van Lier et al., 2015), in which stably accepted adolescents showed decreased dACC activity in response to exclusion, compared to chronically rejected peers. Differences in study designs might explain these discrepant findings. We used a continuous measure of acceptance and a Cyberball task in which information about the peer status of the virtual players was provided. These prior studies compared two groups of adolescents (chronically rejected vs. stably accepted) who had extreme acceptance scores (e.g., upper and lower 10th percentile in the Will et al. study), while we included participants whose acceptance scores covered the full range of possible scores. Additionally, these studies used a Cyberball task without information about the virtual player's popularity. Providing information about the characteristics of the virtual players might make participants more engaged in the task, which could influence activation of brain areas implicated in the processing of emotional salience, such as the dACC. Future studies should examine this hypothesis by directly comparing designs in which information about the virtual players is and is not provided.

4.3. Effects of the virtual players' popularity

Participants' neural responses to Cyberball events were influenced by the popularity of the virtual players, but not in the direction we hypothesized. There were no differences in neural responses to exclusion by popular players or players who were average in popularity. Instead, we found a difference in the neural response to inclusion. Inclusion by players who were average in popularity was associated with the most pronounced recruitment of the rACC.

The rACC has frequently been implicated in the processing of negative emotions, such as distress (posterior probability = .80 for distress). However, it is unlikely that the increased rACC activity during inclusion by players who were average in popularity reflects increased distress, since participants did not report more distress during inclusion by players who were average in popularity than by popular players. In fact, they rated the players who were average in popularity as more accepted than the popular players.

Nevertheless, a recent meta-analysis showed that the rACC is particularly activated by positive feedback (Liu, Hairston, Schrier, & Fan, 2011). Davey, Allen, Harrison, Dwyer, and Yucel (2010) found that receiving positive peer feedback activated the rACC in adolescents. Given that participants rated the players who were average in popularity as more accepted than the popular players, the enhanced rACC response to inclusion by the players who were average in popularity may reflect increased emotional salience or positive affect induced by being included by more accepted peers (posterior probability = .93 for happy faces, and posterior probability = .79 for salience network). This hypothesis needs to be tested in future research by comparing neural responses to inclusion between players who vary in acceptance but are matched on popularity.

4.4. Interaction between participants' popularity and the popularity of the virtual players

Adolescents' popularity correlated positively with VS/basal forebrain and mPFC activity in response to exclusion by popular players, compared to exclusion by players who were average in popularity. These regions have been implicated in emotional salience processing (VS/basal forebrain: posterior probability = .74 for distress) and understanding others' emotions and self-referential processing (mPFC: posterior probability = .85 for theory of mind and posterior probability = .78 for self-referential). Being excluded by popular players might be more salient and self-relevant for adolescents who are more popular themselves, as they might see it as a threat to their status (cf. Lansu et al., 2014).

4.5. Strengths and limitations

The current study has several strengths. To our knowledge, we are the first to examine whether the popularity of virtual Cyberball players influences neural responses to social exclusion and inclusion, and whether participants' own peer status interacts with these responses. Further, we made an important distinction between acceptance and popularity, and showed that these distinct forms of high peer status are differentially associated with neural responses to (incidental) exclusion. The present study included a relatively large sample of adolescents, and used a Cyberball design that allowed us to maximize signal-to-noise ratio.

Nevertheless, limitations need to be mentioned as well. We did not include a third team of highly unpopular virtual players. Future studies could use between-subjects designs to study whether responses to exclusion and inclusion by unpopular players differ from players who are average in popularity and popular players. Further, we used fictitious Cyberball players instead of actual classmates. The use of fictitious players provided optimal experimental control, as participants were not influenced by confounding factors, such as previous (negative) encounters with the other players or differences in popularity between the classmates of different participants. However, it remains an empirical question whether the same findings would be observed with actual classmates.

Even though we used Neurosynth to support our interpretation of the fMRI activations, these interpretations are still

speculative. Future studies should test our interpretations more directly, for instance by directly measuring or manipulating the use of emotion-regulation strategies or perspective taking during Cyberball. Finally, in order to better interpret findings associated with the processing of incidental exclusion, future studies could administer social distress questions that specifically distinguish between not receiving the ball during an exclusion period and during an inclusion period.

5. Conclusions

Two distinct types of high peer status were differentially associated with neural responses to exclusion. Participants' acceptance was positively associated with activation of the dACC during exclusion. Participants' popularity interacted with player popularity, in that more popular participants showed increased activation of the mPFC and VS in response to being excluded by popular players, compared to being excluded by players who were average in popularity. The popularity of the virtual players influenced neural responses to inclusion. The rACC response to inclusion by players who were average in popularity but who were rated as more accepted, was stronger than the response to inclusion by popular players. Together, these findings indicate that distinct types of high peer status were differentially associated with neural responses to exclusion. Higher acceptance was associated with increased activation of a brain area implicated in social distress processing and regulation. Higher popularity, on the other hand, was associated with increased activation of brain areas involved in perspective-taking, self-referential processing and emotional salience processing, but only when the excluders were also popular. These findings underscore that popularity and acceptance are distinct types of high peer status in adolescence, with not only distinct behavioral correlates, but also distinct neural correlates.

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Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.cortex.2017.02.018>.

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