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Neural response to prosocial scenes relates to subsequent giving behavior in adolescents: A pilot study

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Abstract

Adolescence is characterized by extensive neural development and sensitivity to social context, both of which contribute to engaging in prosocial behaviors. Although it is established that prosocial behaviors are linked to positive outcomes in adulthood, little is known about the neural correlates of adolescents' prosociality. Identifying whether the brain is differentially responsive to varying types of social input may be important for fostering prosocial behavior. We report pilot results using new stimuli and an ecologically valid donation paradigm indicating (1) brain regions typically recruited during socioemotional processing evinced differential activation when adolescents evaluated prosocial compared with social or noninteractive scenes ($N = 20$, ages 13–17 years, $M_{Age} = 15.30$ years), and (2) individual differences in temporoparietal junction recruitment when viewing others' prosocial behaviors were related to adolescents' own charitable giving. These novel findings have significant implications for understanding how the adolescent brain processes prosocial acts and for informing ways to support adolescents to engage in prosocial behaviors in their daily lives.

Keywords

Adolescence; Donating; Prosocial; fMRI; Temporoparietal junction

Adolescence is often portrayed as a time of engaging in risky and thrill-seeking behaviors. Yet, for many adolescents, this is also a period of tremendous social-cognitive growth and development of positive behaviors toward others. Complex social-cognitive skills such as mentalizing, perspective taking, and metacognition are refined during this developmental

priod (Burnett, Sebastian, Cohen Kadosh, & Blakemore, 2011), and these skills are supported by structural and functional changes in brain regions involved in social information processing and cognition (Blakemore, 2008; Nelson, Jarcho, & Guyer, 2016; Rilling & Sanfey, 2011; van den Bos, van Dijk, Westenberg, Rombouts, & Crone, 2011). These behavioral skills and neural networks are thought to facilitate positive, other-oriented behavior (often termed "prosocial behavior" or actions intended to help others), which is beneficial for myriad psychosocial outcomes (Aknin et al., 2013; Bandura, Caprara, Barbaranelli, Pastorelli, & Regalia, 2001; Layous, Nelson, Oberle, Schonert-Reichl, & Lyubomirsky, 2012; Telzer, Fuligni, Lieberman, & Galván, 2014). Using a new task, we explored neural mechanisms that relate to prosocial behavior during adolescence.

Prosocial behavior is a multifaceted construct. Generally, prosocial behavior is considered to be voluntary, intentional behavior that benefits another person (Eisenberg & Miller, 1987). Prosociality encompasses altruistic acts, defined as prosocial behaviors motivated by a desire to benefit another person without any expectation of benefit to the actor (Feigin, Owens, & Goodyear-Smith, 2014). Prosociality includes a range of affective and behavioral components including empathy, compassion, helping, sharing, cooperating, volunteering, and donating (Radke-Yarrow, Zahn-Waxler, & Chapman, 1983). Some of these elements have direct benefits to the actor, for example fostering social relationships, whereas others align with more traditional views of altruism. Prosocial behavior has been linked to numerous positive outcomes, including increased happiness (Aknin et al., 2013), peer acceptance (Layous et al., 2012), self-esteem (Bandura et al., 2001), and lower depressive symptoms (Telzer et al., 2014). In addition, engaging in prosocial behaviors may ward off social isolation, which has long-term negative health consequences (Caspi, Harrington, & Moffitt, 2006). Identification of mechanisms underlying individual tendencies to behave prosocially is particularly important given the positive impact of prosociality on adult outcomes (Aknin et al., 2013; Roth et al., 2013).

Adolescents are a unique population in which to study individual differences in prosocial tendencies because they undergo a social reorientation whereby they are intensely cued in to their social environments (Nelson et al., 2016). Much of adolescent research investigates this social change in terms of peer influence, risk taking, and seeking hedonic rewards. However, adolescents also demonstrate an improvement in perspective-taking skills (Eisenberg, Cumberland, Guthrie, Murphy, & Shepard, 2005; Symeonidou, Dumontheil, Chow, & Breheny, 2016; van den Bos et al., 2011), which is an important component of social decision-making. As adolescents age, they become more focused on others' thoughts, feelings, and behaviors, a shift that coincides with social network brain development (Blakemore & Mills, 2014; van den Bos et al., 2011). The social brain network, commonly identified as the medial prefrontal cortex (mPFC), temporoparietal junction (TPJ), superior temporal sulcus (STS), and temporal poles, changes in structure and function during adolescence (Blakemore, 2008; Mills, Lalonde, Clasen, Giedd, & Blakemore, 2014; Nelson et al., 2016). Compared with adults and children, adolescents demonstrate increased activation in the social brain network when processing social information (Blakemore & Mills, 2014; Somerville 2013). This network has been implicated in perspective taking (Frith & Frith, 2006) as well as self-reported altruistic and prosocial behavior (Hare, Camerer, Knoepfle, O'Doherty, & Rangel, 2010; Tankersley, Stowe, & Huettel, 2007; Tusche,

Bockler, Kanske, Trautwein, & Singer, 2016). It remains unknown whether, during this period of increased attention to one's social environment, adolescents differentially recruit regions of the social brain network when evaluating prosocial information compared with other types of social information. During adolescence, the brain may be more malleable through environmental input (Galván, 2014). Thus, identifying whether the social brain network is differentially responsive to varying types of social input in adolescence may be important for understanding how to support adolescents' engagement in prosocial behaviors. In this study, we probed whether differential engagement of the social brain network to prosocial versus social and noninteractive stimuli related to adolescents' own prosocial giving.

Prior research on neural correlates of prosociality has primarily sought to determine how the brain responds during prosocial tasks. These efforts have identified neural activation during prosocial giving that resembles activation during one's own receipt of monetary rewards in adults (Moll et al., 2006) and adolescents (Telzer et al., 2014). In social contexts, individuals activate regions of the social brain when behaving prosocially toward someone who has previously been excluded from the social group (van der Meulen, van Ijzendoorn, & Crone, 2016). Other adolescent work has demonstrated engagement of the social brain network during prosocial giving and increased activation in these regions when being observed acting prosocially by peers (Van Hoorn, Van Dijk, Güroglu, & Crone, 2016). Although this prior work elucidates neural mechanisms at play during prosocial behavior, it does not explore whether the adolescent brain differentiates prosocial behavior from other types of positive social interaction. Additionally, these studies did not link neural activation to prosocial tendencies outside of the scanner, lacking the data to determine whether individual differences in recruitment of social brain regions relate to prosociality.

The current pilot study paired a new task presenting scenes of others engaged in prosocial, social, and noninteractive behaviors with an ecologically valid donations task to test two primary hypotheses: (1) adolescents show distinct neural correlates of evaluating others engaged in prosocial behaviors compared with social or noninteractive behaviors, and (2) individual differences in neural response to others' prosocial behaviors relate to one's own actual charitable giving behavior, over and above existing prosocial tendencies. Unlike much of the former research on prosocial behavior that focused on how the brain responds during prosocial acts (e.g., Telzer et al., 2013; Van Hoorn et al., 2016), we investigated whether adolescents differentially engaged the social brain network when viewing *others* engaged in prosocial behavior. This question was of particular interest due to the increased salience of social information during adolescence (Crone & Dahl, 2012). Additionally, we probed whether the magnitude of this neural activation to prosocial scenes related to charitable giving outside of the scanner, rather than giving during the fMRI task. This *brain-as-predictor* approach (Berkman & Falk, 2013) is particularly useful when investigating behaviors such as prosociality that have a social component and may be prone to conformity effects or bias in self-report (Cascio, Scholz, & Falk, 2015).

Method

Participants

Participants included 20 adolescents (seven female, M_{Age} = 15.30 years, SD =.98, range: 13–17 years). Males and females did not differ on age, $t(18)$ = –2.01, p =.059, ethnicity, $t(18)$ = 1.03, p >.25, or maternal education, $t(18)$ =.21, p >.25 (see Table 1). Adolescent participants completed written assent, and parents completed written consent in accordance with the university's Institutional Review Board. Although we conducted this study in a small sample, sample size was determined prior to data collection based on funding constraints, prior studies investigating altruism in adults (Marsh et al., 2014; Tusche et al., 2016), and guidelines in the field regarding acceptable minimum sample sizes for pilot studies (Mumford, 2012). Recruitment was discontinued at our predetermined target of 20 participants.

Materials and procedures

All participants were tested individually in laboratory sessions lasting approximately 1 hour. During testing sessions, participants completed self-report questionnaires, the social-scene task in the MRI scanner, and the donation task. Participants completed written consent and assent in accordance with the university's Institutional Review Board and were compensated for their participation.

Social-scene task—Participants rated their affective response to 90 static scenes varying by type of social interaction. Thirty scenes depicted social behavior with prosocial content (e.g., helping an injured sports opponent), 30 scenes depicted social behavior without prosocial content (e.g., playing a card game with friends), and 30 scenes depicted actors alone or in noninteractive social settings (e.g., walking on campus; see Fig. 1). The task was designed to evaluate whether participants distinguished among prosocial, social, and noninteractive scenes at the behavioral and neural level. Participants rated how they felt while viewing each scene on a scale of 1 to 4 (1 = *not* good, 2 = *ok, 3 = good,* and 4 = *very good).* Ratings were captured to probe whether adolescents reported more positive emotions in response to prosocial versus social scenes given prior work suggesting engaging in prosocial behavior is rewarding (e.g., Moll et al., 2006; Telzer et al., 2014; van der Meulen et al., 2016). Reaction times (RTs) were recorded and represented how quickly participants rated their feelings about the observed scenes. Scene types were randomly presented, each for a maximum of 5,000 ms. The stimuli offset after the participants provided their rating. Jittered interstimulus intervals ranged from 750 ms to 6,250 ms (M = 2,251.67 ms, SD = 1,344.20 ms). The task and stimuli are available via Open Science Framework (OSF; https://osf.io/ve4dw/).

Prior to testing, a larger set of stimuli were rated to confirm scene categorization by an independent sample of participants. On average 27, people rated each scene. Participants were asked to make four judgments about the scenes: (1) How do you feel about what is happening in this picture on a scale of 1 *(very bad)* to 6 (very good)?*;* (2) How old are the people in this picture?: 1–10 years, 11–15 years, 16–20 years, 20–30 years, 30+ years; (3) What do you think is happening in this picture? (open-ended response); and (4) Are the

people in this photo doing something: altruistic/prosocial, social, or neither? (category rating). Stimuli used for the final study had a category rating of at least 75% accuracy (average: prosocial, 90%; social, 94%; noninteractive, 85%) and an open-ended description response of at least 76% accuracy (average: prosocial, 96%; social, 100%; noninteractive, 100%). Given the importance of peers during adolescence, individuals depicted in the stimuli were primarily adolescents and young adults. Fifty-eight percent of ratings for the age of the actors were between 11 and 20 years (5% 1–10 years, 18% 11–15 years, 40% 16–20 years, 24% 20–30 years, 14% 30+ years). To adapt the task for the scanner button box and because only 2.3% of scenes were rated as *very bad* or *bad,* we collapsed the 6-point scale to a 4-point scale (1 = *not good,* 2 = *ok,* 3 = *good,* 4 = *very good*) for the final study. Participants rated scenes using the 4- point scale by pressing buttons with their right hand (index finger = 1, pinky finger = 4) while undergoing MRI.

Donation task—After the scan, participants received $30 in cash as compensation for their participation (two $10, one $5, and five $1 to give participants donation options). Participants were handed a form that briefly described a charity for foster youth and were told that as part of the study they could donate any portion of the study compensation they received to the charity, but that they did not have to donate anything. Participants were asked to complete the form with the amount they wished to donate and to insert the form and any amount of money they wished to donate into an envelope marked "Donations." Experimenters left the room while participants completed this part of the study. At no point were participants asked how much they donated, nor was the donation envelope opened in front of them. All donations were given to the California Youth Connection (CYC; http://www.calyouthconn.org/) at the end of the study. CYC was selected as the study charity because it helps adolescents of a similar age to the participants and was located in the participants' home state.

Altruistic Personality Scale—Prior to the scan, participants completed a commonly used measure of prosocial experiences. The Altruistic Personality Scale (APS) is a 20-item inventory designed to measure altruistic tendency by gauging the frequency with which one engages in altruistic acts primarily toward strangers (Rushton, Chrisjohn, & Fekken, 1981). Each item is rated from 1 (*strongly agree*) to 4 (*strongly disagree*). Cronbach's alpha for the APS was a =.86. Ratings were summed for each item, and the average for the 20 scale items was used in all analyses.

FMRI data acquisition

The scan was conducted on a Siemens Magnetom Prisma MRI scanner with a 32-channel head coil. Parameters for image acquisition were as follows: voxel size = $3.0 \times 3.0 \times 4.0$ mm, slices = 34, slice thickness = 4.0 mm, repetition time (TR) = 2,000 ms, echo time (TE) = 30 ms, flip angle = 90 degrees, interleaved slice geometry, field of view (FOV) =192 mm. AutoAlign was used, which conducts automated positioning and alignment of the anatomy-related slices using anatomical landmarks. The social-scene task was self-paced and lasted an average of 6.19 minutes (range: 5.05–8.38 min). We chose to allow self-paced ratings to prevent unnecessary missing rating and RT data. Preprocessing was conducted using FEAT (FMRI Expert Analysis Tool) Version 6.00, part of FSL (FMRIB Software Library,

www.fmrib.ox.ac.uk/fsl). Preprocessing consisted of slice timing correction, nonbrain removal using BET, high-pass filtering (100-s cutoff), and spatial smoothing using a Gaussian kernel of FWHM 5 mm. Motion correction was performed with MCFLIRT using 24 standard and extended regressors (six motion parameters, the derivatives of those parameters, and the squares of the derivatives and the original parameters) as well as confound matrices for each participant using FSL Motion Outliers. Average maximum translation was .481 mm, average maximum rotation was .008 mm, maximum translation range: .077–2.076, maximum rotation range: .001–.049. No participants were excluded due to excessive motion and age was not correlated with motion. A magnetization-prepared rapid-acquisition gradient echo (MPRAGE) anatomical scan was acquired for registration purposes (TR: 1,900 ms; TE 2.26 ms; FOV: 250 mm; slice thickness: 1mm; 176 slices). Each participant's functional data were registered to their MPRAGE using boundary based registration (BBR; Greve & Fischl, 2009) and then to Montreal Neurological Institute (MNI) stereotaxic space with 12 degrees of freedom using FSL's registration method via FLIRT. Alignment was visually confirmed for all participants.

FMRI data analysis

At the individual level, one general linear model (GLM) was defined for the social-scene task. The GLM included multiple regressors for each scene type: prosocial behaviors, social behaviors, and noninteractive behaviors. Events were modeled with a canonical (double-gamma) hemodynamic response function for a duration from stimulus onset to participant RT (stimuli offset after a rating was made). The jittered interstimulus intervals were not explicitly modeled and therefore served as a baseline. Temporal derivatives were included as covariates of no interest for all regressors, allowing a better fit for the whole model and reducing unexplained noise.

Group-level analyses were performed using the FMRIB Local Analysis of Mixed Effects (FLAME 1) module in FSL (Beckmann, Jenkinson, & Smith, 2003), with outliers deweighting using mixture modeling (Woolrich, 2008), a cluster-forming threshold of $Z > 2.3$, and an extent threshold of $p < .05$ familywise error corrected using the theory of Gaussian random fields (Poline, Worsley, Evans, & Friston, 1997). Contrasts of interest were defined as prosocial versus social scenes, prosocial versus noninteractive scenes, social versus prosocial scenes, and noninteractive versus prosocial scenes.

Conjunction analyses for the prosocial > social ∩ prosocial > noninteractive contrasts were performed using the easythresh_conj script in FSL (Nichols, 2007) and using the same threshold for the group-level analyzes ($Z > 2.3$, cluster size $p = .05$) in order to identify regions commonly activated for prosocial scenes (Price & Friston, 1997). Parameter estimates for the conjunction analysis were extracted from each contrast using fslmeans, and then averaged in SPSS. Parameter estimates were extracted using a binarized mask of significant activation from the conjunction analysis. Binarized masks of significant activation were also created for each of the left and right hemispheres, and analyses were repeated with average activation in each of the left and right TPJ. Parameter estimates were then regressed against psychological variables of interest. Unthresholded statistical maps are available via OSF (https://osf.io/ve4dw/).

Results

Correlations for all variables of interest are presented in Table 2.

Donation behavior

Participants donated on average $3.25 ($SD$ = $3.43, range $0–$14), and did not vary by participant age or gender. Seven participants donated $0, assuring us that there was no experimenter coercion. One participant presented as an outlier, donating $14 (skew = 1.52, kurtosis = 3.90). Thus, we conducted analyses with the actual donation amount and with the winsorized amount to account for nonnormality. To winsorize this outlier, we reduced the donation amount to the next highest donation ($6) plus 1 to equal $7 (winsorized donations $M_{donations}$ = $2.90, SD = $2.51, range: $0–$7, skew = −.52, kurtosis = −1.69). Results presented here use the winsorized amount. Results were the same using actual amounts.

Scene differentiation

To determine whether participants distinguished between scene type, we conducted two univariate ANOVAs to determine whether affective response and RT varied by type of scene. Main effects revealed that participants distinguished between scene type with regard to affective rating, $F(2, 57) = 13.63$, $p < .001$, $\eta\rho^2 = .32$, but not with regard to RT, $F(2, 57) = .17$, $p > 25$, $\eta\rho^2 = .01$. Tukey HSD post hoc tests revealed that, with respect to ratings, participants distinguished between prosocial and noninteractive scenes, $M_{diff} = .83$, 95% CI [.44, 1.22], $p < .001$, but not prosocial and social scenes, $M_{diff} = .25$, 95% CI [−.14, .64], $p > .25$. Social scenes were also distinguished from noninteractive scenes, $M_{diff} = .58$, 95% CI [.19, .97], $p = .002$. On average, prosocial scenes were rated most positive ($M = 3.28$, $SD = .56$, 95% CI [3.05, 3.51]), followed by social scenes ($M = 3.03$, $SD = .55$, 95% CI [2.80, 3.26]), and lastly noninteractive scenes ($M = 2.45$, $SD = .42$, 95% CI [2.22, 2.68]). Ratings and RTs did not significantly correlate with donation amount for any type of scene. Results were the same covarying for age. Ratings and RTs had no significant skew or kurtosis.

fMRI results

The main question of interest regarding brain activation was whether adolescents engaged regions of the social brain network differentially when viewing scenes of others engaged in prosocial versus social or noninteractive behaviors. Whole-brain analyses revealed greater activation in the bilateral temporoparietal junction (TPJ), bilateral posterior superior temporal sulcus (pSTS), and right anterior temporal pole (ATP) when viewing prosocial scenes versus viewing social scenes (see Fig. 2 and Table 3). Results were the same controlling for age.

Bilateral TPJ, bilateral pSTS, and right ATP emerged as significant regions for the prosocial versus noninteractive contrast (see Fig. 2 and Table 3). Results were the same controlling for age. There was no significant activation for the contrast of social scenes versus prosocial scenes or for the contrast of noninteractive scenes versus prosocial scenes.

Conjunction analysis—Group-level analyses revealed similar patterns of activation for contrasts of prosocial versus social and prosocial versus non-interactive contrasts. We

conducted a formal conjunction analysis for prosocial > social ∩ prosocial > noninteractive to identify regions commonly activated for prosocial scenes. Bilateral TPJ emerged as significant regions from the conjunction analysis (see Fig. 3 and Table 3). Results were the same controlling for age.

Neural response and donation behavior—To probe the relation between TPJ activation and donation behavior, we regressed contrast parameter estimates against donation amount. Parameter estimates for the conjunction analysis were extracted from each contrast (prosocial > social and prosocial > noninteractive) using a binarized mask of significant activation from the conjunction analysis. Values were then averaged across the two contrasts to obtain one average value for analyses. Given the broad age range of our participants, we controlled for age. Additionally, because APS scores were significantly related to donations (see Table 2), we controlled for APS scores. Controlling for APS scores allowed us to determine whether neural response to prosocial scenes was associated with donations over and above preexisting behavioral tendencies. Age, APS scores, and neural activation had no significant skew or kurtosis. Histograms for each variable used in regression analyses are presented in the Supplemental Materials (Fig. S1).

Linear regression results revealed a significant relation between bilateral TPJ activation and donation amount, controlling for age and APS scores, $p = .004$ (see Table 4 and Fig. 4). Participants with greater activation in the TPJ when viewing prosocial images donated more to charity after the task.

Binarized masks of significant activation were also created for each of the left and right hemispheres, and analyses were repeated with average activation in each of the left and right TPJ. Regression results revealed significant associations between activation in each of the left and right TPJ clusters and donation amount, controlling for age and APS scores, left: $R^2 = .50$, $F(3, 16) = 5.42$, $p = .009$, $B = .03$, $t(16) = 3.04$, $p = .008$; right: $R^2 = .55$, $F(3, 16) = 6.47$, $p = .004$, $B = .04$, $t(16) = 3.42$, $p = .004$. All results were the same using the raw donation amounts (see Supplemental Materials, Table S1).

Discussion

Adolescence is a time of heightened social awareness and increased engagement of social brain regions compared with other developmental periods, but little is known about the degree to which social brain regions differentiate prosocial behaviors from other types of social behaviors and how activation in these regions relates to actual prosocial behaviors in adolescents. The present study used a set of new stimuli paired with a donations task to identify neural and behavioral correlates of prosocial giving in adolescents. Participants distinguished between scenes of prosocial, social, and noninteractive behaviors, evaluating their feelings about prosocial and social scenes as more positive than noninteractive scenes. However, participants did not differ in their affective rating for prosocial versus social scenes. Similarly, participants did not spend more time evaluating prosocial scenes compared with social or noninteractive scenes, as evinced in no significant differences in reaction time. Despite the similarities between prosocial and social scenes in rating and reaction time, adolescents distinguished between others engaged in prosocial versus social

and noninteractive behaviors at the neural level. Evaluating prosocial scenes robustly activated the bilateral TPJ and the magnitude of greater activation in the TPJ when evaluating prosocial scenes compared with social or noninteractive scenes related to the size of adolescents' own charitable donations. Using the brain as a predictor of prosocial behavior, independent of the fMRI task, improves upon prior investigations of prosociality in terms of ecological validity and has implications for future work seeking to promote prosocial behavior in adolescents.

Conjunction analyses demonstrated that TPJ activity was particularly prominent when adolescents evaluated others engaged in prosocial versus social or noninteractive behaviors. Our results contribute new neurobiological evidence supporting the idea that the extent to which the TPJ is recruited in prosocial contexts is associated with an individual's propensity to behave prosocially. Although our study was conducted in a small pilot sample, this finding aligns with research in adults showing that the structure and function of the TPJ relates to cognitive perspective taking as an antecedent of altruism (Morishima, Schunk, Bruhin, Ruff, & Fehr, 2012; Tusche et al., 2016). The TPJ has also been linked to greater perspective taking in adolescents (van den Bos et al., 2011), suggesting the evaluation of prosocial scenes in the present study may have required perspective-taking skills relevant for engaging in prosocial behavior. Extensive neural development occurs during adolescence, reflecting both biological maturation and experience. As neural systems develop, neural response to experienced situations becomes stronger and more automatic, while neural response to nonexperienced input becomes reduced (Nelson et al., 2016). During adolescence, engagement of the TPJ increases (Blakemore, den Ouden, Choudhury, & Frith, 2007). Thus, adolescence may be a window of opportunity to expose adolescents to prosocial behavior, potentially encouraging development of enduring prosocial tendencies.

The present study points to individual differences in recruitment of the social brain network as a potential mechanism for differences in prosocial behavior. The social-scene task can be used to examine neural antecedents of differences in prosocial behavior for antisocial and typically developing adolescents. Prior work with antisocial youth has linked perspective-taking training to increases in prosocial behavior (Chalmers & Townsend, 1990). Even in early childhood, affective perspective taking has been associated with prosocial behavior (Vaish, Carpenter, & Tomasello, 2009). Identifying the role of TPJ activation to prosocial behavior may have important implications for improving prosocial behavior, and the malleability of the brain in adolescence highlights the importance of studying brain–behavior links for antisocial and typically developing adolescents.

Adolescence is a time for maladaptive behavior but also is one of opportunity for positive development (Crone & Dahl, 2012). Growing evidence indicates social contexts strongly influence brain development and decision-making in adolescence (e.g., Gardner & Steinberg, 2005; Schriber & Guyer, 2016). Uniquely, in the current study, donation decisions were made anonymously, providing evidence that social context influences brain function and decision-making even in the absence of peer evaluation. Additionally, we assessed actual donation behavior, as opposed to points or theoretical donations, requiring participants to relinquish some of their study compensation to donate. This required a self-

sacrifice without any expectation of reciprocation and, as a result, reduced confounds compared with tasks that involve giving to a friend or being evaluated for prosocial behavior.

Another innovation of this pilot study is the assessment of brain activity when viewing others engaged in prosocial acts rather than when the participant was engaged in prosocial acts themselves, as previous research has done (e.g., Moll et al., 2006; Telzer et al., 2013; Van Hoorn et al., 2016). Much of prior work investigating neural activation during prosocial behavior focuses on whether prosocial giving is rewarding. The current study design allowed us to assess whether individual differences in neural response to social context (e.g., interpreting and evaluating social behavior of others) related to independent prosocial giving. The finding that adolescents distinguished between prosocial and social scenes as a function of greater TPJ activity to prosocial scenes, and that this activation related to subsequent giving behavior, expands our understanding of links between neural activation in the social brain and prosociality. Using comparison scenes that included people, rather than inanimate objects, provides evidence that the TPJ is differentially engaged when evaluating prosocial behavior, not merely because social content is presented. Additionally, comparison across scene types rather than exposure to only one type of scene allowed us to demonstrate that, at the neural level, participants differentiated between prosocial and social behavior in others. Future work should investigate how neural activation in mesolimbic circuitry during one's own prosocial behavior relates to the extent of social brain engagement when evaluating the prosocial behaviors of others. By studying the interplay of these processes, we may better understand whether the extent to which an individual feels rewarded by engaging in prosocial behavior influences their differentiation of prosocial versus other types of social content at the neural level. Thinking about others' intentions during prosocial behavior specifically, rather than other types of more general social behavior, may be a key component of what motivates adolescents to act in prosocial ways and may be related to the extent to which these adolescents perceive prosociality as rewarding.

We assessed self-reported experiences with prosocial behavior. APS scores, representing different experiences with prosocial behaviors, correlated with donation behavior, as did TPJ activation for prosocial versus social and noninteractive scenes. Importantly, TPJ activation related to the amount of money donated over and above age and APS scores, suggesting brain-based differences in responsivity to social context inform a tendency toward prosocial behavior beyond what is explained by self-reported prior experience. Higher APS scores were also correlated with higher ratings of prosocial scenes, calling for future work to better disentangle the motivating factors contributing to adolescent prosocial behavior, including prior experience and relative value structures with regard to prosocial behavior.

Interpretation of the current findings should be made in the context of study specifics. Although our sample size was small, it was predetermined based on funding constraints, prior studies investigating prosociality (Marsh et al., 2014; Tusche et al., 2016), and guidelines in the field regarding minimum sample sizes for pilot studies (Mumford, 2012). Future work should explore neural correlates of prosocial behavior in larger adolescent samples, and our results should be interpreted as preliminary. Participants donated to a charity for foster youth, which more closely aligns with traditional views of altruism rather than prior studies on prosocial behaviors toward family and friends (e.g., Telzer, Masten,

Berkman, Lieberman, & Fuligni, 2011). We did not assess participants' feelings regarding the charity in this study. Thus, it may be possible that donations would differ if participants chose a charity that was personally important to them. Therefore, extrapolations to other types of prosocial behaviors should be made with caution. Additionally, the present study was correlational and cannot establish a causal direction for the association between TPJ activation and prosocial giving.

In conclusion, we used an ecologically valid donations task paired with neuroimaging to probe neural and behavioral contributors to prosociality in adolescence. Adolescents distinguished prosocial behavior from other types of social interactions in both neural and affective response. Differential brain activation to prosocial scenes were related to subsequent monetary giving, suggesting potential mechanisms related to individual differences in prosocial behavior. The numerous positive psychosocial and health benefits conferred by prosociality and the importance of social context during adolescence call for continued work exploring neural mechanisms and contextual motivators of prosocial behavior during adolescence.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Acknowledgments

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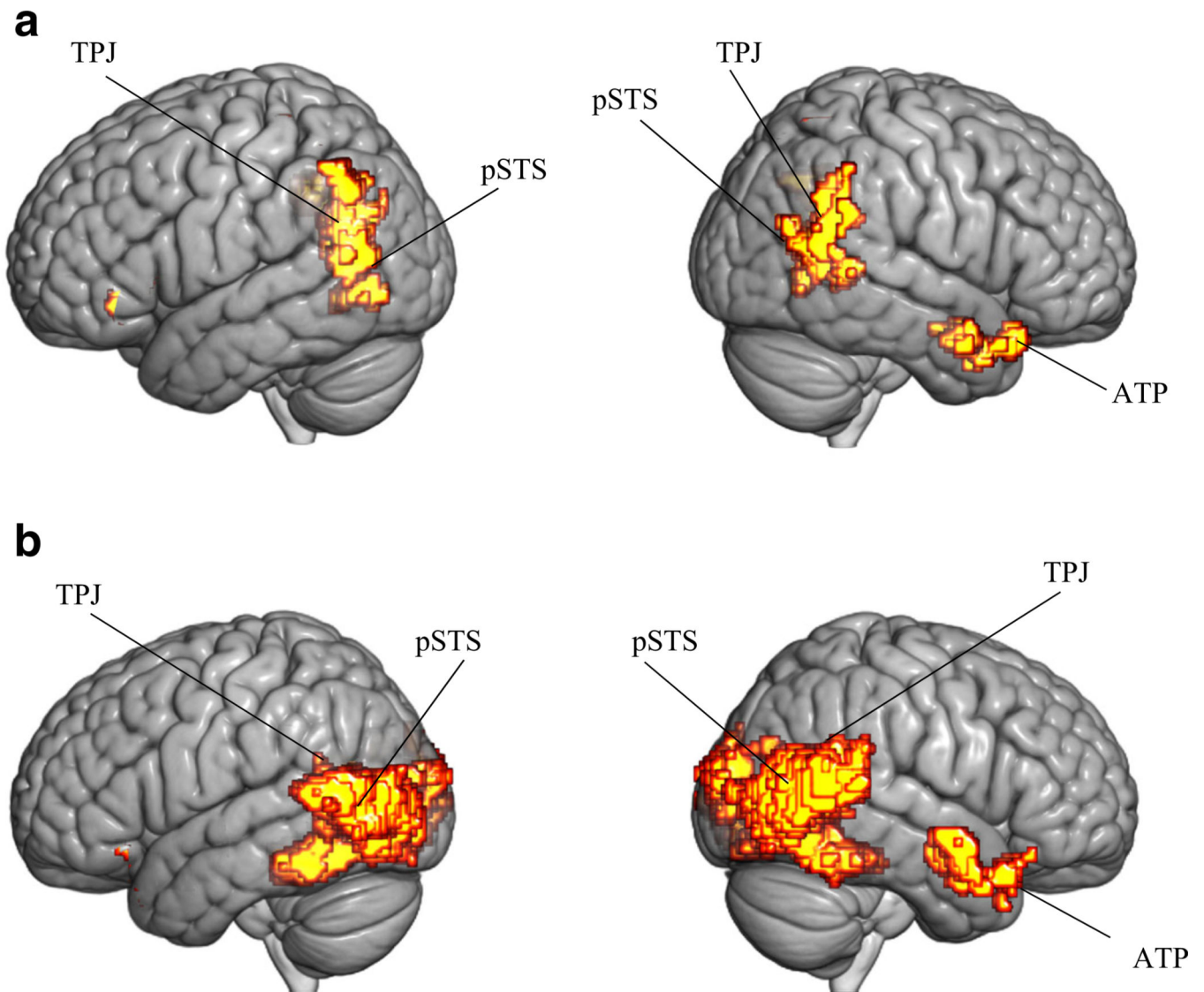Woolrich M (2008). Robust group analysis using outlier inference. Neuroimage, 41, 286–301. [PubMed: 18407525]

Fig. 1.

Examples of images used in the social-scene task. **a** prosocial scenes, **b** social scenes, **c** noninteractive scenes.

Fig. 2.
Visualization of significant activation for the contrasts of (**a**) prosocial versus social scenes and (**b**) prosocial versus noninteractive scenes. Significant regions for both contrasts include the left temporoparietal junction (TPJ), left posterior superior temporal sulcus (pSTS), right TPJ, right pSTS, and right anterior temporal pole (ATP). FLAME 1, $Z > 2.3$, $p < .05$, outlier deweighting, $N = 20$.
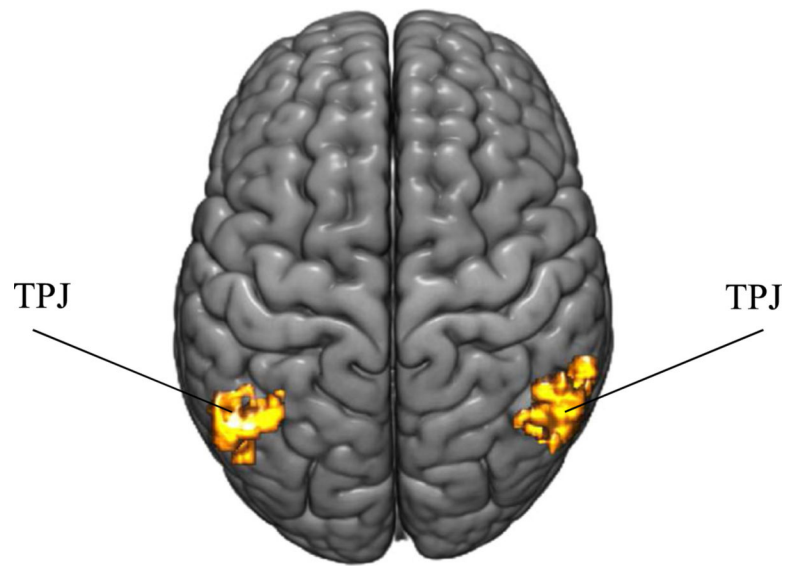
Fig. 3.
Visualization of significant activation in the bilateral temporoparietal junction (TPJ) for prosocial > social ∩ prosocial > noninteractive scenes. FLAME 1, $Z > 2.3$, $p < .05$, outlier deweighting, $N = 20$.
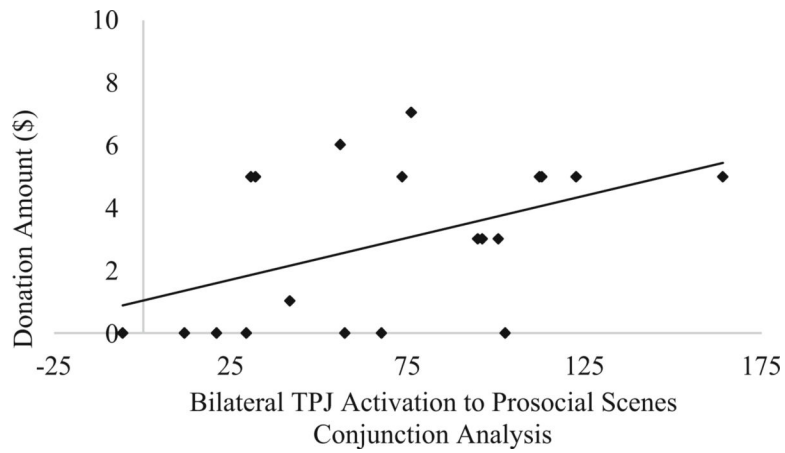
Fig. 4.
Scatter plot showing a visual depiction of the relation between winsorized donation amount (dollars) and bilateral temporoparietal junction (TPJ) activation (contrast parameter estimates). Parameter estimates for the conjunction analysis were extracted from each contrast (prosocial > social and prosocial > noninteractive) using a binarized mask of significant activation from the conjunction analysis, FLAME 1, cluster corrected $Z > 2.3$, p <.05, outlier deweighting, $N = 20$. Values were then averaged across the two contrasts to obtain one average value for analysis

Table 1

Demographic information for participants

Ethnicity	% of sample	Maternal education	% of sample
African American	35%	Doctorate	25%
Hispanic/Latino	25%	Master's	20%
Caucasian	25%	4-year college	5%
Asian American	10%	Associates	5%
Other	5%	Some college	20%
		High school/GED	10%
		Some high school	10%
		Middle school only	5%

Note. $N = 20$, seven female, $M_{Age} = 15.30$ years, $SD = .98$, range: 13–17 years

Table 2

Bivariate correlations for behavioral variables of interest

Variable	1	2	3	4	5	6	7	8	9	10	11	12
1. Donation amount	-											
2. Bilateral TPJ activation conjunction analysis	.47*	-										
3. L TPJ activation conjunction analysis	.43†	.96***	-									
4. R TPJ activation conjunction analysis	.48*	.98***	.89***	-								
5. APS score	.47*	−.20	−.20	−.19	-							
6. Prosocial scene rating	.18	−.03	.03	−.06	.45*	-						
7. Social scene rating	−.04	−.19	−.18	−.18	.32	.59**	-					
8. Noninteractive scene rating	.06	−.22	−.22	−.21	.41†	.44†	.69**	-				
9. Prosocial scene RT	−.33	−.38	−.28	−.44†	−.21	−.14	−.08	−.06	-			
10. Social scene RT	−.34	−.27	−.18	−.33	−.25	−.08	−.14	−.09	.94***	-		
11. Noninteractive scene RT	−.27	−.47*	−.40†	−.50*	−.02	.14	.15	.06	.91***	.88***	-	
12. Age	.14	−.14	−.18	−.10	.30	.10	.52*	.29	−.12	−.20	−.07	-

Note. N = 20, seven female, M_{Age} = 15.30 years, SD = .98, range: 13–17 years.

†
p <.10

*
p <.05

**
p <.01

***
p <.001. Ratings and RT (reaction time) are based on averages for each individual across each of 30 prosocial, 30 social, and 30 noninteractive scenes. APS = Altruistic Personality Scale

Table 3

Significant clusters for the contrast of prosocial > social and prosocial > noninteractive

Region	R/L	Peak MNI coordinates			Max	Voxels	p value
		x	y	z	Z value	(mm³)	
Prosocial > Social							
Occipital cortex, middle temporal gyrus	L	−56	−64	16	4.16	1,239	<.001
Angular gyrus, supramarginal gyrus	R	52	−50	30	3.70	1,010	<.001
Cingulate gyrus, precuneous cortex	L	−6	−48	32	3.54	441	.011
Temporal pole	R	50	22	−26	3.68	393	.022
Prosocial > Noninteractive							
Occipital cortex, Middle temporal gyrus	R	50	−62	14	5.24	6,660	<.001
Occipital cortex, middle temporal gyrus	L	−48	−64	14	5.05	3,228	<.001
Superior temporal gyrus, middle temporal gyrus	R	50	−6	−16	6.40	565	<.001
Conjunction Prosocial > Social ∩ Prosocial > Noninteractive [a]							
Angular gyrus, middle temporal gyrus, occipital cortex	R	54	−56	14	2.62	695	.002
Occipital cortex, middle temporal gyrus	L	−50	−62	11	1.58	471	.026

Note. x, y, and *z* refer to MNI coordinates; voxels refer to each significant cluster; L = left hemisphere and R = right hemisphere.

[a] Center of gravity coordinates

Table 4

Linear regression predicting winsorized donation amount

Factor	Model 1			Model 2		
	B	**SE**	**β**	**B**	**SE**	**β**
Age	.36	.60	.14	.004	.58	.001
APS score				2.17	1.05	.47
Bilateral TPJ activation						
R^2	.02			.22		
F	.38			2.37		
$\triangle R^2$				.20		

Note. Temporoparietal junction (TPJ) contrast parameter estimates were extracted from the averages of the significant activation from the conjunction analysis of prosocial > social ∩ prosocial > noninteractive, FLAME 1, cluster corrected $Z > 2.3$, $p < .05$, outlier deweighting, $N = 20$.

*
$p < .05$

**
$p < .01$

***
$p < .001$. APS = Altruistic Personality Scale