Familiarity and Audience Effects on Giving; an fMRI Study

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Abstract

Giving is often characterized by the conflicting decision to give up something of value to benefit others. Recent evidence indicated that giving is highly context dependent. To unravel the neural correlates of social context, in this study young adults ($N = 32$) performed a novel giving fMRI paradigm, in which they divided coins between self and known others (friends) or unknown (unfamiliar) others. A second manipulation included presence of others; giving decisions were made with an audience or anonymously. Results showed that participants gave more coins to a friend than to an unfamiliar other, and generally gave more in the presence of an audience. On a neural level, medial prefrontal cortex and the right insula were most active for relatively generous decisions. These findings possibly reflect that aversion of norm deviation or fairness concerns drive differences in the frequency of giving. Next, activation in separate sub regions of the TPJ-IPL (i.e., a region that comprises the temporo-parietal junction and inferior parietal lobule) was found for target and audience contexts. Overall, our findings suggest that donation size and social contextual information are processed in separable brain regions and that TPJ-IPL plays an important role in balancing self- and other-oriented motives related to the social context.

Keywords: Giving, Target, Audience, fMRI, Social Brain

Familiarity and Audience Effects of Giving; an fMRI Study

Giving is an important form of prosocial behavior that is essential for forming and maintaining social relationships (Cutler & Campbell-Meiklejohn, 2019; Schreuders et al., 2018), especially when young individuals make the transition to becoming adult members of society (Guassi Moreira et al., 2018). Giving is characterized by the conflicting decision to give up something of value to benefit others, and as such is highly context-dependent (Obeso et al., 2018). For example, giving is more prevalent when it is less costly, when the giver has a relationship with the target, or when the decision is being observed by others, as these situations may align interests of the giver and target (Crone & Fuligni, 2019; Güroğlu, van den Bos, et al., 2014; Obeso et al., 2018; Schreuders et al., 2018; Telzer et al., 2015; Van de Groep et al., 2019; Van Hoorn et al., 2016). There currently is little understanding of the neural mechanisms driving context-dependent giving in young adults. Therefore, the goal of this study was to investigate whether neural regions associated with giving are differentially activated due to variation in 1) familiarity of the target of giving and 2) whether an audience was present or not. These two social contextual task manipulations have previously been found to be most powerful in influencing giving behavior.

Previous neuroimaging studies provided insights in motivations to give by employing variations of the Dictator Game (Cutler & Campbell-Meiklejohn, 2019; Do et al., 2019; Güroğlu et al., 2009; Van Den Bos et al., 2009; Van Hoorn et al., 2016). The Dictator Game is an economic game, in which participants can share valuable resources with others. Prior behavioral studies showed that people give away 20-30% of their resources in anonymous settings and settings without future transactions (Van de Groep et al., 2019; Will & Güroğlu, 2016), but they give more when they have a relationship with the target (Güroğlu, van den Bos, et al., 2014) or

when they are being observed by others (Lamba & Mace, 2010; Van Hoorn et al., 2016). So far, prior neuroimaging studies mainly focused on anonymous giving and showed involvement of the medial prefrontal cortex (mPFC) as a hub region that integrates several affective and social processes (Crone & Fuligni, 2019). For example, the mPFC has been implicated in affective processing, together with activity in the ventral striatum; as well as in self-regulation, mentalizing, and the processing of social norms and saliency of stimuli, together with activity in the dorsolateral prefrontal cortex (dlPFC), superior temporal sulcus (STS), anterior insula (AI), temporo-parietal junction (TPJ), and inferior parietal lobe (IPL; (Blakemore, 2008; Cutler & Campbell-Meiklejohn, 2019; Güroğlu, Will, et al., 2014; Schreuders et al., 2018; Telzer et al., 2011). Note that the TPJ and IPL are closely interrelated parietal areas consisting of functionally heterogeneous sub regions that serve a global function of inferring mental states, integrating social contexts, and thinking about self and others, and will henceforth be referred to as TPJ-IPL (Carter & Huettel, 2013; Schurz et al., 2014). Although involvement in aforementioned social brain regions has been revealed in fMRI tasks measuring anonymous giving to unknown others, the direction of effects across studies is conflicting. That is, studies sometimes show increased activation for more, and sometimes for less giving. Furthermore, the extent to which patterns of neural activation are modulated by different social motivations to give in young adulthood is not yet well understood (Carter & Huettel, 2013).

Understanding the neural correlates of familiarity and audience effects on giving is especially important during young adulthood as this is a period in life in which behaviors are increasingly shaped by social context. For example, whereas young adults vary their giving behavior based on the target of the donations, this is not yet always seen in childhood and early to mid-adolescence (Güroğlu, van den Bos, et al., 2014; van den Bos et al., 2012). Furthermore,

young adulthood is a period in which social relations are developed outside the family context,

and social acceptance and reputational concerns make young adulthood a particularly interesting

period to study audience effects on giving (Van Hoorn et al., 2016). Possibly, the familiarity of

the target and presence of an audience increase the likelihood to give because young adults

perceive giving in these contexts to be less costly or in conflict with their own social norms, as it

prevents loss of resources to out-group members and helps them to meet reputational goals

(Cutler & Campbell-Meiklejohn, 2019; Telzer et al., 2015; Van de Groep et al., 2019).

Even though most brain imaging studies focused on anonymous giving, several recent

studies showed that neural responses to giving are influenced by the target to whom giving is

directed (Schreuders et al., 2018; Telzer et al., 2015). Specifically the mPFC, a brain region that

is implicated in anonymous self and other-directed giving choices (Cutler & Campbell-

Meiklejohn, 2019), is more active when interacting with friends compared to unfamiliar others

(Güroğlu et al., 2008). Interestingly, the mPFC is also more strongly activated when giving

choices are observed by an audience (Van Hoorn et al., 2016). Furthermore, the TPJ-IPL is also

involved when interacting with friends or when being observed (Schreuders et al., 2018; Van

Hoorn et al., 2016), but no studies to date examined whether both of these contexts activate the

same regions (including mPFC and TPJ-IPL) within the same individuals and experimental

design. To unravel the overlapping and unique roles of neural regions involved in these two

forms of social context sensitivity, it is of importance to manipulate both within the same design;

as this allows for testing the additive and interaction effects of familiarity and audience

manipulations.

Taken together, several studies point to a role of the mPFC and TPJ-IPL in social context

related giving, but it remains to be determined whether target related activity and audience related

activity reflect the same neural process. Currently, this can only be assessed by comparing studies with largely dissimilar between-subjects designs, which may hamper the reliability of drawn conclusions. Therefore, the present study used a novel, within-subjects, fMRI paradigm based on the Dictator Game (Kahneman et al., 1986; Van de Groep et al., 2019), to elucidate whether similar or separable neural regions are involved in giving to friends or to unfamiliar others, and in giving anonymously or with an audience.

We designed a giving paradigm in which young adults divided coins between themselves and another target. The task was designed to compare neural activity under conditions where participants could only make small donations (i.e., 1, 2, or 3 out of 7 coins) to neural activity under conditions where participants could only make large donations (i.e. 4, 5, or 6 out of 7 coins). This manipulation allowed us to compare small to large donations within individuals, thereby controlling for individual differences in giving. We took this approach because some individuals show little or no giving under unrestricted giving conditions, which has been reason to exclude participants in prior studies, thereby limiting generalizability (Do et al., 2019; Telzer et al., 2015). Within the contexts of small and large donations participants could decide on the magnitude of donation, ensuring a sense of volition (Gagné, 2003; Murayama et al., 2013). We expected participants to give relatively more in the small donation condition than the large donation condition (Güroğlu, Will, et al., 2014), which we expected to be reflected in more activation in areas previously associated with self-gain, saliency signalling, and norm violation, including mPFC, AI, and the ventral striatum (Cutler & Campbell-Meiklejohn, 2019; Güroğlu, Will, et al., 2014; Schreuders et al., 2018; Van Den Bos et al., 2009).

Secondly, we manipulated social context related to target (i.e., giving to a friend or unfamiliar other) and audience (i.e., giving publicly or anonymously). We hypothesized

participants would give more to a friend than an unfamiliar other (Güroğlu, van den Bos, et al., 2014; Schreuders et al., 2018; Van de Groep et al., 2019), and expected increased activation in the mPFC and TPJ-IPL when participants played for a friend versus unfamiliar other. Prior studies showed that these regions are more strongly activated for liked compared to neutral or disliked persons (Güroğlu et al., 2008; Schreuders et al., 2018), although it should be noted that some studies showed increased activation in these regions while contrasting out-group versus in-group donations as a function of group identity (Telzer et al., 2015). As such, one of the aims of the current study was to shed more light on the contradictory findings with regard to activation in social brain regions pertaining to donation size and target. With regard to the audience, we hypothesized participants would give more with an audience present than in anonymous situations (Hofmann et al., 2018; Lamba & Mace, 2010), and expected increased activation for audience compared to anonymous conditions in the mPFC and TPJ-IPL (Izuma et al., 2010, 2010; Van Hoorn et al., 2016).

Method

Participants

Thirty-two participants (17 females) between ages 20 and 25 (M_{age} = 22.57, SD_{age} = 1.58; age range 20.26 – 25.75 years) participated in this study, which was part of a larger study on prosocial behavior in young adulthood. Participants were recruited via local advertisements and provided written informed consent. All participants had normal or corrected-to-normal vision, and had not been previously diagnosed with an intellectual disability (i.e., their IQ > 70). Participants were screened for neurological or psychiatric disorders or diseases, and MRI contraindications via a private telephone conversation. The study was approved by the local

medical ethical committee. Participants received €40 for their participation plus additional

earnings from the fMRI task.

Materials

fMRI Donation task.

Basic task design: small and large donations. To measure participants' giving behavior,

we developed a novel economic game inspired by the Dictator Game (Kahneman et al., 1986). In

this game, participants divided seven coins between themselves and someone else. Giving

behavior was measured as the number of coins that was given to the other person, who could not

reject the decision (Kahneman et al., 1986). In the small donation condition, participants could

donate 1, 2, or 3 of 7 coins. In the large donation condition, participants could donate 4, 5, or 6 of

seven coins. To ensure comparability of the small and large donation condition participants could

not give 0 coins (i.e., nothing), 7 coins (i.e., everything), or make an equal split.

Targets of giving: friend and unfamiliar peer. Participants were instructed they would

divide coins between themselves and an unfamiliar peer (same-sex, similar-age), or between

themselves and their closest friend (same-sex, similar-age). On each trial, the name of either the

friend (as indicated by the participant during instructions) or the unfamiliar other was displayed

at the top of the screen to indicate the target of the donation (see Figure 1). Participants were

instructed that the coins represented real money, but no information was given about how the

coins translated to real-life money. They were instructed before the scan that the computer would

randomly select a few trials, which would be paid out to the participant, their friend, and the

unfamiliar other after completion of the experiment. Participants received a set payment (i.e.,

independent of decisions) for both themselves (€1.50) and their friend (€1), and experimenters

transferred the payment to the unfamiliar other (€0.50), which was another, anonymous

participant in the study.

Peer presence: anonymous and audience donations. The task included two blocks in

which participants made anonymous choices, and two blocks in which participants' decisions

were evaluated by peers at a later time (see Figure 1). During the practice session, participants

watched a video clip of six age-matched peers (three males and three females) with neutral

expressions. To prevent deception of participants, the peers in the video clip were invited after

completion of the study to observe and evaluate anonymised decisions that were made during the

donation task. Experimenters masked the screen in the control room to ensure anonymous

decision making. Participants were aware of this masking. Screens indicating whether blocks

were anonymous or not were shown at the start of each block, but not during trials to prevent

differences in visual complexity (and thus neural activation) between anonymous and audience

trials.

Task duration and stimuli. The task was presented in the MRI scanner via E-prime

version 2 (Schneider et al., 2012). Each block started with a 4000 millisecond display indicating

whether it was an anonymous or audience block (see Figure 1). Each trial within a block started

with a jittered fixation cross 0 – 4400 ms ($M = 550$ ms) which was optimized using OptSeq

(Dale, 1999). After fixation, three possible distributions (i.e., 1, 2, and 3 within the small

donation condition and 4, 5, and 6 within the large donation condition) were presented.

Participants had to respond within 2000 ms by pressing a response button with their right index,

middle, or ring finger. Choices were confirmed for 1000 ms through a white selection frame at

the bottom of the screen. If participants did not respond in time, a 'too late' screen was displayed

for 1000 ms and these trials were excluded from analysis (.02% of the trials). The total duration

of the experiment, excluding instructions and breaks, was approximately 15 minutes.

   Order of blocks and trials. Before the scanning session, participants performed a practice

version of the task consisting of four trials per condition in randomized order. The fMRI task

during the scanning session consisted of four blocks presented in two runs, in which the order of

anonymous and audience blocks was counterbalanced across participants (i.e., there were 4

possible orders). In total there were 160 trials, separated in four blocks of 40 trials. All

combinations of conditions (donation size, target, and audience/anonymous) were equally divided

across the trials. The order of trials was optimized using OptSeq (Dale, 1999). There was a short

break between the second and third block of the task.

   Giving behavior. Participants' giving behavior was measured using a button response

box, where pressing the left button was coded as 1, the middle as 2, and the right as 3. To enable

comparison of the small and large donation conditions, scores were transferred to percentages. As

such, the lowest outcomes (1 and 4 donated coins) were recoded as 33.33%, the middle outcomes

(2 and 5) as 66.66%, and the highest outcomes (3 and 6) as 100%. These scores were used to

examine average giving behavior and whether giving differed as a function of task conditions.

We also examined whether there were any reaction time differences between conditions.

   Exit question. Participants were asked to rate how important the targets were to them and

how much they liked them on a 7-point scale, ranging from 1 (not at all) to 7 (very much).

Procedure

   Participants received information about the study by telephone and a digital information

letter. After agreeing to participate, participants filled out questionnaires prior to the scanning

session. During the scanning session, participants received instructions about the MRI session in a quiet laboratory room. Prior to scanning, participants performed a practice version of the donation task. As the current study was part of a larger project, the MRI session consisted of a structural MRI scan, a resting state scan, functional scans for the donation task, functional scans for a reward-task, and a Diffusion Tensor Imaging (DTI) scan. During testing outside of the scanner, participants also performed several behavioral tasks and filled out questionnaires, either before or after the scanning session.

MRI Data Acquisition

MRI scans were acquired using a 3T MRI scanner (Philips Achieva TX, Erlangen, Germany) with a standard whole-head coil. Stimuli were displayed to participants using a screen they could see through a mirror attached to the head coil. Functional scans were acquired during two runs, which consisted of 178 and 205 dynamic scans, respectively. We collected T2* weighted gradient echo planar images (EPI) (TR = 2.2 s, TE = 30 ms, flip angle 8°, sequential acquisition: 38 slices, voxel size = 2.75 x 2.75 x 2.75 mm, 80x80 matrix, field of view [FOV] = $220 \times 220 \times 115$ mm). 5 dummy scans were acquired before the start of the first functional scan of each run. To provide anatomical reference, a high-resolution 3D T1-weighted anatomical image was collected prior to the functional scans (TR = 7.9 ms, TE = 3.5 ms, flip angle 8°, 3D matrix size for 3D acquisitions: 228x177x155 slices, axial slice orientation, voxel size: 1.1 x 1.1 x 1.1 mm, FOV = 250 x 196 x 170 mm). The duration of this scan was 4 minutes and 12 seconds. T1 stabilization dummy scans were automatically discarded by the scanner. All scans were acquired using a fast field echo pulse sequence. To avoid head motion, participants' head motion was limited with foam inserts at both sides of the head when possible. No participants had to be

excluded due to excessive head motion, as translational movement parameters did not surpass 3 mm for all directions, participants and scans (movement range: .00–1.61 mm, $M = .07$, $SD = .06$).

MRI Data Analyses

Preprocessing. Data were analysed using SPM8 (Wellcome Department of Cognitive Neurology, London, United Kingdom). Preprocessing steps of the functional images included realignment, slice-time correction, spatial normalization using segmentation parameters, and spatial smoothing with a 6-mm FWHM isotropic Gaussian kernel. The normalization algorithm used a 12-parameter affine transform with a nonlinear transformation involving cosine basis functions and resampled the volumes to 3-mm cubic voxels. Templates were based on MNI-305 stereotaxic space.

General Linear Model. To analyse individual participants' data, we used the general linear model in SPM8. The fMRI time series were modelled as a time series with the length of the reaction times convolved with the hemodynamic response function (HRF). Note that a model with stick function showed largely similar results, expect for some differences when contrasting small versus large donations on a whole brain level (i.e., the stick function model also showed increased activation in the right striatum, dlPFC, and bilateral insula). Here, we report results using a reaction times model to account for differences in reaction times between conditions. The modelled events (i.e., donation condition: small or large; target: friend or unfamiliar other; and audience: anonymous or audience present) were used as regressors in a general linear model, along with a basic set of cosine functions that high-pass filtered the data (cutoff: 120 seconds). The start screens in which participants were presented with anonymous or audience conditions were modelled separately. In addition, six motion parameters were included as nuisance regressors. Trials on which participants failed to respond were modelled separately as covariate

of no interest and were excluded from analyses. The least-square parameter estimates of the

height of the best-fitting canonical hemodynamic response function for each condition were used

in pair-wise contrasts. These pairwise comparisons resulted in subject-specific contrast images,

which were submitted to second-level group analyses.

Confirmatory ROI Analyses. To test whether small or large donations, giving to a friend

or unfamiliar other, and giving anonymous or with an audience resulted in increased activity in

similar brain regions, we created targeted ROIs using the MarsBaR toolbox (Brett et al., 2002);

http://marsbar.sourceforge.net/) for SPM8 for which we extracted parameter estimates. Based on

prior literature we created ROIs of the mPFC and nucleus accumbens (a subregion of the ventral

striatum) for their role in mentalizing and reward processing (Braams et al., 2014; Cutler &

Campbell-Meiklejohn, 2019), and of the TPJ-IPL as this region has been shown to be

differentially activated depending on the target and audience (Braams et al., 2014; Schreuders et

al., 2018; Van Hoorn et al., 2016). ROIs consisted of a 10 mm sphere around peak coordinates

reported in prior meta-analyses: mPFC [x = 8, y = 50, z = -8] (Campbell-Meiklejohn et al., 2017;

Cutler & Campbell-Meiklejohn, 2019), left TPJ-IPL [x = 46, y = -63, z = 41] and right TPJ-IPL

[x = 47, y = -61, z = 39] (Schurz et al., 2014). NAcc ROIs were extracted from the Harvard-

Oxford subcortical atlas with a threshold of 40%. The left nAcc consisted of 28 voxels [x = -9.57

, y = 11.70, z = -7.10] and the right nAcc consisted of 26 voxels [x = 9.45, y = 12.60, z = -6.69].

We report nAcc ROI analyses collapsed across hemispheres as there were no significant

differences between the left and right hemispheres. ROI analyses were performed with a

threshold of $p \leq .05$.

Whole Brain Analyses. To explore neural responses across the whole brain we computed

a 2 (donation condition: small or large) x 2 (target: friend or unfamiliar other) x 2 (audience:

anonymous or audience present) ANOVA at the group level to examine the following whole-brain contrasts: 'small donation condition versus large donation condition', 'friend versus unfamiliar other', and 'audience versus anonymous', and to test for possible interaction effects between conditions. Task-related responses were deemed significant when they exceeded false discovery rate (FDR) cluster correction of $p < .05$, with an initial uncorrected threshold of $p < .001$ (Woo et al., 2014).

An additional way to examine the neural responses associated with generosity is to compare response options within the small and large donation condition, respectively. That is, to compare relatively generous response options (i.e., donating 2 or 3 coins, or 5 or 6 coins) to response options that reflect minimal giving (i.e., donating 1 or 4 coins, respectively). Therefore, we also examined the following whole-brain contrast: generous giving vs. minimal giving. This whole brain analysis was performed collapsed across the small and large conditions to ensure robust analyses with on average 91.75 ($SD = 36.60$) trials for minimal giving and 65.66 ($SD = 36.16$) trials for generous giving. The analysis was performed for 30 participants as two participants never showed generous giving. All reported whole brain analyses are available on NeuroVault (Gorgolewski et al., 2015), see https://neurovault.org/collections/MADDFZPG/.

Results

Assumption checks were performed for all analyses. No violations were observed, except that there were a few outliers as assessed by inspection of a boxplot (i.e., values greater than 3 box-lengths from the edge of the box), which were therefore winsorized (Tabachnick & Fidell, 2013). Specifically, five participants were outliers on one variable each. Results did not change before and after winsorizing. Here, we report the winsorized results.

Manipulation check

Participants rated friends as more important (M = 6.56, SD = .67) than unfamiliar others

(M = 2.75, SD = 1.19), as indicated by a paired-samples t-test, $t(31)$ = 17.54, p < .001.

Participants also liked their friends (M = 6.66, SD = .60) more than unfamiliar others (M = 4.00,

SD = .00), $t(31)$ = 24.98, p < .001. As such, the manipulation check confirmed that participants

differentiated between friends and unfamiliar others.

Behavioral results

Donating behavior. To examine whether participants' giving behavior was modulated by

donation condition (small or large), target (friend or unfamiliar other), and audience (audience

present or anonymous), we performed a repeated measures ANOVA with donation condition,

target, and audience (all with two levels) as within-subject variables, and giving (in percentages)

as dependent variable. There was a significant main effect of donation condition, $F(1, 31)$ =

48.50, p < .001, η^2_p = .61, such that participants gave more in the small donation condition (M =

67.78 %, SD = 20.26) than in the large donation condition (M = 42.33 %, SD = 10.09). There was

also a main effect of target, $F(1, 31)$ = 50.63, p < .001, η^2_p = .62, and a two-way interaction

between donation condition and target, $F(1, 31)$ = 16.43, p < .001, η^2_p = .35. As shown in Figure

2, participants gave more to friends, but the difference between giving to a friend and unfamiliar

other was larger in the small donation condition, $F(1, 31)$ = 47.88, p < .001, η^2_p = .61, than in the

large donation condition, $F(1, 31)$ = 18.44, p < .001, η^2_p = .37. Finally, there was a main effect of

audience, $F(1, 31)$ = 8.15, p = .008, η^2_p = .21, such that participants gave more in the audience (M

= 56.03, SD = 12.43) compared to anonymous condition (M = 54.08, SD = 12.32), but the two-

way interactions between donation condition and audience, and between target and audience were

not significant, (p's > .378). There was no significant three-way interaction (p = .760).

Reaction times. Next, we performed a 2 (target: friend or unfamiliar other) x 2 (donation condition: small or large) x 2 (audience: anonymous or audience present) repeated measures ANOVA to test whether reaction times differed for the task conditions. We found a main effect of target, $F(1, 31) = 7.53$, $p = .010$, $\eta^2_p = .20$, which was qualified by a two-way interaction between target and donation condition, $F(1, 31) = 14.32$, $p = .001$, $\eta^2_p = .32$. Follow-up analyses revealed no differences in RTs between friends and unfamiliar others in the small donation condition, $F(1, 31) = .03$, $p = .861$, $\eta^2_p = .00$, $M_{friend} = 1029.20$, $SD = 236.05$, $M_{unfamiliar\ other} = 1032.25$, $SD = 256.08$, but longer RTs for giving to a friend than an unfamiliar other in the large donation condition, $F(1, 31) = 28.12$, $p < .001$, $\eta^2_p = .48$, $M_{friend} = 1043.94$, $SD = 254.47$, $M_{unfamiliar\ other} = 975.185$, $SD = 241.18$ (see Figure 2). There were no other main or interaction effects.

Neural results

Confirmatory ROI results. For each of the a priori defined ROIs we tested for main effects and interactions of task-conditions using donation x target x audience repeated measures ANOVAs. mPFC was collapsed across left and right hemispheres, given that this was a midline region. For nAcc and TPJ-IPL hemisphere was added to the ANOVA.

For the mPFC and nAcc we found main effects of donation condition, reflecting higher activation for small versus large donations in mPFC $F(1, 31) = 7.01$, $p = .013$, $\eta^2_p = .19$; and in nAcc, $F(1, 31) = 9.07$, $p = .005$, $\eta^2_p = .23$, see Figure 3. There were no other main or interaction effects.

For TPJ-IPL, we found a main effect of audience, showing increased activation for audience versus anonymous donations, $F(1, 31) = 10.22$, $p = .003$, $\eta^2_p = .25$. There was also a main effect of hemisphere, showing that the right TPJ-IPL was more active than the left

regardless of task condition, $F(1, 31) = 17.84$, $p < .001$, $\eta^2_p = .37$. No other main or interaction effects were found. There were no effects of target for any of the confirmatory ROIs.

Whole-brain full factorial ANOVA. To examine neural responses during the task at the whole brain level, we performed a whole-brain full factorial ANOVA with the following within-subject factors: donation condition (small or large), target (friend or unfamiliar other), and audience (anonymous or audience present).

The main effect of donation condition revealed activation in the mPFC (i.e., in the superior medial gyrus), the occipital cortex and cerebellum (see Figure 4). Paired samples t-tests showed that all aforementioned brain regions were more active in the small compared to the large donation condition, t's ≥ 4.39, p's $\leq .001$.

The main effect of target revealed activation in the left and right TPJ-IPL, right cuneus, as well as occipital and cerebellar regions (see Figure 4). Paired samples t-tests revealed that all brain regions were more active for friend than unfamiliar other, t's ≥ 5.29, p's $\leq .001$, except for the left TPJ-IPL, as this region did not survive cluster correction in the post-hoc paired samples t-test.

No significant clusters of activation were found for the main effect of audience, nor did we observe any interactions between conditions.

To directly test whether giving in the different contexts of the task relied on overlapping or different neural regions, we performed conjunction analyses. These analyses confirmed no overlap in activation between donation condition, target, and audience.

Exploratory whole-brain analysis of choice differences.

The main effects of donation condition could be influenced by choice differences. To gain additional insight in neural responses related to generous vs. minimal giving we examined the whole brain contrast 'generous (i.e., giving 2, 3, 5, or 6 coins) > minimal giving (i.e., giving, 1 or 4 coins)', collapsed across small and large donation conditions. The contrast generous > minimal giving resulted in significant clusters of activation in the mPFC and right AI (see Figure 5). To further visualize this effect, we extracted these clusters as ROIs. As can be seen in Figure 5, activation in the mPFC and right AI was higher when participant showed relatively generous giving (i.e., giving 2, 3, 5, or 6 coins) compared to minimal giving (giving 1 or 4 coins). Follow up analyses for small and large donation conditions separately revealed that this effect was mainly driven by the large donations condition, such that giving 5-6 coins (generous) resulted in more activation than giving 4 choices (minimal), for both the mPFC, $F(1, 17)= 20.62, p \leq .001$ and for the right insula, $F(1, 15)= 14.12, p \leq .001$. These effects were not significant for the small donation condition, i.e., giving 2-3 coins (generous) versus giving 1 coin (minimal) in both ROIs (p's > .53).

Discussion

The goal of the current study was to get a better understanding of neural correlates of giving in different social contexts in young adults, specifically giving to a friend versus unfamiliar other, and anonymously versus being observed by an audience. Consistent with prior studies, young adults gave more when costs for self were low (i.e., in the context of small donations), when the beneficiary was a friend, and when being observed by an audience (Gächter et al., 2015; Gagné, 2003; Güroğlu, Will, et al., 2014; Hofmann et al., 2018; Van de Groep et al., 2019; Van Hoorn et al., 2016). These findings show that motivations for giving are strongly context dependent (Güroğlu, van den Bos, et al., 2014). Neural findings demonstrated dissociable

processes for small versus large donations, and for giving to friends and unknown others, as will be outlined in the next sections.

We used neuroimaging to test whether giving in general (i.e., small and large donations) and in specific social contexts (i.e., target familiarity, being observed) was associated with similar or separable patterns of neural activation in mPFC, as this region was previously implicated in decision-making for self and others (Cutler & Campbell-Meiklejohn, 2019). As expected, confirmatory ROI and exploratory whole-brain analyses revealed involvement of the mPFC for small relative to large donations. Thus, overall mPFC was more sensitive to giving less to others. Follow up analyses revealed that within the large donation condition mPFC and AI were more active for generous choices rather than minimal giving choices (e.g. giving 5 or 6 rather than 4 coins). Taken together, mPFC was generally more sensitive to giving less to others, but also to generous giving. Within the context of fairness-related decision making in economic games, activation in the mPFC and AI has previously been linked to choices that deviate from the equity norm (Feng et al., 2015). A prior meta-analysis showed that activation in the AI may reflect a cognitive detection mechanism for norm violation, whereas the mPFC has been linked to computing the value of fairness as well as other normatively valued goods (Feng et al., 2015). In the current study, it was not possible to make equity choices, as none of the conditions allowed for giving 50% of the stakes. However, in Dictator Games, equal distributions are often not considered the norm, as participants generally give away some, but not half of their stakes (Van de Groep et al., 2019; Will & Güroğlu, 2016). Possibly, giving 4 coins was interpreted as the norm, and small donations as well as generous giving were experienced as deviations from this norm, although more research is necessary to confirm this hypothesis. Interestingly, in prior research the mPFC has been associated with both self-beneficial and other-beneficial choices,

possibly because of individual differences in the value assigned to fair decision making (Cutler &
Campbell-Meiklejohn, 2019; Feng et al., 2015).

The activation in the mPFC and AI associated with generous decisions may, apart from
the processing of norm deviations, also reflect feelings of empathy, generosity, fairness, or the
inhibition of selfish responses (Crone & Fuligni, 2019; Cutler & Campbell-Meiklejohn, 2019;
Güroğlu, Will, et al., 2014). Especially for generous choices in the large donation condition
activation could be associated with generosity or empathy. This interpretation is further upheld
by previous studies that postulated that AI activation upon giving without extrinsic rewards is
indicative of empathy (Cutler & Campbell-Meiklejohn, 2019), and that activation in the mPFC is
often observed in giving situations that require mentalizing or impulse control (Crone & Fuligni,
2019; Güroğlu, Will, et al., 2014). Future studies should examine these norm deviation and
generosity hypotheses in more detail, for example by increasing the possibilities to deviate from
minimal giving.

We observed that the NAcc ROI, which is considered to be part of the ventral striatum,
was more active in the small donation condition than in the large donation condition. A prior
meta-analysis showed greater activation in this region for selfish choices in economic games
without extrinsic rewards (Cutler & Campbell-Meiklejohn, 2019). Interestingly, economic games
that measure strategic giving (i.e., games in which the participant can improve their situation via
reciprocity, reputation, or public good) often show increased striatal activation for other-
beneficial compared to selfish choices, possibly because this is associated with an extrinsic
reward. Future work could examine whether these seemingly contradictory results could be
explained by individual differences in the subjective value of giving.

The next goal was to examine how neural patterns are influenced by two salient social contexts: the target of giving and being observed by an audience. In line with our expectations and ROI analyses, the whole-brain analysis showed the importance of an anterior subregion of the TPJ-IPL in differentiating between social contexts related to target, specifically considering giving to a friend versus unfamiliar other. Prior studies demonstrated that this region is important for mentalizing, thinking about the self in relation to others, and processing or adjusting to different social contexts (Blakemore, 2008; Carter & Huettel, 2013; Crone & Fuligni, 2019; Geng & Vossel, 2013; Schreuders et al., 2018; Van Hoorn et al., 2016). We showed that neural activity in the anterior TPJ-IPL is higher when considering giving to friends (Braams et al., 2014; Crone & Fuligni, 2019; Schreuders et al., 2018), which fits well with recent findings that costly giving to a friend compared to a disliked other engaged bilateral TPJ-IPL and putamen in young adults (Schreuders et al., 2018). Seemingly contradictory to our results, some studies have observed increased activation in the TPJ-IPL for out-group compared to in-group donations (Telzer et al., 2015), but only when accounting for individual differences in group identity and this was in a more posterior region of the TPJ-IPL. Taken together, activation in the anterior TPJ-IPL may facilitate giving to close but not distant others (Schreuders et al., 2018; Strombach et al., 2015).

We also addressed the question whether neural patterns were different when being observed, relative to not being observed by an audience, based on prior studies showing that being observed results in stronger activity in the medial PFC (Somerville, 2013; Van Hoorn et al., 2016). However, despite the finding that participants gave more when an audience observed them, we found no whole-brain audience effects. Instead, ROI analyses pointed to a role of a posterior subregion of the TPJ-IPL for being observed by an audience. This is in line with prior work showing that the TPJ-IPL is involved in mentalizing and establishing and integrating social

contextual information into decisions about self and others (Carter & Huettel, 2013; Van Hoorn et al., 2016). Possibly, the activation we found in TPJ-IPL in response to the audience reflects mentalizing to meet reputational goals (Cutler & Campbell-Meiklejohn, 2019). For example, other studies have also shown increased activation in the TPJ-IPL in the presence of peers and this was associated with increased donation amounts (Van Hoorn et al., 2016). In another study increased activation in left TPJ-IPL when receiving trust was associated with more advanced forms of social perspective taking (i.e., greater consideration of the risk one took by trusting; van den Bos et al., 2011).

Notably, our a priori selected posterior subregion of the TPJ-IPL (Schurz et al., 2014) for which we found an audience effect did not show overlap with the TPJ-IPL subregion found for the whole-brain contrast comparing donations to friends and unfamiliar others, with a more anterior location. Meta-analyses and diffusion weighted tractography have suggested that TPJ-IPL is a conglomerate with a global function of predicting mental states and processing information about self and others, consisting of various sub regions with different functions (i.e., applying the global function to different types of information) and connectivity patterns (Mars et al., 2012; Schurz et al., 2014). In line with this, the current study suggests that separable sub regions of the TPJ-IPL play distinct roles in the neural processing of target and audience contexts, respectively. As such, the current study expands findings suggesting that TPJ-IPL is important for establishing social context for behavior (Carter & Huettel, 2013) by examining its contribution to prosociality for distinct types of social contexts. Future research should aim to replicate the finding that the more anterior sub region of the TPJ-IPL codes for the social context directly relevant to the decision (e.g. the target or evaluators; (Schreuders et al., 2018; Van Hoorn et al., 2016), whereas the more posterior sub region codes for the broader social context (e.g.,

being observed). Perhaps the dissociation between these social contexts in the brain, but proximity in the TPJ-IPL region, reflects a different degree of perspective taking for familiarity versus audience contexts. Taken together, we demonstrated that donation size and social contexts pertaining to the target of giving and being observed by an audience are processed in separable brain regions. The TPJ-IPL emerged as a general processing area of different social contexts (Carter & Huettel, 2013), in which separate sub regions are activated by distinct social contexts.

Limitations

Some caveats and future directions should be noted. First, the audience in our study was pre-recorded and provided ratings of giving behavior later in time, whereas other studies used a real-time audience (Izuma et al., 2010; Somerville, 2013; Van Hoorn et al., 2016), which might be an explanation for not finding audience effects in the mPFC. Second, our sample was relatively homogenous with regard to age and background. Future studies should test whether the current results replicate in more diverse populations and can use this diversity to clarify the role of individual differences in giving as a function of familiarity and audience. Third, based on the current study, it cannot be dissociated whether increased activation in the TPJ-IPL for audience compared to anonymous choices is due to being observed or being observed while making prosocial choices. Nonetheless, there are reasons to believe that this brain region plays a pivotal role not only in social behavior in general but also prosocial behavior in particular because of its role in mentalizing and integrating social contextual information into decisions about self and others (Carter & Huettel, 2013). For instance, prior studies suggest that the TPJ-IPL is more strongly activated for prosocial compared to social or non-interactive situations (Tashjian et al., 2018) and that activation in this region while observing other people's prosocial acts or being

observed by others during prosocial decisions is associated with increased donation amounts (Tashjian et al., 2018; Van Hoorn et al., 2016).

Conclusion

We demonstrated separable motivations to give and their neural correlates in young adulthood, a period characterized by changes and increasing autonomy in social contexts and relationships (Guassi Moreira et al., 2018). By manipulating social contexts of giving related to target familiarity and audience, we showed that mPFC and the anterior AI were more strongly activated for generous compared to minimal giving. In contrast, two separate sub regions of the TPJ-IPL were activated in relation to target and audience contexts, respectively. Our findings suggest that the TPJ-IPL plays an important role in distinguishing between various social contexts when balancing self- and other-oriented motives. Efforts to understand or increase giving behavior in young people should take this context-dependency into account rather than focusing on generalized giving behavior as giving behaviors may not generalize across all social contexts. Acknowledging and abiding by this context-dependency may be a next step towards interventions that will successfully foster prosociality and its benefits in young adults (Lam, 2012; Schreuders et al., 2018).

Table 1

MNI coordinates of local maxima activated for the F-test and t-test for small > large donation condition. Results were calculated using a primary voxel-wise threshold of p < .001 (uncorrected), with a cluster corrected threshold of $p < .05$ FDR corrected. The reversed large > small donation contrast did not result in significant effects.

Area of activation	MNI Coordinates			Test statistic	Cluster Size
	x	y	z	F/t	
F-test Donation Condition (FDRc < 0.001 = 25.54)					
Left Lingual	-9	-82	-5	82.99	518
Right Lingual	12	-73	-8	42.30	349
Right Frontal Superior Medial (i.e., Medial Prefrontal Cortex)	3	50	4	19.26	221
Left Occipital	-9	-100	4	34.41	43
t-test Small > Large Donation Condition (FDRc < 0.001 = 316)					
Right Lingual	12	-73	-8	6.50	421
Right Frontal Superior Medial (i.e., Medial Prefrontal Cortex)	3	50	4	4.30	316

Note: Names were based on the aal toolbox in SPM. For functional regions discussed throughout the paper, both the aal label and functional label (between brackets) are displayed. See https://neurovault.org/collections/MADDFZPG/ for a full, untresholded overview of activation.

Table 2

MNI coordinates of local maxima activated for the F-test and t-test for friend > unfamiliar target. Results were calculated using a primary voxel-wise threshold of p < .001 (uncorrected), with a cluster corrected threshold of $p < .05$ FDR corrected. The reversed unfamiliar > familiar target contrast did not result in significant effects.

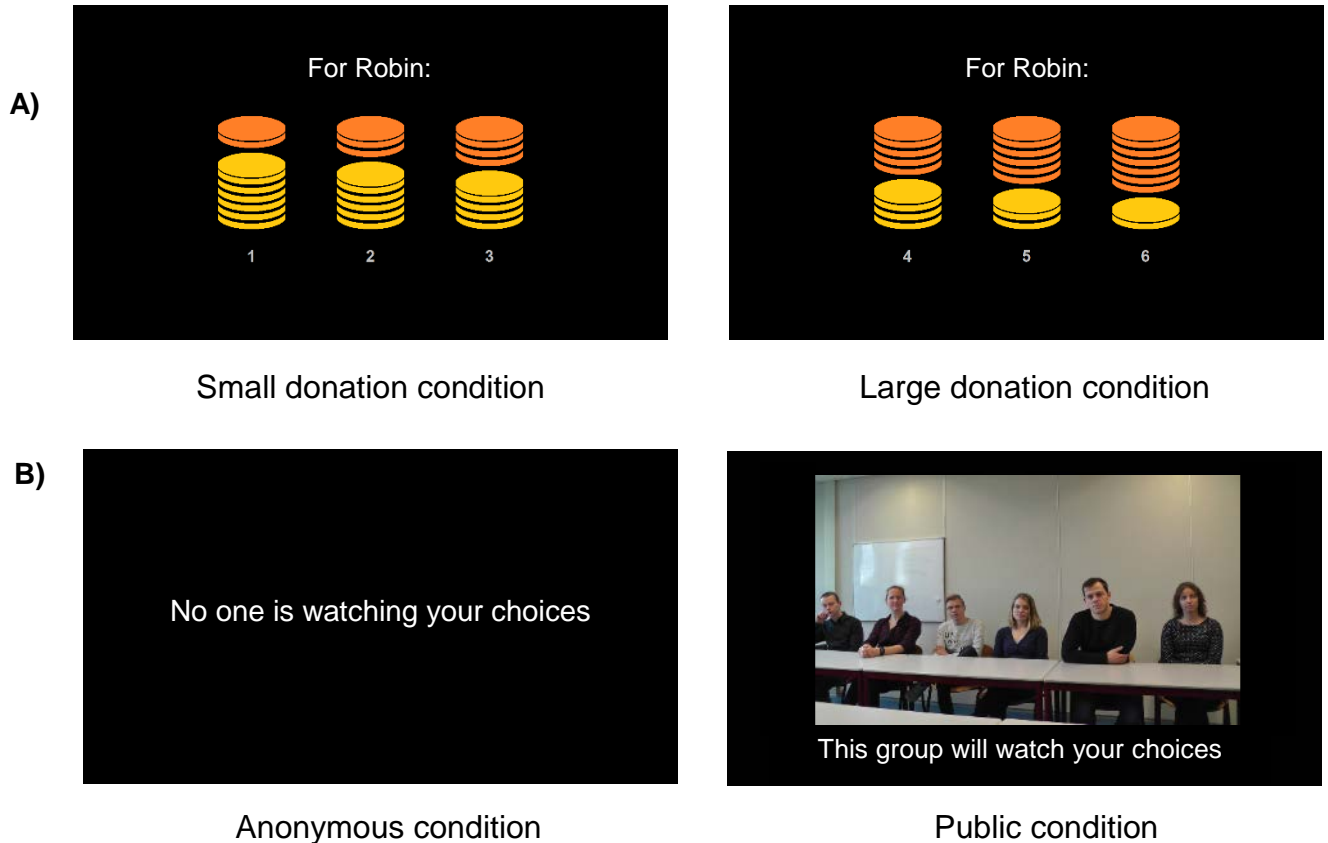| Area of activation	MNI Coordinates			Test Statistic	Cluster Size
	x	y	z	F/t	
Target (FDRc < 0.001 = 28.02)					
Left Inferior Occipital	12	-79	-8	37.01	370
Left Inferior Occipital	-36	-82	-8	28.02	304
Right Inferior Parietal (i.e., Right TPJ-IPL)	48	-34	49	28.81	240
Left Inferior Parietal (i.e., Right TPJ-IPL)	-45	-40	46	19.32	38
Right Cuneus	9	-85	28	21.93	30
t-test Friend > Unfamiliar Target (FDRc < 0.001 = 313)					
Left Inferior Occipital	12	-79	-8	6.08	456
Left Inferior Occipital	-36	-82	-8	5.29	378
Right Inferior Parietal (i.e., Right TPJ-IPL)	48	-34	49	5.37	313

Note: Names were based on the aal toolbox in SPM. For functional regions discussed throughout the paper, both the aal label and functional label (between brackets) are displayed. See https://neurovault.org/collections/MADDFZPG/ for a full, untresholded overview of activation.

Table 3

MNI coordinates of local maxima activated for the t-test comparing generous giving (response options 2, 3, 5 and 6) to minimal giving (response options 1 and 4). Results were calculated using a primary voxel-wise threshold of p < .001 (uncorrected), with a cluster corrected threshold of $p < .05$ FDR corrected. The reversed minimal > generous giving contrast did not result in significant effects.

Area of activation	MNI Coordinates			t	Cluster Size
	x	y	z		
Generous > Minimal Giving (FDRc < 0.001 = 77)					
Right Lingual	15	-76	-8	7.57	256
Left Anterior Cingulum (i.e., Medial Prefrontal Cortex)	-9	38	22	5.28	199
Right Insula (i.e., Right Anterior Insula)	33	14	-11	4.47	77

Note: Names were based on the aal toolbox in SPM. For functional regions discussed throughout the paper, both the aal label and functional label (between brackets) are displayed. See https://neurovault.org/collections/MADDFZPG/ for a full, untresholded overview of activation.

Figure 1. A. The small and large donation conditions of the donation task, in which participants could give away 1, 2, or 3 coins, or 4, 5, or 6 coins, respectively (depicted in orange). The remainder of the 7 coins (depicted in yellow) would be kept to themselves. The name of the target (which could either be a friend or unfamiliar other) was displayed on top of the screen for each trial. B. In two of the four blocks of the donation task, participants were told at the start of the block that their choices were anonymous. In the other two blocks, participants were told at the start of the block that the group depicted on the screen would watch their choices later (i.e., the public condition). Blocks were presented in counterbalanced order.
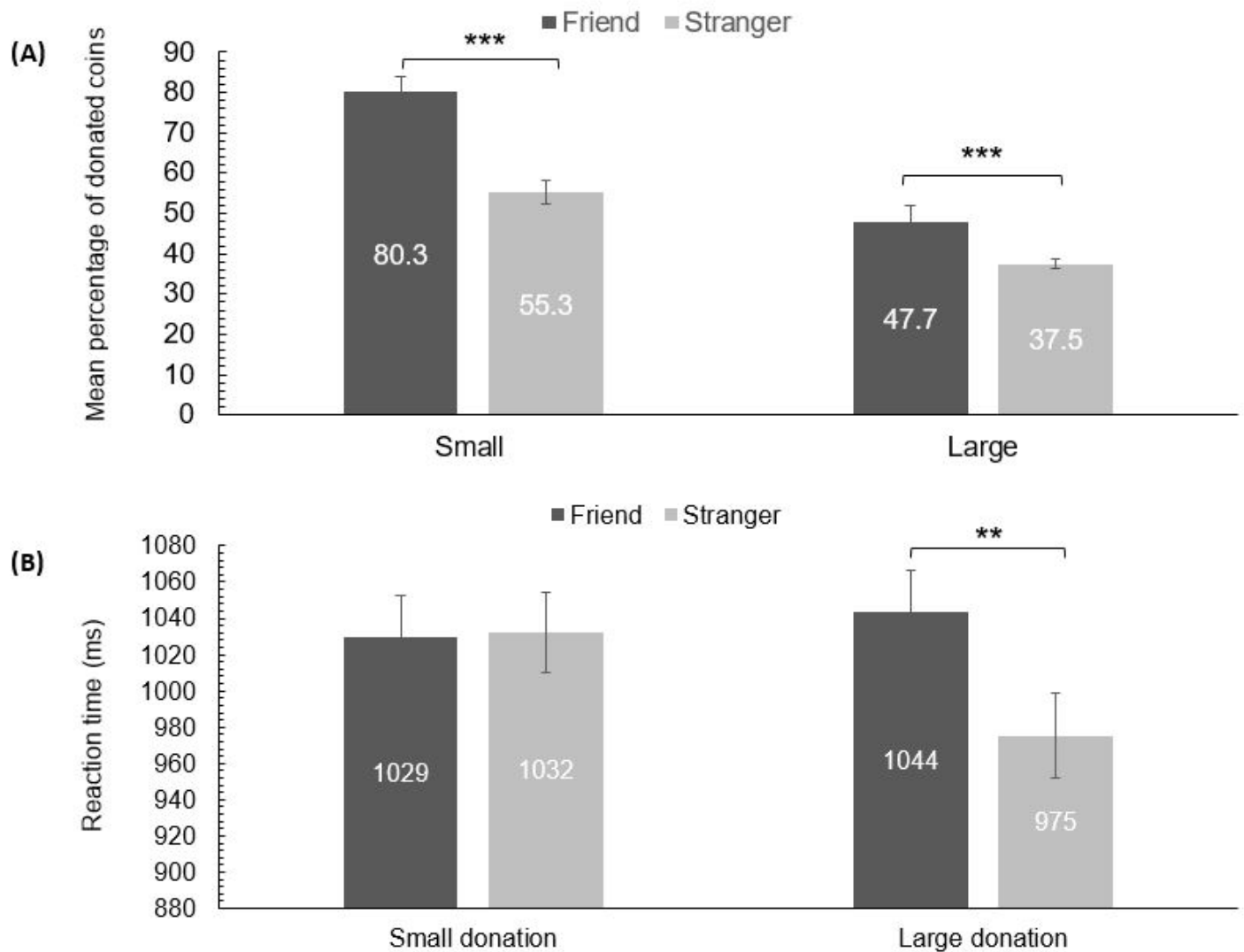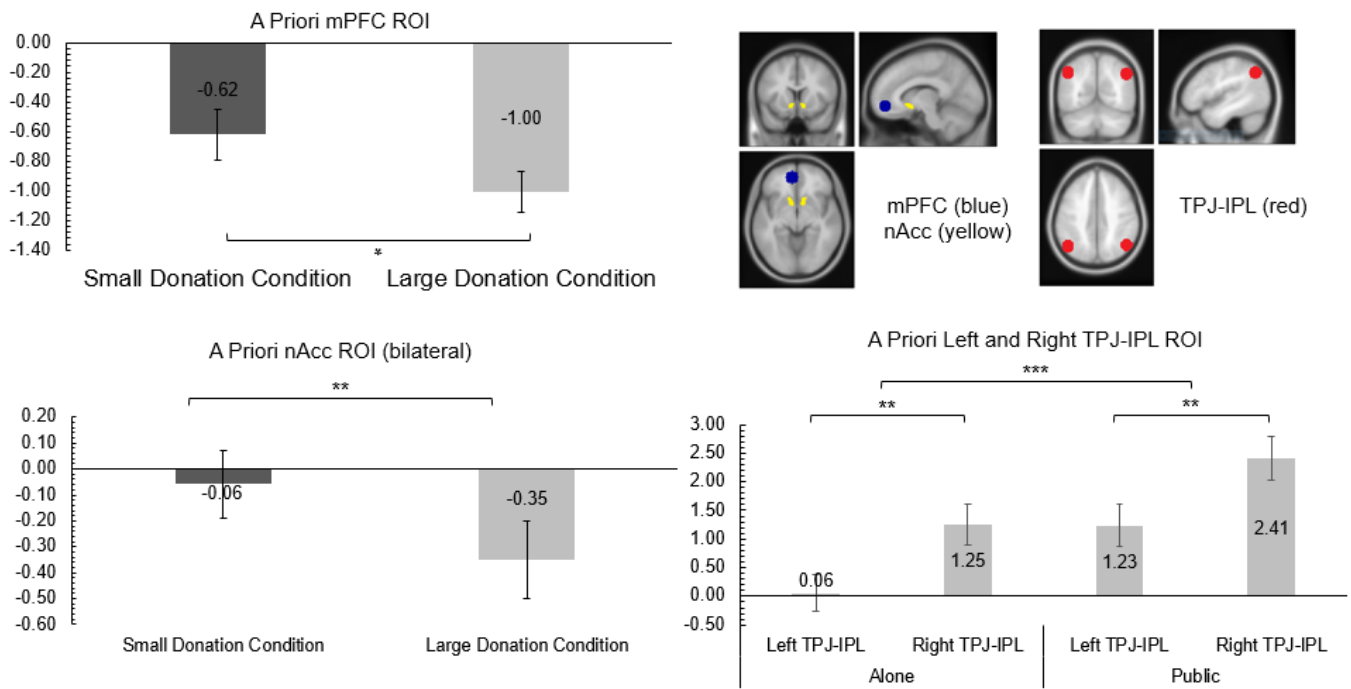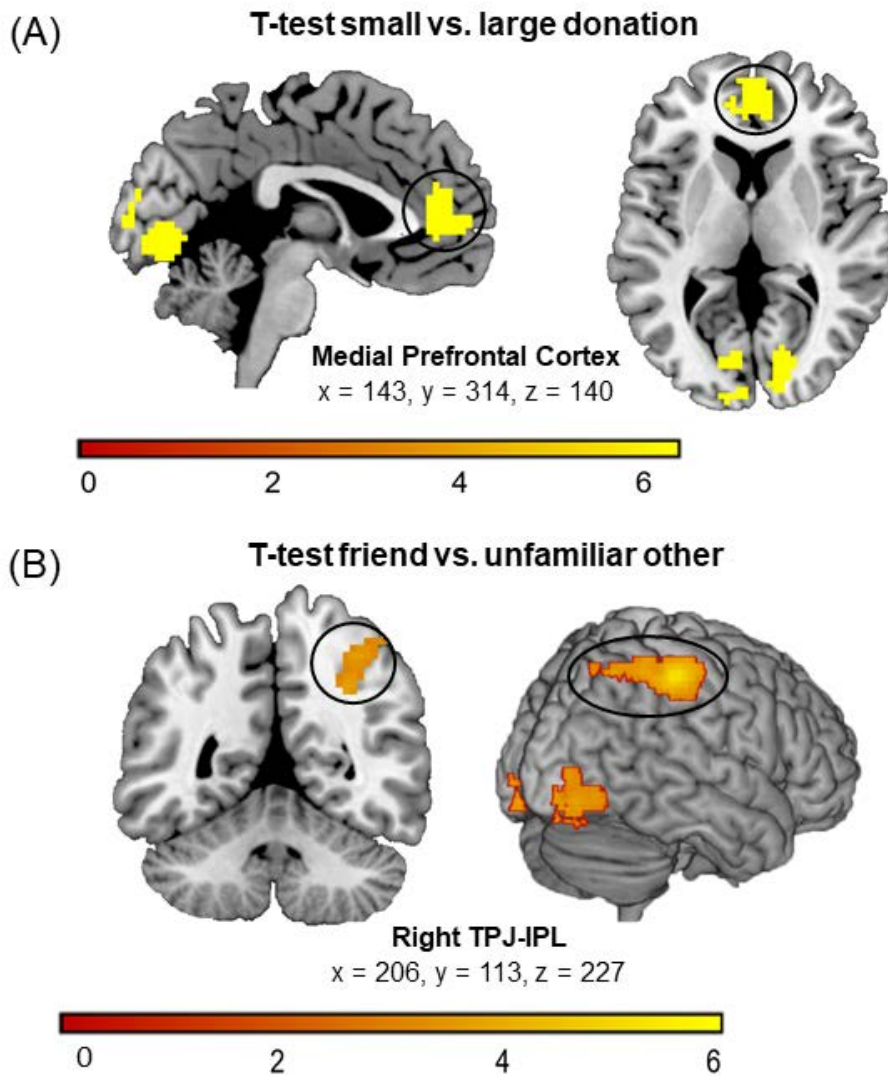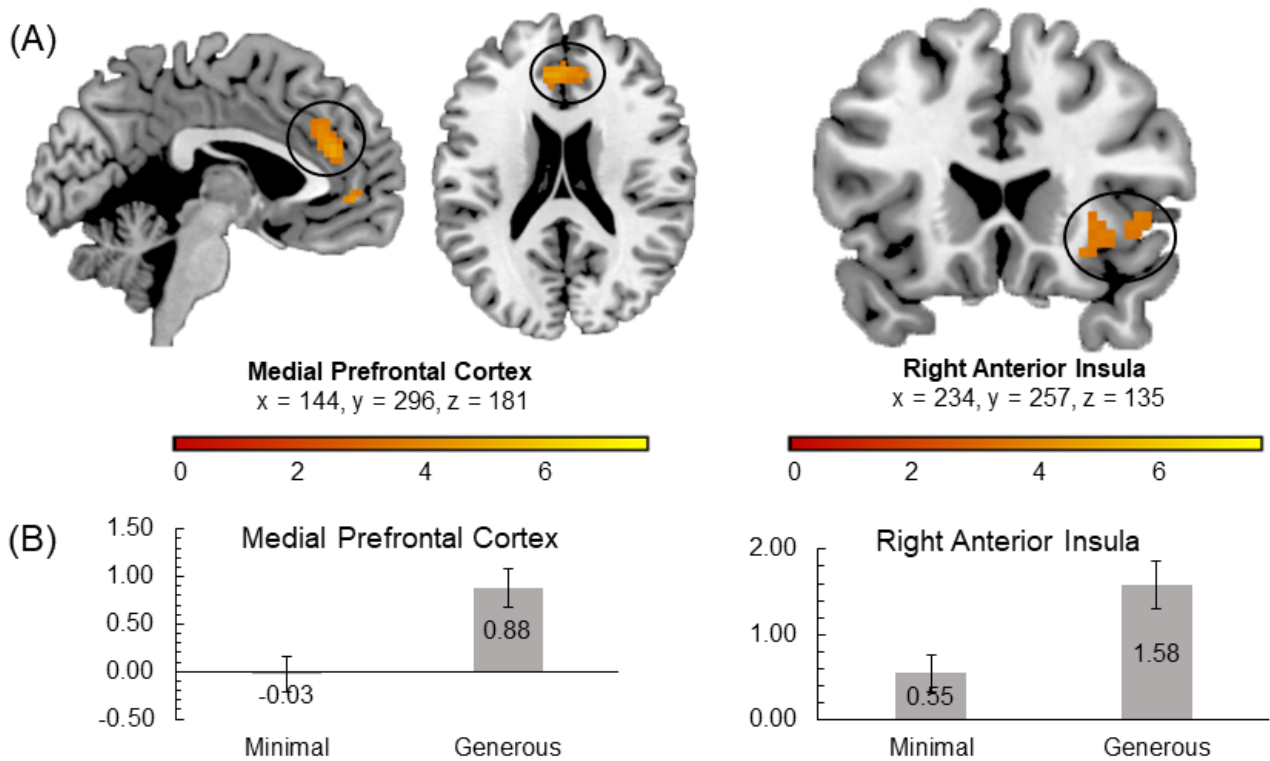
Figure 2. (A) Mean percentage of coins that were donated to a friend and unfamiliar other in the small and large donation condition. (B) Reaction times associated with donations to a friend and unfamiliar other in the small and large donation condition. ***=<.001, **=≤.010

Figure 3. Task condition effects in pre-defined ROIs. The mPFC and nAcc showed more activation (i.e., less de-activation) in the small compared to the large donation conditions. Left and right TPJ-IPL showed increased activation in the public compared to the anonymous condition. Furthermore, averaged over conditions, activation was higher in the right compared to left TPJ-IPL.

Figure 4. (A) Whole-brain *t*-test for the small versus large donation condition. (B) Whole-brain *t*-test for friend versus unfamiliar other. Results are displayed with a primary voxel-wise threshold of $p < .001$ (uncorrected) and FDR cluster correction of $p < .050$.

Figure 5. (A) Whole-brain *t*-test for generous giving vs. minimal giving, *N* = 30. (B) Neural activation in the mPFC and Right Anterior Insula for generous giving (2,3, 5 or 6 coins) versus minimal giving (1 or 4 coins). Note that activations could only be calculated for participants who selected this option at least once. Results are displayed with a primary voxel-wise threshold of *p* < .001 (uncorrected) and FDR cluster correction of *p* < .05.

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