

Full Length Articles

Neuroanatomy of intergroup bias: A white matter microstructure study of individual differences



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ABSTRACT

Intergroup bias—the tendency to behave more positively toward an ingroup member than an outgroup member—is a powerful social force, for good and ill. Although it is widely demonstrated, intergroup bias is not universal, as it is characterized by significant individual differences. Recently, attention has begun to turn to whether neuroanatomy might explain these individual differences in intergroup bias. However, no research to date has examined whether white matter microstructure could help determine differences in behavior toward ingroup and outgroup members. In the current research, we examine intergroup bias with the third-party punishment paradigm and white matter integrity and connectivity strength as determined by diffusion tensor imaging (DTI). We found that both increased white matter integrity at the right temporal-parietal junction (TPJ) and connectivity strength between the right TPJ and the dorsomedial prefrontal cortex (DMPFC) were associated with increased impartiality in the third-party punishment paradigm, i.e., reduced intergroup bias. Further, consistent with the role that these brain regions play in the mentalizing network, we found that these effects were mediated by mentalizing processes. Participants with greater white matter integrity at the right TPJ and connectivity strength between the right TPJ and the DMPFC employed mentalizing processes more equally for ingroup and outgroup members, and this non-biased use of mentalizing was associated with increased impartiality. The current results help shed light on the mechanisms of bias and, potentially, on interventions that promote impartiality over intergroup bias.

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Introduction

Intergroup bias is the tendency to behave more positively toward an ingroup member than an outgroup member (Hewstone et al., 2002). This tendency can promote ingroup cohesion but foster intergroup conflict (e.g., Fiske, 2002; Fu et al., 2012; Tajfel and Turner, 1979). Although primarily investigated as a universal tendency (e.g., Brewer, 1979), intergroup bias is characterized by significant individual differences. Understanding the sources of individual differences in intergroup bias can shed light on the mechanisms of bias and, potentially, on interventions that promote impartiality.

Prior attempts to explain sources of individual differences in intergroup bias have been mixed, however. For example, personality measures are relatively inconsistent predictors of intergroup bias

(Hewstone et al., 2002), perhaps due to the issues inherent in self-report. As an alternative, neuroanatomical differences can be objectively indexed, free from personal biases and demand characteristics and can effectively reveal sources of individual differences in behavior and social cognition. (Cikara and Van Bavel, 2014; Kanai and Rees, 2011). One study, to our knowledge, has examined neuroanatomical differences and intergroup bias. Baumgartner et al. (2013) indexed cortical volume and intergroup bias and found that increased volume in the temporal-parietal junction (TPJ) and the dorsomedial prefrontal cortex (DMPFC) was associated with increased impartiality, i.e., reduced intergroup bias. Structural differences in the TPJ and DMPFC thus appear to explain sources of individual differences in intergroup bias.

However, the TPJ and the DMPFC share rich, reciprocal neural connections and functional connectivity during decision making between these regions is associated with intergroup bias (Barbas et al., 1999; Baumgartner et al., 2012). Further, TPJ and DMPFC comprise part of a network that mediates mentalizing processes, such as perspective taking (Behrens et al., 2009; Carter et al., 2012; Frith and Frith, 2006; Hampton et al., 2008; Klapwijk et al., 2013; Van Overwalle, 2009, 2011). Mentalizing processes are key in reducing intergroup bias (Batson et al., 1997; Mitchell, 2009; Pettigrew and Tropp, 2008). Thus,

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the quality and quantity of connective white matter tracts should impact communication between these two brain areas, and accordingly, impact mentalizing processes and intergroup bias.

We measured white matter integrity and connectivity strength using diffusion tensor imaging (DTI, [Mori and Zhang, 2006](#)). White matter integrity and connectivity strength both have been related to clear, functional consequences ([Kanai and Rees, 2011](#)). For example, better cognitive functioning across the lifespan is related to increased white matter integrity and connectivity strength ([Catani et al., 2007](#); [Forstmann et al., 2010](#); [Gong et al., 2009](#); [Kochunov et al., 2012](#); [Madden et al., 2009](#)). We thus expected that increased white matter integrity and connectivity strength in fibers connecting the TPJ and DMPFC would be associated with better functioning, i.e., egalitarian mentalizing and reduced intergroup bias. We also expected that this association between increased white matter integrity at and connectivity strength between the TPJ and the DMPFC and reduced intergroup bias would be mediated by egalitarian mentalizing for ingroup and outgroup members.

Materials and methods

Participants

The same 56 healthy participants from [Baumgartner et al. \(2013\)](#) were analyzed (mean age \pm SD = 22.3 ± 3.47 years, 26 females). Participants gave informed written consent before behavioral and MRI data collection (which was approved by the local ethics committee). All participants were right-handed and reported no psychiatric illness or neurological disorder. Participants received 40 Swiss francs (CHF 40; CHF 1 = about US\$1) for study completion, in addition to the money earned in the third-party punishment paradigm (see below).

Data collection and social groups

Online questionnaires were administered to a large undergraduate sample. Participants completed questions about personal interests (about soccer, politics, music, etc.), identification of personal ingroup and outgroup (in either soccer or politics), and the Sport Spectator Identification Scale (SSIS, adapted for supporters of political parties, i.e., the term “your preferred political party” replaced “your preferred soccer team”) to index ingroup identification ([Wann and Branscombe, 1993](#)). From this sample, strong supporters of soccer clubs ($N = 16$) and political parties ($N = 40$) were recruited—two groups with a proven proclivity for intergroup bias ([Ben-Ner et al., 2009](#); [Hein et al., 2010](#); [Koopmans and Rebers, 2009](#)). Independent *t*-tests revealed that the two social groups did not differ in our main dependent variable of intergroup bias (partiality score, see below) during trials with unilateral defection ($t(54) = -.228, p = 0.82$, our main condition of interests) and bilateral defection ($t(54) = -1.63, p = 0.11$). As such, we combined these two social groups in our brain analyses.

Behavioral and MRI data collection for the current study took place over two sessions. In the first session, participants completed the third-party punishment paradigm. As a third-party observer (player C), participants were given the opportunity to punish either an ingroup member or an outgroup member of a rival social group. Soccer supporters always interacted with other soccer supporters, and political supporters always interacted with political supporters. In the second session, participants completed the MRI scans. Approximately 3–4 weeks separated the online assessments, and the third-party punishment paradigm session and 4–6 weeks separated the behavioral paradigm session and the MRI session.

Third-party punishment paradigm

To index intergroup bias, participants completed the third-party punishment paradigm (e.g., [Bernhard et al., 2006](#)). Participants in the role of

a third-party observer (player C) were confronted with the behavior of a number of real, prior interactions in a simultaneous prisoner's dilemma game (PDG), and were given the opportunity to punish unfair behavior. In a single trial of this PDG, two players, here termed player A and player B, were each given 20 points (which could be exchanged after the game for money, see rates below). They could then chose to either cooperate (C) by passing these points to the other player or to defect (D) by keeping the points. Passed points doubled. Thus, if player A defected and player B cooperated, player A would acquire 60 points (20 kept + 40 passed) and player B would earn nothing. Four decisional configurations were possible: both players A and B cooperate (CC), both players A and B defect (DD), player A cooperates and player B defects (CD), and player A defects and player B cooperates (DC). There were no repeated interactions between player A and B and all interactions were anonymous. Participants (player C) observed these PDG decisions and could punish one player's behavior by assigning punishment points (to either player A or B) during each of the trials. For the purpose of administering punishment, player C received 10 points at the beginning of each punishment trial. One point assigned for punishment reduced the punished player's income by three points. Points not used for punishment were exchanged into real money and paid to player C at the end of the experiment (10 points = 2 Swiss francs = about US\$2).

We recoded player C's decisions so that player A always refers to the player that could be punished. Thus, two group pairings were examined in this experiment (see [Fig. 1](#)): (1) player A was an outgroup member and player B was an ingroup member (termed OUT/IN), and (2) player A was an ingroup member and player B was an outgroup member (termed IN/OUT). The PDG decisions of players A and B were selected so that player C observed the same 20 decisional configurations, in random order. DC decisions (i.e., instances in which player A defected and player B cooperated, our main condition of interest) were presented four times (in each group pairing), and all other conditions were presented twice (CC, CD, DD, in each group pairing). The group affiliation and the behavioral decisions of player A and B were presented both in text (your group/other group; keeps points/transfers points) and in pictures (symbol of the political parties/jerseys of the soccer clubs) on the computer screen. Prior to beginning the task, participants were instructed that there were no repeated interactions in the paradigm (i.e., participants never viewed the same players more than once) and that all interactions were conducted in complete anonymity in order to control for reputation effects.

To measure individual differences in intergroup bias, a partiality score was computed as the average punishment points used by player C against outgroup perpetrators minus the average punishment points used against ingroup perpetrators (OUT/IN minus IN/OUT), separately calculated for DC and DD trials (as in [Baumgartner et al., 2013](#)). Thus, higher numbers indicate more partiality or intergroup bias, i.e., participants were more punitive toward defecting outgroup members as compared to defecting ingroup members, whereas a score closer to zero indicates more impartiality.

Mentalizing processes

Following the third-party punishment task, participants responded to three questions to assess the use of mentalizing processes in judging DC decision trials (we focused on our main condition of interest) for both ingroup and outgroup perpetrators (as player A). They answered the following questions on a scale from 1 (strongly disagree) to 6 (strongly agree): (1) It was easy for me to put myself in the position of player A; (2) I am sure player A had a justifiable reason for his or her behavior; and (3) Putting myself in the position of player A helped me to make my punishment decision. A composite mentalizing bias score was computed as the average mentalizing score with ingroup perpetrators minus the average mentalizing score with outgroup perpetrators (IN/OUT minus OUT/IN). Higher values indicate a more biased use

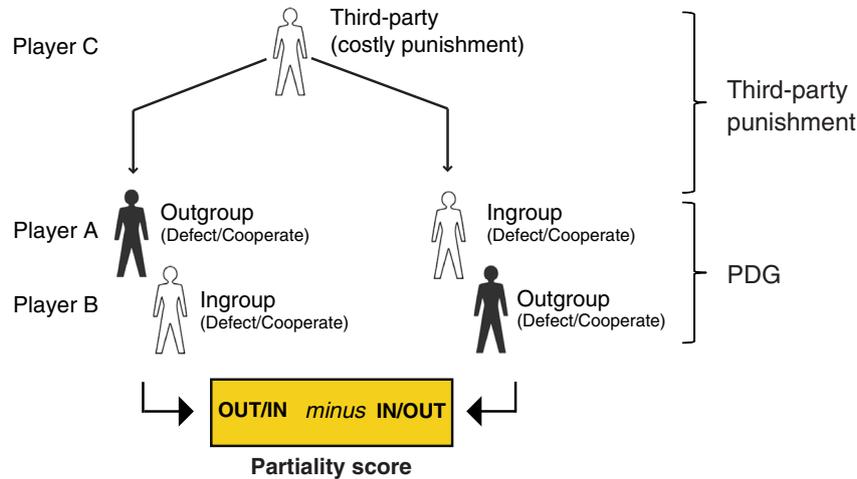


Fig. 1. Schematic representation of the study design. Depicted is the third-party punishment paradigm. Participants in the role of an uninvolved third party (player C) were confronted with norm-violating and norm-abiding behavior (defection or cooperation in a prisoner's dilemma game) committed by both ingroup and outgroup members of real social groups (player A and B). Player A always refers to the player that could be punished. In total, third parties were confronted with two different group situations: player A is an outgroup member and player B is an ingroup member (termed OUT/IN) or player A is an ingroup member and player B is an outgroup member (termed IN/OUT). Comparing punishment decisions in these two group situations (OUT/IN–IN/OUT) reveals third parties' propensity for intergroup bias, quantified by the partiality score: high values indicate strong tendencies to partiality and low values indicate strong tendencies to impartiality.

of mentalizing in judging ingroup and outgroup perpetrators. A score closer to zero indicates a more balanced use of mentalizing.

Scanning procedure

MRI data were collected using a 3 T whole body MR system (Magnetom Verio, Siemens Healthcare, Germany) equipped with a standard twelve-channel head coil. Whole brain diffusion-weighted images (58 slices of 2.5 mm thickness, TR = 9000 ms, TE = 82 ms, FOV = 320 × 240 mm, 128 × 96 in-plane matrix) were acquired using 64 diffusion directions and $b = 900 \text{ s/mm}^2$. A reference image with no diffusion weighting ($b = 0 \text{ s/mm}^2$) was also acquired. Additionally, anatomical images were acquired with a 3D magnetization prepared rapid gradient-echo (MPRAGE) sequence. The following acquisition parameters were used: TR (repetition time) = 2000 ms, TE (echo time) = 3.4 ms, TI (inversion time) = 1000 ms, flip angle = 8°, FOV (field of view) = 25.6 cm, acquisition matrix = 256 × 256 × 176, voxel size = 1 mm × 1 mm × 1 mm. A sagittal volume covering the entire brain was acquired in 7.5 min.

White matter integrity analyses: fractional anisotropy (FA) and partial volume fraction estimates (f1 and f2)

DTI data were processed using the Diffusion Toolbox (Version 3.0) implemented in FSL (Version 5.0.2.1, Smith et al., 2004; Woolrich et al., 2009; <http://www.fmrib.ox.ac.uk/fsl/index.html>). We applied the following recommended procedures to the data: (1) motion and eddy current corrections, (2) removal of skull and nonbrain tissue using the brain extraction tool, and (3) voxel-by-voxel calculation of the diffusion tensors and fractional anisotropy (FA) volumes using DTIFIT. Next, we used tract-based spatial statistics (TBSS, Smith et al., 2006) for the following processing steps: (1) nonlinear alignment of each participant's FA volume to the 1 × 1 × 1 mm³ standard MNI152 space via the FMRIB58_FA template using the FMRIB's nonlinear registration tool, (2) calculation of the mean of all aligned FA images, (3) creation of a representation of white matter tracts common to all subjects (a white matter skeleton), and (4) perpendicular projection of the highest FA value (local center of tract) onto the skeleton, separately for each subject. Because the interpretation of FA values in areas with crossing fibers can be ambiguous, we extended the basic TBSS processing steps by an additional procedure (tbss_x), as recommended in the paper by Jbabdi et al. (2010). This procedure incorporates the crossing

fiber model by Behrens et al. (2007) into the TBSS framework by using the partial volume fraction estimates from BedpostX (a main step from the tractography analyses, described below) instead of FA at each voxel. BedpostX can model two measures that each relate to a different fiber orientation within each voxel (i.e., the contribution of each fiber population to the diffusion MR signal is associated with a different direction), producing a main fiber direction and a secondary fiber direction labeled f1 and f2, respectively. The use of partial volume fraction estimates has been demonstrated to increase the interpretability of the results in crossing fiber areas (Jbabdi et al., 2010), and thus we will focus our analyses on f1 and f2 instead of FA. Nevertheless, we also report the analyses using the FA values for comprehensiveness.

Connectivity strength analyses: probabilistic tractography

To further probe whether individual differences in white matter pathways between the TPJ and the DMPFC determine intergroup bias in third-party punishment, we conducted probabilistic tractography to characterize white matter connectivity strength. For that purpose, we used the same diffusion toolbox (version 3.0) and entered the eddy current and motion-corrected and skull-stripped DTI images into tractography analyses. Voxel-wise estimates of fiber orientation distribution were calculated using the BedpostX tool (Behrens et al., 2007)—a Bayesian method that selects the appropriate number of tract orientations in each voxel and thus is able to account for regions that might contain crossing fibers. Essentially, the tractography approach draws a number of lines, or 'streamlines', from a seed region that follow the main diffusion directions in each voxel. In voxels with multiple fiber directions, the orientation that is closest to the previous orientation is selected.

We positioned a seed region near the right TPJ based on the results of the white matter integrity analyses, defined as a 10 mm sphere around the F1 peak ($x = 44, y = -48, z = 2$, see Fig. 2, MNI space). A target region, defined as a 10 mm sphere, was also positioned near the DMPFC (centered at $x = 10, y = 50, z = 28$, MNI space) based on the anatomical study by Baumgartner et al. (2013) that showed a strong negative correlation of the partiality score with gray matter volume of the DMPFC. Because the peak in this analysis was clearly in gray matter, we changed the x-coordinate slightly from $x = 2$ to $x = 10$ and thus moved the ROI into white matter, in order to allow for reliable tractography (Gschwind et al., 2012; Hagmann et al., 2006). Furthermore, an exclusion mask in the left hemisphere was used, i.e., pathways that cross into the left

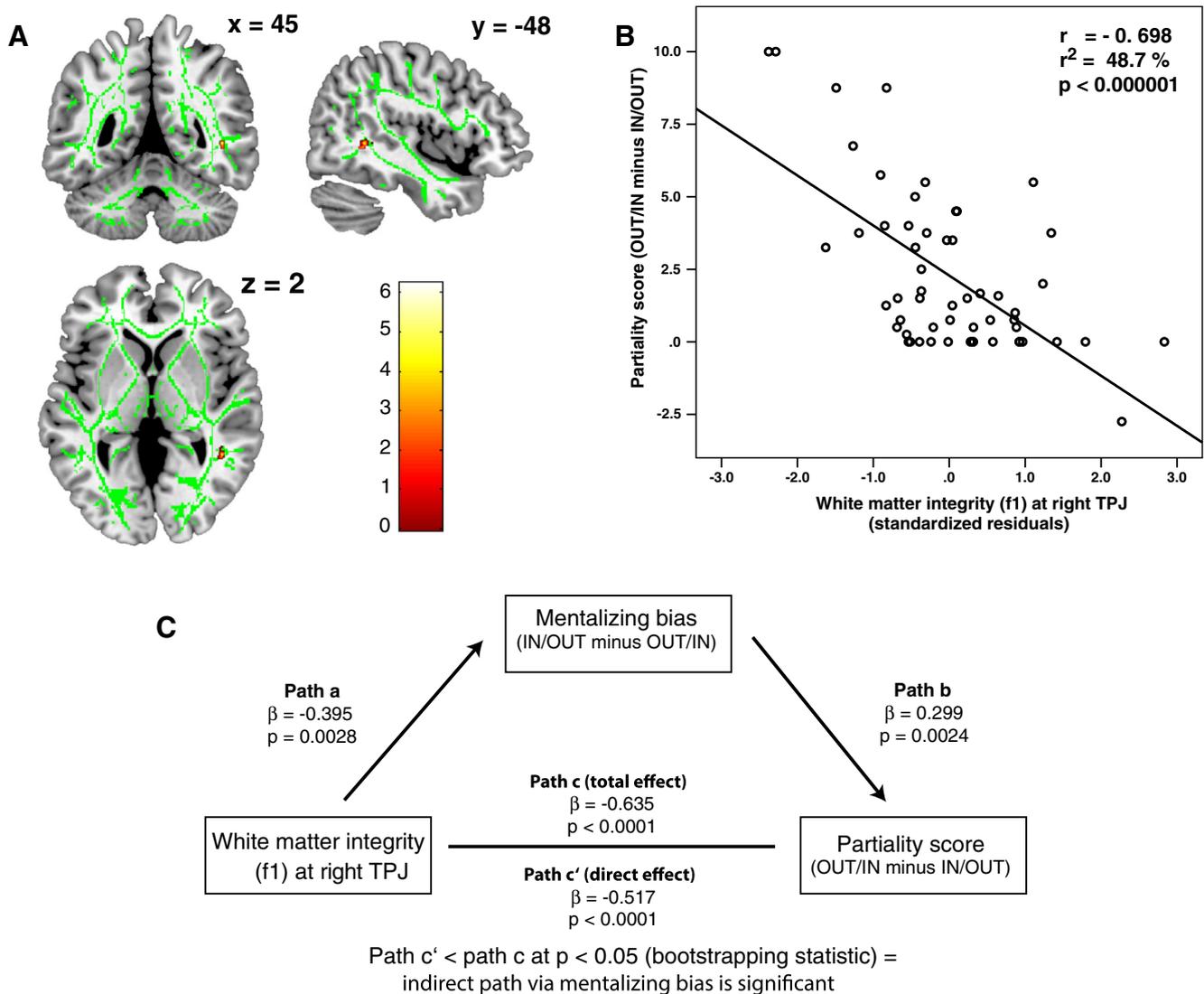


Fig. 2. White matter integrity at the right TPJ predicts individual differences in intergroup bias. (A) White matter integrity measured with partial volume fraction estimate f_1 at the right TPJ (peak coordinate: $x = 44, y = -48, z = 2$, peak t -value = 6.24) is highly significantly (at $p < 0.01$, FWE-corrected for all the voxels in the skeleton, for display purpose depicted at $p < 0.001$ uncorrected) correlated with the partiality score (calculated with DC trials), i.e., the better the structural integrity in this part of the white matter, the lower the intergroup bias in punishment. Depicted in light green is the white matter skeleton mask used for analysis. (B) Scatter plot of the partiality score against the white matter integrity (f_1) values of the significant cluster (mean of all voxels) depicted in (A). Note that the depicted f_1 values are adjusted for all covariates (age, total punishment costs, strength of ingroup identification) and z -standardized. A line of best fit with r , r^2 , and uncorrected p values is also displayed for the entire sample of 56 participants. Note that if we remove the only subject with a negative partiality score from the analysis, the finding is highly similar ($r = -0.664, p < 0.00001$). (C) Mediation model depicting a significant (at $p < 0.05$) indirect path from the white matter integrity (f_1) values at the right TPJ to the partiality score through the mentalizing bias. β indicates standardized regression coefficients. Note that all requirements for a mediation effect are satisfied: path a, path b, and path c are significant and path c' is significantly smaller than path c (see Materials and methods section for details).

hemisphere were removed from the analyses. A total of 10,000 streamlines from each voxel within the seed ROI were drawn in each subject at 0.5 mm step lengths and a curvature threshold = 0.2. The same process was conducted in the opposite direction, tracking connectivity strength from the DMPFC to the seed region in the TPJ. This double-seed approach increases the accuracy of the estimated tract (Gschwind et al., 2012). Connectivity strength in each participant was assessed as the average number of streamlines that reached the target in both directions (from TPJ to DMPFC and vice versa). Note that all fiber tracking analyses were conducted in the individual native DTI space. In order to bring the seed and target ROIs from the MNI space into the individual space, the inverse nonlinear registration warp field (from the first TBSS processing step, see above) was applied to the ROIs.

In order to visualize the results of the described tractography analysis, the probabilistic connectivity distribution maps from individual participants were thresholded, i.e., we only selected voxels where more

than 500 streamlines passed (a usual threshold used for visualization of tracts). The resulting maps were then binarized, transferred into MNI space (using the nonlinear registration warp field), and summed up across participants to obtain the connectivity probability map of the group. Because this visualization revealed (see Fig. 3) that two well-known fiber tracts connect the TPJ and DMPFC (the superior longitudinal fasciculus [SFL] and the inferior occipito-frontal fasciculus [IOFF]), we conducted two additional tractography analyses. The goal of these two analyses was to separately estimate the number of streamlines in the two pathways. We achieved this by positioning an exclusion mask (a 15 mm sphere) in the pathway of the SLF (at $x = 36, y = -34, z = 30$) in the first analyses and an exclusion mask in the IOFF (at $x = 38, y = -22, z = -6$) in the second analyses. Thus, all streamlines passing an exclusion mask were removed from consideration. Fig. 4A shows that this procedure successfully disentangled the two fiber tracts.

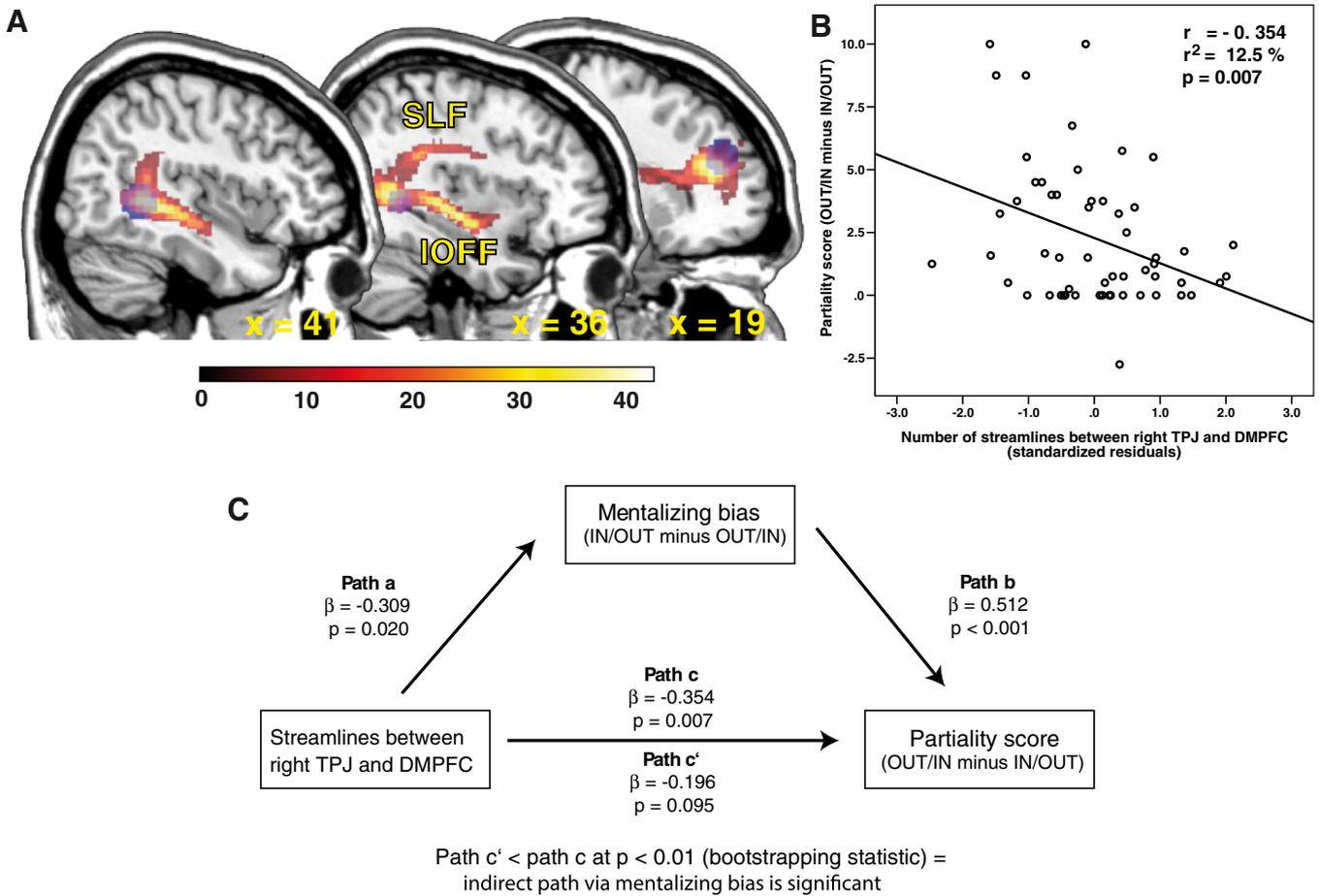


Fig. 3. White matter connectivity strength between the right TPJ and the DMPFC predicts individual differences in intergroup bias. (A) As expected, tractography analyses revealed that two well-known fiber tracts (superior longitudinal fasciculus and inferior occipito-frontal fasciculus) consistently connect the white matter areas of right TPJ and DMPFC in our subjects. The depicted tracts overlapped in at least 10 participants. Note that in most areas of the tracts, there is a strong overlap in most subjects; see the yellow parts of the tracts. The blue circles show the position of the two seed and target areas (right TPJ and DMPFC) used for tractography analyses. (B) Scatter plot of the partiality score (calculated with DC trials) against the number of streamlines (mean of both directions) of the two fiber tracts depicted in (A). Note that the depicted streamline values are log-transformed, adjusted for all covariates (age, brain size, volumes of the ROIs, total punishment costs, strength of ingroup identification) and z-standardized. A line of best fit with r , r^2 , and p values is also displayed for the entire sample of 56 participants. Note that if we remove the only subject with a negative partiality score from the analysis, the finding is highly similar ($r = -0.353$, $p = 0.008$) (C) Mediation model depicting a significant (at $p < 0.01$) indirect path from the connectivity strength between right TPJ and DMPFC to the partiality score through the mentalizing bias. β indicates standardized regression coefficients. Note that all requirements for a mediation effect are satisfied: path a, path b, and path c are significant and path c' is significantly smaller than path c (see Materials and methods section for details).

Statistical analysis

Voxel-wise analyses were performed to examine the association between white matter integrity measures (f1, f2, and FA) and intergroup bias, quantified in our third-party paradigm as the partiality score. These analyses were conducted with the individual white matter skeleton maps derived from the TBSS analyses described above. We examined the association between white matter integrity and partiality with age, SSIS, and total punishment costs entered as covariates (for detailed explanation of these covariates, please see next section). We used $p < 0.05$ family-wise error corrected for all the voxels in the white matter skeleton as the criterion to detect voxels with a significant correlation with the partiality score. Please note that if we instead conduct a whole brain voxel-wise analysis using smoothed (4 mm full-width-at-half-maximum Gaussian kernel) and thresholded (0.2, in order to restrict the analysis to white matter) whole brain f1, f2, and FA maps (instead of using the white matter skeleton maps), we derive the same results at the same family-wise error corrected threshold. Thus, our findings are robust, irrespective of whether we apply a more conventional whole brain voxel-wise analysis approach or a

newer approach that limits the analysis to the core of the white matter tracts.

To examine whether connectivity strength between right TPJ and DMPFC was associated with intergroup bias, we regressed the partiality score on the number of streamlines from the TPJ to the DMPFC (log-transformed to reduce skew), with age, brain size, volumes of the seed and target ROIs, SSIS, and total punishment costs entered as covariates (again see next section). We conducted separate regression analyses for streamlines in the SLF and the IOFF.

Finally, we conducted mediation analyses in order to explore whether mentalizing processes mediate the impact of white matter (integrity and connectivity strength) on intergroup bias. For that purpose, we used the SPSS macro programmed by Andrew F. Hayes (Preacher and Hayes, 2008). It is based on a standard three-variable path model (Baron and Kenny, 1986) that investigates whether an independent variable (X , in our case the different DTI measures) affects a dependent variable (Y , in our case the partiality score) through one or more intervening variables, or mediators (M , in our case the mentalizing bias). Variable M is a mediator if X significantly accounts for variability in M (path a), X significantly accounts for variability in Y (path c, representing the total effect), M

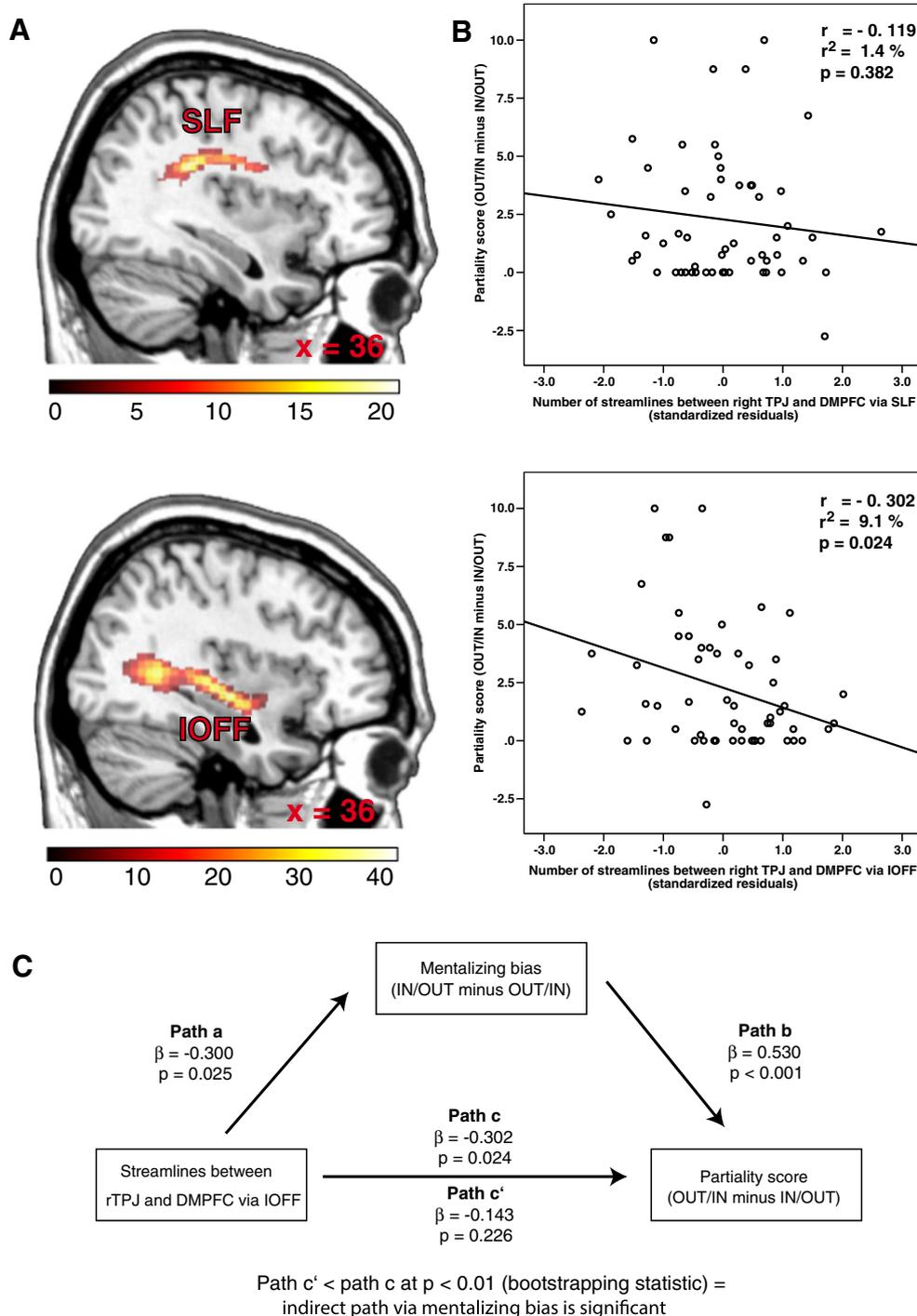


Fig. 4. White matter connectivity strength between the right TPJ and DMPFC via the inferior occipito-frontal fasciculus predicts individual differences in intergroup bias. (A) Depicted are the findings from the tractography analyses in which we separated (with the help of exclusion masks, see Materials and methods section for details) the two fiber tracts depicted in Fig. 3A. The two separated tracts overlapped in at least 10 participants. Note that in most areas of the tracts, there is a strong overlap in most subjects; see the yellow parts of the tracts. (B) Scatter plots of the partiality score (calculated with DC trials) against the number of streamlines (mean of both directions) of the two separated fiber tracts depicted in (A). Note that the depicted streamline values are log-transformed, adjusted for all covariates (age, brain size, volumes of the ROIs, total punishment costs, strength of ingroup identification) and z-standardized. A line of best fit with r , r^2 , and p values is also displayed for the entire sample of 56 participants. Findings revealed that only connectivity strength between right TPJ and DMPFC via the inferior occipito-frontal fasciculus predicts individual differences in intergroup bias. Note that if we remove the only subject with a negative partiality score from the analyses, all findings are highly similar (SLF: $r = -0.065$, $p = 0.639$; IOFF: $r = -0.321$, $p = 0.017$). (C) Mediation model depicting a significant (at $p < 0.01$) indirect path from the connectivity strength between right TPJ and DMPFC via the IOFF to the partiality score through the mentalizing bias. β indicates standardized regression coefficients. Note that all requirements for a mediation effect are satisfied: path a, path b and path c are significant and path c' is significantly smaller than path c (see Materials and methods section for details).

significantly accounts for variability in Y when controlling for X (path b), and the effect of X on Y decreases substantially when M is entered simultaneously with X as a predictor of Y (path c', representing the direct effect). Estimates of all paths are calculated using OLS regression. In order to test whether the mediated, indirect effect through M

is significant (i.e., whether the direct effect [path c'] is significantly smaller than the total effect [path c]), bootstrapping tests for statistical significance were used (Preacher and Hayes, 2008). We used 10000 bootstrap samples to generate bootstrap confidence intervals (CIs at 90%, 95% and 99%) for the indirect effects.

Covariates

We used the same covariates (with one DTI specific exception, see below) as in the Baumgartner et al. (2013) anatomy study (brain volume/thickness) on intergroup bias, given that we reexamined the same subjects within the same intergroup paradigm. In all statistical analyses, we controlled for age, SSIS, and total punishment costs. Age was included because it has been demonstrated to affect brain anatomy (e.g., Silk and Wood, 2011). SSIS was included to control for differences in the strength of ingroup identification to rule out the possibility that even though we recruited strongly identified individuals, impartial behavior could yet be due to remaining variance in ingroup identification (Aberson et al., 2000). Total punishment costs was included to control for the mere willingness to part with money. In the statistical analyses with the tractography measurements, we further controlled for brain size and volume of the seed and target ROIs. Brain size was included due to a potential relationship with connectivity strength. The volumes of the ROIs were included to control for (slightly) different ROI volumes that might have been caused by transforming the ROIs from MNI space to the individual native space of the subjects (see Materials and methods section: connectivity strength analyses).

Results

Behavioral results

Participants evinced the expected behavioral pattern of intergroup bias, particularly during DC trials (as reported in Baumgartner et al., 2013). Specifically, participants punished an outgroup perpetrator who defected against a cooperating ingroup member more severely than an ingroup perpetrator who committed the same transgression against a cooperating outgroup member (mean punishment difference = 2.28, $SD = 2.78$; $t(55) = 6.13$, $p < 0.001$). Intergroup bias in punishment was also found when both players defected (behavioral pattern DD), but the magnitude was markedly reduced (mean punishment difference $\pm SD = 1.00 \pm 1.99$; paired t -test: $t(55) = 3.7$, $p < 0.001$). No biased punishment pattern was observed when player A cooperated (behavioral pattern CC and CD, all $p > 0.11$).

White matter integrity and intergroup bias

Voxel-wise analyses were conducted to examine the association between each participant's $f1$, $f2$, and FA white matter skeleton maps and the partiality score. Please note that all white matter integrity analyses reported below involved the partiality score calculated from DC trials (trials with unilateral defection of player A, our main condition of interests, see above). However, the main findings from the white matter integrity analyses hold for a partiality score calculated from DD trials (see Supplementary Table 1). Age, SSIS, and total punishment costs were entered as covariates. We used $p < 0.05$ family-wise error corrected for all voxels in the skeleton maps as the criterion to detect voxels with a significant correlation with the partiality score. For the $f1$ values, results showed that a white matter cluster at the right TPJ was negatively associated with the partiality score ($x = 44$, $y = -48$, $z = 2$, $r = -0.698$, $p < 0.000001$, $r^2 = 48.7\%$)—i.e., greater white matter integrity was associated with reduced intergroup bias (see Fig. 2B). No other regions demonstrated a correlation with the partiality score that survived the correction procedure. For the $f2$ values (reflecting the non-dominant white fiber tracts), there were no brain regions that demonstrated a positive or negative correlation with the partiality score that survived the corrected threshold. For the sake of comparison, we conducted the same analyses using FA values (the values which do not account for regions with crossing fibers). Results showed that a white matter cluster at the same area of the right TPJ was negatively associated with the partiality score ($x = 43$, $y = -48$, $z = 2$, $r = -0.596$, $p < 0.00001$, $r^2 = 35.5\%$). As with the $f1$ value, no other

FA values demonstrated a positive or negative correlation with the partiality score that survived the correction procedure. Thus, both $f1$ and FA at the right TPJ were associated with a reduced partiality score, i.e., reduced intergroup bias, but consistent with the idea that accounting for multiple fiber directions increases the interpretability of effects, the partial volume fraction estimate $f1$ showed a stronger association.

We then tested whether the mentalizing bias score ($M = 0.84$, $SD = 1.07$) might mediate the association between white matter integrity and intergroup bias. To test whether the indirect effect through M is significant, bootstrapping tests for statistical significance were used (Preacher and Hayes, 2008). We used 10000 bootstrap samples to generate bootstrap confidence intervals (90%, 95%, and 99%) for the indirect effects. Results demonstrate that the indirect effect ($a \times b = -5.10$) was significantly different from zero (95% CIs between -15.83 and -0.51 , see Fig. 2C). In other words, our analysis suggests that increased white matter integrity ($f1$) at the right TPJ predicts a lower mentalizing bias (a more balanced use of mentalizing processes, regardless of group membership), which in turn predicts a reduced propensity for intergroup bias.

White matter connectivity strength and intergroup bias

Tractography analyses revealed that two pathways consistently connected the right TPJ and the DMPFC in our participants—the superior longitudinal fasciculus (SLF) and the inferior occipito-frontal fasciculus (IOFF, see Fig. 3A). As with the white matter integrity analyses, all our white matter connectivity strength analyses reported below involved the partiality score calculated from DC trials (our main condition of interests). Again, however, white matter connectivity strength results also hold for a partiality score calculated from DD trials (see Supplementary Table 1).

To examine whether connectivity strength between right TPJ and DMPFC was associated with individual differences in intergroup bias, we regressed the partiality score on the number of streamlines between the right TPJ and the DMPFC (log-transformed to reduce skew), with age, brain size, volumes of the seed and target ROIs, SSIS, and total punishment costs entered as covariates. Paralleling the $f1$ and FA results, results showed a negative relationship between the number of streamlines from the region near the right TPJ to the region near the DMPFC and the partiality score, $r = -0.354$, $p < 0.007$, $r^2 = 12.5\%$ (see Fig. 3B). That is, an increased number of streamlines connecting these brain regions was associated with reduced intergroup bias.

Next, we tested whether mentalizing processes might similarly mediate the association between white matter connectivity strength between the right TPJ and the DMPFC and intergroup bias. Analyses revealed that the indirect effect ($a \times b = -0.44$) was again significantly different from zero (99% CIs between -1.20 and -0.03 , see Fig. 3C). These results further support the idea that connectivity strength between the right TPJ and the DMPFC is associated with a reduced propensity for intergroup bias due to engaging a more impartial use of mentalizing processes.

Next, we examined each pathway's separate contribution to the association between connectivity strength between the right TPJ and the DMPFC and the partiality score. We conducted separate regression analyses (using the same covariates) for streamlines in the SLF only and the IOFF only. Results revealed that whereas the SLF streamlines were not significantly related to the partiality score, $r = -0.119$, $p = 0.382$, $r^2 = 1.4\%$, the IOFF streamlines remained a significant predictor, $r = -0.302$, $p = 0.024$, $r^2 = 9.1\%$, such that more streamlines through the IOFF was associated with a reduced partiality score (see Fig. 4B). Furthermore, the link between connectivity strength via the IOFF and reduced partiality was again mediated by mentalizing processes (indirect effect $a \times b = -.45$, 99% CIs between -1.21 and -0.02 , see Fig. 4C).

Finally, we conducted the very same three tractography analyses (combined and separated tracts) on the left hemisphere to examine

whether the above-reported associations between connectivity strength and partiality are specific (or not) to the right hemisphere. We mirrored the *x*-coordinates of the seed and target regions used for the analyses on the right hemisphere. As expected, the same fiber tracts consistently connect the left TPJ and DMPFC (see Supplementary Fig. 1A). Interestingly, however, we did not find any evidence that the connectivity strength between left TPJ and DMPFC is associated with intergroup bias (for details, please see Supplementary Fig. 1B). Thus, these findings suggest that the link between intergroup bias and connectivity strength between TPJ and DMPFC is indeed specific for the right hemisphere, reflecting the white matter integrity finding which is also specific for the region of the right TPJ.

Discussion

This study is the first to examine whether neuroanatomical connections explain individual differences in intergroup bias. The results demonstrated that increased white matter integrity specifically at the right TPJ and connectivity strength between the right TPJ and DMPFC was associated with reduced intergroup bias in the third-party punishment paradigm. These results thus support the idea that differences in structural connectivity can help determine sources of individual differences in intergroup bias (Cikara and Van Bavel, 2014; Nash et al., 2014).

Increased white matter integrity and connectivity strength are both reliably related to better functioning (Kanai and Rees, 2011). As such, increased white matter integrity at the right TPJ and connectivity strength between the right TPJ and the DMPFC should be associated with better functioning within this network. Because the TPJ and DMPFC are thought to comprise part of a neural network involved in mentalizing (Behrens et al., 2009; Carter et al., 2012; Frith and Frith, 2006; Hampton et al., 2008; Klapwijk et al., 2013; Van Overwalle, 2009, 2011), better functioning should be associated with better mentalizing ability. Consistent with this, we found that people with greater white matter integrity at the right TPJ and connectivity strength between the TPJ and the DMPFC appear to use mentalizing more equally for ingroup and outgroup members, and this leads to reduced intergroup bias. We assume that the biological mechanisms for these effects are, in general, more elaborate and efficient networks. That is, increased white matter integrity at the TPJ should reflect increased axon caliber, fiber density, and/or myelination. Connectivity strength between the TPJ and the DMPFC reflects more fibers linking these two regions. These more elaborate networks allow for more efficient conduction and better functioning, i.e., better mentalizing ability.

The current findings significantly extend the only other study (to our knowledge) on neuroanatomy and individual differences in intergroup bias. Baumgartner et al. (2013) found that increased DMPFC and TPJ volume was associated with reduced intergroup bias. The authors speculated that such findings implicated not just circumscribed brain regions but rather a psychologically relevant neural network. These speculations are validated by the current demonstration that intergroup bias depends upon the degree of connectivity between the TPJ and DMPFC. Further, the mediation findings in Baumgartner et al. (2013) were replicated here in two separate analyses using independent measures of white matter. Overall, across both studies, the effects of cortical volume, white matter integrity, and white matter connectivity strength in the mentalizing system on intergroup bias were all mediated by the degree to which mentalizing processes were used equally for ingroup and outgroup members. Thus, these two structural studies together demonstrate that individual differences in intergroup bias are explained by neuroanatomical differences in an interconnected mentalizing system.

We contend that these structural findings explain why functional studies find increased activation in the TPJ and DMPFC for ingroup members in comparison with outgroup members and why this activation is often associated with higher levels of intergroup bias (Baumgartner et al., 2012; Falk et al., 2012; Harris and Fiske, 2006). Equal treatment

of ingroup and outgroup members is a difficult task. It appears to require elaborate coordination between two regions in the mentalizing system. Unequal treatment, i.e., intergroup bias, involves a less elaborate system that is only recruited for ingroup members. A difference in activity for ingroup compared to outgroup members may reflect failure to similarly employ this system for outgroup members.

We speculate that this reasoning might also explain prior evidence in which transient disruption of the right TPJ caused decreased intergroup bias (Baumgartner et al., 2014). Participants in this TMS study demonstrated high levels of intergroup bias in general. This would suggest that people within this biased sample tended to possess a poor mentalizing system. Thus, disruption of the TPJ would have knocked out biased employment of mentalizing processes, i.e., the use of mentalizing only for ingroup members but not outgroup members. Consequently, disruption of biased mentalizing processes would lead to a reduction in intergroup bias, as was reported in that study. On the other hand, if a sample tends to possess an elaborate or highly functioning TPJ and DMPFC network, could transient disruption of the TPJ have the opposite effect and increase intergroup bias? This is a research question ripe for testing.

Also ripe for consideration is recent research that suggests that the TPJ is involved in social distance processes. Strobach et al. (2015) found that the right TPJ showed increasing activation during generous choices as social distance increased between the participant and their playing partner. Thus, the TPJ appeared to incorporate other-regarding preferences in to the decision-making process, particularly as social distance increased. In relation to the current study, social distance is presumably greater for outgroup as opposed to ingroup members. Perhaps a more elaborate structure and improved functioning at the TPJ might allow individuals to better incorporate other-regarding preferences of socially distant outgroup members into non-biased decision-making? Notably, we found that increased connectivity strength in the IOFF, and not in the SLF, was associated with increased non-biased mentalizing and reduced intergroup bias. Although research is in incipient stages, the IOFF appears related to visuospatial processing (Voineskos et al., 2012). Thus, there is an intriguing overlap between the function associated with the IOFF, the function associated with the TPJ, and the results demonstrated here. Might social distance processes involve visuospatial processes? Neural networks are often employed in different domains or co-opted for different behaviors. Future research could probe whether TPJ and IOFF involvement in social distance-related processing may reflect a common visuospatial process.

We note certain limitations that may be addressed by further research. First, the current research may appear to assume a deterministic view of individual differences, i.e., people with certain stable brain differences are fated to enact ingroup bias or not. Rather, ours is an interactionist approach (e.g., see Declerck et al., 2013; Flesoon, 2001; Lewin, 1946). We assume that neuroanatomical differences predispose individuals toward certain behaviors and these dispositions interact with other neural systems and contextual influences to produce behavior. Thus, neuroanatomical differences incline one toward or away from respective psychological processes or behavior but do not fully determine behavior. Further, neuroanatomical differences are themselves malleable (Kanai and Rees, 2011). Future research could explore whether improving mentalizing might be achieved via changes to the mentalizing neural system affected through experience or training techniques. For example, neurofeedback and repeated practice of certain skills have the capacity to increase cortical volume and white matter integrity in relevant systems (e.g., Ghaziri et al., 2013; Scholz et al., 2009; Takeuchi et al., 2010). The current research lends confidence to the idea that the mentalizing network explains individual differences in intergroup bias. Thus, training has the potential to alleviate intergroup bias by targeting the right TPJ, the DMPFC, and/or the white matter connecting these regions.

The current methodology was strongly predicated on a priori hypotheses derived from our prior research involving the same behavioral task. For example, the probabilistic tractography methods followed

directly from the current white matter integrity results and the anatomical results in Baumgartner et al. (2013). Alternatively, subsequent research could functionally localize mentalizing processes in the TPJ and DMPFC to determine whether an increase in the precision of anatomical identification would replicate the current findings. Additionally, other brain regions have been associated with mentalizing processes (e.g., temporal poles; Gallagher and Frith, 2003) and ingroup bias (e.g., amygdala, orbitofrontal cortex; Krämer et al., 2014; Van Bavel et al., 2008; for a recent review, see Amodio, 2014, Molenberghs, 2013). White matter connectivity strength differences between these regions could further explain individual differences in intergroup bias and reveal mechanisms of bias.

In sum, the current research demonstrated that increased white matter integrity at the right TPJ and increased connectivity strength between the right TPJ and the DMPFC are associated with reduced intergroup bias. These associations were mediated by a more balanced use of mentalizing processes for both ingroup and outgroup members. These results provide further support for the notion that neuroanatomical differences in the TPJ and DMPFC network help determine individual differences in intergroup bias and buttress a prevailing notion in intergroup research in which mentalizing is central to overcoming intergroup bias, in terms of overcoming both discrimination (Pettigrew and Tropp, 2008) and violent intergroup conflicts (Kelman, 1986).

Conflict of interests

The authors declare no conflict of interests

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.neuroimage.2015.08.011>.

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