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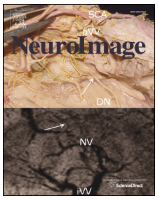

Impartiality in humans is predicted by brain structure of dorsomedial prefrontal cortex

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ABSTRACT

The moral force of impartiality (i.e. the equal treatment of all human beings) is imperative for providing justice and fairness. Yet, in reality many people become partial during intergroup interactions; they demonstrate a preferential treatment of ingroup members and a discriminatory treatment of outgroup members. Some people, however, do not show this intergroup bias. The underlying sources of these inter-individual differences are poorly understood. Here we demonstrate that the larger the gray matter volume and thickness of the dorsomedial prefrontal cortex (DMPFC), the more individuals in the role of an uninvolved third-party impartially punish outgroup and ingroup perpetrators. Moreover, we show evidence for a possible mechanism that explains the impact of DMPFC's gray matter volume on impartiality, namely perspective-taking. Large gray matter volume of DMPFC seems to facilitate equal perspective-taking of all sides, which in turn leads to impartial behavior. This is the first evidence demonstrating that brain structure of the DMPFC constitutes an important source underlying an individual's propensity for impartiality.

Introduction

Justice's most iconic figure is *lady justice*, an allegorical representation of the moral forces lying at the heart of the ideal provider of justice. *Lady justice* is often depicted as blindfolded to shield her judgment from morally irrelevant information, such as group affiliation. Yet, when granted the position of provider of justice if the own group is implicated in a conflict, ignoring the blindfold and falling into partiality is human nature (Bowles, 2009; Brewer, 1999; Haushofer et al., 2010). This unequal treatment of ingroup and outgroup members, i.e. ingroup favoritism and outgroup hostility, has been documented in many laboratory and field studies in psychology, sociology, and economics (e.g. Bernhard et al., 2006; Brewer, 1979; Halevy et al., 2008; Levine et al., 2005; Tajfel et al., 1971). Despite the widespread occurrence of this intergroup bias, however, there is considerable inter-individual heterogeneity in the degree of this bias. This raises the question: What sets apart impartial people (i.e. people who treat ingroup and outgroup members equally) from those whose judgments are biased in favor of their ingroup?

There is a long psychological tradition of relating personality to differences in partiality (e.g. Batson and Burris, 1994; Graham et al., 2011; Hewstone et al., 2002; Kreindler, 2005; Pratto and Shih, 2000). However, correlations between these personality difference measures and partiality are rather low, suggesting that personality measures generally have limited predictive power (Hewstone et al., 2002). The use of more objective individual markers might therefore help explain inter-individual differences in the propensity for impartiality. Recent applications of brain morphometry indicate that individual differences in brain structure might be such a useful, objective marker because brain structure has been demonstrated to be relatively stable over time in healthy adults and can be used to predict individual differences in various traits (e.g. Baur et al., 2012; DeYoung et al., 2010), skills (e.g. Jancke et al., 2009; Steinbeis et al., 2012), and behavior (e.g. Bickart et al., 2011; Ersche et al., 2012; Morishima et al., 2012). No previous study, however, has examined whether variables reflecting neuroanatomical individual differences, such as gray matter volume or cortical thickness, may help predict individual differences in human's propensity for impartiality.

Previous studies on the neural underpinnings of partiality measured brain activity during the decision-making process rather than examining task-independent neuroanatomical characteristics. Thus, it is difficult to derive clear hypotheses based on these studies. Nevertheless, these studies do allow for speculation about the potential neural structures driving the propensity for impartiality. These studies (e.g. Baumgartner et al., 2012; Falk et al., 2012; Harris and Fiske, 2006) showed that differences in judgment of and behavior towards ingroup and outgroup members are associated with differential activity patterns in areas known to play a key role in social cognition

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(Adolphs, 2003; Van Overwalle, 2009), including the dorsomedial prefrontal cortex (DMPFC) and bilateral temporo-parietal junction (TPJ).

In order to investigate whether anatomical differences in certain brain structures explain inter-individual differences in impartiality, we applied structural magnetic resonance imaging and measured a person's propensity for impartiality with a third-party punishment paradigm. In this paradigm, judges in the role of an uninvolved third-party were confronted with norm-abiding and norm-violating behavior committed by both ingroup and outgroup members of real social groups (see Material and methods section for details) and had to decide whether to punish this behavior at their own expense (see Fig. 1).

More precisely, subjects in the role of a third-party (player C) were given the opportunity to punish the behavior of players who had previously played a prisoner's dilemma game (PDG). In the PDG, players A and B (either ingroup members, or outgroup members) were each endowed with 20 points and each had to decide simultaneously whether to keep all of the points or to pass them to the other player. Passed points were doubled. Thus, keeping the points equals defection (denoted as D) and passing the points equals cooperation (denoted as C). For example, if player A retained the 20 points while player B transferred the 20 points (behavioral pattern DC), player A earned a total of 60 points (40 points from the transfer plus the initial endowment of 20 points) and player B earned nothing. In order to be able to punish the decisions made by players A and B in the PDG, subjects in the role of player C received an endowment of 10 points at the beginning of each punishment trial. Assigning 1 punishment point cost player C 1 point and cost the sanctioned player 3 points. Points not used for punishment could be retained as income. Notably, we only allowed player C to punish the behavior of one player (either A or B) during each of the punishment trials played. In order to simplify the nomenclature, we recoded all of player C's decisions such that player A always refers to the player that C can punish, while player B always refers to the player that C cannot punish.

To measure subjects' propensity for impartiality, player C was confronted with two different group situations (depicted in Fig. 1). In the group situation OUT/IN, player A was an outgroup member and player B was an ingroup member, whereas in the group situation IN/OUT, player A was an ingroup member and player B was an outgroup member. Comparing player C's punishment decisions between these two group situations reveals player C's propensity for impartiality. Thus, we calculated a partiality score by subtracting punishment points in IN/OUT from punishment points in OUT/IN, separately for all possible behavioral decisions made by players A and B in the PDG (CC, CD, DC, DD). High values on this partiality score indicate that the third-party judges (player C) strongly differed in the treatment of ingroup and outgroup members, i.e. they showed a pronounced tendency towards partiality. Low values on this score indicate that the third-party judges treated ingroup and outgroup members equally, i.e. they demonstrated an impartial punishment pattern. We used this partiality score in order to examine whether inter-individual differences in the propensity for impartiality can be predicted by differences in brain anatomy.

Materials and methods

Subjects

56 healthy subjects were studied (mean age ± S.D. $= 22.3 \pm 3.47$ years, 26 females, 30 males). Subjects gave informed written consent prior to participating in the study, which was approved by the local ethics committee. No subject had a history of psychiatric illness or neurological disorders. Subjects received 40 Swiss Francs (CHF 40; CHF 1 = about $1 U.S.) for participating, in addition to the money earned in the third-party punishment paradigm.

Social groups and ingroup identification scale

We decided to use naturally occurring social groups. We recruited strong supporters of either soccer clubs ($n = 16$) or political parties ($n = 40$) because previous studies using these groups have reported strong behavioral intergroup biases (Ben-Ner et al., 2009; Hein et al., 2010; Koopmans and Rebers, 2009). Subjects in the role of an uninvolved third-party (player C) were given the opportunity to punish supporters of their own or a corresponding rival social group. Note that soccer supporters always interacted with other soccer supporters and political supporters always interacted with other political supporters. Independent t-tests revealed that the two social groups did not differ

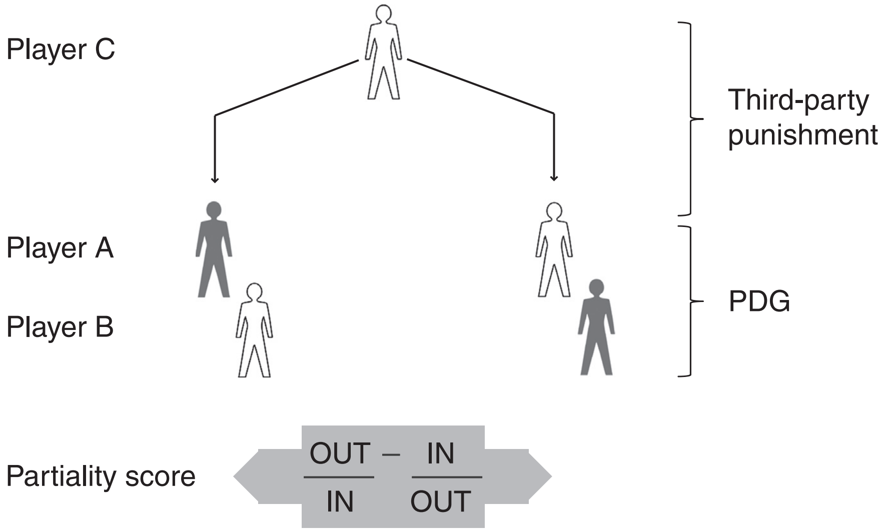

Fig. 1. Schematic representation of the study design. Depicted is the applied third-party punishment paradigm. Player C in the role of a third-party judge was confronted with decisions of player A and player B in a Prisoner's Dilemma Game (PDG) and had the opportunity to assign punishment points to player A. Players A and B either stemmed from the same social group as the third-party judge (ingroup members depicted in white colors) or from a different social group (outgroup members depicted in gray colors). In total, third-party judges 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 third-party judges' punishment decisions in these two group situations (OUT/IN–IN/OUT) reveals their propensity for impartiality, quantified in the partiality score: high values indicate strong tendencies to partiality and low values indicate strong tendencies to impartiality.

with regard to the partiality score (OUT/IN minus IN/OUT) during trials with unilateral defection ($t_{(54)} = -.228$, $p = 0.82$, our main condition of interests,) and bilateral defection ($t_{(54)} = -1.63$, $p = 0.11$). Thus, we do not differentiate between these two social groups in our brain analyses.

Before the third-party punishment paradigm, we measured each subject's strength of ingroup identification with the Sport Spectator Identification Scale (SISS, 5-point likert scale) (Wann and Branscombe, 1993). We adapted this questionnaire slightly for supporters of political parties, for example, the term “your preferred political party” replaced “your preferred soccer team”.

Third-party punishment paradigm

We applied a third-party punishment paradigm with real social groups and the involvement of real monetary stakes and consequences for all involved interaction partners. In this paradigm, subjects in the role of a third-party (player C) were given the opportunity to punish the behavior of players who had previously played a simultaneous prisoner's dilemma game (PDG). In this PDG, two players A and B interacted and could decide either to cooperate or defect. Thus, four behavioral patterns were possible: player A and B cooperate (CC), player A and B defect (DD), player A cooperates and player B defects (CD), and player A defects and player B cooperates (DC). Subjects in the role of an uninvolved third-party (player C) were informed of these PDG decisions and were able to punish player A's behavior by assigning punishment points. For this purpose, they received an endowment of 10 points at the beginning of each punishment trial which they could either keep or use to punish player A. 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 $2 U.S.).

Two group situations were used in the experiment (see Fig. 1): player A is an outgroup member and player B is an ingroup member (termed OUT/IN) and player A is an ingroup member and player B is an outgroup member (termed IN/OUT). The PDG decisions of players A and B were selected such that each player C was confronted with the same 20 decision situations, which were presented in random order. DC decisions (our main condition of interest) were presented four times, and all other conditions were presented twice (CC, CD, DD). 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 (signet of the political parties/shirts of the soccer clubs). The software package z-Tree (Fischbacher, 2007) was used for presenting these computer screens and for collecting behavioral data. Finally, the subjects knew that there were no repeated interactions in the paradigm and that all interactions were conducted in complete anonymity in order to exclude reputation effects.

Questions about mentalizing processes

At the end of the punishment task, subjects were asked to answer the following statements regarding trials with unilateral defection (DC trials) committed by an ingroup or an outgroup perpetrator in the role of player A: (1) It was easy for me to put myself in the position of player A. (2) I am sure player A had good reasons justifying his behavior. (3) Putting myself in the position of player A helped me to make my punishment decision.

Subjects had to indicate on a 6-point likert scale whether they agreed with the statement or not (ranging from “I agree not at all” to “I agree completely”). Based on these questions, we created a mentalizing bias by subtracting perspective-taking with outgroup perpetrators from perspective-taking with ingroup perpetrators (IN/OUT minus OUT/IN). Thus, high values in this mentalizing bias mean that it was easier for individuals to mentalize with ingroup perpetrators, whereas low values mean that individuals did not differ in mentalizing towards ingroup and outgroup perpetrators.

Explicit trait measures

In order to examine whether inter-individual differences in brain anatomy are capable of explaining unique variance in impartiality compared to other explicit measures, subjects answered the following two well-established trait questionnaires measuring group-related attitudes and emotional reactions to injustice known to play a role in intergroup behavior. The social dominance orientation questionnaire (Jost and Thompson, 2000) is a two-dimensional, 16-item measurement of social dominance orientation using 7-point likert scales. One dimension measures general opposition to equality and the other dimension measures support for group-based dominance. The justice sensitivity scale from the observer perspective (Schmitt et al., 2005) is a 10-item questionnaire that measures, on a 7-point likert scale, how strongly subjects in the role of an observer (i.e. a third-party) psychologically and emotionally react to observed injustice.

Implicit attitude measure

Implicit attitudes measured by the implicit association test (IAT) predict actual behavior for some socially sensitive topics even better than explicit trait measures, supposedly because the IAT is less influenced by self-presentational forces (Greenwald et al., 2009). In order to examine whether inter-individual differences in brain anatomy are an even better predictor than this implicit measure, we additionally used an IAT to measure subjects' implicit intergroup attitudes.

More specifically, we determined how strongly subjects automatically associate their in- and outgroup with positive and negative valence (Greenwald et al., 1998). The IAT used here consisted of words belonging to 4 categories: ingroup words (e.g. names of famous politicians/soccer players of the favored party/soccer club), outgroup words (e.g. names of famous politicians/soccer players of the rival party/soccer club), positive words (e.g. “love”) or negative words (e.g. “death”). These words were presented to subjects in the middle of the screen; they then had to sort these words by pressing a key on the left of the keyboard if the word belonged to the category labels presented on the left side of the screen, and a key on the right if the word belonged to the category labels presented on the right side of the screen. For determining the IAT effect, two conditions were compared. In “congruent” blocks, subjects had to press one key when ingroup and positive words appeared, while they had to press another key when outgroup and negative words were shown. In contrast, ingroup and negative words shared the same response key in “incongruent” blocks, while outgroup and positive words shared another response key. It is assumed that categorization is easier when closely associated categories (e.g. ingroup and positive words) share a common response key than when less associated categories (e.g. outgroup and positive words) share a common response key. Thus, the strength of the implicit bias can be measured by calculating the difference in reaction times between incongruent and congruent trials. To adjust for each subject's latency variability, a d-score was computed using the improved scoring algorithm (Greenwald et al., 2003). This d-score is calculated by dividing the reaction time difference between incongruent and congruent trials by the pooled standard deviation in these trials. Positive d-scores indicate a strong association of the ingroup with positive valence and/or a strong association of the outgroup with negative valence.

Mediation analysis

In order to conduct a mediation analysis, we used the SPSS macro programmed by Andrew F. Hayes (Preacher and Hayes, 2008), which is freely available on the internet. It is based on a standard three-variable path model (Baron and Kenny, 1986) which investigates whether an independent variable (X, in our case brain anatomy) 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 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 5000 bootstrap samples to generate bootstrap confidence intervals (90%, 95% and 99%) for the indirect effects.

Acquisition of the neuroimaging data

Measurements were performed on a 3 T whole body MR system (Magnetom Verio, Siemens Healthcare, Germany) equipped with a standard twelve-channel head coil. 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.

Neuroimaging data processing and statistical analyses

Anatomical brain images of 56 individuals were analyzed using voxel-based morphometry version 8 (VBM 8) implemented in statistical parametrical mapping version 8 (SPM 8). VBM 8 is documented and freely available online (http://dbm.neuro.uni-jena.de/vbm/). It is a whole-brain technique capable of discovering subtle, regionally specific changes in gray matter by averaging across subjects. This method is based on high-resolution structural three-dimensional magnetic resonance images, registered in standard space, and is designed to find significant regional differences throughout the brain by applying voxelwise statistics within the context of Gaussian random fields (Ashburner and Friston, 2000). Preprocessing of the data involved spatial normalization, segmentation into gray matter (GM), white matter (WM), and cerebrospinal fluid (CSF), modulation, and spatial smoothing with a Gaussian kernel (full width at half maximum = 8 mm) (Ashburner and Friston, 2000, 2005). In detail, the segmentation approach is based on an adaptive Maximum a Posterior (MAP) technique without the need for a priori information of tissue probabilities, uses a Partial Volume Estimation (PVE) with a simplified mixed model of at most two tissue types, and applies a classical Markov Random Field (MRF) approach, which incorporates spatial prior information of adjacent voxels into the segmentation estimation. Finally, the modulation option we used during preprocessing multiplies the voxel values by the non-linear component derived from the spatial normalization, producing tissue volumes that are already corrected for individual brain size.

A linear regression analysis was performed on the smoothed gray matter volume images in SPM 8 to determine regions in which gray matter volume is associated with impartiality. Total punishment costs, strength of ingroup identification, and age were included in the design matrix as covariates of no interest to model and thus regress out any effects correlated with these factors (see Results section for details). Note that the gray matter volume maps are already corrected for individual brain size; inclusion of individual brain size as an additional covariate was thus not necessary. We used $p < 0.05$ family-wise error corrected for the whole brain volume as the criterion to detect voxels with a significant correlation with impartiality.

In order to corroborate the findings of the VBM 8 analysis and to obtain a more fine-grained understanding of the underlying structural differences driving the relationship between DMPFC gray matter volume and impartiality, we additionally performed a surface-based structural analysis with the Freesurfer image analysis suite, which is documented and freely available for download online (http://surfer.nmr.mgh.harvard.edu/). The technical details of these procedures are described in prior publications (Dale et al., 1999; Fischl and Dale, 2000; Fischl et al., 1999, 2002, 2004). Briefly, T1-weighted MRI images volumes were processed in a fully automated fashion using a cortical surface-based reconstruction that ultimately provides measurement of cortical thickness and surface area throughout the cortical mantle for each individual participant. A trained operator, blind to the hypothesis, manually inspected the results of the cortical reconstruction. In this inspection, no adjustments, modifications, or edits were made; the results of the automated cortical reconstruction were verified as accurate without the need for correction. In order to examine whether thickness or surface area, or a combination of both, drives the relationship between impartiality and gray matter volume in the DMPFC, we extracted the average thickness and surface area in this brain area. We then conducted linear regression analyses with the partiality score as the dependent variable and either the cortical thickness or surface area as the independent variable, controlling for the same potentially confounding factors used in the VBM 8 analyses (total punishment cost, strength of ingroup identification, age, total intracranial brain volume). Notably, if we perform an exploratory statistical analysis of the whole cortical mantle using cortical thickness or surface area as measurement of interests (controlling for all mentioned covariates), no other brain area showed an association with impartiality that survived whole brain false discovery rate (FDR) correction. This finding further corroborates the results from the VBM 8 analyses.

Results

Behavioral results

In agreement with prior research (e.g. Bernhard et al., 2006; Goette et al., 2006), behavioral results of 56 healthy subjects in the role of a third-party judge revealed the expected biased punishment pattern. Partiality in punishment was particularly pronounced in DC trials, i.e. when player A defected and player B cooperated (behavioral pattern DC). In other words, an outgroup perpetrator who defected against a cooperating ingroup member was more severely punished than an ingroup perpetrator who committed the same norm violation against a cooperating outgroup member (mean punishment difference ± standard deviation = 2.28 ± 2.78; paired *t*-test: $t_{(55)} = 6.13$, $p < 0.001$). Partiality in punishment was also found when both players defected (behavioral pattern DD), but the magnitude was markedly reduced (mean punishment difference ± SD = 1.00 ± 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 $p > 0.11$). The observed biased punishment patterns, however, demonstrated considerable inter-individual variability, i.e. while some subjects strongly differed in the punishment of ingroup and outgroup perpetrators, others did not (DC trials: maximum = 10, minimum = −2.75; DD trials: maximum = 10, minimum = −1).

Brain anatomy and human impartiality

In order to assess whether these inter-individual differences in impartiality can be explained by neuroanatomical differences, we performed quantitative morphometric analysis of T1-weighted MRI data using voxel-based morphometry (VBM) implemented in SPM software. VBM is a whole brain technique capable of discovering subtle, regionally specific changes in gray matter volume (see Material and methods section for details). Because both brain size and age are known to affect brain anatomy (Im et al., 2008; Silk and Wood, 2011), we controlled for these two covariates in all our analyses, in line with previous studies (e.g. Bickart et al., 2011; Ersche et al., 2012). Furthermore, because punishment was costly, we controlled for the total points used for punishment in order to rule out the possibility that altruistic and egoistic behavioral tendencies instead of impartial or partial considerations account for the difference in brain anatomy. Finally, although we only recruited subjects who were strong supporters of the ingroups, slight differences in the strength of ingroup identification cannot be prevented. Thus, we controlled for the strength of ingroup identification using a questionnaire measure (see Material and methods section) in order to rule out that differences in impartiality are simply caused by differences in the strength of ingroup identification, i.e. that subjects who demonstrate impartial behavior simply identify less with the specific ingroup on hand than those subjects demonstrating partial behavior (Aberson et al., 2000).

We applied linear regression analyses with gray matter volume as the dependent variable and the partiality score (difference in punishment: OUT/IN minus IN/OUT) as the independent variable, controlling for the mentioned covariates. We focused on the partiality score from trials with unilateral defection of player A (behavioral pattern DC), i.e., the trials in which we found the strongest partiality in punishment (see above). Note that similar findings can be obtained if we instead use the partiality score from trials with bilateral defection (behavioral pattern DD) as the independent variable (for details of these analyses please see supplementary Table S1).

Findings revealed (at $p < 0.05$, family-wise-error corrected for the whole brain) that the gray matter volume in the DMPFC ($x = 2$, $y = 50$, $z = 28$, peak t-value $= 5.38$, explained variance $= 36.2\%$, Brodmann area 9/10), a key region involved in social cognition (Adolphs, 2003; Van Overwalle, 2009), is strongly negatively correlated with the partiality score. In other words, the larger the gray matter volume in this brain area, the lower the partiality in punishment, i.e. the stronger individuals' propensity for impartiality (see Fig. 2). No other brain region demonstrated a positive or negative correlation with the partiality score that survived this whole brain correction procedure. Only if the significance threshold was strongly lowered (to $p < 0.005$, uncorrected, voxel extent threshold 15 voxels, Lieberman and Cunningham, 2009), did we find another region involved in social cognition, the right TPJ ($x = 35$, $y = -57$, $z = 33$, peak t-value $= 3.05$, explained variance $= 15.4\%$), which demonstrated a negative correlation similar to that of the DMPFC. Moreover, the two correlational patterns in DMPFC and right TPJ were similarly pronounced in males and in females (see supplementary Table S2). We are reluctant, however, to make any interpretations based on the correlational findings in the TPJ due the lenient threshold.

The reported regression analysis demonstrated a particularly strong impact of gray matter volume in the DMPFC on human's propensity for impartiality. However, because this analysis is based on the partiality score, i.e. the difference in punishment between an outgroup perpetrator in OUT/IN compared to an ingroup perpetrator in IN/OUT, this analysis cannot reveal whether inter-individual differences in gray matter volume affects the punishment of outgroup perpetrators, ingroup perpetrators, or both. In an attempt to answer this question, we extracted the gray matter volume in the structural cluster of the DMPFC depicted in Fig. 2A (thresholded at $p < 0.0001$), split subjects into three groups using the 33rd and 66th percentiles of this volume measure, and calculated the mean punishment of these three groups, separately for the two group situations, OUT/IN and IN/OUT (see Fig. 3). The resulting pattern demonstrated that only those individuals with large gray matter volume showed a strong propensity for impartiality, i.e. they demonstrated an equally strong punishment of both ingroup and outgroup perpetrators (paired *t*-test: $t_{(18)} = 1.76$, $p > 0.10$). In contrast, individuals with medium gray matter volume exhibited partiality in punishment (paired *t*-test: $t_{(18)} = 5.58$, $p < 0.001$), mainly due to weaker punishment of ingroup perpetrators (group situation IN/OUT, independent *t*-test large versus medium gray matter volume group: $t_{(36)} = -2.03$, $p = 0.05$), suggesting that they treat ingroup perpetrators preferentially. Finally, individuals with small gray matter volume not only favored ingroup perpetrators (independent *t*-test small versus large gray matter volume: $t_{(35)} = -2.26$, $p = 0.03$), but further demonstrated harsher punishment of outgroup perpetrators (group situation OUT/IN) compared to the other two groups (independent *t*-test small versus medium gray matter volume group: $t_{(35)} = 2.28$, $p = 0.02$; small versus large gray matter volume group: $t_{(35)} = 2.01$, $p = 0.05$). Thus, only individuals

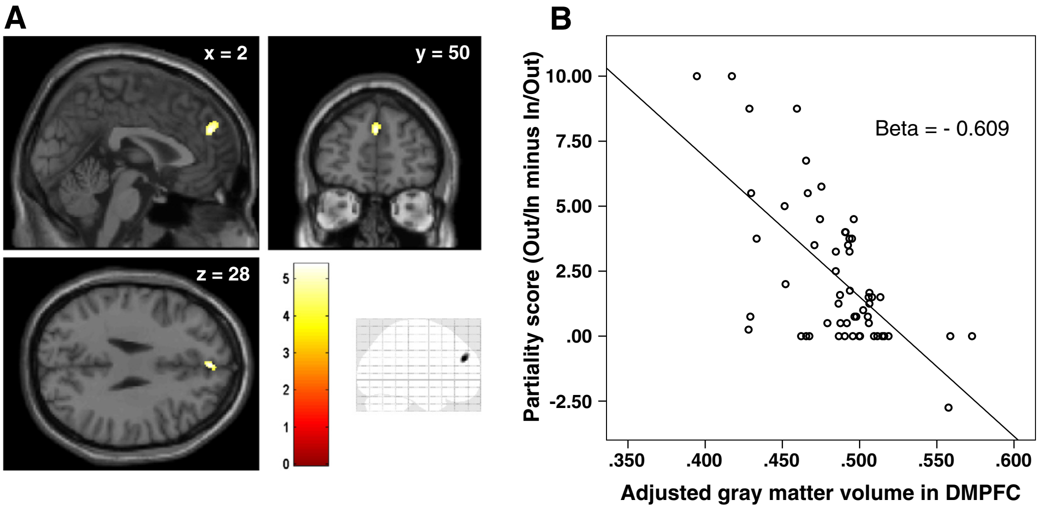

Fig. 2. Gray matter volume in DMPFC is linked to human impartiality. Depicted in (A) is the region of the DMPFC demonstrating a strong negative correlation with the partiality score (at $p < 0.05$, family-wise error corrected for the whole brain, for display purposes depicted at $p < 0.0001$). The glass brain view in the lower right corner demonstrates the specificity of the finding in the DMPFC depicted at the same uncorrected threshold. Findings thus suggest that the gray matter volume in the DMPFC is strongly associated with individuals' propensity for impartiality. (B) Scatter plot of the partiality score (y axis) against the gray matter volume in the DMPFC (x axis), which is based on the significant cluster depicted in (A) and adjusted for all covariates (age, brain size, total punishment costs, strength of ingroup identification). A line of best fit with standardized regression coefficient is also displayed for the entire sample of 56 individuals.

with small gray matter volume showed partiality in punishment (paired *t*-test: $t_{(17)} = 5.46$, $p < 0.001$) driven by discriminatory treatment of outgroup perpetrators. Taken together, the findings suggest that the amount of gray matter volume in the DMPFC can predict individual differences in impartiality and that only individuals with large gray matter volume in the DMPFC seem to be capable of behaving impartially by avoiding both the preferential treatment of ingroup perpetrators as well as the discriminatory treatment of outgroup perpetrators.

Mentalizing processes as a potential mediator between brain structure and impartiality

Our study demonstrates that a key area involved in social cognition in the DMPFC seems to be an important neuroanatomical source of inter-individual variability in human impartiality. Several recent meta-analyses (Denny et al., 2012; Van Overwalle, 2009, 2011) have consistently demonstrated that taking the perspective of others, also known as mentalizing or theory of mind, is one of the key social cognitive functions associated with the same area in the DMPFC we found in the present study. This part of the brain plays a critical role in inferring the goals, intentions, desires, and dispositions of others in order to judge their behavior (Frith and Singer, 2008; Young and Saxe, 2009). Thus, we wondered whether we could provide evidence that the amount of gray matter volume in the DMPFC indeed affects the way individuals mentalize about ingroup and outgroup perpetrators and whether these differential mentalizing processes have an impact on individuals' propensity for impartiality. For that purpose, individuals had to answer several questions (immediately after the end of the behavioral paradigm) about their mentalizing processes that took place during the punishment decisions against ingroup and outgroup perpetrators. For example, they had to report how well they were able to put themselves into the shoes of ingroup or outgroup perpetrators and whether they thought that the ingroup or outgroup perpetrators had good reasons justifying their behavior (see Material and methods section for details). Based on these questions, we created a mentalizing bias by subtracting perspective-taking with outgroup perpetrators from perspective-taking with ingroup perpetrators (IN/OUT minus OUT/IN). Thus, high values on this mentalizing bias indicate that participants better understood and more readily justified the behavior of ingroup perpetrators compared to that of outgroup perpetrators, whereas low values mean that individuals did not differ in mentalizing towards ingroup and outgroup perpetrators, suggesting that their mentalizing processes were less biased by partial considerations (negative values did not occur, suggesting that mentalizing with an outgroup perpetrator was not easier for any of our subjects). We used this bias in a mediation analysis in order to test whether mentalizing is a significant mediator between gray matter volume and impartial behavior (Preacher and Hayes, 2008). Findings provide significant evidence (bootstrapping statistics comparing path c with path c′: $p < 0.01$, see Fig. 4) that mentalizing processes are a significant partial mediator. In other words, our analysis suggests that the larger the gray matter volume in the DMPFC, the lesser an individual's mentalizing is biased, which in turn seems to increase his or her propensity for impartiality.

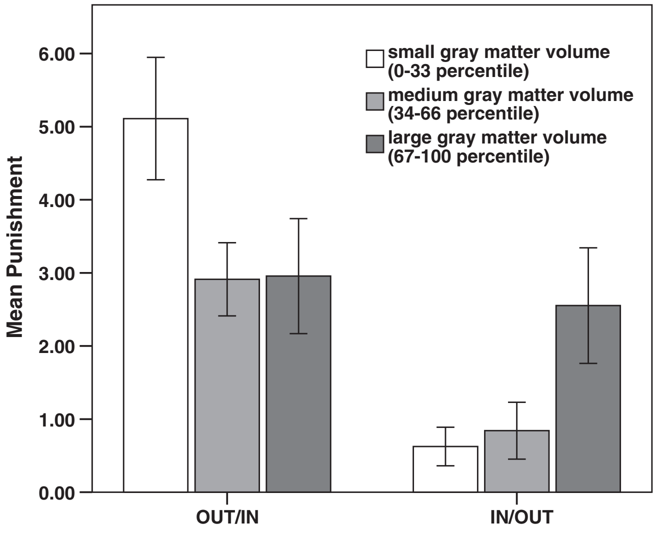

Fig. 3. Third-parties' punishments of outgroup and ingroup perpetrators, broken down by three groups with differing amount of gray matter volume in the DMPFC. In order to gain an improved understanding of the regression analyses using the partiality score (visualized in Fig. 2), we split our subjects into three groups based on the amount of gray matter volume in the DMPFC (using the 33rd and 66th percentile), and calculated the mean punishment of these three groups, separately for the two group situations OUT/IN and IN/OUT. Findings revealed an impartial punishment pattern (depicted are means ± SEM) only in those subjects with large gray matter volume. These subjects neither showed an exaggerated punishment of outgroup perpetrators (group situation OUT/IN) as demonstrated by subjects with small gray matter volume, nor a marginal punishment of ingroup perpetrators (group situation: IN/OUT) as demonstrated by subjects with small and medium gray matter volume.

Cortical thickness or surface differences?

In order to obtain a more fine-grained understanding of the underlying structural differences driving the relationship between DMPFC gray matter volume and impartiality, we additionally performed a vertex-based structural analysis with the Freesurfer image analysis suite (see Material and methods section for details). Freesurfer allows us to look at the two components of gray matter volume separately, i.e. cortical thickness and cortical surface. This analysis is thus able to provide evidence of whether the differences we observe in gray matter volume of the DMPFC are due to differences in cortical thickness, cortical surface, or a combination of both. In order to answer this question, we conducted linear regression analyses with either the cortical thickness or the cortical surface component in the DMPFC as the independent variable and the partiality score as dependent variable, controlling for all the covariates used in the brain analyses described above (total punishment costs, strength of ingroup identification, age, and intracranial brain volume; see Material and methods section for details). Results showed that only cortical thickness was negatively associated with the partiality score (standardized beta $= -0.577$, $t = -4.41$, $p < 0.001$), whereas cortical surface was not (standardized beta $= 0.081$, $t = 0.53$, $p = 0.596$).

Brain structure in DMPFC explains unique variance in impartiality

In a final step, we sought to examine whether the amount of gray matter volume in the DMPFC is capable of explaining unique variance in impartiality that other explicit or implicit measures cannot explain. To this end, we measured two well-established trait questionnaires related to group-based attitudes and emotional reactions to injustice known to play a role in intergroup behavior (social dominance orientation, Jost and Thompson, 2000; justice sensitivity scale, Schmitt et al., 2005). Moreover, we applied the implicit association test (IAT) (Greenwald and Banaji, 1995), which measures subjects' implicit intergroup bias (see Material and methods section for details). The IAT has been demonstrated to predict actual behavior for some socially sensitive topics even better than explicit trait measures, presumably because self-presentational forces exert less influence on the IAT (Greenwald et al., 2009; Stanley et al., 2011). We conducted a hierarchical linear regression analysis using the partiality score as dependent variable and added the different measurements block-wise (for details please see supplementary analysis S1 and supplementary Table S3). This analysis showed that the amount of gray matter volume

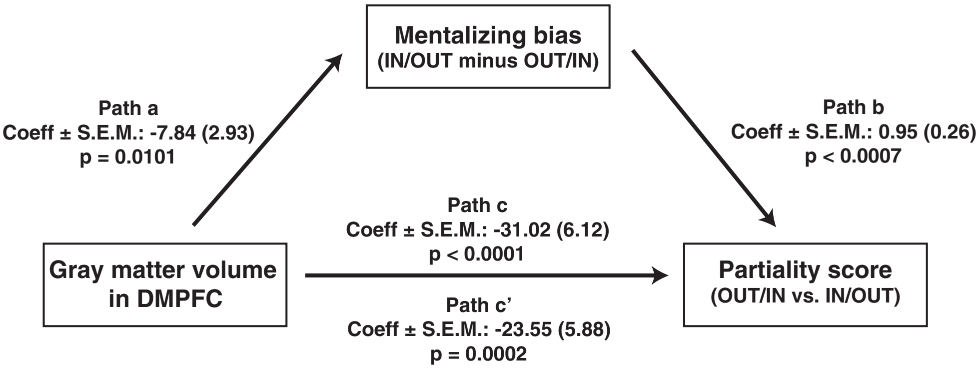

Fig. 4. Mentalizing partially mediates the impact of gray matter volume of the DMPFC on human impartiality. Depicted is the path diagram (including regression coefficients ± s.e.m. and p-values) of the mediation analysis demonstrating that gray matter volume affects individuals' propensity for impartiality through mentalizing processes. All four 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. In detail, path a represents the effect of gray matter volume on the mentalizing processes. Path b represents the impact of the mentalizing processes on impartiality, controlling for gray matter volume. Together, path a and path b represent the indirect (mediated) effect of gray matter volume on impartiality through the mentalizing processes. Path c′ represents the direct effect of gray matter volume on impartiality and is calculated controlling for the indirect, mediated effect. Path c represents the total (mediated and direct) effect of gray matter volume on impartiality. Finally, the decisive statistical test to examine whether mediation occurs is the statistical test between path c and path c′. Bootstrapping statistics (see Materials and methods section for details) revealed that path c′ is significantly smaller than path c ($p < 0.01$), providing evidence that the mentalizing processes are indeed a significant mediator. Because the direct path c′ is still significant, the mentalizing processes are a partial mediator.

in the DMPFC is capable of explaining considerable unique variance in impartiality, which cannot be explained by explicit and implicit psychological measures. More precisely, all these measures together are able to explain 42.6% of the inter-individual variance in impartiality (we report corrected R-squared values, i.e. the amount of variance in the dependent variable that the model explains in the population). However, almost half of this variance, namely 18.2%, could be accounted for solely by differences in gray matter volume of DMPFC. Thus, the gray matter volume in the DMPFC is a highly significant predictor of impartiality (standardized $\beta = -.478$, $p = 0.001$), even though several important implicit and explicit group-related measures are included in the regression model. Finally, a similar picture emerged for the thickness measure derived from the Freesurfer analysis, namely 15.7% of the variance in impartiality could be explained solely by differences in thickness of the DMPFC.

Discussion

The present study demonstrates the first link between inter-individual differences in human impartiality and neuroanatomical brain structure. Findings reveal that the phylogenetically (Krueger et al., 2009) and ontogenetically (Giedd et al., 1999) late maturing dorsomedial prefrontal cortex is strongly associated with individuals' propensity for impartiality. Whereas individuals with small gray matter volume in the DMPFC demonstrate a strong propensity for partiality, individuals with large gray matter volume in the DMPFC demonstrate a strong propensity for impartiality, i.e. they demonstrate an impartial punishment pattern characterized by reduced susceptibility for both favoritism towards ingroup perpetrators and hostility towards outgroup perpetrators.

Neuroanatomical studies in healthy adults consistently suggest that larger cortical volume or thickness is associated with better computational efficacy of a cortical region (for a recent review please see Kanai and Rees, 2011). Thus, our findings suggest that a more elaborated and sophisticated neural structure in the DMPFC seems to be critical for demonstrating impartial behavior. It is noteworthy that avoiding the preferential treatment of ingroup perpetrators seems to require more gray matter volume or thickness in the DMPFC (i.e. a more elaborated neural structure) compared to avoiding the discriminatory treatment of outgroup perpetrators (see Fig. 3).

Our study also sheds light on previous functional neuroimaging studies which demonstrated that differential treatment and judgment of ingroups and outgroups are associated with a differential activity pattern in the DMPFC (among other regions), i.e. individuals more strongly activate the DMPFC in interactions with ingroup members than in interactions with outgroup members (Baumgartner et al., 2012; Falk et al., 2012; Harris and Fiske, 2006). These findings gave rise to the speculation that the DMPFC drives partiality, i.e. the better the functioning of this brain area, the stronger the tendencies toward partiality. In contrast, our study suggests that an elaborated DMPFC helps to behave impartially. How can this discrepancy be resolved? We conjecture that individuals with large gray matter volume in the DMPFC are capable of upholding an impartial stance because they succeed in equally recruiting the same social cognitive processes when judging the behavior or the attitudes of both ingroup and outgroup members. Individuals with a less sophisticated neural structure in the DMPFC fail to recruit the same social cognitive processes for ingroup and outgroup members and consequently are less able to uphold an impartial stance. This failure in the recruitment of the same social cognitive processes could then be observable in neuroimaging studies as a differential activity pattern in the DMPFC.

In search of a potential mechanisms that explains the link between brain structure of DMPFC and impartiality we found that one of the social cognitive processes that plays an important role in upholding an impartial stance might be perspective taking. Individuals with large gray matter volume in the DMPFC do not differentiate in perspective taking towards ingroup and outgroup perpetrators. This evidence is consistent with various theories of negotiating peace between opposing sides (Kelman, 1986; Ross and Stillinger, 1991). These theories suggest that a fundamental roadblock in negotiating peace is the inability to take the opposing side's perspective. Our findings substantiate these assumptions by providing evidence that a neuroanatomical region, the DMPFC, previously shown to be associated with perspective taking, in fact seems to be important in overcoming this roadblock. A highly developed DMPFC seems to facilitate equal consideration of all sides, which in turn increases impartial behavior.

Finally, our findings raise questions ripe for future research: What might cause these neuroanatomical differences in DMPFC? Do certain genes, the environment, or a combination of both drive this effect? An understanding of the factors that influence volume and thickness of the DMPFC would be a heartening perspective for future intergroup conflicts and their peaceful settlement. Because there is growing evidence that certain training programs (e.g. meditation techniques and neurofeedback) can increase the volume of certain brain structures (e.g. Holzel et al., 2011; Luders et al., 2009; Zatorre et al., 2012), an improvement in human impartiality seems possible, and this might help build human societies with an increased capability to avoid or solve intergroup conflicts.

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Conflict of interests

The authors declare no conflict of interests.

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.neuroimage.2013.05.047.

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