1 **Title**

2 Neural signatures of prosocial behaviors

3

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Abstract

Prosocial behaviors are hypothesized to require socio-cognitive and empathic abilities—engaging brain regions attributed to the mentalizing and empathy brain networks. Here, we tested this hypothesis with a coordinate-based meta-analysis of 600 neuroimaging studies on prosociality, mentalizing and empathy (~12,000 individuals). We showed that brain areas recruited by prosocial behaviors only partially overlap with the mentalizing (dorsal posterior cingulate cortex) and empathy networks (middle cingulate cortex). Additionally, the dorsolateral and ventromedial prefrontal cortices were preferentially activated by prosocial behaviors. Analyses on the functional connectivity profile and functional roles of the neural patterns underlying prosociality revealed that in addition to socio-cognitive and empathic processes, prosocial behaviors further involve evaluation processes and action planning, likely to select the action sequence that best satisfies another person's needs. **By characterizing the multidimensional construct of prosociality at the neural level, we provide insights that may support a better understanding of normal and abnormal social cognition (e.g., psychopathy).**

Introduction

Prosociality refers to behaviors that are intended to benefit others at a cost to the self (de Waal, 2008; Jensen, 2016). Prosocial behaviors comprise a broad range of acts, which include caring, sharing, donating, helping, and volunteering (Dovidio, 2001; Padilla-Walker and Carlo, 2014; Penner et al., 2005). Three aspects are central to prosocial behaviors: (i) an agent intentionally carries out an act (ii) to benefit others (iii) without selfish motivations—as personal gains are an unintended by-product and not the goal of the prosocial act (Batson, 1987; Batson et al., 1981; Jensen, 2016). Previous research has suggested that these behaviors represent a broad and multidimensional construct constituted of cognitive and motivational processes (Coke et al., 1978; Padilla-Walker and Carlo, 2014).

Socio-cognitive abilities (e.g., mentalizing) are required for prosocial acts to understand another person's needs, infer goals across variable and novel contexts, and recognize when to engage in helping behavior (Warneken, 2015). Humans support those who are in need and ask for help, and they are more likely to do so if the latter are friends or ingroup members (Abrams et al., 2015; Warneken and Tomasello, 2009b; Weller and Hansen Lagattuta, 2013; Young et al., 1999). Prosocial acts require these abilities because they presuppose representations of self- and other-related intentions and goals (Batson, 1991; Brownell et al., 2006; Smiley, 2002), and ontogenetic evidence indicates that the development of complex prosocial behaviors is concomitant with the refinement of mentalizing abilities (Abrams et al., 2015; Eisenberg et al., 2015; Warneken and Tomasello, 2009a).

Further, the motivation to help (e.g., empathic concern) is required to resonate with the other's needy situation and to be motivated to see the other's needs satisfied (Dovidio and Penner, 2007). Such motivation has been proposed to be an evolutionary outcome of empathy (de Waal, 2008; Rumble et al., 2009; Xu et al., 2018). Humans exhibit empathic

74 concerns about the welfare of others (Batson, 2011) and based on these concerns, they feel

75 committed to alleviate others' distress and pain (de Waal, 2008; Warneken, 2015;

76 Warneken and Tomasello, 2009a).

77   Building on this evidence, a qualitative review of the neuroimaging literature has

78 proposed a set of brain regions that are likely involved in prosociality (Chakroff and

79 Young, 2014). On the one hand, socio-cognitive abilities are instantiated in brain areas

80 broadly associated with the mentalizing network (Bzdok et al., 2012) to support processes

81 that lead to the recognition of another person's needs and the circumstances in which

82 prosocial behaviors are appropriate. Candidate regions involve brain areas previously

83 implicated in social trait attributions and social event knowledge, such as the posterior

84 cingulate cortex (PCC) and medial prefrontal cortex (mPFC) (Hackel et al., 2015; Krueger

85 et al., 2009; Mitchell et al., 2009; Murray et al., 2012). On the other hand, the motivation

86 for a prosocial act is instantiated in brain regions broadly associated with the empathy

87 network (Bzdok et al., 2012; Fan et al., 2011) to support processes that lead to identifying

88 oneself with another person's needy situation and thus to the emergence of empathic

89 concerns (Chakroff and Young, 2014). Brain regions like the middle cingulate cortex

90 (MCC) and anterior insula (AI) might play a central role given their involvement in

91 vicarious affective experiences (e.g., pain, disgust, and distress) that promote empathic

92 concern (Corradi-Dell'Acqua et al., 2016; Fan et al., 2011).

93   One limitation of the current literature is that brain regions involved in prosociality

94 have been inferred from task-based functional MRI (fMRI) investigations of single

95 prosocial behaviors (Hackel et al., 2015; Karns et al., 2017; Moll et al., 2006; Park et al.,

96 2017). Evidence of the common neural network underlying all these prosocial acts is still

97 lacking. Further, small sample sizes and analytic flexibility (combined with publication

98 bias) pertain to other concerns for individual fMRI studies (Feredoes and Postle, 2007;

99 Raemaekers et al., 2007). Moreover, even though a recent comparative meta-analysis has

100 provided preliminary evidence for the involvement of the mPFC in giving behaviors

101 (Cutler and Campbell-Meiklejohn, 2019), it is still unclear to which extent the neural

102 underpinnings of other prosocial behaviors are part of the mentalizing and empathy brain

103 networks hypothesized to be involved in those very behaviors. Because prosociality is

104 such a composite and multidimensional construct, a quantitative meta-analysis of the

105 neuroimaging evidence on its components might be the most suitable means to unearth its

106 neural underpinnings.

107   Here, we aimed at testing the presence of the above-mentioned cognitive and

108 motivational modules of prosocial behaviors at the neural level and whether there are brain

109 patterns preferentially associated with prosociality. As prosocial behaviors imply carrying out

110 actions that help others, brain regions associated with action-outcome evaluations and action

111 planning might be involved as well. We performed a quantitative meta-analysis implementing

112 the activation likelihood estimation (ALE) algorithm (Eickhoff et al., 2009) and meta-analytic

113 connectivity analyses to identify the meta-analytic neural profile of prosociality, mentalizing,

114 and empathy, and examined their convergences and divergences. Finally, to characterize the

115 functions of the emerging neural patterns, we employed functional decoding (FD) analyses

116 (Eickhoff et al., 2017).

117

118 **Methods**

119 **ALE meta-analyses**

120 *Literature search and selection.* In this work, we performed three meta-analyses to identify

121 meta-analytic brain regions consistently engaged by (1) prosociality, (2) mentalizing, and (3)

122 empathy. A systematic online database search was performed on PubMed and Google Scholar

123 by entering various combinations of relevant search items referring to behaviors that the

124 literature had identified as prosocial behaviors. The following keywords were used for the

meta-analysis on prosociality: 'generosity', 'altruism', 'cooperation', 'charity', 'donation', 'prisoner's dilemma', 'prosocial', 'prosociality', 'altruistic behavior', 'prosocial behavior', 'dictator game', 'fMRI', 'magnetic resonance imaging', and 'neuroimaging', 'PET', 'positron emission tomography'.

The meta-analyses on empathy and mentalizing were built on previous meta-analyses (Bzdok et al., 2012; Fan et al., 2011; Lamm et al., 2011). **Given the massive number of new studies on empathy and mentalizing since those meta-analyses, we decided to update this previous work and test whether those results still hold with the new investigations added to the literature. Hence, our work directly builds on those previous meta-analyses (by including the experiments they analyzed) and aims to replicate and extend their results with a larger dataset including the newer studies from the literature, which provides more robust results.** Keywords for empathy were as follows: 'empathy', 'empathic', 'fMRI', 'magnetic resonance imaging', and 'neuroimaging', 'PET', 'positron emission tomography'. Keywords for mentalizing were as follows: 'mentalizing', 'theory of mind', 'perspective taking', 'false belief', 'fMRI', 'magnetic resonance imaging', and 'neuroimaging', 'PET', 'positron emission tomography'.

Also, we explored several other sources for all meta-analyses, including (a) the BrainMap database (http://brainmap.org), (b) work cited in review papers, and (c) direct searches on the names of frequently occurring authors. The studies were considered for the meta-analysis if they met the following criteria: (i) participants were free from psychiatric or neurological diagnoses; (ii) participants were adults; (iii) no pharmacological modulations were reported; (iv) fMRI was used as the imaging modality (no PET studies were found under the searched terms); (v) participants underwent a task in which they made a prosocial decision (only for prosociality); (vi) the prosocial decision implied some costs and was not exclusively advantageous to the participants (only for prosociality); (vii) whole-brain analyses were applied (excluding region of interest [ROI] analyses); (viii) fMRI results were derived from a

general linear model based on either a binary contrast or parametric analyses in within-subject

comparisons; and (ix) activations were presented in a standardized stereotaxic space

(Talairach or Montreal Neurological Institute, MNI). Note that Talairach coordinates were

converted into MNI space using the GingerALE software (https://www.brainmap.org/ale/)

with Brett's algorithm.

ALE algorithm. To determine the brain regions consistently activated across the identified

studies, we employed a coordinate-based meta-analytic approach using the ALE algorithm

(in-house MATLAB 2016b scripts) (Eickhoff et al., 2009). ALE determines the convergence

of foci reported from different functional neuroimaging studies with coordinates of peak

activations in standardized space (Laird et al., 2005; Turkeltaub et al., 2002). Foci are

interpreted as spatial probability distributions. Their widths are based on empirical estimates

of the spatial uncertainty based on between-subject and between-template variability of the

neuroimaging data (Eickhoff et al., 2009). The sample sizes of the studies reporting the foci

are used to weight the between-subject variability. Thereby, the ALE algorithm presupposes a

more reliable approximation to the 'true' activation for larger sample sizes, which are

modeled with smaller Gaussian distributions (Eickhoff et al., 2009).

An ALE map is obtained by calculating the union of the individual modulated

activation maps created from the maximum probability associated with anyone's focus

(always the closest one) for each voxel (Turkeltaub et al., 2012). This ALE map is determined

against a null-distribution of random spatial association between studies employing a non-

linear histogram integration algorithm (Eickhoff et al., 2012; Turkeltaub et al., 2012).

Significant results were assessed at a cluster-level family-wise error (*cFWE*) correction at $p <$

0.05 with a cluster defining threshold of $p < 0.001$ and 10,000 permutations (Eickhoff et al.,

2012; Eklund et al., 2016). To meet the criteria of robust unbiased results, clusters were

considered significant only if the most dominant experiment contributed to the significant

177   cluster on average less than 50%, and the two most dominant experiments contributed, on

178   average less than 80% (Bellucci et al., 2017; Bellucci et al., 2018; Eickhoff et al., 2016).

179   Experimental contributions were represented by the fraction of the ALE value accounted for

180   by each experiment contributing to the significant cluster. This average non-linear

181   contribution to the ALE value was computed from the ratio of the ALE values at the location

182   of the cluster with and without each contributing experiment (Eickhoff et al., 2016).

183   The following number of experiments, foci, and subjects were found for our three

184   meta-analyses: *prosociality* had 67 experiments, 433 foci, 1,642 subjects (i.e., an average of

185   24.7 subjects per experiment; see *Supplementary list of study for prosociality*); *empathy* had

186   273 experiments, 3,267 foci, 5,485 subjects (an average of 21.3 subjects per experiment; see

187   *Supplementary list of study for empathy*); and *mentalizing* had 240 experiments, 2,483 foci,

188   4,867 subjects (an average of 21.3 subjects per experiment; see *Supplementary list of study for*

189   *mentalizing*).

190

191   *Contrast and conjunction of ALE results.* To investigate differences and convergences

192   between the meta-analytic results for prosociality, empathy and mentalizing, two contrast and

193   conjunction analyses were performed. Contrast analyses were based on voxelwise differences

194   of the Z-scores obtained from the ALE maps. Significance was tested with a permutation test.

195   **Thereby, the experiments of each meta-analysis were pooled and randomly divided into**

196   **two groups of the same size as the two original datasets**. The ALE scores of these two

197   randomly generated groups were voxelwise subtracted from each other to generate a map of

198   ALE score differences. This procedure was repeated 10,000 times, yielding an empirical null-

199   distribution of maps of ALE score differences. Finally, the ALE maps of 'true' differences

200   were thresholded at a posterior probability of $p > 95\%$. Conjunction analyses were performed

201   by computing a minimum conjunction with a *cFWE* < 0.05 and a voxelwise, cluster-forming

202   threshold of $p < 0.001$ (Nichols et al., 2005).

203

Meta-analytic functional profiles

Task-free resting-state functional connectivity analysis. Task-free resting-state functional connectivity (RSFC) of the prosociality brain regions was estimated from fMRI images of 192 healthy volunteers from the Enhanced Nathan Kline Institute – Rockland Sample, who underwent a resting-state scan right before which they were instructed to look at a fixation cross, not to think of anything in particular and not to fall asleep (Nooner et al., 2012). The re-analysis of the data was approved by the local ethics committee of the Heinrich-Heine University in Düsseldorf. Functional images were acquired with a Siemens TimTrio 3T scanner using a gradient-echo, echo-planar imaging (EPI) pulse sequence (repetition time = 1.4s; echo time = 30 ms, flip angle = 65, voxel size = $2.0 \times 2.0 \times 2.0$ mm; number of slices = 64).

After minimal preprocessing (unwrap and realign), FIX (FMRIB's ICA-based Xnoiseifier, version 1.061 as implemented in FSL 5.0.9) (Griffanti et al., 2014; Salimi-Khorshidi et al., 2014) was used to remove physiological and movement artifacts by decomposing the data into independent components and identifying noise components with the help of a large number of distinct spatial and temporal features via pattern classification. Unique variance related to the artefactual independent components was regressed from the data together with 24 movement parameters (including derivatives and second-order effects as previously described and evaluated) (Satterthwaite et al., 2013). After having excluded the first four scans, functional images were preprocessed using SPM8 (Wellcome Trust Centre for Neuroimaging, London) and in-house MATLAB scripts as follows: functional images were corrected for head movement using a two-pass affine registration (alignment to the initial volume followed by alignment to the mean after the first pass); the mean image was then spatially normalized to the ICBM-152 reference space using the "unified segmentation" approach (Ashburner and Friston, 2005); using the resulting deformation parameters, the

9

229 individual functional images were subsequently smoothed with a 5-mm full width at half

230 maximum Gaussian kernel to improve the signal-to-noise ratio and compensate for residual

231 anatomic variations. The time-course of each seed was extracted by computing the first

232 eigenvariate of the time-series of all voxels within 5 mm of the seed coordinates.

233 **To reduce spurious correlations, variance explained by the mean white matter**

234 **and cerebral spinal fluid signal were removed from the timeseries, which was then band-**

235 **pass filtered with a filter ranging between 0.01 and 0.08 Hz. Afterwards, the functional**

236 **connectivity profile of each seed was estimated by correlating each seed's timeseries with**

237 **the timeseries of all other gray-matter voxels across the brain (Pearson correlation).**

238 Correlation coefficients were transformed into Fisher's z-scores, which were entered in a

239 second-level ANOVA for group analysis, including age and **sex** as covariates of no interest.

240 The data was then subjected to non-parametric permutation-based inference and cluster-level

241 thresholded at $p < 0.05$ to correct for multiple comparisons.

242

243 *Task-based meta-analytic connectivity mapping.* The task-based co-activation profile of each

244 prosociality brain region was estimated employing task-based meta-analytic connectivity

245 mapping (MACM), which uses patterns of co-activations reported in standardized space by

246 neuroimaging studies in the BrainMap database (http://www.brainmap.org/) (Laird et al.,

247 2009; Langner et al., 2014) and related to activations of between-condition differences from

248 whole-brain neuroimaging contrasts in healthy individuals. Studies including between-group

249 differences (e.g., age, **sex** or handedness), effects of interventions (e.g., pharmacological or

250 training-based), and clinical populations were excluded.

251 **We used a 5-mm radius around the peak coordinates of the meta-analytic clusters**

252 **from the prosociality meta-analysis (i.e., of the four prosociality brain regions).** The

253 following experimental contrasts, number of foci and participants were identified for each

254 prosociality brain region: dlPFC (96 experimental contrasts; 1,356 foci; 1,417 participants),

255 dPCC (117 experimental contrasts; 1,415 foci; 1,749 participants), vmPFC (245 experimental

256 contrasts; 2,862 foci; 3854 participants), and MCC (404 experimental contrasts; 5,806 foci;

257 5,896 participants). Whole-brain peak coordinates of all those studies from BrainMap that

258 reported at least one focus of activation within the respective seeds were downloaded.

259 Coordinates were then analyzed with the ALE algorithm to detect areas of convergence of co-

260 activations with the two seeds. Finally, the ALE maps were thresholded at $p < 0.05$ cluster-

261 level corrected (voxelwise, cluster-forming threshold: $p < 0.001$) and converted into z-scores

262 for display.

263

264 *Conjunction of meta-analytic connectivity profiles.* To determine the robustly interconnected

265 areas from the task-free and task-based meta-analytic connectivity profiles of prosociality, a

266 conjunction analysis was performed using the minimum conjunction of the previous

267 functional connectivity results thresholded with a *cFWE* < 0.05 and a voxelwise, cluster-

268 forming threshold of $p < 0.001$ (Nichols et al., 2005). To further single out brain areas that

269 were engaged exclusively by prosociality and neither mentalizing nor empathy, two exclusive

270 conjunctions were conducted between the extended prosociality network and both mentalizing

271 and empathy brain regions identified in the previous ALE analysis. The union of these

272 exclusive maps yielded overlapping brain regions that were preferentially associated with

273 prosociality.

274

275 **Functional characterization of meta-analytic clusters**

276 **The functional role of the prosociality brain regions were characterized based on the**

277 **behavioral domains (BD)in the BrainMap database by using forward and reverse**

278 **inference (Müller et al., 2013; Rottschy et al., 2012).** In the forward inference, the

279 functional profile was determined by identifying BD for which the probability of finding

280 activation in the respective set of regions was significantly higher than the overall (*a priori*)

281 chance across the entire database. That is, we tested whether the conditional probability of

282 activation given a particular BD, i.e., P(Activation|Domain), was higher than the baseline

283 probability of activating the regions in question *per se*, namely, P(Activation). Significance

284 was established using a binomial test using the standard $\alpha = 0.05$, corrected for multiple

285 comparisons using the false discovery rate (*FDR*). In the reverse inference, the functional

286 profile was determined by identifying the most likely BD, given activation in a particular set

287 of regions. This likelihood P(Domain|Activation) can be derived from P(Activation|Domain)

288 as well as P(Domain) and P(Activation) using Bayes' rule. Significance was then assessed

289 using a chi-squared test (with *FDR* < 0.05 for correction of multiple comparisons).

290

291 **Anatomical labeling and data visualization**

292 The SPM Anatomy toolbox (www.fz-juelich.de/ime/spm_anatomy_toolbox, v.2.2b, Eickhoff

293 et al., 2007), and MRIcron (http://people.cas.sc.edu/rorden/mricron/install.html/) were used

294 for   anatomical   labeling.   **MRIcroGL**

295 **(https://www.mccauslandcenter.sc.edu/mricrogl/home/)   was   used   for   brain**

296 **visualizations (with default settings).**

297

298 # Results

299 **Meta-analytic clusters for prosociality, empathy and mentalizing**

300 We first identified brain regions consistently activated by prosociality, empathy, and

301 mentalizing. For prosociality, we searched both broad and general keywords, such as

302 prosocial and prosocial behaviors, as well as more specific key terms describing single

303 prosocial behaviors, such as generosity, altruism, charity, and donation. Moreover, to be able

304 to include all appropriate and relevant behaviors, scientific paradigms known to

305 experimentally investigate forms of prosocial behaviors were searched as well, like prisoner's

306 dilemma and dictator game. For empathy and mentalizing, we searched key terms related to

307 these psychological phenomena, such as empathic and theory of mind, similarly to previous

308 work (Bzdok et al., 2012; Fan et al., 2011; Lamm et al., 2011).

309   We observed that prosocial behaviors consistently activated the ventromedial PFC

310 (vmPFC), left dorsolateral PFC (dlPFC), MCC, and dorsal PCC (dPCC)—a cluster between

311 the PCC and precuneus (**Fig. 1 & Tab. 1 & Tab S1**). Replicating and extending previous

312 findings, we observed that empathy consistently activated, among other regions, the bilateral

313 AI, bilateral amygdala, and MCC (**Fig. 2a & Tab. S2**). Finally, we observed that mentalizing

314 consistently activated, among other regions, the bilateral temporal cortex (TC) extending from

315 the temporoparietal junction (TPJ) to the temporal pole (TP), PCC and mPFC (**Fig. 2b & Tab.**
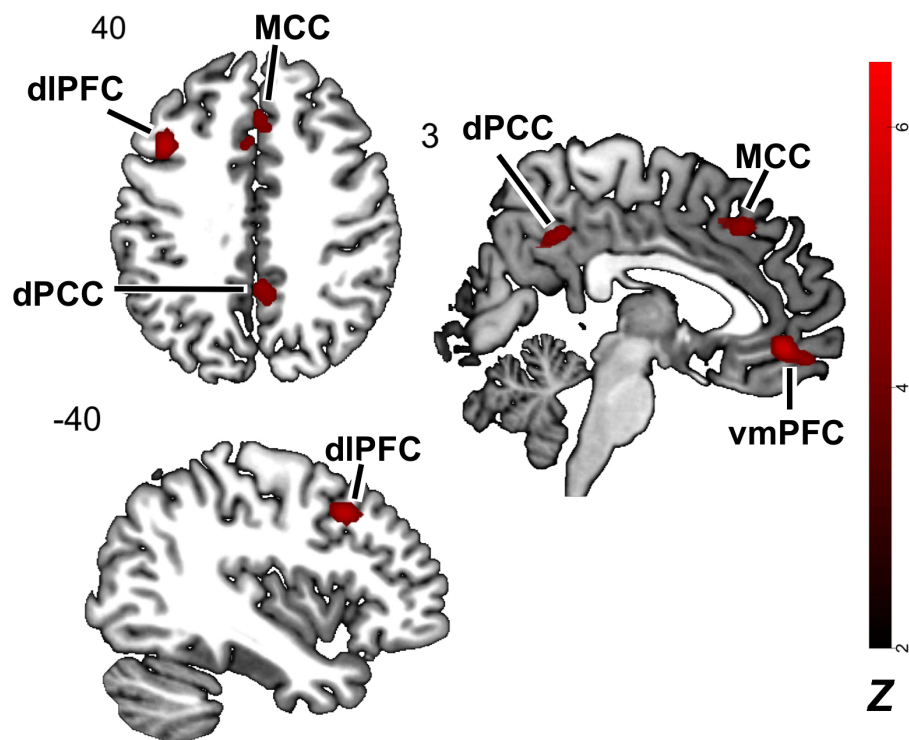
316 **S3**).

317

Figure 1. Prosociality brain regions. ALE meta-analysis results showing brain regions consistently engaged by prosocial behaviors. Results were cluster-level familywise-error corrected for multiple comparisons (*cFWE* < .05). Depicted are *Z* values. dlPFC, dorsolateral prefrontal cortex; dPCC, dorsal posterior cingulate cortex; MCC, middle cingulate cortex; vmPFC, ventromedial prefrontal cortex; ALE, activation likelihood estimation.
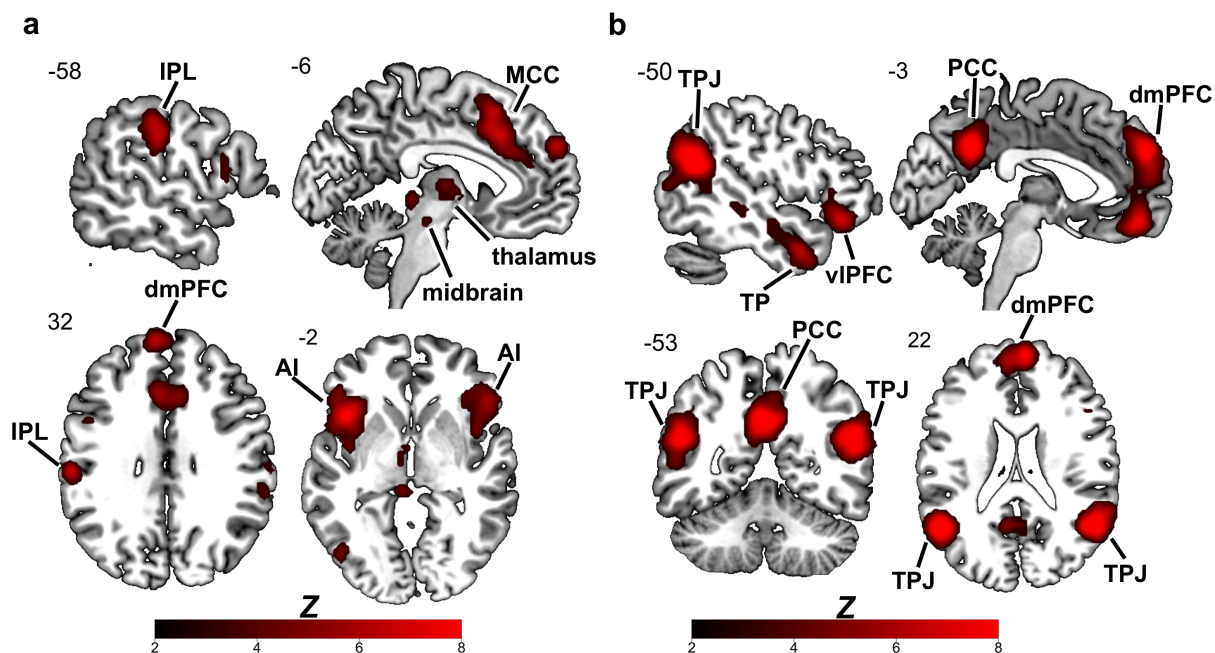
318

Figure 2. Empathy and mentalizing brain regions. ALE meta-analyses results showing brain regions consistently engaged by empathy (**a**) and mentalizing (**b**). Results were cluster-level familywise-error corrected for multiple comparisons (*cFWE* < .05). Depicted are *Z* values. IPL, inferior parietal lobule; dmPFC, dorsomedial prefrontal cortex; MCC, middle cingulate cortex; AI, anterior insula; TPJ, temporoparietal junction; TP, temporal pole; vlPFC, ventrolateral prefrontal cortex; PCC, posterior cingulate cortex; dmPFC, dorsomedial prefrontal cortex; ALE, activation likelihood estimation.

319

Brain Regions	Anatomical location	BA	Coordinates			Z score	Cluster Size	Contributing experiments	MDE	2MDE
			x	y	z					
vmPFC	middle orbital gyrus	10 (Fp2/s32)	0	46	-8	6.21	263	16 (23.9%)	11.2%	22.4%
L dlPFC	middle frontal gyrus	44	-40	18	40	4.71	90	11 (16.4%)	23.3%	43.0%
MCC	superior medial gyrus	32	0	22	42	3.42	108	12 (17.9%)	17.0%	32.8%
dPCC		31	0	-52	36	3.51	119	9 (13.4%)	20.3%	39.3%

Table 1. Coordinates of prosociality brain regions. Meta-analytic results for brain regions associated with prosociality. Listed are clusters consistently activated for prosocial behaviors with MNI coordinates (in mm), *Z* scores at the peak, cluster size (in voxels), number of contributing experiments (with their percentage in parentheses based on the total number of experiments), and the contribution percentages of the most dominant experiments. vmPFC, ventrolateral prefrontal cortex; dlPFC, dorsolateral prefrontal cortex; MCC, middle cingulate cortex; dPCC, dorsal posterior cingulate cortex; BA, Brodmann area; anatomical assignment based on the Anatomy toolbox in parentheses; L, left; ALE, activation likelihood estimation; MNI, Montreal Neurological Institute; MDE, most dominant experiment; 2MDE, two most dominant experiments.

320 **Converging and diverging neural patterns between prosociality, empathy and**

321 **mentalizing**

322 Once we identified the meta-analytic clusters consistently activated by prosociality, empathy,

323 and mentalizing, **we set out to test to which degree the neural patterns of prosociality**

include brain regions that are part of the empathy and mentalizing meta-analytic maps.

Given the hypothesis on the cognitive level that prosocial behaviors require socio-cognitive and empathic abilities, we should observe a certain degree of convergence. We ran two conjunction analyses between the meta-analytic map for prosociality and those for empathy and mentalizing identified in the previous analyses to estimate these neural convergences (**Tab. S4**). We observed that the MCC was commonly activated by prosociality and empathy (**Fig. 3a**), whereas the vmPFC and dPCC were commonly activated by prosociality and mentalizing (**Fig. 3b**). These results confirm on the neural level that some brain regions associated with empathic and socio-cognitive processes were engaged by prosocial behaviors as well.

However, it is still an open question whether any of the meta-analytic clusters identified by the ALE analyses are preferentially activated by prosocial behaviors but neither empathy nor mentalizing. Therefore, we ran two contrast analyses between the meta-analytic map for prosociality and those for empathy and mentalizing. We observed that the left dlPFC, dPCC, and vmPFC were preferentially activated by prosocial behaviors as opposed to empathy (**Fig. 3c & Tab. S5**), whereas the MCC, AI, amygdala and inferior parietal lobule (IPL) were preferentially engaged by empathy as opposed to prosociality (**Fig. 3c & Tab. S5**). On the contrary, in the second contrast analysis between prosociality and mentalizing, we observed that the vmPFC, left dlPFC, and MCC were preferentially activated by prosocial behaviors (**Fig. 3d & Tab. S5**), while the TPJ, lateral PFC, and dorsal mPFC were preferentially engaged by mentalizing (**Fig. 3d & Tab. S5**).
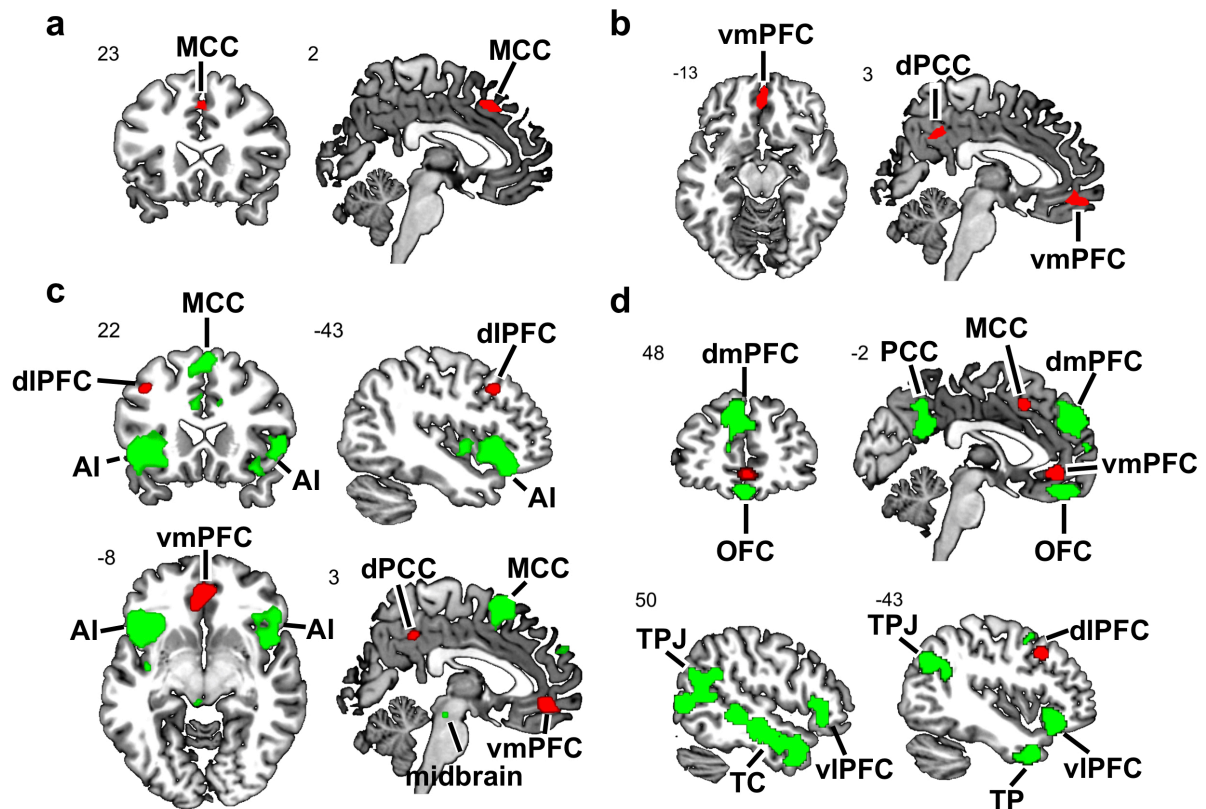
Figure 3. Contrast and conjunction analyses. Conjunction analyses to identify brain regions commonly engaged by prosociality and empathy (**a**) and by prosociality and mentalizing (**b**). **Contrast analyses to identify diverging neural patterns between prosociality (red) and empathy (green) (c) and between prosociality (red) and mentalizing (green) (d)**. MCC, middle cingulate cortex; vmPFC, ventromedial prefrontal cortex; dPCC, dorsal posterior cingulate cortex; dlPFC, dorsolateral prefrontal cortex; AI, anterior insula; dmPFC, dorsomedial prefrontal cortex; PCC, posterior cingulate cortex; OFC, orbitofrontal cortex; TPJ, posterior temporoparietal junction; TC, temporal cortex; vlPFC, ventrolateral prefrontal cortex; TP, temporal pole.

345

346   These findings suggest that prosocial behaviors involve both socio-cognitive and

347   empathic processes, recruiting some of the brain regions that are part of the mentalizing

348   network (e.g., dPCC) and some of the brain regions that are part of the empathy

349   network (e.g., MCC). However, our contrast analyses further revealed brain regions like

350   the vmPFC and dlPFC that were more consistently engaged by prosocial behaviors than

351   empathy and mentalizing, suggesting a preferential role for these brain regions in

352   prosociality.

353

354   **Connectivity and co-activation analyses of the prosociality brain regions**

355   We next set out to examine whether the brain regions underlying prosocial behaviors form an

356   interrelated functional connectivity network. **A good match between resting-state networks**

357   **and task networks has been shown before, which has led to the hypothesis that**

358   **functional networks interact with each other at rest with the same functional hierarchy**

359   **that is observed during task performance (Cole et al., 2014; Smith et al., 2009).**

360   **Specifically, resting-state functional connectivity maps onto a layout of activity patterns**

361   **elicited by different cognitive domains (Raichle, 2015; Tavor et al., 2016). Hence,**

362   **identifying the meta-analytic functional connectivity networks of a specific brain region**

363   **during both rest and task, and analyzing their convergence help to robustly determine**

364   **the consistent functional connectivity profile of that region.** We employed two whole-

365   brain connectivity analyses, namely, task-free RSFC and task-based MACM across more than

366   70 cognitive domains, **to first determine the whole-brain functional connectivity layout of**

367   **each prosociality brain region and then their exclusive convergence for prosociality as**

368   **opposed to mentalizing or empathy.**

369   These analyses revealed a broad and converging functional connectivity profile for the

370   prosociality brain regions (**Fig. 4a-b & Tab. S6-7**). In particular, the dPCC and vmPFC were

371   similarly coupled to brain areas such as the TPJ, angular gyrus, and TC, whereas the MCC

372   and dlPFC were more closely coupled with lateral parietal and prefrontal areas like the

373   bilateral IPL and lateral PFC. Further, the vmPFC reveled functional connectivity with the

374   striatum and orbitofrontal cortex, whereas the dlPFC was also functionally coupled with the

375   PCC and TPJ. A conjunction of these connectivity profiles revealed a common functional

376   connectivity network involving the four ALE meta-analytic brain regions (i.e., dlPFC, dPCC,

377   MCC and vmPFC) with functional connectivity with cortical and subcortical regions, like the

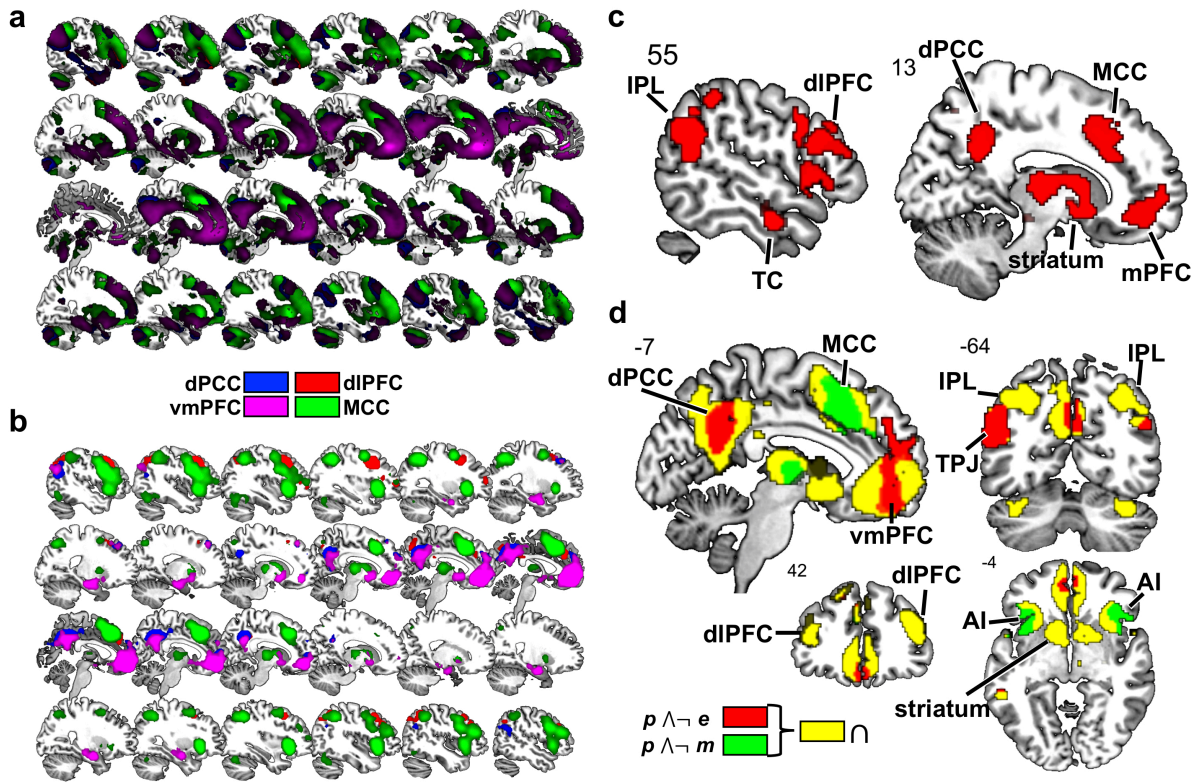378   striatum, bilateral TC and IPL with overlaps in the TPJ (**Fig. 4c & Tab. S8**).

Figure 4. Functional connectivity and co-activation analyses. Results of task-free resting-state connectivity (**a**) and task-based co-activations (**b**) of the four meta-analytic clusters consistently engaged by prosocial behaviors. Conjunction analyses of the task-free and task-based functional connectivity profiles to identify the extended prosociality network (**c**). Common brain regions (yellow) of the two maps yielded by the exclusive conjunctions of the prosociality network and empathy (red), and the prosociality network and mentalizing (green) (**d**). dPCC, dorsal posterior cingulate cortex; dlPFC; dorsolateral prefrontal cortex; vmPFC, ventromedial prefrontal cortex; MCC, middle cingulate cortex; IPL, inferior parietal lobule; TC, temporal cortex; mPFC, medial prefrontal cortex; TPJ, temporoparietal junction; AI, anterior insula; *p*, prosociality network; *e*, empathy; *m*, mentalizing; ∧, logical 'and'; ¬, logical negation; ∩, conjunction.

379   Part of these common functional connectivity patterns includes regions previously

380   observed to be associated with the mentalizing and empathy meta-analytic maps. Hence, to

381   single out brain regions preferentially coupled with the meta-analytic activation patterns of

382   prosocial behaviors, we further computed an exclusive conjunction analysis between this

383   functional connectivity profile of prosociality and each of the mentalizing and empathy meta-

384   analytic maps (**Fig. 4d**). We observed that the striatum, bilateral dlPFC, and IPL were

385   preferentially part of the functional connectivity profile of prosocial behaviors.

386

387   **Functional characterization of the prosociality brain regions**

To gain insights into the different computational processes undertaken by the emerged meta-analytic neural patterns for prosociality, we implemented FD analyses using forward and reverse inferences, which characterized the functional roles of the identified prosociality brain regions. Functional roles were characterized using the BD in the BrainMap database, which describe categories (i.e., action, cognition, emotion, interception, and perception) and subcategories (e.g., reward, social cognition, language, working memory) of the mental operations likely isolated by the experimental contrasts stored in the database (Fox and Lancaster, 2002; Fox et al., 2014; Laird et al., 2009). **We performed forward and reverse inferences to identify the experiments that engage a particular brain region, and then analyzed the experimental meta-data that describe the experimental settings employed in the studies (Bellucci et al., 2020; Camilleri et al., 2018)—enabling statistical inference on the type of tasks that evoke activations in a certain brain region.**

Forward and reverse inferences provide converging results (**Fig. 5a-b**). In particular, we found that the dPCC was mainly associated with social cognition and the vmPFC with an affective domain involving fear, reward, and gustative perception, but also with cognitive functions such as reasoning and, like the dPCC but to a lesser extent, social cognition. Both the dlPFC and the MCC were associated with forms of cognitive control, but while the MCC was mainly related to a cognitive domain involving reasoning and semantics, the dlPFC, like the vmPFC, further yielded functional associations with an affective domain. However, the specific affective processes associated with the dlPFC were different from the ones associated with the vmPFC, suggesting different functional roles of these two brain regions in affective processing. These results indicate both similarities and differences in the functional roles of the prosociality brain regions. In particular, they refer to partly converging, but still distinct functional modules undertaking separate aspects of the processes underlying a prosocial act.
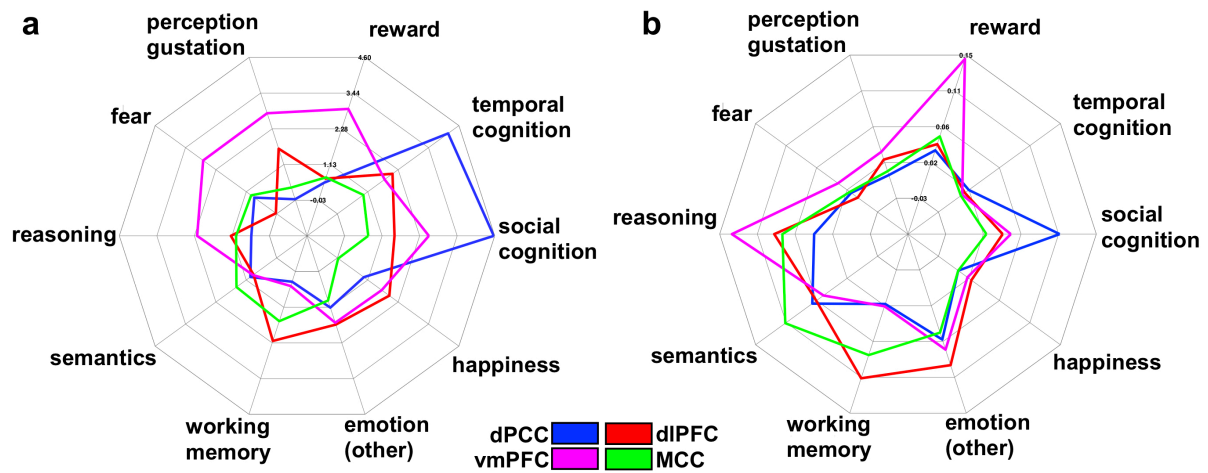
Figure 5. Functional decoding analyses. Forward (**a**) and reverse (**b**) functional decoding analyses to characterize the functional roles of the four meta-analytic clusters consistently engaged by prosocial behaviors. For forward functional decoding analyses, the likelihood ratios are depicted, whereas probability values are depicted for reverse functional decoding. dPCC, dorsal posterior cingulate cortex; dlPFC; dorsolateral prefrontal cortex; vmPFC, ventromedial prefrontal cortex; MCC, middle cingulate cortex.

413

Discussion

414

415   Prosocial behaviors refer to a wide range of acts aimed at benefitting others (e.g., helping,

416   sharing, and caring). Psychological accounts posit that the psychological components of

417   prosocial behaviors comprehend socio-cognitive abilities to understand the other's goals, and

418   empathic concern to be motivated to help. This hypothesis predicts the engagement of the

419   mentalizing and empathy brain networks on the neural level. Here, we found partial evidence

420   to support this hypothesis. In particular, brain regions consistently activated by prosocial

421   behaviors do engage areas associated with mentalizing (dPCC) and empathy (MCC).

422   However, we also observed other brain regions (dlPFC and vmPFC) preferentially activated

423   by prosociality with functional connectivity with subcortical and lateral frontoparietal areas.

424

425   *Understanding another person's goals*

426   To act prosocially, an agent has to understand the intentions and goals of another individual.

427   Mentalizing is hence a prerequisite of prosocial behaviors. Socio-cognitive abilities enable the

428   helping agent to realize whether and how particular actions help another to reach her goals

429   (Frith and Frith, 2003; Tomasello et al., 2005). Ontogenetic evidence indicates that only

430   rudimental forms of prosociality are present in preschool children with non-fully developed

431   mentalizing abilities and only in contexts that do not require inferences on complex goals

432   (Brownell et al., 2006; Warneken and Tomasello, 2009a).

433   Our results showed that prosociality consistently activated the dPCC, which was

434   commonly recruited by prosociality and mentalizing, and was more strongly associated with

435   prosociality than empathy. Connectivity analyses revealed that the dPCC was coupled to brain

436   areas typically part of the mentalizing network (Buckner et al., 2008; Frith and Frith, 2003;

437   Ingvar, 1974) and functional decoding pointed to a role in social cognition for this region.

438   Given these results and previous evidence on its importance in perspective-taking (Cavanna

439   and Trimble, 2006), the dPCC is a good candidate for a role in evaluations of another person's

440   goals in prosocial behaviors. A previous fMRI study found the dPCC to be recruited for

441   intentional causality and prospective memory in a task where participants had to identify the

442   intentions of consequential actions and bear in mind an intention to act (den Ouden et al.,

443   2005). With this respect, the dPCC might help an agent to prospectively embed her prosocial

444   act into an action sequence that conforms to another individual's goals. This hypothesis is also

445   consistent with other functions attributed to the dPCC, such as visual imagery in episodic

446   memory (Fletcher et al., 1995; Fletcher et al., 1996) and preparation and execution of

447   intentionally guided actions (Astafiev et al., 2003).

448   Contrary to the predictions of a previous qualitative review of the neural correlates of

449   prosociality (Chakroff and Young, 2014), we did not observe any consistent activations in the

450   TPJ. Unlike the dPCC, the TPJ has been associated with belief representations and with the

451   justification of a belief (Koster-Hale et al., 2017; Young et al., 2010). Interestingly, the neural

452   signal in the TPJ is predictive only of prosocial behaviors in situations of advantageous

453   inequality (e.g., giving to those who are poorer but not wealthier than oneself) with no links to

454   other prosocial behaviors (Morishima et al., 2012). Even though the TPJ was not

preferentially recruited by prosocial behaviors in our study, it was still part of the functional connectivity network of the prosociality brain regions, suggesting that it plays an essential role in supporting their underlying computations. **Future work might consider clarifying the role of intentionality and perspective-taking in prosocial behaviors to provide better insights into the involvement of specific mentalizing brain regions**.

Motivated to help others

Further, prosocial behaviors require a motivation to help another—arguably triggered by empathic concerns (Batson et al., 1987; Coke et al., 1978; Eisenberg et al., 1994). Individual differences in empathic skills (Bird and Viding, 2014; Blair, 2005; Decety and Jackson, 2004) have been linked to prosocial tendencies and prosocial learning, that is, learning when to benefit others (Lockwood et al., 2016; Lockwood et al., 2014). Importantly, vicarious distress is not enough to motivate prosocial behaviors if it is not accompanied by other-oriented empathic concerns (FeldmanHall et al., 2015).

In our study, the only brain area consistently engaged by prosocial behaviors that overlapped with the empathy network was the MCC. Connectivity analyses revealed that this region was functionally coupled with lateral parietal and prefrontal areas generally part of a central-executive network (Bressler and Menon, 2010). Functional decoding analyses characterize the MCC as having a specific role in cognitive control. These results are in line with previous studies proposing cognitive-motor control as the core functional computation of this region (Botvinick et al., 2004; Guo et al., 2013; Hoffstaedter et al., 2014; Shackman et al., 2011; Shenhav et al., 2014; Singer et al., 2004). As our results indicate that the MCC was preferentially related to a cognitive domain rather than an affective or social domain, the MCC might be a good candidate for representations of empathic concern, signaling the motivational component of empathy that prompts to take action to change the emotionally painful situation of another person's needy condition.

481   Contrary to previous hypotheses, we found no associations between prosociality and

482   the AI, which is considered a central region to empathic processes (Lamm et al., 2011; Lamm

483   et al., 2017; Singer et al., 2004). These results might reflect the two different roles of the AI

484   and MCC in empathy. Unlike some neuroimaging accounts that lump together the functions

485   of the AI and MCC in a general role in "affect sharing" (Lamm et al., 2017), others suggest

486   that the MCC represents a cognitive-evaluative form of empathy, whereas the AI represents

487   an affective-perceptual form (Fan et al., 2011). Our results seem to confirm this functional

488   distinction, suggesting that the cognitive form of empathy, in particular, its motivational

489   component, might play a more central role in prosociality.

490

491   *Enacting prosocial behaviors*

492   Further, our contrast analyses demonstrated that the vmPFC and, in particular, the dlPFC were

493   preferentially associated with prosociality as opposed to empathy and mentalizing. Our

494   functional decoding analyses revealed that these regions were closely related to both cognitive

495   and affective domains, suggesting that they integrate cognitive and affective signals relevant

496   for prosocial behaviors.

497   Functional connectivity analyses revealed functional coupling of the vmPFC with both

498   mentalizing areas (e.g., TPJ) and subcortical brain regions (e.g., striatum). Functional

499   decoding analyses suggested a role for the vmPFC in both socio-cognitive and affective

500   processes. Given these results and previous evidence on its role in signaling outcome

501   expectancies and behaviorally-relevant value information (Bellucci et al., 2019a; Bellucci et

502   al., 2019b; Iigaya et al., 2019; Na et al., 2019), the vmPFC might be responsible for the

503   integration of cognitive and affective signals in prosocial behaviors to prospectively evaluate

504   actions and outcomes associated with a prosocial act. In particular, in concert with the

505   striatum and TPJ, which have been shown to play a role in feelings of happiness during

506   generous decisions (Park et al., 2017), the vmPFC might evaluate the positive consequences

507   that a prosocial act has for the helping agent. This resonates with a recent study indicating that

508   individuals report the positive feelings following a prosocial act to be the second-most

509   influential reason to behave prosocially (after "helping those in need" and before "feelings of

510   empathy") (Sisco and Weber, 2019).

511   Importantly, the dlPFC was the only brain area preferentially engaged by prosocial

512   behaviors and activated by neither empathy nor mentalizing. Connectivity analyses linked the

513   dlPFC with both cognitive control regions (e.g., parietal cortex) and mentalizing regions (e.g.,

514   PCC, TPJ). Functional decoding analyses linked the dlPFC to roles in both cognitive and

515   affective processing. This configuration of activation patterns involving the dlPFC, PCC and

516   parietal cortex is often observed when flexible behavioral adaptation to the current social

517   interaction is required based on beliefs about the character and reputation of the interacting

518   partner (Hackel et al., 2015; Igelström et al., 2016; Mende-Siedlecki et al., 2013). A recent

519   neuroimaging study has demonstrated that neural signal in these regions is not only

520   informative of the character traits of another person but also predicts an individual's

521   willingness to trust that person in a later interaction (Bellucci et al., 2019a). Hence, our results

522   suggest that the recruitment of the dlPFC allows the tracking of another person's behavior for

523   inferences on her intentions and planning on the adequate course of actions.

524

525   *Limitations*

526   A couple of limitations have to be addressed. First, the neuroimaging literature, unlike

527   psychological work, has not yet tackled the specific neural patterns underlying the different

528   components of empathy (with the exception of some attempts (Fan et al., 2011)), leaving in

529   particular the neural signatures of empathic concerns underspecified. Given its role in

530   cognitive-motor control, we have here proposed that the MCC might signal behaviorally-

531   relevant motivational states, such as empathic concern (Kolling et al., 2016). However, as

532   neuroimaging studies have so far primarily neglected this motivational component of empathy

533 and the BrainMap does not even contain a behavioral domain for motivation or empathic

534 concern in its catalog, we were here unable to test this hypothesis. Second, we here aimed at

535 identifying the common neural patterns underlying prosocial acts. However, it still remains an

536 open question whether different types of prosocial acts recruit differing neural patterns. Given

537 the few experiments for each of the prosocial acts here considered, future studies are needed

538 to tackle this question. **Moreover, we note that most investigations on prosociality use**

539 **economic paradigms (see *Supplementary list of studies for prosociality*). For more robust**

540 **and generalizable results, future studies might consider other types of paradigms, such**

541 **as vignettes to test individuals' tendency to prosocial behaviors in different contexts (like**

542 **in studies on third-party punishment; Bellucci et al., 2020), virtual reality to more**

543 **ecologically simulate situations requiring prosocial actions or longitudinal studies with**

544 **chronic (as opposed to acute) manipulation of prosocial behaviors to investigate the**

545 **effects of being prosocial on the brain (Lyubomirsky et al., 2005; Park et al., 2017). For**

546 **these future studies, our results provide meta-analytic clusters that could be used as**

547 **regions of interest to test specific hypotheses in investigations with other methods such**

548 **as functional near-infrared spectroscopy and transcranial magnetic stimulation.** Despite

549 these limitations, we were able to reliably characterize the specific activation patterns,

550 connectivity profile and functional roles of brain areas consistently activated by prosocial

551 behaviors.

552

553 *Conclusions*

554 Taken together, we found a set of brain regions that were consistently activated by prosocial

555 behaviors. These activation patterns partially overlapped with mentalizing and empathy brain

556 regions, lending support to the hypothesis based on psychological research that socio-

557 cognitive and empathic abilities are central to prosociality. However, we also found that the

558 vmPFC and, in particular, the dlPFC were preferentially recruited by prosocial acts,

559   suggesting that prosocial behaviors require the involvement of other important processes.

560   Analyses on their functional connectivity profile and functional roles suggest that the vmPFC

561   and dlPFC might be involved in valuation and planning of prosocial actions, respectively.

562   These results clarify the role of mentalizing and empathic abilities in prosociality and

563   provides useful insights into the neuropsychological processes underlying human social

564   behaviors. For instance, they might help understand where and how things go awry in

565   different neural and behavioral disorders such as psychopathy and antisocial behavior (Blair,

566   2007).

567

Author contribution

G.B. conceived the study idea. G.B. and F.K. designed the study. G.B. collected the data. G.B. and J.A.C. carried out the data analysis. S.B.E. provided analysis tools. G.B. wrote the manuscript with edits from F.K., J.A.C. and S.B.E.. All authors approved the final version of the manuscript.

Conflict of Interest

The authors declare no conflicts of interest, financial or otherwise.

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