



Development of functional network architecture explains changes in children's altruistically motivated helping

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Abstract

Childhood is marked by profound changes in prosocial behaviour. The underlying motivational mechanisms remain poorly understood. We investigated the development of altruistically motivated helping in middle childhood and the neurocognitive and -affective mechanisms driving this development. One-hundred and twenty seven 6–12 year-old children performed a novel gustatory costly helping task designed to measure altruistic motivations of helping behaviour. Neurocognitive and -affective mechanisms including emotion regulation, emotional clarity and attentional reorienting were assessed experimentally through an extensive task-battery while functional brain activity and connectivity were measured during an empathy for taste paradigm and during rest. Altruistically motivated helping increased with age. Out of all mechanisms probed for, only emotional clarity increased with age and accounted for altruistically motivated helping. This was associated with greater functional integration of the empathy-related network with fronto-parietal brain regions at rest. We isolate a highly specific neuroaffective mechanism as the crucial driver of altruistically motivated helping during child development.

KEYWORDS

altruistic motivation, development, empathy network, helping, middle childhood, prosocial behaviour

1 | INTRODUCTION

Early childhood is characterized by the emergence of a multitude of prosocial behaviours, such as helping, sharing, and comforting (Warneken & Tomasello, 2006; Zahn-Waxler et al., 1992). These behaviours change radically throughout childhood and become increasingly selective, (i.e., directed increasingly at specific individuals or groups) (Martin & Olson, 2015). Recent studies have shown that different types of prosocial behaviour do not correlate in children (Dunfield et al., 2011) and, to a degree, emerge at different times in development (Zahn-Waxler et al., 1992). Further, early prosociality

is only a poor predictor for later prosocial behavior (Paulus et al., 2015). Such heterogeneity is best explained by divergent developmental mechanisms underlying different types of social behaviours (Steinbeis, 2018). Prosocial behaviours play an important role for subjective well-being (Weinstein & Ryan, 2010), quality of relationships (Cillessen et al., 2005), and long-lasting social bonds (Flitzpatrick & Sollie, 1999). Whereas prior work has mostly focused on the emergence of prosocial behaviour in early childhood around the preschool years (ages 3–5) (Eisenberg, 2000; Warneken & Tomasello, 2006), how prosocial behaviours This is particularly noteworthy as middle childhood has been identified as a crucial developmental period

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(Knudsen, 2004) during which the development of socio-emotional and -cognitive skills supports school transitions (Carr, 2011) and where social difficulties spell the emergence of later mental health problems (Mah & Ford-Jones, 2012; Pedersen et al., 2007). The present study remedies this gap by probing the underlying motivational and neurocognitive and -affective mechanisms of helping, while focusing on the neglected but important developmental period of middle childhood.

Helping others can result from different motivations (Batson et al., 1983). Thus, helping is not always altruistically motivated but instead can be egoistically motivated, when, for example, help is offered to gain a good reputation (Batson et al., 1983). It has been argued that whether helping results from an altruistic or an egoistic motivation is the consequence of the underlying emotional state, namely empathic concern and personal distress, respectively (Batson et al., 1983). Empathic concern refers to the “other-oriented” feelings of sympathy and concern for someone who is suffering, whereas personal distress refers to the “self-oriented” feelings of personal anxiety and unease elicited by someone’s suffering (Zahn-Waxler et al., 1992). Studies on the development of helping have identified self-report, physiological, and facial markers of these emotions in children to predict behavior (Eisenberg et al., 1989). In contrast, in adults, sophisticated experimental paradigms have been used, which manipulate the cost of helping to infer the underlying motivational state (Batson et al., 1983; Hein et al., 2010). In these paradigms, originally developed by Batson and colleagues (Batson et al., 1983) altruistic motivations of helping are disentangled from egoistic motivations by giving participants a choice between either helping another in distress (thus potentially eliciting either empathic concern or personal distress) or an alternative, which varies depending on the condition. In a so-called *Escape condition*, the alternative is a literal escape from the situation, whereas in a so-called *No-escape condition*, participants are forced to witness another’s distress that arises from not receiving help (Batson et al., 1983). Arguably, helping when the alternative is witnessing the other’s distress can arise from *both* egoistic (reducing one’s own personal distress) and altruistic motivations. However, choosing to help when one also has the option to escape suggests a real altruistic motivation grounded in the subjective experience of empathic concern (Batson et al., 1983; Batson et al., 1987; Hein et al., 2010). To our knowledge, no behavioural work has attempted to pinpoint the development of altruistically motivated helping in middle childhood. We conducted a large-scale study using experimental manipulations to study the development of altruistically motivated helping. In addition, we used task-based measures and neuroimaging to probe neurocognitive and -affective mechanisms underlying the development of altruistically motivated helping in middle childhood.

Whether and how altruistically motivated helping changes throughout middle childhood is unknown. Our first aim, therefore, was to study in an experimentally controlled way the development of altruistically motivated helping during middle childhood. Our second aim was to study the cognitive and affective mechanisms underlying the development of altruistically motivated helping. Based on prior work in children and adults, these boil down to three core mechanisms

RESEARCH HIGHLIGHTS

- The underlying motivational mechanisms that drive the development of prosocial behaviours during childhood remain poorly understood.
- In this large-scale study we investigated the development of altruistically motivated helping in middle childhood and explored the underlying neurocognitive and -affective mechanisms.
- Using a novel gustatory costly helping task to differentiate distinct motivations we find that altruistically motivated helping increases with age during middle childhood.
- Emotional clarity accounted in part for altruistically motivated helping being associated with of greater functional integration of the empathy-related network at rest.

that potentially play a crucial role in the empathy-related development of altruistically motivated helping: (1) emotion regulation, (2) emotional clarity, and (3) attentional reorienting. We employed a task-based approach, drawing on well-developed paradigms to study these potential mechanistic links with altruistically motivated helping. Emotion regulation has been argued to be crucial for altruistically motivated helping behavior, through shifting the experience of personal distress into one of empathic concern (Decety & Jackson, 2006). Such a mechanism has also been proposed for the development of altruistic behaviours in children, albeit based on questionnaire and physiological data (Eisenberg, 2000). Questionnaire measures in particular are inherently biased relying either on retrospection and introspection and verbal abilities of young and still developing children or on third person perspectives of parent and teacher reports. Physiological measures on the other hand, such as heart rate or skin conductance have been sometimes found to be unreliable, unspecific and difficult to interpret (Cacioppo & Tassinary, 1990). Our task-based approach thus represents an advance over previous developmental studies that have relied heavily on correlational designs, as it allows for a direct manipulation of the actual emotional and cognitive processes with a certain degree of control and specificity. Emotional awareness represents another mechanisms, which has been reported to play a role in prosocial behaviours (Feldmanhall et al., 2013). Emotional awareness of one’s own emotional states allows for effective empathic responding in social situations and might thus be a prerequisite for the development of prosocial behaviours. An important component of emotional awareness represents emotional clarity, which refers to the ability to unambiguously identify, label and characterize one’s own emotions (Boden & Thompson, 2017). Emotional clarity has been positively associated with emotion regulation capacities across a range of settings (Lischetzke et al., 2011) and could play a crucial role in the development of helping. In the present study, emotion regulation and emotional clarity were assessed within a single paradigm in which children were asked to either to indicate or to regulate their emotional experience in response to negative



or neutral socio-affective images (McRae et al., 2012). In addition, emotion regulation was also assessed through another measure designed to test emotional inhibition (Hare et al., 2008). A further cognitive mechanism that has been hypothesized to relate to the development of altruistically motivated helping is attentional reorienting, which refers to the reorienting of attention towards the appearance of unexpected, but task-relevant objects (Mitchell, 2007). Attentional reorienting and its neural correlates were found to be associated with prosocial behaviours in adults (Tusche et al., 2016), which is why it was also assessed in the present study. This process might be particularly important in the context of altruistically motivated helping by shifting attention from one's own emotional state to that of the suffering person.

The third aim of our study was to study the brain networks associated with the development of altruistically motivated helping. Research in adults has shown that the shared activation of experiencing and observing others' negative emotions recruits a network of brain regions comprising the anterior insula and the anterior cingulate cortex (Kanske et al., 2015). Activation of this network has been associated with the trait differences in empathy (Jabbi et al., 2007), the subjective experience of empathy (Kanske et al., 2015), each of which predicted prosocial motivation and resulting behaviours (Hein et al., 2010; Hein et al., 2016). In particular, activity (Hein et al., 2010) and connectivity (Hein et al., 2016) of the anterior insular (AI) have been found to predict altruistically motivated helping in adults. The AI is part of a network of brain regions that have been consistently implicated in empathy tasks, including the supramarginal gyrus (SMG) and dorsolateral prefrontal cortex (DLPFC) (Kanske et al., 2015). It is known that children as young as 7 years also show empathic brain responses, which then undergo changes throughout development (Decety & Michalska, 2010). There is, however, no evidence in what way such an empathy-related brain network might contribute to the emergence of altruistically motivated helping in children. Evidence suggests that task-based functional network architecture is largely shaped by resting-state network architecture (Cole et al., 2014). Further, developmental studies have shown that changes in resting-state functional connectivity are associated with the maturation of specific emotional and cognitive functions (van Duijvenvoorde et al., 2016). Therefore, we assessed functional connectivity acquired both during an empathy task and at rest.

To achieve these aims, 127 children between 6 and 12 years performed a novel costly helping task using gustatory stimulation that allowed altruistic motivations to be identified (Batson et al., 1983; Hein et al., 2010). To assess the specific neurocognitive and -affective mechanisms associated with the development of altruistically motivated helping, we employed a task-based approach to assess a range of emotional and cognitive functions such as emotion regulation, emotional clarity as well as attentional reorienting. Finally, to assess the functional network of brain regions involved in altruistic helping we also measured children's functional brain activity during an empathy for taste paradigm and during rest.

We hypothesized, in line with the literature, that helping in the Escape condition would occur less often than helping in the No-escape condition (Batson et al., 1987; Hein et al., 2010). It has been proposed that more complex helping behaviors should undergo the most pro-

nounced changes during childhood (Eisenberg et al., 2015). As a result, we hypothesized that altruistically motivated helping as measured in the Escape condition would increase throughout middle childhood. We further hypothesized that the maturation of specific a priori neurocognitive and -affective candidate mechanisms, such as emotion regulation, emotional clarity and attentional reorienting would explain an age-related increase in altruistically motivated helping. Based on previous findings in adults (Hein et al., 2016; Hein et al., 2010), we expected that the brain network associated with empathy in terms of anterior insula activation and functional connectivity during empathy for taste and during resting-state would be associated with increased altruistically motivated helping throughout middle childhood.

2 | METHODS

2.1 | Participants

One-hundred and twenty seven children participated in this study (62 females; mean age = 8.94 years, SD = 1.70, range = 6–12 years). Children were recruited from databases at the Max Planck Institute for Human Cognitive and Brain Sciences. Participants were predominantly White Caucasian and were normally developing. Parental consent was obtained and the study was approved by the ethics committee of the University of Leipzig (Nr. 381-11-12122011). A subsample of children, for which parental consent was obtained for the functional magnetic resonance imaging (fMRI), were recruited from the same databases (N = 69; 34 females; mean age = 8.93, SD = 1.84, range = 6–12 years) and underwent fMRI while performing an empathy for taste paradigm as well as a functional resting-state scan. For those children that underwent fMRI, the behavioural testing session always followed after the scan and a short 15-min break on the same day. The actual scanning time did not exceed 20 min. The behavioural testing session was 30–40 min long, possibly including several 5–10 min breaks.

2.2 | Gustatory costly helping task

At the start of the experiment, participants were told that they would perform a task jointly with another child, who was sat in an adjacent testing room with a second experimenter. They were told that they could observe the other child via live stream during parts of the experiment but would not encounter the child in person; a piece of information that should minimize concerns of reciprocity and reputation formation. First, participants performed an empathy for taste paradigm either behaviourally (see Supporting Information) or inside the MRI, depending on whether they took part in the MRI experiment or not. Afterwards, participants performed the gustatory costly helping task (for details of the apparatus and gustatory stimuli see Supporting Information and also Hoffmann et al., 2015). To avoid experimenter demand effects, children were informed that there were two different roles during the experiment, which would be randomly assigned by lot: In *Role A*, the child would have to drink a small amount of a bitter



solution (quinine) several times and rate its perceived valence. In *Role B*, the child could “take over” for the other child by drinking the bitter solution instead. The experiment was designed such that the child in the first role would have to drink the bitter solution at least five times. For the other 10 times the child in *Role B* could either choose to help or not. Participants were told that the different roles were allocated randomly beforehand and that the other child in the adjacent room would play *Role A*, drinking the bitter solution 15 times, whereas the participant would adopt *Role B*. The participants were then shown a video of the other child waiting in the testing room close by.

The helping task consisted of two different helping conditions. In an Escape condition, participants could choose to either help the other child by drinking the bitter solution for them or watch a short nature movie. In the No-escape condition, participants could choose to either help the other child by drinking the bitter solution for them or watch the other child drink the bitter solution. They could indicate their choices by pressing on related pictures on a touch screen. Each condition had five trials and the order was counterbalanced across subjects. The task was self-paced. After each decision participants had to rate the pleasantness of the quinine solution. Then a cue to swallow the solution appeared on the screen followed by a water rinse. Participants were explicitly told that their decisions would not be judged or observed by the experimenter and that the experimenter would leave the room for this task. Before the start of the task the participants were shown the video of the other child drinking the bitter solution in distress (one of the five times that the child would have to drink the solution at the start). After the gustatory costly helping task children performed a series of tasks assessing specific cognitive and affective mechanisms. The order of these tasks was counterbalanced across participants.

2.3 | Cognitive and affective mechanisms

2.3.1 | Emotion regulation

Our measures of emotion regulation were derived from the ratings in a (a) the emotion regulation task, in which children cognitively reappraised the content of emotional images; and (b) an emotional Go/NoGo task, in which children were asked to respond/inhibit to one of two emotional categories. These two tasks were selected to comprehensively measure emotion regulation in terms of explicit (cognitive reappraisal task) as well implicit (Go/NoGo task) processes (Ahmed et al., 2015).

Cognitive reappraisal

The emotion regulation task was similar to those in previous developmental studies (McRae et al., 2012). Participants were presented with negatively or neutrally valenced IAPS pictures of social scenes (Lang et al., 1997) (e.g., person showing sadness, see Supporting Information for more details and Table S1). The pictures were presented for 5 s on the screen. After the disappearance of the pictures, participants could give their rating of “how they felt” (valence rating) using a nine

point SAM figure (Self-Assessment Manikin; Bradley & Lang, 1994). The rating phase had no time limitation. There were two blocks: the emotion rating block and the emotion regulation block. In the emotion rating block, children were simply asked to identify and rate their own emotion when looking at the pictures showing neutral and negative social scenes (“how do you feel?”). In the emotion regulation block children were asked to cognitively reappraise their own emotion by telling themselves that what they are seeing is “not as bad as it seems”. The emotion rating block and the emotion regulation block both consisted of eight pictures (four negative, four neutral). The pictures used for each condition were counterbalanced across participants and did not differ in valence and arousal ratings from IAPS populations norms (see Supporting Information for more details). Children always started with the emotion rating block, followed by the emotion regulation block.

Emotional inhibition

Emotion regulation was also assessed with an emotional Go/NoGo task, similarly to previous studies (Hare et al., 2008). The emotional Go/NoGo task used happy and fearful face stimuli as Go and NoGo stimuli (intertrial intervals: 1000, 1500, 2000, 2500, and 3000 ms). In this task, participants had to respond quickly with a button-press to the presentation of Go stimuli, while withholding a response to the presentation of NoGo stimuli. Participants performed 120 Go trials (60 happy face stimuli, 60 fearful face stimuli) and 40 NoGo trials (20 happy face stimuli, 20 fearful face stimuli). Counterbalanced across participants, children either started first with happy faces as Go stimuli and fearful faces as NoGo stimuli followed by the second part with fearful faces as Go stimuli and happy faces as NoGo stimuli or the other way around. Emotion regulation in this task was measured by the ability to inhibit the response to NoGo stimuli, calculating a general d' score: $d' = Z(\text{hit rate}) - Z(\text{false alarm rate})$ across happy and fearful face stimuli.

2.3.2 | Emotional clarity

Emotional clarity was derived from response times in the emotion rating condition of the emotion regulation task, in which children were asked to identify and rate their own emotion in terms of valence when looking at the pictures showing neutral and negative social scenes. Emotional clarity is the ability to unambiguously identify, label and characterize one's own emotions (Boden & Thompson, 2017; Lischetzke et al., 2005). Previous research has demonstrated that greater emotional clarity is represented by an individual's faster response times while rating their current affective states and mood, which has been cross-validated with self-report measures of emotional clarity (e.g., Arndt et al., 2018; Thompson et al., 2015). Reaction times of ratings of one's own affective state represent an ecological, indirect, momentary measure of emotional clarity that has clear advantages over global self-report measures based on retrospection (Boden & Thompson, 2017), an ability that still matures during childhood (Ghetti & Bunge, 2012) and thus may confound findings obtained this way. Thus, emotional clarity was assessed through participants' average



response times in rating their current affect in response to the negatively valenced image.

2.3.3 | Attentional reorienting

In this task, participants were instructed to indicate by pressing the left or the right arrow key on the keyboard the location of a visual target stimulus on the left or the right side of the computer screen (Mitchell, 2007). The location of the visual target was either congruent or incongruent to a preceding arrow pointing to the left or to the right (80 trials, 40 congruent, 40 incongruent).

2.4 | Empathy for taste fMRI paradigm

A subsample of participants ($N = 69$) performed a cue-based empathy for taste paradigm while undergoing fMRI. Participants were told that they themselves would have to taste bitter and neutral solutions inside the scanner and rate their pleasantness. They also had to imagine how another child outside the scanner performing the same task would feel tasting the solutions and then rate how pleasant the taste was for the other child. The participants were told that the child was in an adjacent testing room and that they would do some other behavioural tasks together later but via a live-video. The event-related empathy for taste paradigm consisted of a *Self* and an *Other condition*.

Self condition

Self trials were indicated by the word "you" above the picture. In the Self condition, participants saw a picture on the screen representing the neutral or negative taste solution, with a green frame. The green frame functioned as a cue and disappeared after 2000 ms, indicating that now the taste solution would be presented (pumped through the tube, pump phase lasting 1000 ms). For the following taste phase (4000 ms), participants were instructed to keep the solution in their mouth and taste it. Afterwards, an instruction appeared to swallow the solution (3000 ms). The participants then had to indicate the pleasantness of the taste on a rating scale from 1 to 10 using a slider (4000 ms). The rating scale depicted an unhappy, neutral and happy smiley. A water rinse (3000 ms) and another instruction to swallow followed (3000 ms).

Other condition

Other trials were indicated by the words "other child" above the picture. In the Other condition, participants saw a picture on the screen representing the neutral or negative taste solution the other child was about receive. The same cue indicated that now the child was beginning to taste the solution (also pump phase lasting 1000 ms). During the tasting phase of the other child, participants were instructed to imagine how the other child felt experiencing the taste (4000 ms). This was followed by a fixation cross (3000 ms). Afterwards, the participants then had to indicate the pleasantness of the taste for the other child on a rating scale from 1 to 10 using a slider (4000 ms). Then, the pic-

ture appeared indicating that the other child received the water rinse (3000 ms) followed by another fixation (3000 ms).

In between the trials, there was an interstimulus interval of varying lengths (4000–6000 ms). In total, there were 16 trials for each target (Self, Other) condition (eight neutral, eight negative), across four runs of 3.6 min. Participants were instructed to keep the tubes in their mouth throughout the whole experiment. At a pre-visit before the fMRI session, children practiced the task extensively inside a mock scanner. During the scan, children responded on 97.7% of trials suggesting that they were clearly performing the empathy for taste paradigm.

2.5 | Task-based fMRI preprocessing and analysis

Task-based functional data were analyzed using SPM8 (<http://www.fil.ion.ucl.ac.uk/spm/software/spm8/>) on the basis of an event-related model (see Supporting Information for MRI acquisition). In brief, functional volumes were linearly realigned to the first volume to correct for head movements. The functional image was co-registered with the corresponding structural image, non-linearly registered to the MNI152 template, and finally resampled to a voxel size of $3 \times 3 \times 3$ mm³. Evidence suggests that there are minimal structural differences in brain anatomy between children over the age of six and adults that are below the specificity the MRI scanner (Burgund et al., 2002; O'Shaughnessy et al., 2008). Normalization of children's brains to adult brains has been found to have no significant effect on fMRI measures and SPM analysis (Burgund et al., 2002; Muzik et al., 2000). In addition, findings suggest that the brain size of 6-year-old children is already approximately 95% that of adults', while their brain also shows adult-like gyri-fication (Armstrong et al., 1995). Normalized images were smoothed using a Gaussian kernel with a full width at half maximum (FWHM) of 8 mm. A high-pass temporal filter with cutoff of 128 s was applied to remove low-frequency drifts from the data. Volumes with scan-to-scan movement of more than 1 mm were replaced, using ArtRepair (Mazaika et al., 2007), with a "repaired" volume (interpolated values). Runs were excluded in which repaired volumes exceed 25%. Participants were included in the analysis when they had at least two runs in which repaired volumes did not exceed 25%. Three children were thus excluded from further analysis. Out of the remaining 66 children, 61 children had four usable runs, two children three usable runs, three children two usable runs (average percentage of repaired volumes per run = 4.4%).

Analysis was carried out according to the general linear model (Friston et al., 1994). Regressors were defined separately for the four experimental conditions (Self Negative, Self Neutral, Other Negative, Other Neutral) and modeled the length of the event (4000 ms). Regressors were convolved with a canonical hemodynamic response function (HRF). Effects of head motion were corrected for by modeling the six motion parameters for each subject as effects of no interest in the design matrix. Subsequent contrast images were derived by applying linear weights to the parameter estimates for the regressors of each event. Contrast images were entered into one-sample t-tests for random-effects analyses. In line with our aim to investigate anterior



insula functioning as a key node of the empathy-related network, region of interest (ROI) analyses were performed using small volume correction (SVC) for the whole bilateral insula based on the AAL atlas (Maldjian et al., 2003). Using the whole bilateral insula as an ROI was the most conservative and unbiased approach considering the use of a novel empathy of taste fMRI paradigm within a developmental sample, as well as for the purpose of identifying the shared network for self and other during direct experience of and empathy for negative taste in children. Statistical significance was assessed within the ROI using nonparametric tests, which have been suggested to be more conservative in terms of correcting for multiple comparisons than their parametric counterparts (Eklund et al., 2016). Five-thousand permutations were computed and a cluster-wise inference was applied with $p < 0.05$ FWE corrected using a cluster-forming threshold of $p < 0.005$. Regression analyses were performed within the bilateral insula during empathy for negative taste (Other Negative > Other Neutral) compared to empathy for neutral taste including altruistically motivated helping, age and emotional clarity as covariates of interest. For the identification of the shared activation within the insula as previously reported showing similar activation for the experience of and empathy for the negative taste, a conjunction analysis was performed (conjunction contrast: Negative > Neutral: self \cap other; Table S3). Significance of the conjunction analysis within the insula ROI was established using Monte-Carlo Simulation (3D ClusterSim; Ward, 2000) correcting for multiple comparisons. Cluster-size-corrected results are reported (voxel-wise $p < 0.005$, $k_e = 1$) corresponding $p = 0.05$, FWE corrected). The right ventral anterior insula was found to be similarly activated for the first-person experience of and empathy for negative taste and thus functioned as a seed for the task-based and resting-state functional connectivity analyses. Additional whole brain analyses using nonparametric tests were performed (Table S2).

To assess functional connectivity from the anterior insula, we carried out a psychophysiological interaction (PPI) analysis to identify brain regions that show a correlation with activity in the right ventral anterior insula (rvAI) during empathy for negative taste (Other Negative > Other Neutral) compared to empathy for neutral taste, and to assess whether the connectivity of rvAI with distal brain regions might be associated with altruistically motivated helping, age and emotional clarity. We extracted mean-corrected and deconvolved BOLD time-series from the rvAI. The extracted time course, the psychological variables (Other Negative, Other Neutral, Self Negative and Self Neutral) and their interaction term as well as six motion regressors were entered into a GLM on the first level. We used a generalized form of context-dependent psychophysiological interaction analysis (gPPI; McLaren et al., 2012). A first level contrast was computed between the parameter estimates of the two psycho-physiological regressors of interest (Other Negative-Other Neutral). For statistical inference, whole brain regression analyses were then performed on the resulting contrast images on the second level, including altruistically motivated helping, age and emotional clarity as covariates of interest. Statistical significance was assessed in a nonparametric fashion (Nichols & Holmes, 2002). Five-thousand permutations were computed and a

cluster-wise inference was applied with $p < 0.05$ FWE corrected using a cluster-forming threshold of $p < 0.005$.

2.6 | Resting-state fMRI preprocessing and analysis

Data were processed using the data processing assistant for the resting-state fMRI toolbox [R(R)EST/DPARSFA; <http://www.restfmri.net>; Song et al., 2011] for Matlab. The toolbox is based on the Statistical Parametric Mapping toolbox [SPM8, <http://www.fil.ion.ucl.ac.uk/spm>]. In brief, preprocessing discarded the first five volumes to ensure steady state magnetization, performed motion correction and realignment, and co-registered the functional time series to the corresponding T1-weighted MRI. Images underwent DARTEL-based segmentation and registration, followed by nuisance covariate regression to remove effects of average WM and CSF signal, as well as 6 motion parameters (three translations and three rotations). To make our analysis more robust against confounds possibly relating to differential motion artifacts in children, we included the scrubbing approach (Power et al., 2012). In brief, this approach modeled bad time points (based on the framewise displacement threshold, FD (Power), of 0.5 mm or higher; together with one time point before and one time point after each such time point) as separate regressors during the nuisance covariate correction. Time series were band-pass filtered to be within the 0.01 and 0.08 Hz band, normalized to MNI space, resampled to 3 mm voxels, and spatially smoothed using a 8 mm Full-Width-at-Half-Maximum (FWHM) isotropic Gaussian kernel. Resting-state data was acquired for 61 children. In the resting-state session, 14/61 children showed head-motion beyond 3 mm translation or three degrees of rotation. These children were excluded from all further analysis. The final resting-state sample thus consisted of $N = 47$ children. Functional connectivity maps were generated for the right ventral anterior insula seed identified in the task-based functional imaging analysis. Functional connectivity was calculated as the time series correlation between the mean time series of the seed region and the time series of all brain voxels. Time-series correlation coefficients underwent a Fisher r -to- z transformation to render the data more normally distributed. Whole brain regression analyses were run using SPM 8 for the variables of interest (altruistically motivated helping, age and emotional clarity; see Table S5). Similarly to task-based analyses, statistical significance was assessed in a nonparametric fashion (Nichols & Holmes, 2002). Five-thousand permutations were computed and a cluster-wise inference was applied with $p < 0.05$ FWE corrected using a cluster-forming threshold of $p < 0.005$.

2.7 | Commonality analysis

To get a better understanding of the respective contributions of functional connectivity, emotional clarity and age to altruistically motivated helping, we performed a voxelwise commonality analysis with functional connectivity, emotional clarity and age as predictors

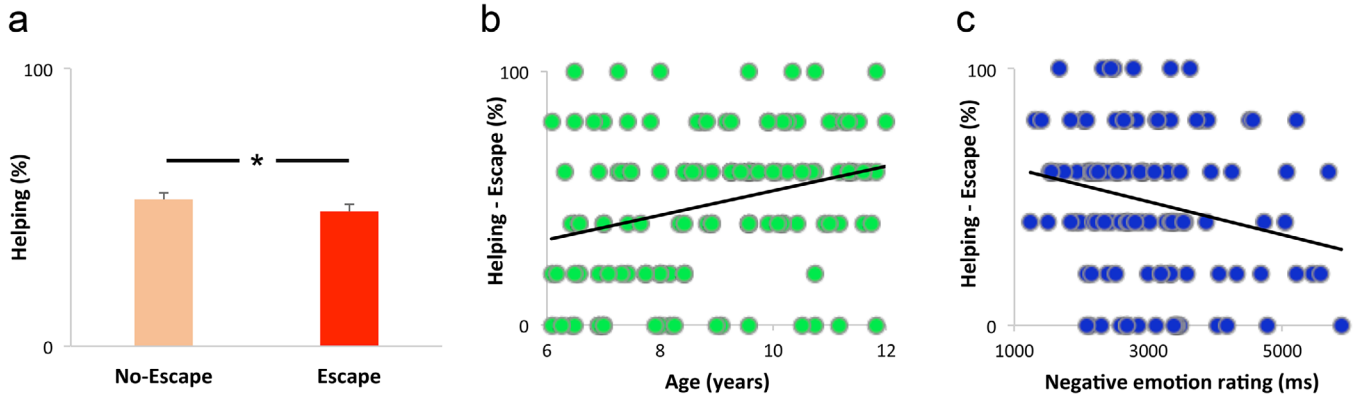


FIGURE 1 Altruistically motivated helping in children and associations with emotional clarity and age (a), Percentages of helping during No-escape and Escape condition. Children were more likely to help in the No-escape condition than the Escape condition. (b), age was positively associated with altruistically motivated helping. (c), emotional clarity was negatively associated with altruistically motivated helping. The error bars show SE. The asterisk indicates significant difference ($p < 0.05$, one-tailed)

for altruistically motivated helping (Wiesmann et al., 2017) (see Supporting Information for details).

3 | RESULTS

3.1 | Gustatory costly helping task

We compared helping rates in the No-escape and the Escape conditions. We predicted lower helping rates in the Escape condition, given that helping in the Escape condition is costlier by virtue of its alternative than helping in the No-escape condition. Indeed, children were more likely to help the other child in the No-escape compared to the Escape condition ($t(126) = 1.78$, $p = .039$, one-tailed, Cohen's $d = 0.2$, see Figure 1(a)). We could thus replicate previous findings (Batson et al., 1983; Hein et al., 2010) with our novel gustatory paradigm in children and demonstrate that the occurrence of helping in our paradigm is sensitive to associated costs.

Our main goal was to study the development of altruistically motivated helping during middle childhood. We did this by correlating helping in the Escape condition with age (continuously). Based on the literature as well as our experimental design, helping in the Escape condition can be seen as a pure measure for altruistically motivated helping (Batson et al., 1983; Hein et al., 2010). Altruistically motivated helping was found to significantly increase with age ($r = .30$, $p = .001$; Figure 1(b)). Helping in the No-escape condition has been linked to both egoistic and altruistic motivations (Batson et al., 1983; Eisenberg et al., 1989). In this scenario, we also found a significant increase with age ($r = .19$, $p = .04$). There was also a moderate correlation between helping in the Escape and No-escape conditions ($r = .52$, $p < .001$). Importantly, we show that when controlling for the other type of helping, the age-related increase in helping in the No-escape condition vanished ($r = .04$, $p = .70$; controlled for helping in the Escape condition) and remained in the Escape condition ($r = .24$, $p = .007$; controlled for helping in the No-escape condition). This suggests that the two forms of helping are dissociable in our developmental sample

and that the age-related increase in helping in the No-escape condition is driven primarily by altruistic motivations. Given the potentially confounded motivations of helping in the No-escape condition, we focus subsequent analyses only on helping in the Escape condition, our measure of altruistically motivated helping.

3.2 | Cognitive and affective mechanisms

3.2.1 | Emotion regulation

Our measures of emotion regulation were derived from the ratings in (a) the emotion regulation task, in which children were asked to cognitively reappraise the content of emotional images; and (b) an emotional Go/NoGo task, in which children were asked to respond/inhibit to one of two emotional categories.

Cognitive reappraisal

There was a significant effect of condition (emotion rating vs. emotion regulation; $F(1, 126) = 153.80$, $p < .001$, $\eta_p^2 = 0.550$), and emotion (neutral vs. negative, $F(1, 126) = 163.78$, $p < .001$, $\eta_p^2 = 0.565$) on emotion ratings. In addition, there was a significant condition by emotion interaction ($F(1, 126) = 34.85$, $p < .001$, $\eta_p^2 = 0.217$). Post-hoc analyses revealed that this effect was stronger for negative scenes ($t(126) = -11.63$, $p < .001$) but still present for neutral scenes ($t(126) = -5.72$, $p < .001$). To investigate any developmental effects, age was included as a covariate in the model. There was a significant interaction between emotion and age ($F(1, 125) = 4.97$, $p = .028$, $\eta_p^2 = 0.038$). Across conditions, ratings for negative images decreased with age, becoming more negative ($r = -.18$, $p = .04$). There was also a significant interaction of condition and age ($F(1, 125) = 5.25$, $p = .024$, $\eta_p^2 = 0.040$). Across emotions ratings (in emotion rating condition) decreased with age, becoming more negative, ($r = -.20$, $p = .02$). There were no other significant interactions with age ($p > .73$). A measure of cognitive reappraisal success was computed (negative emotion regulation rating - negative emotion rating). There was no



significant association of cognitive reappraisal success with altruistically motivated helping ($p > .06$) or age ($p > .20$).

Emotional inhibition

Emotion regulation was also measured by the ability to inhibit the response to emotional NoGo stimuli. A d -prime score was calculated across happy and fearful faces (no difference in d -prime scores between emotions, $p > 0.7$ and a strong association, $r = .54$, $p < .001$). Larger d -prime scores indicate better emotion regulation. There was no association, neither with altruistically motivated helping nor age ($p > 0.25$).

3.2.2 | Emotional clarity

Our measure of emotional clarity was derived from response times in the emotion rating condition of the emotion regulation task, in which children were asked to identify and rate their own emotion when looking at the pictures showing neutral and negative social scenes. There was neither a significant effect of condition (emotion rating vs. emotion regulation; $p > .76$), nor emotion (neutral vs. negative, $p > .28$), on reaction times. There was no significant condition by emotion interaction ($p > .14$). To investigate any developmental effects, age was included as a covariate in the model. There was a main effect of age ($F(1, 125) = 5.17$, $p = .03$, $\eta_p^2 = 0.040$), showing a decrease in reaction times with age ($r = -.20$, $p = .03$). There were no significant interactions with age ($p > .18$).

Based on the literature, we took reaction times in response to negative images as a measure of emotional clarity (where quicker reaction times indicate greater emotional clarity), in terms of how quickly children access and identify their own negative emotions (Boden & Thompson, 2017; Lischetzke et al., 2011; Lischetzke et al., 2005). This measure was significantly negatively associated with altruistically motivated helping ($r = -.23$, $p = .01$, Figure 1(c)). The association persisted after controlling for reaction times for neutral stimuli ($r = -.26$, $p < .003$). Looking at developmental effects of emotional clarity, reaction times in response to negative images decreased with age ($r = -.21$, $p = .02$). In addition, greater emotional clarity was associated with cognitive reappraisal success ($r = -.19$, $p = .04$).

3.2.3 | Attentional reorienting

A difference score on the reaction times and the error percentages was computed as a measure of incongruency cost during attentional reorienting ($RT_{\text{incongruent}} - RT_{\text{congruent}}$; $EP_{\text{incongruent}} - EP_{\text{congruent}}$). There was a significant relationship between attentional reorienting and altruistically motivated helping for reaction times but not for error percentages ($r = -.20$, $p = .03$; $r = -.12$, $p = .17$), suggesting that better reorienting (low incongruency cost in RTs) was related to more altruistically motivated helping. Looking at developmental effects of attentional reorienting, incongruency costs decreased with age in terms of reaction times and error percentages ($r = -.19$, $p = .03$; $r = -.17$, $p = .06$). To derive

a combined measure of attentional reorienting, the difference scores in reaction times and error percentages were z-scored (both measures were associated: $r = .25$, $p = .006$) and aggregated. This attentional reorienting score was significantly associated with altruistically motivated helping and age ($r = -.20$, $p = .02$; $r = -.23$, $p = .01$).

3.3 | Emotional clarity as the single best predictor of altruistically motivated helping

Our next aim was to isolate which of the obtained measures uniquely accounts for children's individual differences in altruistically motivated helping, not accounting for age-related variance, which in a further step would be used to investigate brain-behaviour relationships. A stepwise multiple regression was performed including all relevant measures (*emotional clarity and emotion regulation: (1). negative emotion rating time, (2). neutral emotion rating time, (3). cognitive reappraisal success; emotional inhibition: (4). d-prime score; attentional reorienting: (5). attentional reorienting score*), as well as gender. To deal more thoroughly with the challenge of multiple comparisons in this step, considering the number of predictors, we applied a Bonferroni correction ($p < .05/6$, new alpha level $p = .008$) to reduce type 1 error. Only emotional clarity (negative emotion rating time) significantly predicted altruistically motivated helping, crucially explaining a unique variance of the size in altruistically motivated helping ($B = -.25$, $t = -2.73$, $p = .007$), adjusted R square = .06). Given its significant association with altruistically motivated helping, we focus subsequent analyses of brain-behaviour relationships on emotional clarity.

3.4 | Shared activation in the right ventral anterior insula for experience of and empathy for negative taste

We first performed a whole-brain analysis, identifying areas of brain activation previously related to taste perception and empathy for taste (Table S2). Negative taste perception (Self Negative > Self Neutral) activated right inferior frontal gyrus and anterior insula, extending into amygdala as well as the left hypothalamus. Empathy for negative taste (Other Negative > Other Neutral) activated among other brain regions the occipital lobe and left and right superior parietal lobule and left supplementary motor area. Neutral taste perception (Self Neutral > Self Negative) and Empathy for neutral taste (Other Neutral > Other Negative) did not significantly activate any brain regions (for analyses of fMRI emotion ratings, see Supporting Information and Figure S1).

Based on previous findings showing a specific relationship between anterior insula activation, functional connectivity and altruistically motivated helping in adults (Hein et al., 2016; Hein et al., 2010), we adopted an a priori regions-of-interest (ROI) approach focusing our analysis on the bilateral insulae. The analyses showed that the right ventral insula was significantly activated both during the experience of negative taste (i.e., Self Negative > Self Neutral; Table S3) as well as during empathy for negative taste (i.e., Other Negative > Other Neutral;

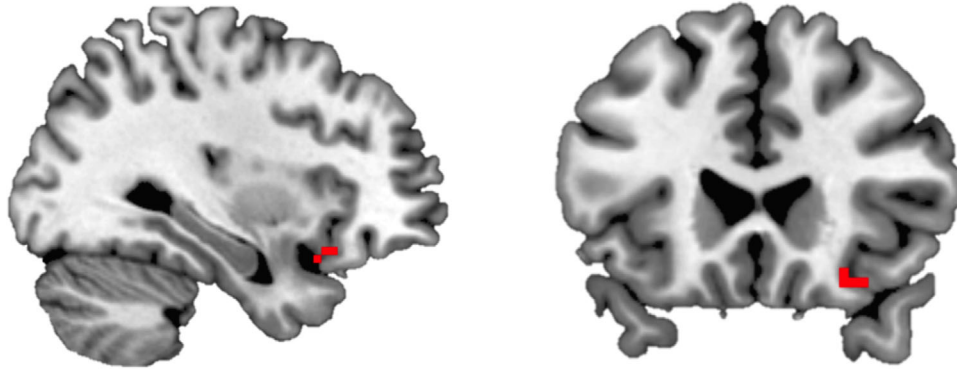


FIGURE 2 Shared activation in the right ventral anterior insula for experience of and empathy for negative taste. In children, the right ventral anterior insula ($k = 9$; $x = 33$, $y = 23$, $z = -17$) was activated during the experience of negative taste as well as during empathy for negative taste (cluster-level FWE-corrected, $p < 0.05$)

Table S3). A conjunction analysis revealed that the right ventral anterior insula (rvAI) was similarly activated by experience of and empathy for negative taste (Figure 2).

To investigate whether anterior insula activation during empathy for negative taste (Other Negative > Other Neutral) was associated with altruistically motivated helping, a regression analysis was performed within the bilateral insula ROI. There was no relationship between activity in the bilateral insulae and altruistically motivated helping, age or emotional clarity. Whole brain regression analyses also revealed no significant results.

3.5 | Right ventral anterior insula functional connectivity during empathy state

Connectivity analyses from the rvAI during empathy for negative taste (vs. neutral taste) showed no increased connectivity to other brain regions, nor was this connectivity associated with altruistically motivated helping, age or emotional clarity.

3.6 | Right ventral anterior insula functional connectivity during resting-state

At rest, the rvAI was connected to a large distributed network that comprised fronto-parietal, fronto-temporal, and subcortical brain regions (Table S4). We then tested for associations between resting-state connectivity from the rvAI and altruistically motivated helping, age, and emotional clarity. There was increased rvAI connectivity to a widespread network of frontal, parietal, and temporal brain regions as a function of altruistically motivated helping. Brain regions included the orbitofrontal cortex (OFC), the striatum, the left parahippocampal gyrus as well as the dorsal medial prefrontal cortex (dMPFC), the right and left anterior prefrontal cortex (aPFC), the right dorsolateral prefrontal cortex (DLPFC), the right pre-supplementary motor area (pre-SMA) as well as the right and left posterior parietal cortex (PPC) (Figure 3(a) and Table S5). Age was positively associated with increased rvAI resting-state functional connectivity to frontal, parietal and occipital brain regions including the left precuneus and posterior

cingulate cortex (PCC), as well as the dMPFC, right aPFC, right DLPFC, right pre-SMA and right and left PPC (Figure 3(b) and Table S5). Finally, emotional clarity was associated with increased rvAI connectivity to frontal, parietal and occipital brain regions, also including the dMPFC, right aPFC, right DLPFC, right pre-SMA as well as right and left PPC (Figure 3(c) and Table S5). We were interested in the overlap of functional connectivity from rvAI as associated with altruistically motivated helping, age and emotional clarity. This overlap occurred in the dMPFC (center of mass $x = -4$, $y = 31$, $z = 53$; $k = 25$), the right aPFC (center of mass $x = 42$, $y = 58$, $z = -6$; $k = 15$) and the right DLPFC (center of mass $x = 33$, $y = 30$, $z = 51$; $k = 12$; center of mass $x = 39$, $y = 11$, $z = 50$; $k = 31$), the right pre-SMA (center of mass $x = 20$, $y = 26$, $z = 60$; $k = 35$) as well as right and left PPC (center of mass $x = 36$, $y = -75$, $z = 42$; $k = 46$, center of mass $x = 48$, $y = -49$, $z = 42$; $k = 51$, center of mass $x = -52$, $y = -52$, $z = 46$; $k = 32$) (Figure 4).

3.7 | Commonality analysis

In a final integrative analytical step, we performed a whole-brain voxelwise commonality analysis with functional connectivity, age and emotional clarity as predictors for altruistically motivated helping. Whereas this analysis was performed whole-brain, we were most interested in the contributions of brain regions which showed an overlap in the previous analysis (dMPFC, right aPFC and DLPFC, right pre-SMA, right and left PPC). Variance in altruistically motivated helping was significantly explained by the shared contribution of resting-state functional connectivity and emotional clarity, and critically, also the shared contribution of resting-state functional connectivity, emotional clarity and age in the brain regions obtained in the previous analysis (cluster-size corrected at $p < .05$; Table S6). In addition, there was a significant unique contribution of resting-state functional connectivity in a small cluster in the right pre-SMA. The significant shared contribution of functional connectivity, emotional clarity and age, in particular, suggests that functional network architecture of a network involved in empathy undergoes development during middle childhood, which is associated with increased emotional clarity and predicts altruistically motivated helping.

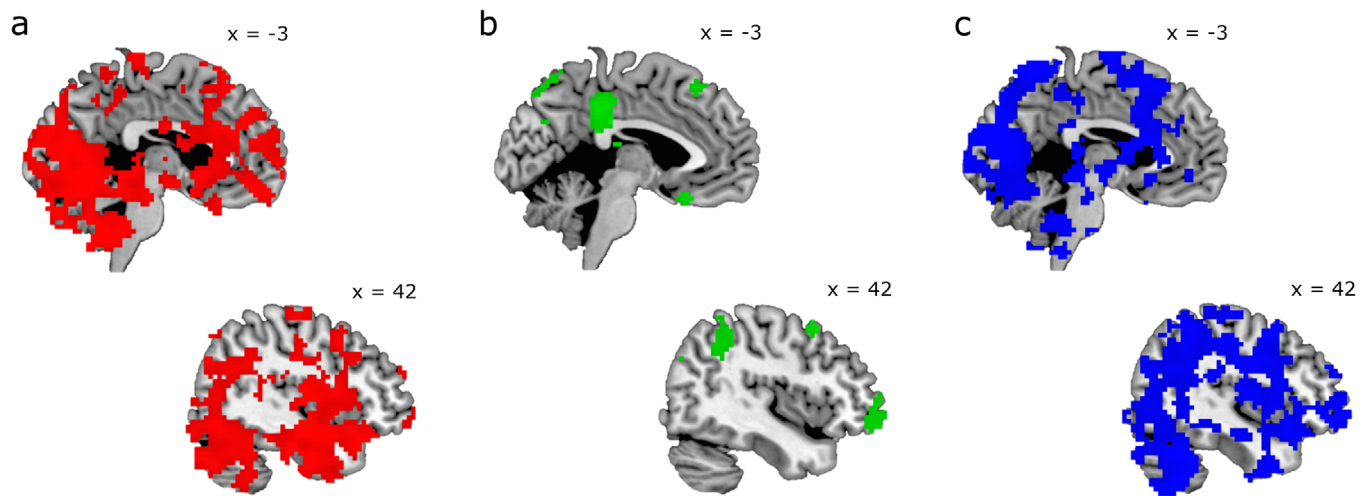


FIGURE 3 Right ventral anterior insula functional connectivity during resting-state. (a) Altruistically motivated helping was associated with increased connectivity to brain regions including OFC, the striatum, left parahippocampal gyrus as well as the dMPFC, right and left anterior prefrontal aPFC, right DLPFC, right pre-SMA as well as right and left PPC. (b), age was associated with increased connectivity to frontal, parietal and occipital brain regions including the left precuneus and PCC, as well as the dMPFC, right aPFC, right DLPFC, right pre-SMA and right and left PPC. (c), and emotional clarity was associated with increased connectivity to frontal, parietal and occipital brain regions, including the dMPFC, right aPFC, right DLPFC, right pre-SMA as well as right and left PPC (cluster-level FWE-corrected, $p < 0.05$)

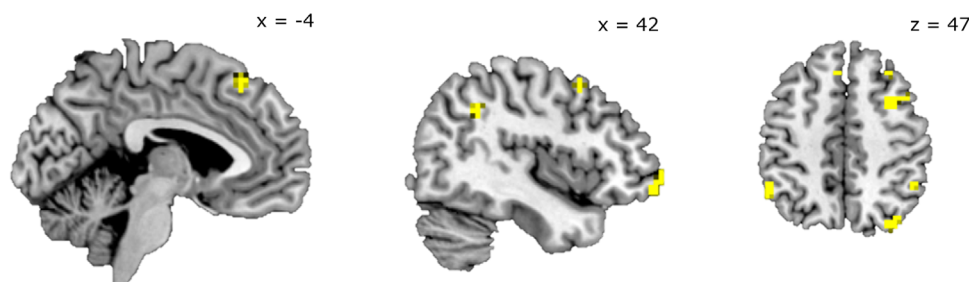


FIGURE 4 Overlapping right ventral anterior insula functional connectivity during resting-state. Right ventral anterior insula functional connectivity as associated with altruistically motivated helping, age and emotional clarity overlapped in a certain set of brain regions including the dMPFC, the right aPFC, the right DLPFC, the right pre-SMA, as well as the right and left PPC

4 | DISCUSSION

Middle childhood is a developmental period crucial for future social relationships and mental health (Mah & Ford-Jones, 2012; Pedersen et al., 2007). In a large-scale study, we investigated the development of altruistically motivated helping during middle childhood in 127 children from age 6 to 12. The first aim was to investigate in an experimentally controlled way the development of altruistically motivated helping during middle childhood using a novel gustatory costly helping task. The second aim was to study the cognitive and affective mechanisms underlying the development of altruistically motivated helping during middle childhood using a task-based approach and probing for specific mechanisms such as emotion regulation, emotional clarity and attentional reorienting. The third aim was to study the neural mechanisms associated with the development of altruistically motivated helping in middle childhood. For that purpose, a subsample of children underwent fMRI in which functional activation and connectivity of the anterior insula was interrogated both during an empathy

for taste paradigm ($N = 69$) as well as during rest ($N = 61$) to assess its contribution to altruistically motivated helping in these children.

We show that helping was modulated by the costs associated with the alternative course of action. Thus, helping occurred less often when escape was possible, making this a particularly costly form of helping. It has been argued that helping when escape is also an option reflects an underlying altruistic motivation (Batson et al., 1983). Importantly, we found that altruistically motivated helping increased throughout middle childhood from the ages of 6 to 12 years. To probe for specific mechanisms driving the age-related changes in altruistically motivated helping, we employed a battery of cognitive and affective tasks. We found that emotional clarity emerged as a unique mechanism predicting altruistically motivated helping in middle childhood. This delivers novel evidence that emotional clarity plays a crucial role in the development of altruistically motivated helping in middle childhood. While emotional awareness more broadly has been linked to prosocial behaviour in adults (Feldmanhall et al., 2013), this is the first time that emotional clarity has been associated with altruistically motivated



behaviour in children. Emotional clarity is the ability to unambiguously identify, label and characterise one's own emotions and might enable children to quickly and efficiently assess their own negative emotional state in relation to someone else's suffering. Such a mechanism potentially allows for more adaptive emotion regulation and an increasing readiness for altruistically motivated behaviours. Greater emotional clarity was indeed associated with greater emotion regulation success, delivering further support that emotional clarity might be crucial for more adaptive and efficient emotion regulation, paving the way to increased altruistically motivated helping.

The fMRI findings showed that the right ventral anterior insula was recruited both for the experience of aversive tastes as well as observing this in others. Whereas previous studies report functional empathy networks early in development, to our knowledge this study demonstrates for the first time that *shared empathy networks* for self and other are already present from 6 years of age. Interestingly, the activation in children was located in the ventral anterior insula, compared to often reported activation of the dorsal anterior insula, as for example in empathy for pain in adults (Lamm et al., 2011). This might potentially be explained by the modality to induce the emotional state, as particularly the ventral anterior insula represents a crucial component of the primary gustatory cortex (Small, 2010).

It has been shown in adults that the functional network architecture of empathic brain responses is particularly sensitive to the motivations underlying social behavior (Hein et al., 2016). We found that functional connectivity of the anterior insula during rest was associated with altruistically motivated helping. Specifically, altruistically motivated helping in children was positively associated with increased connectivity from the rvAI to brain regions previously implicated in the empathy and the theory of mind networks, as well as brain regions such as the striatum and the OFC. These findings importantly suggest that altruistically motivated helping in children is related to an increased functional integration of brain networks that have been individually found to be associated with prosocial behaviours in adults (Hein et al., 2016; Tusche et al., 2016).

Importantly, rvAI resting-state functional connectivity associated with altruistically motivated helping, emotional clarity and age overlapped in the dMPFC, right anterior prefrontal cortex and DLPFC, pre-supplementary motor area, as well as left and right posterior parietal cortex. Within these overlapping regions, variance in altruistically motivated helping was significantly explained by the shared contribution of resting-state functional connectivity, emotional clarity and age. These brain regions are commonly described as part of the executive control network, which is also recruited during goal-oriented emotion regulation (Kohn et al., 2014). Specifically, the anterior prefrontal cortex has been found to be involved during emotion regulation in the context of social emotions whereas the posterior parietal cortex has been repeatedly implicated in self-other distinction during social cognition (Kanske et al., 2015). In general, there has been accumulating evidence that the aPFC seems to play a crucial role in monitoring emotional control strategies and alternative emotional actions (Koch et al., 2018). Throughout development, there is considerable reorganization of functional connectivity in resting-state networks (Power et al., 2010). The anterior insula has been reported to show greater functional and struc-

tural integration with the executive control network in adults compared to children (Uddin et al., 2011). These findings suggest that altruistically motivated helping in middle childhood can be in part explained by a developmental increase in resting-state functional connectivity from the rvAI to prefrontal and parietal brain regions implicated in emotional clarity and emotion regulation.

A number of limitations should be noted. First, whereas resting-state functional connectivity of the rvAI was associated with altruistically motivated helping, age and emotional clarity, task-based functional connectivity of the rvAI was not. One probable reason is that resting-state connectivity offers a better signal to noise ratio compared to task-based approaches (Fox & Greicius, 2010). Task-based fMRI requires a large number of trials and extensive averaging to obtain a signal. In our study, the empathy for taste paradigm had fewer number of trials considering its demands on the children. Second, while helping in the Escape condition is predominantly altruistically motivated as several studies suggest (Batson et al., 1983; Hein et al., 2010), the role of other motivations cannot be totally ruled out. Third, our measure of emotional inhibition may also reflect more general inhibitory control processes that are not emotion specific. Future studies should aim to use purer measures of emotion inhibition. Fourth, to further corroborate and integrate these findings on neural and behavioural levels, future studies should also include additional behavioural measures of empathy. Fifth, the helping rate in the No-escape condition was comparably lower than what has been reported in adult studies (Batson et al., 1987). It must be noted that there is considerable variability in helping rates across different paradigms and populations (Martin & Olson, 2015). Further, as this study shows, helping increases with age and such a difference may reflect overall developmental differences in the propensity to help (Steinbeis, 2018). Further work is required comparing behaviour across multiple paradigms between children and adults to substantiate this.

In this study, we investigated altruistically motivated helping and its underlying cognitive, affective and neural mechanisms in middle childhood. Using a novel gustatory costly helping task in a large-scale study, we show that altruistically motivated helping increased from 6 to 12 years. Importantly, we identified a neuroaffective mechanism accounting for this developmental shift, comprised of increased emotional clarity and greater functional internetwork integration of the empathy-related network with increasing rvAI functional connectivity to prefrontal and parietal brain regions implicated in emotion regulation. These findings importantly contribute to our understanding of how prosocial behaviours emerge and develop in middle childhood, a formative developmental period for social functioning later in life.

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CONFLICT OF INTERESTS

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author on reasonable request.

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