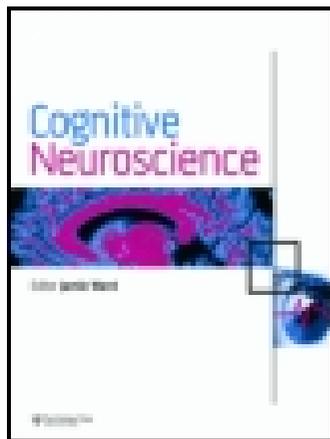


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Anterior cingulate cortex and intuitive bias detection during number conservation

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Anterior cingulate cortex and intuitive bias detection during number conservation

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Children's number conservation is often biased by misleading intuitions but the precise nature of these conservation errors is not clear. A key question is whether children detect that their erroneous conservation judgment is unwarranted. The present study reanalyzed available fMRI data to test the implication of the anterior cingulate cortex (ACC) in this detection process. We extracted mean BOLD (Blood Oxygen Level Dependent) signal values in an independently defined ACC region of interest (ROI) during presentation of classic and control number conservation problems. In classic trials, an intuitively cued visuospatial response conflicted with the correct conservation response, whereas this conflict was not present in the control trials. Results showed that ACC activation increased when solving the classic conservation problems. Critically, this increase did not differ between participants who solved the classic problems correctly (i.e., so-called conservers) and incorrectly (i.e., so-called non-conservers). Additional control analyses of inferior and lateral prefrontal ROIs showed that the group of conservers did show stronger activation in the right inferior frontal gyrus and right lateral middle frontal gyrus. In line with recent behavioral findings, these data lend credence to the hypothesis that even non-conserving children detect the biased nature of their judgment. The key difference between conservers and non-conservers seems to lie in a differential recruitment of inferior and lateral prefrontal regions associated with inhibitory control.

Keywords: Bias detection; Number; Cingulate.

Decades of reasoning and decision-making research have shown that human judgment is often biased by erroneous intuitions. Human reasoners seem to have a strong tendency to base their judgment on fast intuitive impressions rather than on more demanding, deliberative reasoning. Although this intuitive or so-called "heuristic" thinking might sometimes be useful, it can also cue responses that conflict with more logical

or probabilistic considerations and bias our thinking (Evans, 2003, 2010; Kahneman, 2011; Stanovich & West, 2000).

Interestingly, recent studies on bias detection during thinking show that despite the omnipresent bias, adults demonstrate a remarkable sensitivity to violations of logical and probabilistic principles when they reason (e.g., Bonner & Newell, 2010; De Neys

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& Franssens, 2009; De Neys & Glumicic, 2008; Morsanyi & Handley, 2012; Stuppel & Ball, 2008; Villejoubert, 2009; see De Neys, 2012, 2014, for review). That is, although people are often biased and fail to give the correct response, they at least seem to detect that their intuitive heuristic response is questionable. For example, behavioral studies have shown that this intuitive bias detection is associated with increased reasoning times and decreased response confidence (e.g., Bonner & Newell, 2010; De Neys, Cromheeke, & Osman, 2011; De Neys & Glumicic, 2008; De Neys, Rossi, & Houdé, 2013; Stuppel & Ball, 2008; Thompson & Johnson, 2014; Villejoubert, 2009). At the neural level, this bias detection has been linked with increased activation of the anterior cingulate cortex (e.g., De Neys, Moyens, & Vansteenwegen, 2010; De Neys, Vartanian, & Goel, 2008), a region that is often implicated in error monitoring and expectancy violation in cognitive control studies (e.g., Botvinick, Cohen, & Carter, 2004; Brown, 2013; Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004; Ullsperger, Fischer, Nigbur, & Endrass, 2014; but see also Burle, Roger, Allain, Vidal, & Hasbroucq, 2008).

The studies on bias detection during logical and probabilistic thinking have been primarily run with adult reasoners. However, recent findings suggest that when tested with basic, simplified tasks, intuitive bias sensitivity can be demonstrated at the preschool age (De Neys, Lubin, & Houdé, 2014). In their study with preschoolers, De Neys et al. focused on the classic number conservation task. Number conservation boils down to the insight that a numerical quantity will remain the same despite adjustment of its apparent shape or size. Imagine that one is presented with a row of coins that is subsequently being stretched out. Adults and older children will have little trouble grasping that although the stretching makes the row longer, it does not increase the number of coins, of course. However, young children (i.e., until approximately age seven) will intuitively base their judgment on the visuospatial property of length and erroneously conclude that because the row is longer, it also contains more coins (e.g., see Borst, Poirel, Pineau, Cassotti, & Houdé, 2012; Houdé, 1997; Piaget, 1952/1941; Ping & Goldin-Meadow, 2008; Poirel et al., 2012). Hence, in number conservation tasks young children are biased by their visuospatial intuitions (i.e., a so-called “longer-equals-more” heuristic, e.g., Houdé et al., 2011).

De Neys et al. (2014) showed that just like adults in (more complex) logical and probabilistic reasoning tasks, preschoolers who were biased and failed to solve the number conservation task were detecting

the questionable nature of their intuitive response. To demonstrate this, children were given both a classic version of the number conservation task in which the intuitively cued visuospatial longer-equals-more response conflicted with the correct conservation response (i.e., conflict version) and a control or no-conflict version in which this conflict was not present. That is, in the conflict version children initially saw two rows of equal length containing the same number of coins on a computer screen. Next, one of the rows was spread apart so that one was longer than the other and children were asked whether the two rows contained the same number of coins. In the no-conflict version the two rows also had the same number of coins but initially differed in length. Next, the longer row was transformed (i.e., contracted) to give both rows equal length and the child was asked whether the two rows contained an equal number of coins. Hence, the critical difference was that the control problem did not cue an erroneous visuospatial response.

After solving each version children were asked to indicate their response confidence (i.e., how sure they were that their response was correct) on a simplified rating scale. This allowed the authors to measure children’s error detection sensitivity (e.g., De Neys et al., 2010, 2013). If preschoolers do not have an elementary understanding of the conservation principle or do not detect a conflict between their erroneous intuitive answer and this knowledge, their response confidence should not differ after solving conflict and no-conflict problems. However, if children have a minimal awareness of the unwarranted nature of their conservation error, this should decrease their confidence and result in lower confidence ratings after solving conflict than after no-conflict control problems. Results indicated that although the vast majority of preschoolers were biased and failed to solve the conflict version, these same biased children (i.e., the so-called *non-conservers*) were indeed less confident about their response on the conflict than on the no-conflict problem. Hence, although the non-conserving preschoolers did not manage to give the correct response, their confidence indicated that they were not completely oblivious to their error.

Given the link between reasoning bias detection and ACC activation that was established in the studies with logical and probabilistic reasoning tasks (e.g., De Neys et al., 2008, 2010), De Neys et al. (2014) hypothesized that the detection of the erroneous nature of the visuospatial intuition during number conservation might also be mediated by the ACC. In the present study we re-analyze available fMRI data to test this claim. In an earlier fMRI study Houdé

et al. (2011) presented the first neuroimaging data that looked at brain activation associated with number conservation. Houdé et al. tested a group of 5–6-year-old preschoolers and a contrast group of 9–10-year-old children, because children in these two age ranges are known to predominantly fail and succeed at number conservation, respectively (behavioral testing established that this was indeed the case; performance on the conflict problems reached only 2% accuracy in the group of 5–6-year-olds but increased to 98% accuracy for 9–10-year-olds). Children in these two groups were labeled non-conservers and conservers, respectively. All participants were presented with a set of classic conflict number conservation problems and no-conflict control problems in the scanner. fMRI was used to identify brain activation that was associated with correct and incorrect conservation responses. Therefore, Houdé et al. contrasted brain activation in the group of 5–6-year-old non-conservers and 9–10-year-old conservers. Results indicated that correct conservation responses on the conflict problems were associated with increased activation in a parieto-frontal network (encompassing the parietal lobe and inferior frontal and lateral parts of the prefrontal cortex, IFC/LPFC) that has shown to be involved in number processing and inhibitory control (e.g., Aron, Robbins, & Poldrack, 2014; Piazza & Dehaene, 2004). Critically, however, Houdé et al. did not report differential activation for conservers and non-conservers in the ACC region.

As Houdé et al. (2011) noted, the increased activation in regions (i.e., specifically the IFC/LPFC) associated with inhibitory control in the group of conservers supports popular accounts that stress the role of inhibitory processing to override erroneous intuitions in sound conservation (e.g., Bjorklund & Harnishfeger, 1990; Brainerd & Reyna, 2001; Dempster & Brainerd, 1995; Houdé, 2000; Houdé & Tzourio-Mazoyer, 2003; Lubin, Simon, Houdé, & De Neys, 2014). That is, the group of conservers solved the conflict problems correctly and consequently managed to refrain from basing their judgments on the tempting intuitive impression. Hence, the fact that these participants show increased activation in regions associated with inhibitory control is consistent with the idea that they were successful because they succeeded in inhibiting the erroneous intuitive response. Note that such increased IFC/LPFC activation was also observed for correct responses in fMRI studies on bias detection during logical and probabilistic reasoning with adults (e.g., De Martino, Kumaran, Seymour, & Dolan, 2006; De Neys et al., 2008; Goel & Dolan,

2003; Houdé et al., 2000; Stollstorff, Vartanian, & Goel, 2012). However, the key point for our present purposes is that the non-differential ACC activation for conservers and non-conservers in Houdé et al. (2011) lends some credence to the claim that even biased non-conservers detect the erroneous nature of the intuitive response. That is, non-conserving preschoolers might not manage to successfully inhibit the cued intuitive response and consequently show less IFC/LPFC activation in contrast with correctly responding conservers. However, the fact that both groups show similar ACC activation when solving conflict trials is consistent with the claim that the ACC-mediated error or conflict signaling process is equally effective for conservers and non-conservers. Hence, this lends credence to the idea that non-conservers' biased responding does not need to be attributed to a failure to detect the erroneous nature of the intuitive response per se, but rather to a failure to successfully inhibit the intuitive response (e.g., De Neys et al., 2014; Lubin et al., 2014).

It will be clear that the conclusion with respect to the ACC activation pattern in the Houdé et al. (2011) study faces some caveats. First, although the non-differential ACC activation for conservers and non-conservers when solving conflict problems might imply that both groups show a similar ACC activation increase when solving conflict versus no-conflict problems, there is a straightforward alternative explanation. That is, it might be that the ACC is simply not engaged when solving conflict problems (i.e., neither for conservers, nor for non-conservers). Hence, the non-differential activation might result from a lack of ACC engagement in this task. Moreover, Houdé et al. did not specifically consider ACC activation in an independently and a priori circumscribed region. Hence, currently our conclusion with respect to the ACC activation is based on an eyeball analysis of the (absence of) reported activation contrasts in the ACC “ballpark.”

In the present study we address the above issues by re-analyzing the Houdé et al. (2011) data. Therefore, we first determined an a priori specified ACC region that showed most specific conflict and error-related activation in previous independent research (e.g., Klein et al., 2007). For each participant, we calculated the average activation in this ACC region of interest when solving the conflict and control conservation problems. Next, we tested whether ACC activation differed when solving conflict versus control problems and whether the potential ACC activation increase (when contrasting conflict and control problems) differed for conservers and non-conservers.

For completeness, in subsequent control analyses, we also included the IFC/LPFC regions identified by Houdé et al. (2011) as additional regions of interest (i.e., left inferior frontal gyrus, right inferior frontal gyrus, right middle frontal gyrus, and the orbital part of the right middle frontal gyrus). This allowed us to validate the findings and examine how the activation in these regions correlated with activation in the critical ACC region of interest.

METHOD

Participants

Houdé et al. (2011) selected a group of 16 preschoolers aged 5–6 years (mean age = 5.9 years, $SD = 0.7$, range: 5.2–7.2 years, six boys, 12 right-handed) and 16 children aged 9–10 years (mean age = 10.2 years, $SD = 0.6$, range: 9.2–10.9 years, eight boys, 11 right-handed) for their analyses. The study was approved by the local ethical committee and all parents or guardians gave informed consent for the study. The age ranges in question were selected because children in these developmental stages are known to fail and succeed at number conservation, respectively. Following Houdé et al., we will refer to these two groups as non-conservers and conservers, respectively. Behavioral testing confirmed that the selected participants demonstrated the expected behavioral pattern (i.e., correct response on conflict trials averaged 2.5% and 99.7% for non-conservers and conservers, respectively). Accuracy for the no-conflict problems was at ceiling in both groups (+99% for both groups). Note that after the fMRI session, Houdé et al. (2011) also presented participants with a conflict problem in a quiet room using non-computerized material. This posttest confirmed that all conservers managed to solve the problem, while all non-conservers failed to solve it.

For the present study we re-analyzed the fMRI data of these participants. Note that due to technical complications, we did not manage to recover the original data for two participants in the non-conserver group. Hence, the current analyses for the non-conserver group are based on data of 14 participants (mean age = 5.9 years, $SD = 0.9$, range: 5.2–7.2 years, five boys, 10 right-handed, average conflict accuracy = 7.5%, average no-conflict accuracy = 97.7%).

Task stimuli

All children were presented with both a classic version of the number conservation task in which an

intuitively cued response conflicted with the correct conservation response (i.e., conflict version) and a control or no-conflict version in which this conflict was not present (see further for details).

In each conflict problem trial, children were presented with two rows, each containing the same number of objects (five, six, or seven objects). For each trial, children were asked to judge the numerical equivalence of two rows of objects when the rows had the same length. After a jittered inter-stimuli interval of $750 \text{ ms} \pm 250 \text{ ms}$, the objects in one of the rows were spread apart by apparent movement on the computer screen. After the objects in one of the two rows had been moved, the children were again instructed to judge the numerical equivalence of the two rows of objects. Children responded by pressing the “same” button or the “not the same” button of a response box. The question, “Is the number of objects the same in both rows?” was verbally delivered for each trial (2.7 s duration each). Children wore special optical fiber headphones (MR CONFON, Leibniz-Institute for Neurobiology at Magdeburg, Germany) that used the magnetic field of the MRI scanner to drive the headphone membrane. Each trial remained present on the screen until the child responded.

Control/no-conflict trials were similar except that the objects in the two rows could have the same or different colors. Instead of asking children for numerical equivalence, they were now asked, after the spreading apart of one of the rows, whether the objects in both rows had the same color. Children responded by pressing the “same” button or the “not the same” button on the response box. In all other respects stimuli presentation was completely similar to the conflict trials. Hence, as in the study of De Neys et al. (2014), the key feature of the control problems was that they did not cue a biasing erroneous visuospatial response. For completeness, note that Houdé et al. (2011) referred to conflict and no-conflict trials as “Number” and “Color” trials, respectively. We stick here to the conflict and no-conflict labels that were used by De Neys et al. (2014).

Participants solved a total of 21 conflict trials and 21 no-conflict trials. To avoid inter-problem interference Houdé et al. (2011) presented all conflict and no-conflict trials in two separate runs. Note that the conflict trials were presented before the no-conflict trials. Houdé et al. opted for this design to stay as close as possible to Piaget’s original task design (in which no-conflict trials were not presented). Presenting the no-conflict problems before or mixed with the conflict problems could have altered performance on the conflict problems. Children used their preferred hand to give their

answers with the response pad. The inter-trial interval was jittered and lasted 9 s on average, with a standard deviation (*SD*) of 1, and a range from 8 s to 10 s.

fMRI imaging protocol

Images were acquired using a 3T MRI scanner (Achieva, Philips Medical System, the Netherlands). In a first anatomical session, 3D T1-weighted spoiled gradient images (FOV: 256 mm; slice thickness: 1.33 mm; 128 slices; matrix size 192×192 voxels; 5 min, 7 s duration) were acquired while the children passively watched a cartoon on an MRI-compatible screen. After a break outside the scanner, the fMRI session, consisting of two different runs, was conducted with T2*-weighted, gradient echo-planar images (EPI) acquired with a repetition time of 2 s, echo time of 35 ms, and flip angle of 80° for 31 axial slices, 3.5 mm thick, with a 224 mm FOV and 64×64 grid (210 volumes in 7 min for each). Additional anatomical T2*-weighted images were acquired with 60 slices, 2.3 mm thick, and a 112×112 grid (2 min, 10 s duration) to facilitate realignment between T1 and EPI images.

fMRI data analysis

Preprocessing and statistical analysis were carried out using SPM5 software (Penny, Ashburner, Kiebel, Henson, Glaser, & Friston, 2001). Preprocessing included slice-time correction, motion correction, visually checking the realignment of the mean EPI image with the T1 image, normalization using the Montreal National Institute (MNI) template, and spatial smoothing with a 6 mm Gaussian kernel (see Houdé et al., 2011, for details). Comparisons of

interest were implemented using a general linear model with the standard adult hemodynamic response function, as no differences have been reported for children (Kang, Burgund, Lugar, Petersen, & Schlaggar, 2003), convolved with trial onsets, the end of the second response time as an offset, and six motion parameters (*x*, *y*, and *z* axes for translation and rotation) as factors of non-interest.

For the second level analysis Houdé et al. (2011) included their data in a multi-subject fixed-effect analysis to determine significant differences between each group for the conflict and no-conflict trials. All trials were included in the analysis. To avoid confusion, note that due to the design of the study, the conflict trials were correctly solved by the group of conservers and incorrectly by the group of non-conservers. The present analyses focuses on the critical direct contrast of the activation in the conflict and no-conflict trials (i.e., Conflict trials–No-Conflict trials contrast) in the group of conservers and non-conservers.

ROI selection and analysis

ACC region of interest

The exact location of our ACC region of interest (ROI) was based on previous meta-analysis work by Klein et al. (2007). This exact same region was also previously shown to be implicated in the detection of the erroneous nature of biasing intuitions in logical and probabilistic reasoning tasks with adults (De Neys et al., 2008). Following De Neys et al. (2008), the ROI for our current analysis was a sphere with a 12 mm radius centered on the voxel that showed peak activation in the Klein et al. study (center voxel coordinates = 1, 15, 43). Figure 1 illustrates the location of the ROI.

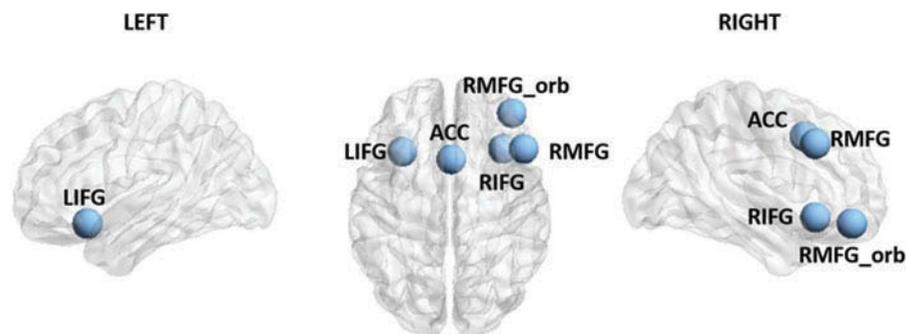


Figure 1. 3D rendering of the different regions of interest (ROI). All ROIs are spheres with a 12 mm radius. Figure was plotted with BrainNet Viewer (Xia, Wang, & He, 2013). ACC, anterior cingulate cortex; LIFG, left insula/inferior frontal gyrus; RIFG, right insula/inferior frontal gyrus; RMFG, right middle frontal gyrus; RMFG_orb, orbital part of the right middle frontal gyrus.

IFC/LPFC regions of interest

In their study, Houdé et al. (2011) identified four different areas within the IFC/LPFC for which the group of conservers showed significantly stronger activation than the group of non-conservers while solving conflict trials. These areas were the left insula/inferior frontal gyrus (LIFG; $-32, 20, -14$), right insula/inferior frontal gyrus (RIFG; MNI coordinates = $36, 22, -10$), right middle frontal gyrus (RMFG; MNI coordinates = $50, 22, 38$), and the orbital part of the right middle frontal gyrus (RMFG orbital; MNI coordinates = $42, 46, -14$). We also included regions of interest centered on these four IFC/LPFC areas in our analysis. In line with the ACC ROI definition, all IFC/LPFC ROIs were defined as spheres with a 12 mm radius. Center of the spheres were the voxels that showed peak activation in the Houdé et al. study. Locations of the IFC/LPFC ROIs is also illustrated in Figure 1.

ROI analysis

All ROIs were built and Blood Oxygen Level Dependent (BOLD) values extracted using MarsBaR (Brett, Anton, Valabregue, & Poline, 2002), a toolbox for SPM which provides routines for region of interest analysis. We extracted the mean positive BOLD signal value in the ACC and IFC/LPFC ROIs from the key contrast of interest (Conflict trials–No-conflict trials) for each participant. Data for voxels in which there was greater BOLD signal for No-conflict than Conflict trials were not included in the calculation of the mean. These mean BOLD values were subjected to statistical analysis. Signal value extractions were performed with normalized images.

RESULTS AND DISCUSSION

ACC ROI

Our key question was whether the ACC shows increased activation when children try to solve conservation problems in which visuospatial intuitions cue an incorrect response (i.e., conflict problems). In our analyses we therefore focused on the differential activation in the conflict versus no-conflict trials (i.e., Conflict–No-conflict contrast). Subtraction of activation in the control/no-conflict condition allows us to unequivocally establish whether the ACC activation differed significantly when solving conflict trials.

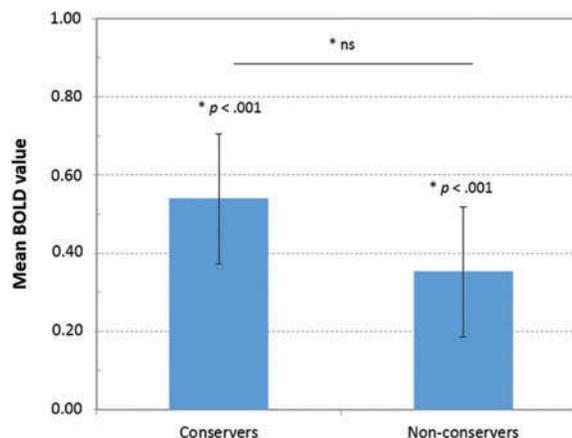


Figure 2. Mean BOLD values for the group of conservers and non-conservers extracted from the conflict vs. no-conflict contrast in the anterior cingulate cortex region of interest (ACC ROI). Results indicate that both conservers and non-conservers showed activation in the ACC ROI that significantly differed from zero. However, the ACC activation did not differ for conservers and non-conservers (ns). Error bars are 95% confidence Intervals.

A first control analysis established that for all participants (conservers and non-conservers combined), the mean BOLD value in the ACC ROI differed significantly from zero, mean BOLD value = 0.45 ($SD = 0.31$), $t(30) = 7.89$, $p < .0001$. This established that at the aggregate group level the ACC was specifically engaged when solving conflict trials. Next, we repeated this analysis for both groups separately. Results are shown in Figure 2. As Figure 2 indicates, when solving conflict problems both conservers, Mean BOLD value = 0.54 ($SD = 0.32$), $t(15) = 6.87$, $p < .0001$, and non-conservers, Mean BOLD value = 0.35 ($SD = 0.29$), $t(13) = 4.51$, $p < .001$, showed ACC activation that was significantly higher than zero. Moreover, the ACC activation for conservers and non-conservers did not differ significantly, $t(28) = 1.69$, $p = .102$. These findings directly establish that the ACC is recruited when faced with conflict trials. However, this does not depend on whether one manages to solve the problems correctly or not. Even biased non-conservers showed the increased ACC activation.

IFC/LPFC ROIs

Table 1 gives an overview of the mean BOLD values extracted from the Conflict–No-conflict contrast for each of the four IFC/LPFC ROIs. As Table 1 indicates, we observed that there was a significantly higher activation for conservers than non-conservers in the right middle frontal gyrus (RMFG) ROI,

TABLE 1

Mean BOLD values (standard deviations in parentheses) in the group of conservers and non-conservers extracted from the conflict vs. no-conflict contrast for regions of interest in the inferior frontal and lateral prefrontal cortex (IFC/LPFC ROIs). The last column shows the correlations in each region with the mean BOLD value in the anterior cingulate cortex region of interest (ACC ROI).

ROI	Non-conservers	Conservers	ACC ROI correlation
Left insula/inferior frontal gyrus	0.35 (0.26)	0.34 (0.15)	.32
Right insula/inferior frontal gyrus	0.27 (0.20) ⁺	0.41 (0.22) ⁺	.72*
Right middle frontal gyrus orbital part	0.32 (0.31)	0.35 (0.14)	.19
Right middle frontal gyrus	0.22 (0.15)*	0.39 (0.19)*	.60*

Notes: ⁺ $p < .07$; * $p < .05$; ROI, region of interest; ACC, anterior cingulate cortex.

$t(28) = 2.57$, $p < .025$, and a marginally significant effect in the right insula/inferior frontal gyrus (RIFG) ROI, $t(28) = 1.89$, $p < .07$. Effects for the other two regions were not significant (all $ps > .63$). For all participants combined (conservers and non-conservers), the activation in the RMFG, $r = .60$, $p < .001$, and RIFG, $r = .72$, $p < .001$, also correlated significantly with the ACC ROI activation. When the ACC ROI correlations were considered in isolation for the group of conservers (RMFG, $r = .57$, $p < .025$; RIFG, $r = .68$, $p < .005$) and non-conservers (RMFG, $r = .51$, $p < .07$; RIFG, $r = .70$, $p < .01$), findings were similar. Correlations with the ACC activation in the RIFG, $p > .93$, and, RMFG, $p > .83$, did not differ significantly for conservers and non-conservers. These correlational patterns are illustrated in the scatterplots in Figure 3.

GENERAL DISCUSSION

In the present study, we re-analyzed available fMRI data from Houdé et al. (2011) to verify the implication of the ACC in the detection of the erroneous nature of cued visuospatial intuitions during number conservation. Therefore, we first determined an a priori specified ACC region that showed most specific conflict and error-related activation in previous independent research (e.g., Klein et al., 2007) and was previously shown to be implicated in the detection of the erroneous nature of biasing intuitions in logical and probabilistic reasoning tasks (e.g., De Neys et al., 2008). For each participant, we calculated the average activation in this ACC region of interest when solving classic and control number conservation problems. In classic conflict trials the intuitively cued visuospatial response conflicted with the correct conservation response, whereas this conflict was not present in the no-conflict control trials. Results showed that ACC activation increased when solving the classic conflict problems. Critically, this increase was observed both in a group of conservers and a group of non-conservers who solved the conflict problems correctly and incorrectly, respectively. Given the postulated role of the ACC in conflict and error monitoring (e.g., Botvinick et al., 2004; Brown, 2013; Ridderinkhof et al., 2004) and previous behavioral findings (De Neys et al., 2014), this lends credence to the hypothesis that even non-conserving preschoolers detect the biased nature of their judgment. If non-conservers are biased because they do not detect that the intuitive response conflicts with the correct conservation response, one would not expect to see increased ACC activation when solving these problems.

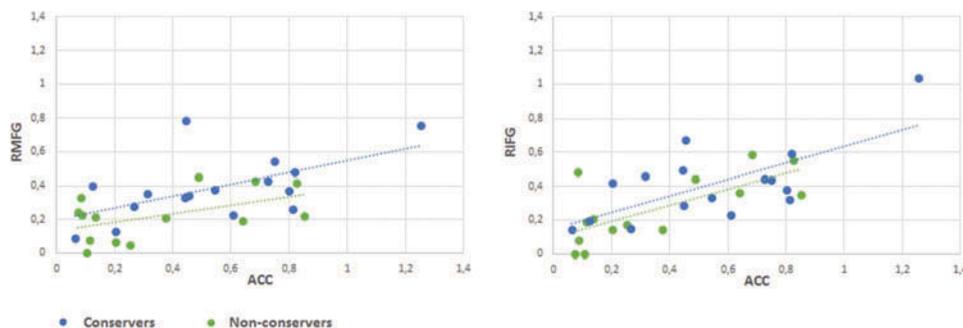


Figure 3. Scatterplots and regression lines illustrating the correlation between activation (mean BOLD values extracted from the conflict vs. no-conflict contrast) in the anterior cingulate cortex region of interest (ACC) and right middle frontal gyrus (RMFG ROI, left panel) and right insula/inferior frontal gyrus (RIFG, right panel) regions of interest for the group of conservers and non-conservers.

In contrast with the ACC findings, we did observe that conservers and non-conservers showed differential activation in inferior frontal and lateral prefrontal regions that were hypothesized to be involved in inhibitory processing by Houdé et al. (2011). In the present analysis, the increased activation for conservers was clearest in the right insula/inferior frontal gyrus and right middle frontal gyrus regions. The activation in these regions also correlated with the ACC activation, both for conservers and non-conservers. Hence, both for conservers and non-conservers alike, a higher ACC activation was associated with a higher IFC/LPFC activation. Given that the average ACC activation for conservers and non-conservers did not differ whereas the average IFC/LPFC did, this pattern tentatively suggests that conservers are specifically efficient in recruiting IFC/LPFC areas in response to conflict (i.e., between the appropriate conservation answer and the incorrect intuitive visual impression) that is detected by the ACC. That is, although the ACC might be signaling the need to block the erroneous cued intuitive response for both groups, conservers might be better at recruiting the IFC/LPFC regions that are mediating the actual inhibition process. Hence, it is not unreasonable to suggest that the higher IFC/LPFC activation for conservers reflects the fact that they succeeded at inhibiting the intuitive response which allowed them to solve the conflict problems correctly (e.g., Houdé et al., 2011). Put simply, although both conservers and non-conservers might be detecting the problematic nature of the intuitive response, conservers will be better at resolving the detected problem (e.g., Lubin et al., 2014).

To be clear, the present study established that out of the four IFC/LPFC regions that were included based on the original Houdé et al. (2011) study, the postulated inhibition-related increased activation for conservers was only observed in the right insula/inferior frontal gyrus (RIFG) and right middle frontal gyrus region (RMFG). To avoid confusion, one needs to bear in mind here that the present analysis focused on the critical direct contrast of activation in the conflict and no-conflict trials (i.e., Conflict trials–No-Conflict trials contrast) in the group of conservers and non-conservers. The original Houdé et al. study simply contrasted activation for conservers and non-conservers in Conflict trials per se (i.e., without subtraction of No-Conflict trials). In this sense the present re-analysis is more stringent. Hence, the present findings indicate that among the IFC/LPFC regions identified by Houdé et al. it is the RMFG and RIFG that are

involved in mediating the conflict resolution and inhibition process during number conservation.

It is vital to stress the importance of the available converging evidence when evaluating the present study. When considered in isolation the findings obviously need to be interpreted with caution. First, the present analyses focused on one specific ACC region. Although there is considerable evidence for the claim that the ACC mediates error-related conflict processing, alternative views about ACC functioning have been presented (e.g., see discussion between Grinband et al., 2011 and Yeung, Cohen, & Botvinick, 2011). Second, although the ACC is assumed to be critical, other regions might be implicated in conflict detection (e.g., Ullsperger et al., 2014). We cannot rule out that the activation pattern would be different in other potential conflict mediating regions. Third, one needs to bear in mind that our group of conservers and non-conservers (by definition) differed in age (i.e., on average, 6- vs. 10-year-olds in the present case). Consequently, potential differential age-related maturation of the cerebral cortex may have affected the findings (e.g., Sheridan, Khartimova, Martin, Chatterjee, & Gabrieli, 2014). Fourth, there are a number of design features of the original Houdé et al. (2011) study that are less than optimal for the present purposes (e.g., the fact that conflict trials were always presented before no-conflict trials and that no-conflict trials did not require a numerical equivalence judgment).

Given the above caveats, it is critical to consider converging evidence. As we noted, the behavioral number conservation study of De Neys et al. (2014) with confidence ratings also indicated that non-conserving preschoolers detect the questionable nature of their incorrect response. In addition, there is imaging data that points to the involvement of the exact same ACC ROI in bias detection during probabilistic reasoning in adults (De Neys et al., 2008). It is in light of this converging evidence that the present study was conceived and that the findings need to be interpreted. Taken together, the findings provide a coherent and convincing case.

Obviously, we readily acknowledge that it will be interesting to complement the present re-analysis of the Houdé et al. (2011) study with a future independent replication. Ideally, such a study could adopt the task design of the behavioral conservation study of De Neys et al. (2014) and also ask children to give confidence ratings in the scanner. This would allow us to directly link the confidence data to ACC brain activation, for example. However, one needs to keep in mind that studies on (unsuccessful) number conservation by definition require testing children at very young (preschool) ages,

and consequently face considerable major logistic challenges for an fMRI study (e.g., only scanning during school holidays, during business hours, both parents and children need to be available, higher likelihood to discard participants because of excessive head motion, etc.). Hence, such de novo experimentation will require a considerable time-frame to be completed. Although we encourage such future work, we believe that in the meantime, the current type of re-analysis has an important scientific role to play and helps to advance the debate.

It might be interesting to link the present work on number conservation to developmental research on bias detection during logical and probabilistic thinking in the reasoning and decision-making field. As we noted, it has been shown that adult reasoners also detect the biased nature of their intuitive logical and probabilistic judgments (e.g., Bonner & Newell, 2010; De Neys, 2012; De Neys & Bonnefon, 2013; Pennycook & Thompson, 2012; Pennycook, Trippas, Handley, & Thompson, 2014; Thompson & Johnson, 2014). However, developmental studies in this field have suggested that the bias detection during logical and probabilistic reasoning is only observed after the onset of adolescence (i.e., by the end of elementary school; e.g., De Neys et al., 2011; De Neys & Feremans, 2013; Rossi, Cassotti, Agogué, & De Neys, 2013; see De Neys, 2013, for a review). This developmental pattern has been linked to the late maturation of the ACC which is known to only achieve full functionality during the adolescent years (e.g., Davies, Segalowitz, & Gavin, 2004; Fitzgerald et al., 2010; Santesso & Segalowitz, 2008). Given these findings, the presently established successful number conservation error detection at the preschool age might seem somewhat surprising at first sight. However, as noted by De Neys et al. (2014), here one needs to take into account that even a less than fully functional ACC does not imply a lack of all conflict detection. Indeed, error monitoring studies have shown that even infants can detect errors in simple tasks that do not cue a strong intuitive response (Berger, Tzur, & Posner, 2006; Lubin et al., 2010; Lyons & Ghetti, 2011). Arguably, in comparison with logical and probabilistic reasoning tasks in which the cued intuitive response typically entails a semantic prior belief or stereotypical information, the critical physical transformation in conservation tasks (i.e., the apparent movement of the objects in the row) can act as a cue that directs children's attention and thereby facilitates monitoring (De Neys, 2013). Hence, detection of intuitive bias in number conservation might be less demanding and can occur at a younger age than in logical and probabilistic reasoning tasks. Although this prediction remains to be tested directly, it does suggest that a promising agenda for

future neuroscientific studies on error monitoring and anterior cingulate cortex development might be to more specifically contrast children's performance across different domains.

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