



# Common Neural Functions during Children's Learning from Naturalistic and Controlled Mathematics Paradigms

Marie Amalric<sup>id</sup> and Jessica F. Cantlon

## Abstract

■ Two major goals of human neuroscience are to understand how the brain functions in the real world and to measure neural processes under conditions that are ecologically valid. A critical step toward these goals is understanding how brain activity during naturalistic tasks that mimic the real world relates to brain activity in more traditional laboratory tasks. In this study, we used intersubject correlations to locate reliable stimulus-driven cerebral processes among children and adults in a naturalistic video lesson and a laboratory forced-choice task that shared the same arithmetic concept. We show that relative to a control

condition with grammatical content, naturalistic and laboratory arithmetic tasks evoked overlapping activation within brain regions previously associated with math semantics. The regions of specific functional overlap between the naturalistic mathematics lesson and laboratory mathematics task included bilateral intraparietal cortex, which confirms that this region processes mathematical content independently of differences in task mode. These findings suggest that regions of the intraparietal cortex process mathematical content when children are learning about mathematics in a naturalistic setting. ■

## INTRODUCTION

When children learn mathematics at school, they need to combine many pieces of information such as the teacher's verbal explanation, formulas or diagrams drawn on the board, reference to a book, and so forth. In contrast to the richness of the school environment, most of what we know about mathematics development in the brain has been established using highly controlled laboratory paradigms that tend to minimize context and extraneous input. Although controlled paradigms are essential to make pure contrasts and test specific hypotheses, they can result in oversimplified and somewhat narrow theories with only limited implications to children's real-life mathematics development (Cantlon, 2020). An alternative approach is to use visually and auditorily rich naturalistic paradigms such as video watching, including cartoon educational videos, to mimic real-world learning conditions as closely as possible. This approach is essential for understanding how human brains function in the real world.

Recent neuroimaging studies have tested children with naturalistic educational videos to measure the similarities between neural processes in children and adults (Lerner, Scherf, Katkov, Hasson, & Behrmann, 2021; Kersey, Wakim, Li, & Cantlon, 2019; Richardson, Lisandrelli, Riobueno-Naylor, & Saxe, 2018; Emerson & Cantlon, 2015; Cantlon & Li, 2013). Those studies use intersubject correlation (ISC) measures to quantify the similarity in brain activation time courses between children and adults.

In ISC, the neural time course at each voxel is tested for temporal correlation among participants. Significant correlation in brain responses among participants indicates the presence of a reliable stimulus-driven neural process in that brain region. These studies established that naturalistic paradigms evoke patterns of activation that associate or dissociate by function and age in predictable and reliable ways. For example, Cantlon and Li (2013) showed that 4- to 8-year-old children exhibited correlated brain activity—also called neural similarity—with adults while watching educational “Sesame Street” videos. Neural similarity between a given child and a group of adults is thought to indicate how adult-like is this child's brain activity, and is thus a measure of neural maturity. In Cantlon and Li's study, children's neural maturity in the parietal cortex predicted their performance on mathematical tests, whereas their neural maturity in Broca's area predicted their performance on verbal tests. Kersey et al. (2019) confirmed the functional dissociation between math- versus reading-related natural viewing activity, and demonstrated that both math- and reading-related networks also show immature neural activity patterns—that is, dissimilar brain activity—in 4- to 8-year-old children relative to adults.

However, in prior naturalistic studies of children, it is unclear how brain activity during naturalistic tasks relates to activity in the more traditional simplified tasks because they were not directly compared. On the one hand, both types of tasks could recruit similar brain circuitry. For example, in 2013, Dastjerdi, Ozker, Foster, Rangarajan, and Parvizi (2013) showed that the neural populations activated during a laboratory arithmetic task also activated

when adult patients were referring to objects with numerical content during natural dialog. On the other hand, critical features of the context of learning may be unique to naturalistic video watching tasks (Sanchez-Alonso & Aslin, 2022; Cantlon, 2020). Indeed, the theory of mind network that Richardson et al. (2018) revealed with a naturalistic task differed from the one predicted by traditional tasks. In 2013, Cantlon and Li showed that math achievement was better predicted by children's brain responses to a naturalistic math task than to a laboratory math task. Moreover, Jovanovic, Fishbein, de la Mothe, Lee, and Miller (2022) recently showed that neural responses to vocalizations in the marmoset's pFC depended on the context—from traditional head-restrained listening to naturalistic free-moving communication—in which they were heard. Note that the two alternatives presented here are not mutually exclusive. If the same brain regions are recruited for both types of tasks, they are not necessarily recruited in the same way.

In this study, to test whether the same brain regions that are engaged during controlled tests of a math concept in the laboratory are also involved when children are taught a lesson about that concept at school, we compare a naturalistic math video lesson and a simplified laboratory math task, which both present the same arithmetic concept: the commutative principle of multiplication. In the naturalistic video, a cartoon teacher explains the formal arithmetic principle of commutativity in an educational narrative, whereas in the simplified laboratory task, the same principle is queried in a traditional two-alternative forced-choice task. Beyond the perhaps trivial difference in their respective involvement of the motor cortex versus auditory and language-related brain regions, our core prediction is that, relative to a naturalistic control video lesson testing nonmathematical content (a grammar lesson), the naturalistic and laboratory arithmetic tasks should evoke overlapping activation within brain regions that process math semantic content. These brain regions are expected to be primarily the intraparietal sulcus (IPS), as well as some frontal regions such as the inferior frontal gyrus (IFG) that are consistently found in studies of mental arithmetic and math processing in both adults and children, and the posterior inferior temporal gyrus (pITG) in adults (for meta-analyses, see the work of Hawes, Sokolowski, Ononye, & Ansari, 2019; Arsalidou, Pawliw-Levac, Sadeghi, & Pascual-Leone, 2018; Yeo, Wilkey, & Price, 2017; Arsalidou & Taylor, 2011; Kaufmann, Wood, Rubinsten, & Henik, 2011; Houdé, Rossi, Lubin, & Joliot, 2010). In these regions, we then investigate similarities and differences in the activation elicited by both types of math tasks.

## METHODS

### Sample Size and Participants

Based on previous studies evidencing the neural dissociation between mathematics and general knowledge

semantics, and others using ISCs in children, we aimed at collecting data in at least 15 adults and 20 children. Data collection was interrupted because of restrictions due to the COVID-19 pandemic, after scanning 39 participants: 24 typically developing children at the end of their third grade year and 15 adult undergraduate students. One adult was excluded from further analyses because of technical issues during the fMRI session, and six children were excluded because of opting out (four participants) or excessive ( $> 3$  mm) head motion (two participants), leaving a total of 32 participants (14 adults: mean age 19.5 years old, 6 men, 8 women; and 18 children: mean age 9.25 years old  $\pm$  2 months, 6 boys, 12 girls).

All adult participants and parents of child participants gave informed consent after reading or being read consent information. All children also gave their assent to participate after being read the consent information. The protocol was approved by the Carnegie Mellon University institutional review board.

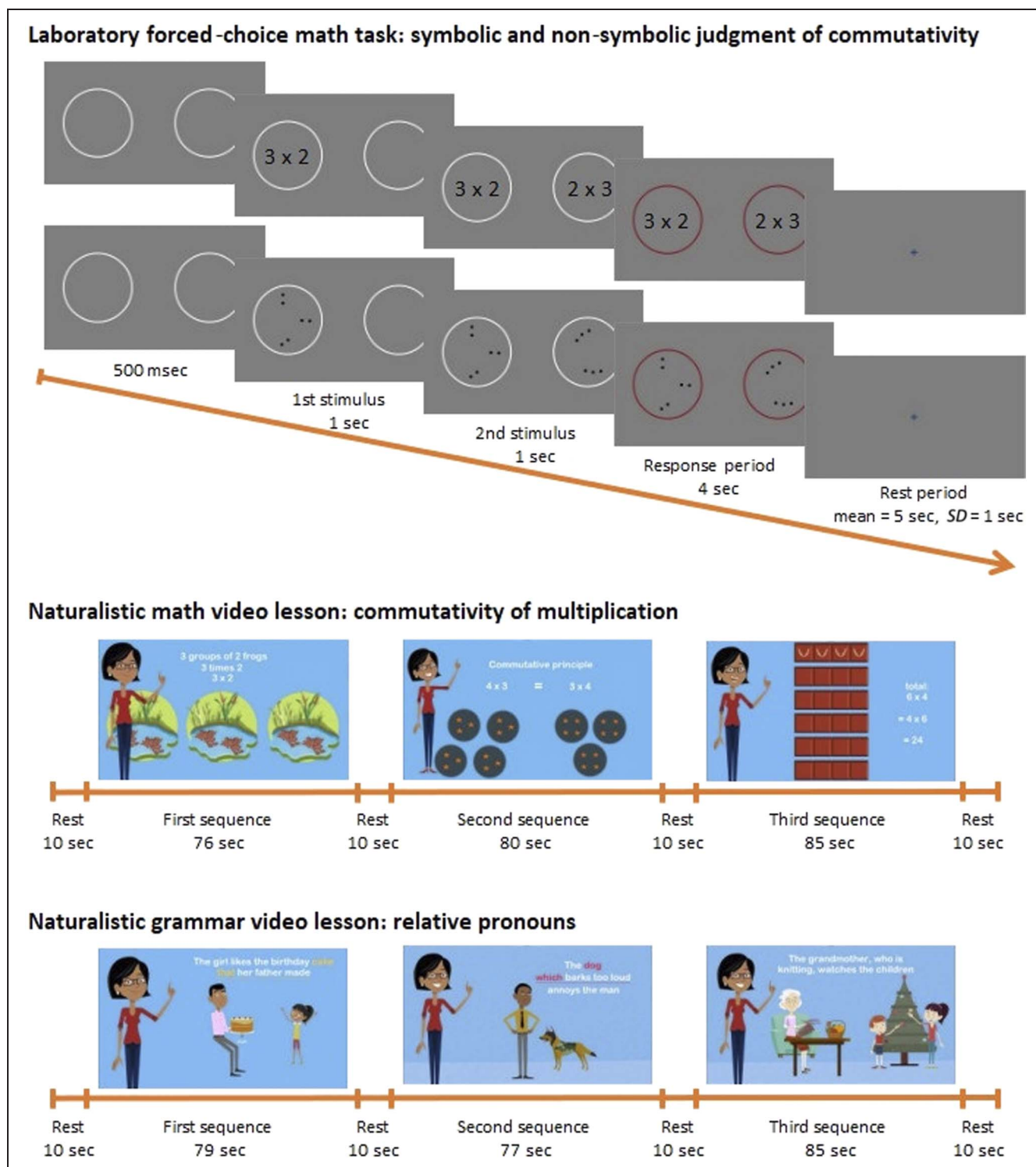
### Protocol and Stimuli

Participants were scanned using fMRI while completing a two-alternative forced-choice math task, a naturalistic mathematics video lesson, and a naturalistic grammar video lesson. Whereas the controlled laboratory math task and math video lesson shared content about the commutative principle of multiplication, the grammar and math videos, in contrast, shared superficial perceptual features of the naturalistic video lesson.

#### *Forced-choice Same/Different Math Task*

The fMRI session started with three runs of the forced-choice task, which tested participants' performance in an arithmetic task with the commutative principle of multiplication. Each run included 24 trials. On each trial, participants were given a few seconds to decide whether two symbolic operations or two dot arrays, including commutative pairs (e.g. " $2 \times 3$ " vs. " $3 \times 2$ "), were numerically equal or not (Figure 1).

Each trial of the same/different task started with two white circles horizontally distributed on a gray background and a blue fixation cross at the center of the screen. After 500 msec, the fixation cross disappeared, and a first operation or dot array appeared in the first circle. At 1500 msec, a second operation or dot array appeared in the second circle. One second later, the color of the two circles turned to red, indicating the beginning of the 4-sec response period. The two operations or dot arrays remained on the screen during the entire response period. Participants were instructed to press a button with their right thumb if they thought that the two operations had the same arithmetic outcome, and to press a button with their left thumb otherwise. Each trial ended with a rest period of variable duration (mean = 5 sec,  $SD = 1$  sec).



**Figure 1.** Protocol. (Top) Timeline of a trial of the two-alternative forced-choice math task. Participants were given 4 sec to decide whether the results of two simple operations or the numbers of dots in two different sets were the same or were different. (Middle and bottom) Timeline of the presentation of both naturalistic arithmetic and grammar video lessons and representative frames extracted from each of the three sequences composing the videos.

The same pairs were presented symbolically and non-symbolically in each run. Symbolic pairs were simple math operations (e.g., “ $2 \times 3$ ” and “ $3 \times 2$ ”). Their nonsymbolic counterparts were sets of dots visually arranged in subgroups (e.g., “2 groups of 3 dots” and “3 groups of

2 dots”). Subgroups of the same size in a set were arranged according to the same pattern. Subgroup arrangements were identical to the ones generated by Ciccione and Dehaene (2020). In each run, eight pairs tested for the understanding of the commutative principle (e.g., “ $4 \times$

**Table 1.** Operations Used in the Laboratory Forced-choice Math Task

<i>Second Item</i>	<i>First Item</i>			
	<i>Same Number - Different Number of Sets</i>		<i>Different Number - Same Number of Sets</i>	
	<i>Same Operation</i>	<i>Different Operation</i>	<i>Same Operation</i>	<i>Different Operation</i>
$2 \times 3$	$3 \times 2$	$1 + 2 + 3$	$2 \times 4$	$5 + 2$
$3 \times 2$	$2 \times 3$	$4 + 2$	$3 \times 4$	$3 + 4 + 5$
$2 \times 4$	$4 \times 2$	$1 + 2 + 2 + 3$	$2 \times 2$	$1 + 3$
$4 \times 2$	$2 \times 4$	$1 + 3 + 4$	$4 \times 3$	$2 + 3 + 3 + 4$

2” and “ $2 \times 4$ ”). We compared them to eight pairs with the same number of items but different math operations (e.g., “ $4 + 2$ ” and “ $3 \times 2$ ”). We also introduced eight pairs controlling for numerosity and ensuring that participants did not simply estimate the number of items but computed exact additions and multiplications (half of them used the same operation: e.g., “ $4 \times 3$ ” and “ $4 \times 2$ ”; and the other half used different operations: e.g., “ $5 + 2$ ” and “ $2 \times 3$ ”). See Table 1 for a list of stimuli.

#### *Naturalistic Video Lessons*

The arithmetic video was a lesson explaining the commutative principle of multiplication. The grammar video was a lesson explaining the principle of combining relative pronouns into phrases. Both the math and grammar videos were created with the on-line application Powtoon (<https://www.powtoon.com/>). They were designed to parallel a real-world school lesson by presenting formal information in a building narrative. Both lessons included the same virtual teacher explaining either a mathematical or grammatical principle over three sequences that followed a natural progression from a simple example, to a more complex example, to a general definition of the principle (Figure 1). The videos had matching visual and auditory frameworks (same teacher, same voice, same blue background, same transition animations and sound effects, same cartoon format, and a combination of symbols and pictures).

Video runs started with a plain blue screen with a central black fixation cross for 10 sec, in order to measure the activation baseline before the video started playing. Both videos consisted of three sequences of  $80 \pm 4$  sec, separated by 10 sec rest periods (Figure 1). Half of the participants watched the math video first, and the other half watched the grammar video first.

#### **fMRI Acquisition and Analyses**

Functional images were acquired on a Siemens Prisma 3-Tesla scanner with multiband imaging sequences (multiband factor = 4, slice acceleration factor = 3, 60 interleaved axial slices, 3-mm thickness and 3-mm in-plane resolution, repetition time = 2000 msec, echo time = 30 msec), with 64 channel headcoil. fMRI data were pre-processed and entered into two-level analyses. At the first

level, we evaluated the level of activation to each task using a standard general linear model (GLM) approach on the one hand and the synchrony across participants’ brain response to each task thanks to ISCs on the other hand.

#### *Preprocessing*

fMRI data were processed with SPM12. Functional images were corrected for slice timing, realigned, despiked, normalized to the standard MNI brain space, resampled to a 2-mm voxel size, and spatially smoothed with an isotropic Gaussian filter of 4-mm full width at half maximum (FWHM), and a 100-sec high-pass filter was applied.

Before completing the ISC analysis, the six framewise displacement parameters extracted from previous realignment were regressed out. Rest periods at the beginning of each run were then trimmed, resulting in two video runs of 276 sec each and three forced-choice task runs of 272 sec each. Each run was finally z-scored (standardized to zero mean and unit variance) for each voxel. An average gray-matter mask was applied before performing any further analyses.

#### *GLM*

Time series from all five runs were modeled altogether by three regressors obtained by convolution of the canonical SPM12 hemodynamic response function with a rectangular kernel capturing the onset and duration of each trial, corresponding to (1) the laboratory math task, (2) the naturalistic math video lesson, and (3) the naturalistic grammar video lesson. Regressors of noninterest corresponded to the six movement parameters for each run. Individual contrast images for each task (laboratory math task, naturalistic math video lesson, naturalistic grammar video lesson) relative to rest were then calculated and smoothed with an isotropic Gaussian filter of 5-mm FWHM.

#### *ISCs*

The technique of ISC is a data-driven analysis technique that consists of identifying brain regions where the response to a stimulus is systematic over time, that is, correlated among participants (Nastase, Gazzola, Hasson, &

Keyesers, 2019). Both within groups (children and adults) and between children and adults, the ISC was calculated using the leave-one-out approach. This means that, at each voxel, each participant's time series (i.e., each run) was correlated with the average time series of all other participants. This approach directly gave us five R-maps for each participant (one for the math video, one for the grammar video, and three for the laboratory math task). Correlating each child's time series with the average time series of the group of adults gave us five additional R-maps per child, which are typically interpreted and referred to as the child's neural maturity maps (Kersey et al., 2019; Cantlon & Li, 2013). All R-maps were converted into z-maps using the Fischer transformation. The three z-maps calculated from each run of the laboratory math task were finally averaged into one mean z-map for further analysis.

### Group-level Analyses

At the group level, to evaluate similarities and differences in activation level or ISCs between tasks, we performed Bayesian tests on the individual contrast maps or z-maps obtained for each task. We used the default prior that consists of a Cauchy distribution centered on 0 with a scale parameter of 0.707 (Rouder, Speckman, Sun, Morey, & Iverson, 2009). This analysis gave us the Bayes factor (BF), which indicates how many times more likely the data are under the alternative hypothesis compared with the null hypothesis. If BF is equal to 1, both the null and alternative hypotheses are equally likely.  $BF = 1-3$  (respectively,  $.33-1$ ) provides anecdotal evidence in favor of the alternative (respectively, null) hypothesis;  $BF = 3-10$  (respectively,  $.10-.33$ ) provides moderate evidence in favor of the alternative (respectively, null) hypothesis; and  $BF = 10-30$  (respectively,  $.03-0.10$ ) provides strong evidence in favor of the alternative (respectively, null) hypothesis (Jeffreys, 1961). Here, we only report at least moderate evidence. Bayesian statistics are robust to variation in sample size—a BF greater than 3 indicates that the data are reliable. In cases without enough power to detect an effect, BF will be close to 1, which indicates inadequate evidence in favor of either hypotheses. Thus, the Bayesian approach of model comparison presents many advantages over classical frequentist null hypothesis testing methods: It not only provides a metric of evidence both for and against the null hypothesis, it is also robust to variation in sample size (Schönbrodt, Wagenmakers, Zehetleitner, & Perugini, 2017; Williams, Bååth, & Philipp, 2017; Dienes, 2014).

### ROI Analysis

To evaluate fine-grained similarities and differences between both the naturalistic and laboratory math tasks, we conducted a series of analyses within regions where they were found to functionally overlap, that is, in parietal, inferior frontal, and inferior temporal regions. These regions are similar to regions consistently found in studies

of calculation and math semantics processing (e.g., Amalric, 2021; Hawes et al., 2019; Yeo et al., 2017; Ansari, 2016; Arsalidou & Taylor, 2011). Based on these studies, we selected four bilateral a priori defined math-related regions of the brain: both anterior and posterior intraparietal sulcus (aIPS and pIPS), the pITG, and the IFG. These regions were defined functionally from two independent studies, as the intersection of the contrast of “calculation versus sentences” from localizer scans performed in a cohort of 83 participants (Pinel et al., 2007)—that also served to define the ROIs used by Amalric and Dehaene (2016, 2019)—and the contrast of “known math versus control nonmath statements” in a cohort of 21 participants (Amalric, Roveyaz, & Dehaene, in preparation). To ensure the generalizability of math-related character of these ROIs, we verified that they included and were even centered around the main parietal, frontal, and inferior temporal coordinates found by Arsalidou and Taylor (2011) and by Yeo et al. (2017) in their meta-analyses of calculation and number tasks.

Within each region and for each task, we extracted the ISC values (i.e.,  $z$  values) for each adult (relative to the other adults) and for each child (relative to the other children) and applied two types of analyses: direct comparisons of mean  $z$  values using Bayesian tests and representational similarity analysis. Representational similarity analysis is a kind of multivoxel pattern analysis that measures the spatial similarity of the BOLD signal elicited by various stimuli within a given region. Here, we applied it to test the spatial similarity of the synchronous neural activity elicited by our three tasks. To do so, we evaluated for each participant the correlation of ISC values across voxels during each of our three tasks for each math-related ROI. We then used  $t$  tests to compare the correlation values of both math tasks (naturalistic vs. controlled laboratory math) versus the correlation values of both video lessons (naturalistic arithmetic vs. grammar videos). A Bonferroni correction for the number of ROIs was applied to all test results.

## RESULTS

### Behavioral Results in the Laboratory Forced-choice Math Task

Children correctly answered  $89.0 \pm 1.84\%$  of the trials on the forced-choice math task. Children's accuracy did not significantly differ from adults' accuracy ( $92.4 \pm 2.69\%$ ,  $t(30) = 1.11$ ,  $p = .275$ ), although they generally answered more slowly than adults (children:  $1.97 \pm 0.077$  sec; adults:  $1.08 \pm 0.108$  sec;  $t(30) = 7.03$ ,  $p < .001$ ). Children failed to respond on 13.7% of the trials whereas adults only missed 1.98% of trials. When counting missed trials as errors, children reached an overall accuracy of  $76.9 \pm 2.43\%$ , significantly lower than adults' accuracy ( $90.8 \pm 2.98\%$ ,  $t(30) = 3.58$ ,  $p < .002$ ). Whether considering missed trials or not, children performed significantly better than chance for each condition (symbolic/nonsymbolic  $\times$

3 categories of pairs; all  $ps < .05$ ), and so did adults (all  $ps < .001$ ).

### **Whole-brain Differences in Activation to the Naturalistic Math Video Lesson Compared with the Controlled Laboratory Math Task and the Naturalistic Grammar Video Lesson**

We first searched for activation differences between both types of math tasks on the one hand and between both naturalistic video lessons on the other hand. Differences in both the global intensity and the intersubject synchrony of activation were evaluated. In children and adults, respectively, we computed BF to quantify the strength of evidence in favor of activation differences between the tasks. The resulting maps, thresholded at  $BF > 3$  to indicate at least moderate evidence, are displayed on Figure 2, and the main peak coordinates are reported in Tables 2 and 3.

In adults and children alike, the naturalistic math video lesson elicited greater activation than the laboratory-controlled math task along the bilateral superior temporal sulcus, extending to the posterior middle temporal gyrus and to the temporal pole, as well as at various sites of the mesial superior and left middle frontal regions. In turn, the laboratory forced-choice task elicited greater activation than the math video lesson bilaterally in the motor cortex, the insula, along the brain midline in the anterior Cingulate, and along a large swath across the superior and middle frontal gyri. There was no more than weak evidence ( $1 < BF < 3$ ) for a difference between adults and children.

When evaluating ISCs instead of a standard GLM, we found overall similar results, but yet noticed variations. If the swath of superior and middle frontal gyri that exhibited greater activation to the controlled math task than to the math video lesson did not show more synchronized activation, differences between the math video lesson and the controlled math task were found in a larger network when using an ISC-based approach compared with a GLM-based approach. Indeed, in addition to temporal activity, the math video lesson elicited more correlated activity than the forced-choice task in the bilateral inferior and middle frontal gyri, precuneus, and in children's IPS, especially in the right hemisphere. Differences between children and adults were also found, the adults exhibiting additional correlated activity in response to the arithmetic video lesson compared with the controlled laboratory math task in the bilateral angular gyrus and the pITG.

We then evaluated brain regions that showed greater activity during the arithmetic video lesson than during the grammar one. For both children and adults, the resulting activation maps revealed clusters in parietal areas of both hemispheres. In the pITG, a large cluster was found in the adults' left hemisphere and a small cluster in children's right hemisphere. Correlated activity was in parietal areas and in the right IFG of children and adults alike. Additional correlated activity was found among adults in

the occipital cortex, the cuneus, and the bilateral posterior inferior temporal gyri.

The converse contrast of grammar versus arithmetic video lessons revealed greater variations between the GLM-based and ISC-based approaches. The grammar lesson induced more activation than the math lesson for both children and adults along the left superior temporal sulcus, in the left IFG, and in the right posterior superior temporal sulcus and temporal pole. Activation of the left superior temporal sulcus, however, did not exhibit stronger ISCs. Grammar-related correlated activity was found in the postcentral gyrus and in various frontal regions for both children and adults. In adults, such frontal clusters were mostly in the left IFG pars triangularis and in the superior frontal gyrus. Children exhibited extensive bilateral grammar-related correlated activity in the middle and inferior frontal gyri, at the temporo-parietal junction, and along the right superior temporal sulcus.

If both GLM- and ISC-based approaches yielded comparable results in various regions of the brain, they also exhibited clear differences. Although traditional GLM analyses are good for identifying differences in the amplitude of activation between conditions, they cannot capture differences in the fluctuation of neural activity over time. On the contrary, ISC statistics have the potential to reveal regions showing common patterns of activity over time across participants. Here, especially in math-related regions of the brain, the ISC-based approach is more sensitive than GLM-based analyses. In the following, we use the ISC-based approach.

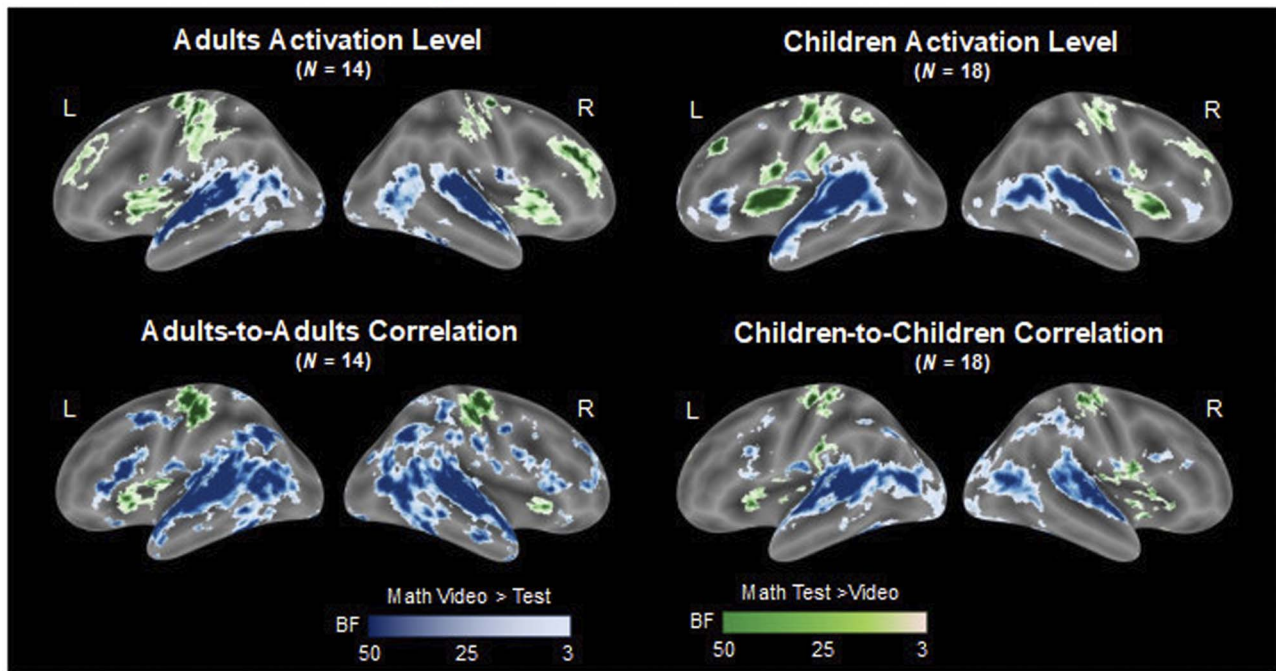
### **Functional Overlap between the Naturalistic and the Controlled Laboratory Mathematics Tasks in Relation to the Naturalistic Grammar Task**

Next, we evaluated the functional overlap between our three tasks, with the ultimate goal to compare neural responses elicited by the laboratory forced-choice arithmetic task to those from the naturalistic arithmetic video lesson. ISC commonalities between both math tasks are represented in light blue on Figure 3. They are distinguished from the general overlap of all three tasks that shared a visual input modality (light green areas on Figure 3) and from the overlap of both videos that had auditory inputs (pink areas on Figure 3).

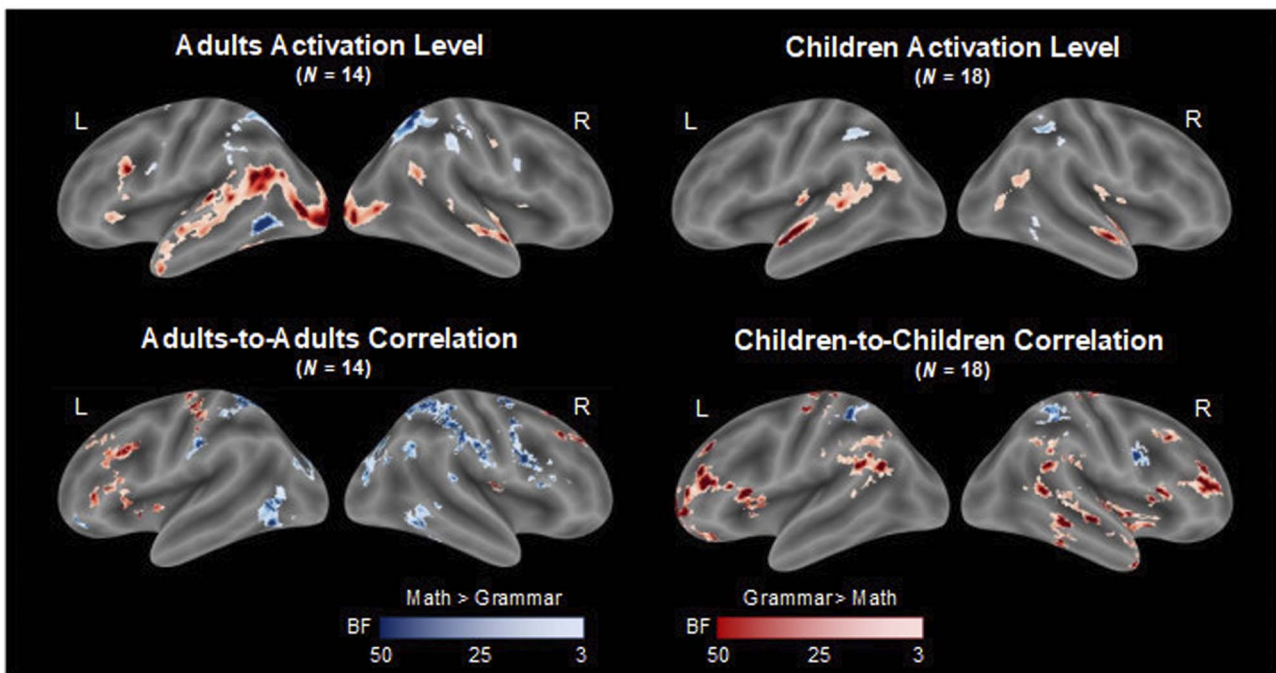
All three tasks overlapped in the occipital cortex, fusiform gyri, precuneus, and inferior parietal lobule in both adults and children. In adults, this general overlap also extended to the left IFG pars opercularis. Correlated activity between children and adults for all three tasks minimally overlapped in the inferior and middle occipital cortex, the fusiform gyri, and in two bilateral small sites of the posterior inferior parietal lobule.

The arithmetic and grammar video lessons overlapped in the lingual gyri, bilateral superior and middle temporal gyri, and bilateral inferior frontal sites (particularly in the left hemisphere in adults). Children's adult-like neural

### A Naturalistic vs Laboratory Math Tasks



### B Mathematics vs Grammar Naturalistic Video Lessons



**Figure 2.** Main contrasts between tasks. (A) Whole-brain maps showing the comparison of activity elicited by both math tasks, the naturalistic video lesson in blue, and controlled laboratory task in green. The top row displays comparison in activation levels obtained from a GLM, and the bottom row displays comparison in temporally correlated activation across participants. Comparisons among adults and children are respectively displayed on the left and on the right. The maps are thresholded such that BF is greater than 3, showing at least moderate evidence in favor of a difference between both math tasks. (B) Same as (A) for the contrast of both naturalistic video lessons, the arithmetic lesson in blue and the grammar lesson in red.

**Table 2.** MNI Peak Coordinates for the Contrasts of the Naturalistic Math Video Lesson versus the Controlled Laboratory Math Task

Cortical Region	Hemisphere	Activation Level (GLM)								ISCs							
		Adults				Children				Adults				Children			
		<i>x</i>	<i>y</i>	<i>z</i>	<i>BF</i>	<i>x</i>	<i>y</i>	<i>z</i>	<i>BF</i>	<i>x</i>	<i>y</i>	<i>z</i>	<i>BF</i>	<i>x</i>	<i>y</i>	<i>z</i>	<i>BF</i>
<i>Math Naturalistic Video Lesson &gt; Math Forced-choice Task</i>																	
Superior Temporal Sulcus	Left	-60	-22	10	>50	-56	-24	10	>50	-56	-20	4	>50	-62	-18	8	>50
Superior Temporal Sulcus	Right	62	-20	0	>50	62	-26	2	>50	54	-20	-6	>50	62	-24	0	>50
Middle Temporal Gyrus	Left	-44	-58	12	>50	-50	-52	8	>50	-48	-58	0	>50	-42	-56	10	>50
Middle Temporal Gyrus	Right	48	-68	4	>50	53	-52	16	>50	44	-70	8	>50	46	-62	12	>50
Temporal Pole	Left					-58	8	-14	>50	-52	18	-20	>50				
Temporal Pole	Right	56	4	-8	>50	58	14	-14	>50	60	4	-10	>50				
Fusiform Gyrus	Left	-40	-54	-16	>50	-32	-60	-12	>50	-44	-46	-20	>50	-30	-50	-12	>50
Fusiform Gyrus	Right	44	-38	-28	>50	38	-26	-28	>50	22	-42	-12	>50	30	-50	-4	>50
Superior Frontal Gyrus	Bilateral	2	60	28	>50	-2	57	22	>50	-2	40	36	>50				
Inferior Frontal Orbitalis	Bilateral	-2	52	-10	>50	-4	48	-8	>50								
IFG	Left					-54	30	-4	>50	-46	14	22	>50	-52	18	30	>50
IFG	Right									52	8	24	>50	54	36	20	>50
Inferior Frontal Triangularis	Left									-52	22	2	>50				
Middle Frontal Gyrus	Left									-36	-14	36	>50				



**Table 2.** (continued)

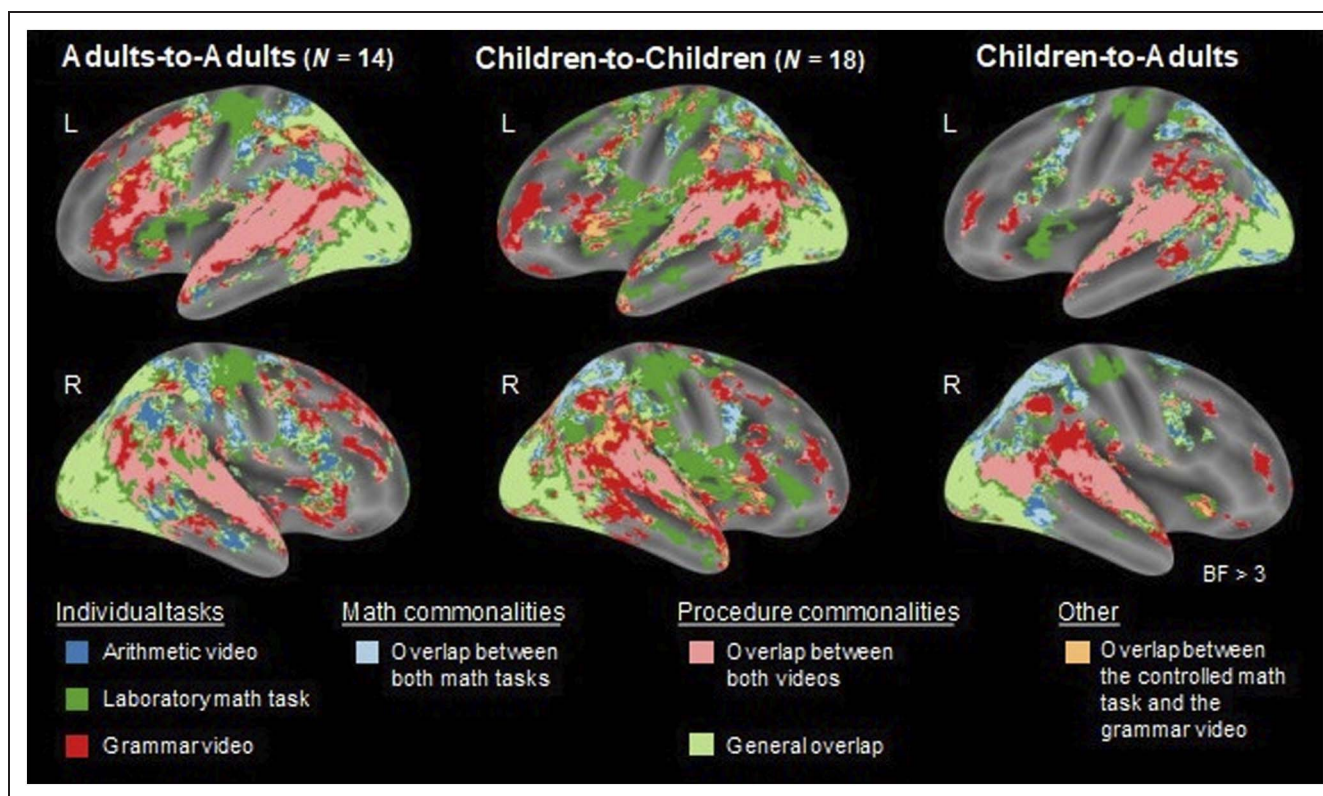
<i>Cortical Region</i>	<i>Hemisphere</i>	<i>Activation Level (GLM)</i>								<i>ISCs</i>							
		<i>Adults</i>				<i>Children</i>				<i>Adults</i>				<i>Children</i>			
		<i>x</i>	<i>y</i>	<i>z</i>	<i>BF</i>	<i>x</i>	<i>y</i>	<i>z</i>	<i>BF</i>	<i>x</i>	<i>y</i>	<i>z</i>	<i>BF</i>	<i>x</i>	<i>y</i>	<i>z</i>	<i>BF</i>
Inferior Occipital Gyrus	Left	-20	-100	-4	>50					-12	-102	4	>50				
Inferior Occipital Gyrus	Right	24	-92	-6	>50												
Angular Gyrus	Left									-36	-64	34	>50				
Angular Gyrus	Right									48	-62	38	>50	44	-66	54	>50
Superior Parietal Lobule	Right													16	-54	64	>50
Precuneus	Bilateral									2	-66	24	>50	-8	-66	34	>50
<i>Math Forced-choice Task &gt; Math Naturalistic Video Lesson</i>																	
Superior/Middle Frontal Gyrus	Left	-34	52	22	>50	-30	36	36	>50								
Superior/Middle Frontal Gyrus	Right	34	38	30	>50	38	52	22	>50								
Insula	Left	-38	8	4	>50	-38	14	4	>50	-34	24	8	>50	-40	-4	-2	>50
Insula	Right	38	14	6	>50	36	14	8	>50	40	12	-6	>50	46	10	4	>50
Postcentral Gyrus	Left	-54	-20	34	>50	-54	-20	26	>50	-40	-26	46	>50	-40	-22	54	>50
Precentral Gyrus	Right	34	-14	64	>50	38	-12	54	>50	48	-20	44	>50	36	-30	62	>50
SMA	Bilateral	6	0	64	>50	-6	-4	60	>50	-2	-10	54	>50	-6	0	60	>50
Anterior and Middle Cingulate	Bilateral	8	2	42	>50	8	16	38	>50					12	24	32	>50

**Table 3.** MNI Peak Coordinates for the Contrasts of the Naturalistic Math Video Lesson versus the Naturalistic Grammar Video Lesson

Cortical Region	Hemisphere	Activation Level (GLM)								ISCs							
		Adults				Children				Adults				Children			
		x	y	z	BF	x	y	z	BF	x	y	z	BF	x	y	z	BF
<i>Math Naturalistic Video Lesson &gt; Grammar Naturalistic Video Lesson</i>																	
Superior Parietal Lobule	Left	-12	-70	54	>50					-26	-50	62	>50				
Superior Parietal Lobule	Right	54	-28	58	>50					28	-52	62	>50				
Inferior Parietal Lobule	Left	-46	-40	56	>50	-36	-46	42	14	-54	-28	44	>50	-32	-40	48	>50
Inferior Parietal Lobule	Right	46	-46	54	>50	38	-42	46	49					38	-40	52	>50
Inferior Temporal Gyrus	Left	-56	-66	-12	>50					-48	-58	-2	>50				
Inferior Temporal Gyrus	Right					56	-60	-18	26	56	-58	-14	>50				
Left Sup Frontal Gyrus	Left	-28	-4	66	>50					-22	-8	52	>50				
Right Inf Frontal Gyrus	Right	54	14	42	>50					58	14	26	>50	52	4	30	>50
Calcarine/Lingual Gyrus	Right									12	-68	4	>50				
Cuneus	Bilateral									2	-72	24	>50				

Table 3. (continued)

Cortical Region	Hemisphere	Activation Level (GLM)								ISCs							
		Adults				Children				Adults				Children			
		x	y	z	BF	x	y	z	BF	x	y	z	BF	x	y	z	BF
<i>Grammar Naturalistic Video Lesson &gt; Math Naturalistic Video Lesson</i>																	
Superior Temporal Sulcus	Left	-46	-34	4	>50	-64	-38	4	>50								
Superior Temporal Sulcus	Right													48	-22	-6	>50
Temporal Pole	Right	58	2	-12	>50	48	2	-14	>50					34	12	-42	>50
Temporo-Parietal Junction	Left	-46	-58	16	>50	-42	-56	28	49					-42	-60	20	>50
Temporo-Parietal Junction	Right	44	-52	24	>50	50	-66	20	25					50	-48	24	>50
Inferior Occipital Gyrus	Left	-20	-96	-10	>50												
Inferior Occipital Gyrus	Right	18	-92	-4	>50												
Insula	Left					-38	-20	14	>50	-36	14	-8	>50	-38	14	0	>50
Inferior Frontal Opercularis	Left	-36	14	22	>50												
Inferior Frontal Opercularis	Right													50	14	10	>50
Inferior Frontal Triangularis	Left									-44	36	2	>50				
Superior Frontal Gyrus	Left									-24	32	42	>50				
Superior Frontal Gyrus	Right									18	40	34	>50				
Middle Frontal Gyrus	Left													-30	48	8	>50
Middle Frontal Gyrus	Right													34	40	8	>50
Left Postcentral Gyrus	Left									-54	-16	46	>50	-40	-22	52	>50



**Figure 3.** Functional overlap of all three tasks. Maps showing the significant correlations of brain activation time course during each task, and their respective overlaps. Red, dark blue, and dark green clusters reveal correlated activation, respectively, associated with the grammar video lesson, the arithmetic video lesson, and the laboratory forced-choice math task. Light blue clusters, mostly found in the parietal cortex, represent correlated activation common to both math tasks, whereas pink clusters, mostly found in the superior temporal cortex, represent correlated activation common to the viewing of both educational videos. Light green clusters locate the brain regions exhibiting significantly correlated activation for all three tasks together. All maps are thresholded at  $BF > 3$ .

responses that were common to both arithmetic and grammar video lessons were also found mostly in the lingual gyri, bilateral superior and middle temporal gyri, and bilateral inferior frontal sites. This suggests that visual and auditory processing of the videos happened similarly in children and adults.

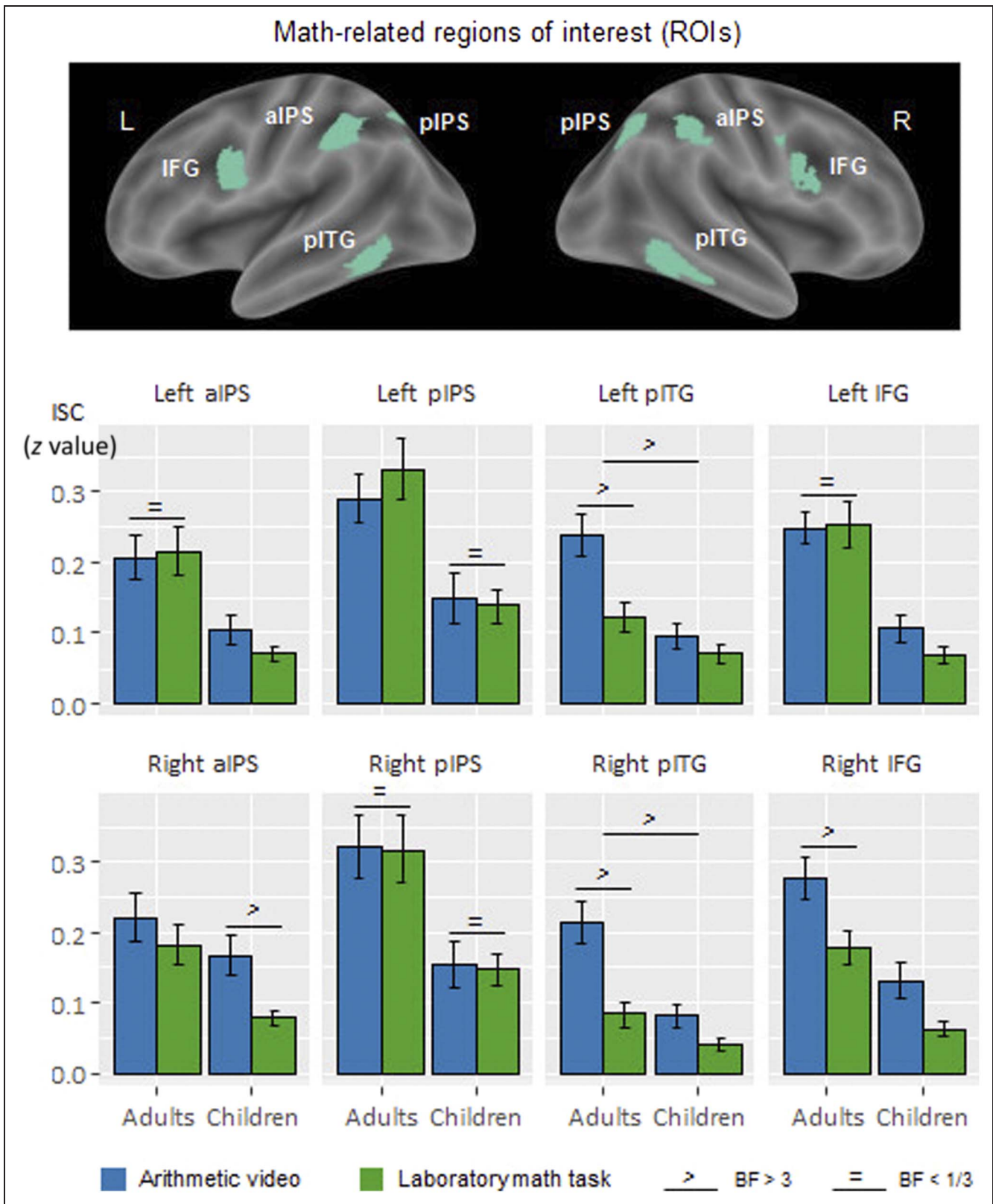
We finally observed significant overlap of correlated activity for the naturalistic and laboratory math tasks among children in the bilateral parietal cortex, and the right IFG. Adults showed the same functional overlap patterns as children but showed additional overlapping activation between tasks in the right pITG. Both types of math tasks elicited adult-like neural responses in children's bilateral IPS, especially in the right hemisphere, in the left inferior frontal extending toward the precentral gyrus, and in the right pITG.

### Similarities and Differences in Neural Responses Elicited by the Naturalistic versus the Controlled Laboratory Mathematics Tasks in Math-related Regions of the Brain

The spatial overlap of neural responses elicited by both naturalistic and laboratory math tasks indicated the common involvement of brain regions similar to regions known to be generally involved in math-related processes.

Here, we analyzed neural response patterns within those regions to compare spatial patterns of activation. Within eight main math-related ROIs (bilateral aIPS, bilateral pIPS, bilateral pITG, and bilateral IFG), we first measured the similarity between spatial patterns of ISC activity across tasks. For each participant, across all voxels of our math-related ROIs, we computed the correlation coefficients between the ISC values observed during each pedagogical video as well as during the forced-choice math task. We then compared the correlation of ISC values corresponding to the two math tasks versus the correlation of ISC values corresponding to the two videos (paired  $t$  tests). In children and adults, ISCs in the left and right IPS were more spatially correlated between the naturalistic arithmetic video lesson and the laboratory forced-choice arithmetic task than between the naturalistic arithmetic and grammar video lessons (left aIPS:  $t(31) = 3.46$ , uncorrected  $p = .0016$ , Bonferroni corrected  $p = .0127$ ; right aIPS:  $t(31) = 2.37$ , uncorrected  $p = .0241$ , Bonferroni corrected  $p = .193$ ; right pIPS:  $t(31) = 6.39$ , uncorrected  $p < 5.10^{-7}$ , Bonferroni corrected  $p < 5.10^{-6}$ ). These relations hold for children and adults separately ( $ps < .03$ ).

Next, we evaluated the similarities and differences in the synchrony of activation elicited by the two math tasks within each math-related ROI (see Figure 4). We



**Figure 4.** Similarities and differences in the systematic response elicited by the naturalistic math task compared with the controlled math task in math-related ROIs. (Top) A priori defined math-related ROIs composed of the left and right aIPS, left and right pIPS, left and right pITG, and left and right IFG. (Bottom) Mean ISC values ( $z$  values) extracted from each math-related ROI, for the naturalistic arithmetic video lesson in blue and the controlled laboratory math task in green. Error bars equal 1 SEM. Equals and greater signs indicate at least moderate evidence, respectively, in favor of an absence of difference and in favor of a difference, between tasks as well as between adults and children.

computed the BF of a comparison between mean ISC values from the naturalistic and controlled laboratory math tasks to quantify the strength of evidence in favor of the null hypothesis, “naturalistic and controlled math tasks elicit similar correlated activity,” versus the alternative hypothesis, “naturalistic math task elicits more correlated activity than the controlled math task.” In both adults and children, we found that the naturalistic and controlled laboratory math tasks elicited similar correlated activity in the right pIPS (adults:  $BF = 0.271$ ; children:  $BF = 0.252$ ). In children, they elicited similar correlated activity in the left pIPS ( $BF = 0.256$ ), and a difference in activity in the right aIPS ( $BF = 5.75$ ). In adults, both types of math tasks elicited similar correlated activity in the left aIPS ( $BF = 0.277$ ) and the left IFG ( $BF = 0.273$ ), whereas the naturalistic math video lesson elicited more correlated activity than the controlled laboratory math task in the right IFG ( $BF = 8.18$ ) and bilateral pITG (left:  $BF = 21.3$ ; right:  $BF = 110$ ). This difference in the bilateral pITG was greater in adults than in children (left:  $BF = 5.09$ ; right:  $BF = 5.56$ ). We note that no such differences were found when comparing correlated activation induced by the grammar video lesson versus the controlled math task. This allowed us to verify that the difference we observed between the naturalistic and the controlled laboratory math tasks was not directly explained by video features unrelated to the content, such as animacy, color, and so forth. Distilling across these findings, the naturalistic mathematics lesson elicited a broader pattern of systematic activation in both children and adults than the controlled laboratory mathematics task.

## DISCUSSION

We compared children’s neural activity during a naturalistic arithmetic video lesson, in which information unfolds in a rich narrative, to their neural activity during a more traditional laboratory two-alternative forced-choice task. ISC measures were more sensitive to detect math-related brain activity than a GLM of the level of activation. ISC measures revealed reliable neural signals across participants in the parietal cortex during the two types of mathematics tasks, and this pattern differed from that of the grammar task. Within the math-related network, the naturalistic math video lesson elicited more widespread systematic activation than the controlled laboratory task, especially in the right aIPS among children.

Regions of the parietal cortex, particularly the IPS, are often implicated in arithmetic processing (Peters & De Smedt, 2018; Arsalidou & Taylor, 2011; Ansari, 2008; Dehaene, 2004) and more generally in conceptual processing of mathematics (Amalric & Dehaene, 2016, 2019; Vogel, Goffin, & Ansari, 2015; Cantlon & Li, 2013; Zhang, Chen, & Zhou, 2012). Mathematical expertise and giftedness are supported by enhanced connectivity and generally greater activity of the posterior parietal cortex (Jeon, Kuhl, & Friederici, 2019; Prescott, Gavrilescu, Cunnington,

O’Boyle, & Egan, 2010; O’Boyle et al., 2005). Arithmetic training impacts the structural and functional properties of the IPS in children (e.g., Jolles et al., 2016; Zamarian, Ischebeck, & Delazer, 2009; Rivera, Reiss, Eckert, & Menon, 2005), and weak IPS responses during arithmetic problem-solving are associated with developmental dyscalculia (Ashkenazi, Rosenberg-Lee, Tenison, & Menon, 2012; Price, Holloway, Räsänen, Vesterinen, & Ansari, 2007).

Here, we confirm and extend those prior findings by comparing two tasks in which the semantic content is the same, but the format of the stimuli differs—both tasks target the same arithmetic principle of commutativity, but one is a naturalistic educational lesson and the other a forced-choice laboratory task. Both the naturalistic and laboratory mathematics tasks systematically modulated neural activation in the IPS among participants and dissociated from the grammar task. Findings from our ROI analysis suggest that both types of math tasks engaged the IPS in a systematic way over time across participants and evoked spatially similar patterns of activation. Previous studies found functional overlap in IPS regions for symbolic and nonsymbolic numerical processing in children (Cantlon, 2015; De Smedt, Noël, Gilmore, & Ansari, 2013; Holloway, Price, & Ansari, 2010; Ansari, 2008), and neural responses during arithmetic processing in children dissociate from control tasks in those regions (Kersey et al., 2019; Price, Mazocco, & Ansari, 2013; Bugden, Price, McLean, & Ansari, 2012). In adults, the cortical networks for high-level mathematics processing and basic numerical processing functionally overlap and dissociate from networks involved in language processing (Kersey et al., 2019; Amalric & Dehaene, 2016, 2017; Kanjlia, Lane, Feigenson, & Bedny, 2016; Maruyama, Pallier, Jobert, Sigman, & Dehaene, 2012; Monti, Parsons, & Osherson, 2012; Baldo & Dronkers, 2007; Klessinger, Szczerbinski, & Varley, 2007). The similarities in the underlying neural processes across a range of mathematics tasks from many studies are argued to be semantic in nature (e.g., Ansari, 2008; Dehaene & Cohen, 2007). Similarly, in the current study, the functional overlap and similarity between the naturalistic and controlled mathematics task, but not the grammar task, likely reflects the shared arithmetic content between the mathematics tasks.

The naturalistic and laboratory tasks exhibited some differences in various regions of the brain. The controlled laboratory task elicited greater activation than the naturalistic math video lesson in the motor cortex whereas the math lesson elicited greater activation in the auditory and language-related brain areas. These differences likely reflect the difference in modalities between both math tasks: Participants answered by pressing buttons in the controlled math task, and they followed a verbal narrative in the math video lesson. Activation to the controlled forced-choice task was also found in the bilateral insula, and across the superior and middle frontal gyrus. These regions are often found in meta-analyses of math activity, and they have, respectively, been associated with participant’s intrinsic motivation in the task, and active planning

and working memory processes (Arsalidou et al., 2018; Houdé et al., 2010; Uddin & Menon, 2009; Delazer et al., 2003; Simon, Mangin, Cohen, Le Bihan, & Dehaene, 2002). Differences between both math tasks in the insula remained when evaluating the level of synchrony in activation among participants, but disappeared in the superior frontal gyrus. This might suggest that while the laboratory math tasks required more planning than the naturalistic math video lesson, temporal fluctuations of planning-related activity were disparate among participants. Overall, the differences we observed between both math tasks are likely because of modality differences and likely due to the active character of the forced-choice task compared with the passivity of natural viewing.

Children and adults showed largely similar patterns of synchronized activation during both the naturalistic and controlled mathematics tasks within the math-responsive brain network. Both groups systematically engaged the IPS and inferior frontal regions for both the naturalistic and laboratory-controlled mathematics tasks. However, unlike in children, the naturalistic mathematics task yielded greater activation in adults than the controlled mathematics task in the pITG. In adults, the pITG has been shown to be involved in the visual processing of Arabic numbers (Conrad, Wilkey, Yeo, & Price, 2020; Yeo, Pollack, Merkley, Ansari, & Price, 2020; Skagenholt, Träff, Västfjäll, & Skagerlund, 2018; Shum et al., 2013; Park, Hebrank, Polk, & Park, 2012), and is implicated in adult mathematics processing more generally (Amalric & Dehaene, 2016, 2019; Grotheer, Jeska, & Grill-Spector, 2018; Pinheiro-Chagas, Daitch, Parvizi, & Dehaene, 2018). Yet no clear number-specific responses have been found in the pITG in fMRI studies of children (Soltanlou et al., 2019; Dehaene-Lambertz, Monzalvo, & Dehaene, 2018; Cantlon, Pinel, Dehaene, & Pelphrey, 2011). The absence of systematic activation of the pITG in children could suggest that these math-related neural responses develop later in childhood.

In adults, but not in children, the naturalistic mathematics task also yielded greater activation than the controlled mathematics task in the angular gyrus, which is often found in studies of mental calculation (Arsalidou & Taylor, 2011; Grabner et al., 2009; Ansari, 2008; Ischebeck et al., 2006; Delazer et al., 2005; Dehaene, Piazza, Pinel, & Cohen, 2003). The angular gyrus is generally seen as a semantic and conceptual hub, as it is involved in word and sentence comprehension, memory retrieval, spatial attention, and reasoning among other functions (e.g., Zhou et al., 2018; Boylan, Trueswell, & Thompson-Schill, 2015; Price, Bonner, Peelle, & Grossman, 2015; Seghier, 2013; Binder, Desai, Graves, & Conant, 2009). Our finding provides converging evidence with previous studies that the angular gyrus has a protracted developmental trajectory in mathematics (Soltanlou, Sitnikova, Nuerk, & Dresler, 2018; Zamarian et al., 2009; Rivera et al., 2005), just as observed in other domains such as reading (Church, Coalson, Lugar, Petersen, & Schlaggar, 2008; Booth et al., 2004).

In children, within brain regions that are thought to respond to math semantics, the naturalistic and laboratory tasks differed in their neural signatures particularly in the anterior part of the right IPS. Many previous studies suggest that the right IPS matures faster and plays a greater role than the left IPS in young children's early numerical development (Matejko & Ansari, 2021; Vogel et al., 2015; Ansari, 2008; Cantlon, Brannon, Carter, & Pelphrey, 2006). Children appear to have a right lateralization bias for mathematics processing in the parietal cortex whereas activity in the left IPS emerges gradually over development and tracks the acquisition of formal symbolic numerical knowledge (Emerson & Cantlon, 2015; Bugden et al., 2012; Kaufmann et al., 2011; Cantlon et al., 2006). Our results indicate that naturalistic mathematics learning systematically engages a greater expanse of the dominant right IPS in children compared with the controlled math task and mostly showed equivalent activation to the controlled task in the left IPS. One possibility is that children engage greater neural resources within the parietal mathematics network during the naturalistic task compared with the more stripped-down controlled task.

Naturalistic learning is a key phenomenon to understand in human brain development, and although this is a new area of enquiry, several studies have made progress toward comparing naturalistic learning with controlled laboratory performance in children (see the work of Cantlon, 2020, p. 20; Vanderwal, Eilbott, & Castellanos, 2019, for reviews). We found that a naturalistic mathematics lesson systematically evoked functional activation in brain regions that are classically involved in mathematics tasks. Our comparison of arithmetic versus grammar lessons yielded the predicted dissociation between math and language networks. The data revealed key functional similarities between math-related neural processes during qualitatively different tasks that probe the same arithmetic functions, one a naturalistic video lesson and the other a laboratory task. These findings suggest that regions of the intraparietal cortex process mathematical content when children are learning about mathematics in the real world. Moreover, the naturalistic math task engaged a broader expanse of the math-responsive network compared with the controlled math task, suggesting that naturalistic educational tasks may be more powerful than controlled tasks for eliciting activation within the math network—or for revealing functions that cut across math-specific and domain-general functions.

Reprint requests should be sent to Marie Amalric, Department of Psychology, Carnegie Mellon University, 5000 Forbes Avenue, Pittsburgh, Pennsylvania 15213–3815, or via e-mail: [marie.amalric@normalesup.org](mailto:marie.amalric@normalesup.org).

### Author Contributions

Marie Amalric: Conceptualization; Data curation; Funding acquisition; Investigation; Methodology; Visualization;

Writing—Original draft; Writing—Review & editing. Jessica F. Cantlon: Conceptualization; Funding acquisition; Methodology; Project administration; Supervision; Validation; Writing—Original draft; Writing—Review & editing.

### Funding Information

This work was supported by the National Institutes of Health (<https://dx.doi.org/10.13039/100000002>), grant number 5R01HD091104 to J. C., by a postdoctoral fellowship attributed by the Fyssen Foundation (<https://dx.doi.org/10.13039/501100003135>) to M. A., and by the chair sponsors Ronald J. and Mary Ann Zdrojowski.

### Data Availability

The data that support the findings of this study are openly available in OSF at <https://osf.io/3a8hf/>.

### Ethics Approval Statement

All participants gave informed consent after reading or being read consent information. The protocol was approved by the Carnegie Mellon University institutional review board.

### Diversity in Citation Practices

Retrospective analysis of the citations in every article published in this journal from 2010 to 2021 reveals a persistent pattern of gender imbalance: Although the proportions of authorship teams (categorized by estimated gender identification of first author/last author) publishing in the *Journal of Cognitive Neuroscience (JoCN)* during this period were  $M(\text{an})/M = .407$ ,  $W(\text{oman})/M = .32$ ,  $M/W = .115$ , and  $W/W = .159$ , the comparable proportions for the articles that these authorship teams cited were  $M/M = .549$ ,  $W/M = .257$ ,  $M/W = .109$ , and  $W/W = .085$  (Postle and Fulvio, *JoCN*, 34:1, pp. 1–3). Consequently, *JoCN* encourages all authors to consider gender balance explicitly when selecting which articles to cite and gives them the opportunity to report their article's gender citation balance.

### REFERENCES

- Amalric, M. (2021). Cerebral underpinning of advanced mathematical activity. In *Heterogeneous contributions to numerical cognition* (pp. 71–92). Elsevier. <https://doi.org/10.1016/B978-0-12-817414-2.00009-9>
- Amalric, M., & Dehaene, S. (2016). Origins of the brain networks for advanced mathematics in expert mathematicians. *Proceedings of the National Academy of Sciences, U.S.A.*, 113, 4909–4917. <https://doi.org/10.1073/pnas.1603205113>, PubMed: 27071124
- Amalric, M., & Dehaene, S. (2017). Cortical circuits for mathematical knowledge: Evidence for a major subdivision within the brain's semantic networks. *Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences*, 373, 20160515. <https://doi.org/10.1098/rstb.2016.0515>, PubMed: 29292362
- Amalric, M., & Dehaene, S. (2019). A distinct cortical network for mathematical knowledge in the human brain. *Neuroimage*, 189, 19–31. <https://doi.org/10.1016/j.neuroimage.2019.01.001>, PubMed: 30611876
- Amalric, M., Roveyaz, P., & Dehaene, S. (in prep). Can a short math video enhance the brain's mathematical networks?
- Ansari, D. (2008). Effects of development and enculturation on number representation in the brain. *Nature Reviews Neuroscience*, 9, 278–291. <https://doi.org/10.1038/nrn2334>, PubMed: 18334999
- Ansari, D. (2016). The neural roots of mathematical expertise. *Proceedings of the National Academy of Sciences, U.S.A.*, 113, 4887–4889. <https://doi.org/10.1073/pnas.1604758113>, PubMed: 27095847
- Arsalidou, M., Pawliw-Levac, M., Sadeghi, M., & Pascual-Leone, J. (2018). Brain areas associated with numbers and calculations in children: Meta-analyses of fMRI studies. *Developmental Cognitive Neuroscience*, 30, 239–250. <https://doi.org/10.1016/j.dcn.2017.08.002>, PubMed: 28844728
- Arsalidou, M., & Taylor, M. J. (2011). Is  $2 + 2 = 4$ ? Meta-analyses of brain areas needed for numbers and calculations. *Neuroimage*, 54, 2382–2393. <https://doi.org/10.1016/j.neuroimage.2010.10.009>, PubMed: 20946958
- Ashkenazi, S., Rosenberg-Lee, M., Tenison, C., & Menon, V. (2012). Weak task-related modulation and stimulus representations during arithmetic problem solving in children with developmental dyscalculia. *Developmental Cognitive Neuroscience*, 2, S152–S166. <https://doi.org/10.1016/j.dcn.2011.09.006>, PubMed: 22682904
- Baldo, J. V., & Dronkers, N. F. (2007). Neural correlates of arithmetic and language comprehension: A common substrate? *Neuropsychologia*, 45, 229–235. <https://doi.org/10.1016/j.neuropsychologia.2006.07.014>, PubMed: 16997333
- Binder, J. R., Desai, R. H., Graves, W. W., & Conant, L. L. (2009). Where is the semantic system? A critical review and meta-analysis of 120 functional neuroimaging studies. *Cerebral Cortex*, 19, 2767–2796. <https://doi.org/10.1093/cercor/bhp055>, PubMed: 19329570
- Booth, J. R., Burman, D. D., Meyer, J. R., Gitelman, D. R., Parrish, T. B., & Mesulam, M. M. (2004). Development of brain mechanisms for processing orthographic and phonologic representations. *Journal of Cognitive Neuroscience*, 16, 1234–1249. <https://doi.org/10.1162/0898929041920496>, PubMed: 15453976
- Boylan, C., Trueswell, J. C., & Thompson-Schill, S. L. (2015). Compositionality and the angular gyrus: A multi-voxel similarity analysis of the semantic composition of nouns and verbs. *Neuropsychologia*, 78, 130–141. <https://doi.org/10.1016/j.neuropsychologia.2015.10.007>, PubMed: 26454087
- Bugden, S., Price, G. R., McLean, D. A., & Ansari, D. (2012). The role of the left intraparietal sulcus in the relationship between symbolic number processing and children's arithmetic competence. *Developmental Cognitive Neuroscience*, 2, 448–457. <https://doi.org/10.1016/j.dcn.2012.04.001>, PubMed: 22591861
- Cantlon, J. F. (2015). Analog origins of numerical concepts. In D. C. Geary, D. B. Berch, & K. M. Koepke (Eds.), *Mathematical cognition and learning* (Vol. 1, pp. 225–251). Elsevier. <https://doi.org/10.1016/B978-0-12-420133-0.00009-0>
- Cantlon, J. F. (2020). The balance of rigor and reality in developmental neuroscience. *Neuroimage*, 216, 116464. <https://doi.org/10.1016/j.neuroimage.2019.116464>, PubMed: 31874256
- Cantlon, J. F., Brannon, E. M., Carter, E. J., & Pelphrey, K. A. (2006). Functional imaging of numerical processing in adults



- and 4-y-old children. *PLoS Biology*, *4*, e125. <https://doi.org/10.1371/journal.pbio.0040125>, PubMed: 16594732
- Cantlon, J. F., & Li, R. (2013). Neural activity during natural viewing of sesame street statistically predicts test scores in early childhood. *PLoS Biology*, *11*, e1001462. <https://doi.org/10.1371/journal.pbio.1001462>, PubMed: 23300385
- Cantlon, J. F., Pineda, P., Dehaene, S., & Pelphrey, K. A. (2011). Cortical representations of symbols, objects, and faces are pruned back during early childhood. *Cerebral Cortex*, *21*, 191–199. <https://doi.org/10.1093/cercor/bhq078>, PubMed: 20457691
- Church, J. A., Coalson, R. S., Lugar, H. M., Petersen, S. E., & Schlaggar, B. L. (2008). A developmental fMRI study of Reading and repetition reveals changes in phonological and visual mechanisms over age. *Cerebral Cortex*, *18*, 2054–2065. <https://doi.org/10.1093/cercor/bhm228>, PubMed: 18245043
- Ciccione, L., & Dehaene, S. (2020). Grouping mechanisms in numerosity perception. *Open Mind*, *4*, 102–118. [https://doi.org/10.1162/opmi\\_a\\_00037](https://doi.org/10.1162/opmi_a_00037), PubMed: 34485793
- Conrad, B. N., Wilkey, E. D., Yeo, D. J., & Price, G. R. (2020). Network topology of symbolic and nonsymbolic number comparison. *Network Neuroscience*, *4*, 714–745. [https://doi.org/10.1162/netn\\_a\\_00144](https://doi.org/10.1162/netn_a_00144), PubMed: 32885123
- Dastjerdi, M., Ozker, M., Foster, B. L., Rangarajan, V., & Parvizi, J. (2013). Numerical processing in the human parietal cortex during experimental and natural conditions. *Nature Communications*, *4*, 2528. <https://doi.org/10.1038/ncomms3528>, PubMed: 24129341
- De Smedt, B., Noël, M.-P., Gilmore, C., & Ansari, D. (2013). How do symbolic and non-symbolic numerical magnitude processing skills relate to individual differences in children's mathematical skills? A review of evidence from brain and behavior. *Trends in Neuroscience and Education*, *2*, 48–55. <https://doi.org/10.1016/j.tine.2013.06.001>
- Dehaene, S. (2004). Arithmetic and the brain. *Current Opinion in Neurobiology*, *14*, 218–224. <https://doi.org/10.1016/j.conb.2004.03.008>, PubMed: 15082328
- Dehaene, S., & Cohen, L. (2007). Cultural recycling of cortical maps. *Neuron*, *56*, 384–398. <https://doi.org/10.1016/j.neuron.2007.10.004>, PubMed: 17964253
- Dehaene, S., Piazza, M., Pinel, P., & Cohen, L. (2003). Three parietal circuits for number processing. *Cognitive Neuropsychology*, *20*, 487–506. <https://doi.org/10.1080/02643290244000239>, PubMed: 20957581
- Dehaene-Lambertz, G., Monzalvo, K., & Dehaene, S. (2018). The emergence of the visual word form: Longitudinal evolution of category-specific ventral visual areas during reading acquisition. *PLoS Biology*, *16*, e2004103. <https://doi.org/10.1371/journal.pbio.2004103>, PubMed: 29509766
- Delazer, M., Domahs, F., Bartha, L., Brenneis, C., Lochy, A., Trieb, T., et al. (2003). Learning complex arithmetic—An fMRI study. *Cognitive Brain Research*, *18*, 76–88. <https://doi.org/10.1016/j.cogbrainres.2003.09.005>, PubMed: 14659499
- Delazer, M., Ischebeck, A., Domahs, F., Zamarian, L., Koppelstaetter, F., Siedentopf, C. M., et al. (2005). Learning by strategies and learning by drill—Evidence from an fMRI study. *Neuroimage*, *25*, 838–849. <https://doi.org/10.1016/j.neuroimage.2004.12.009>, PubMed: 15808984
- Dienes, Z. (2014). Using Bayes to get the most out of non-significant results. *Frontiers in Psychology*, *5*, 781. <https://doi.org/10.3389/fpsyg.2014.00781>, PubMed: 25120503
- Emerson, R. W., & Cantlon, J. F. (2015). Continuity and change in children's longitudinal neural responses to numbers. *Developmental Science*, *18*, 314–326. <https://doi.org/10.1111/desc.12215>, PubMed: 25051893
- Grabner, R. H., Ansari, D., Koschutnig, K., Reishofer, G., Ebner, F., & Neuper, C. (2009). To retrieve or to calculate? Left angular gyrus mediates the retrieval of arithmetic facts during problem solving. *Neuropsychologia*, *47*, 604–608. <https://doi.org/10.1016/j.neuropsychologia.2008.10.013>, PubMed: 19007800
- Grotheer, M., Jeska, B., & Grill-Spector, K. (2018). A preference for mathematical processing outweighs the selectivity for Arabic numbers in the inferior temporal gyrus. *Neuroimage*, *175*, 188–200. <https://doi.org/10.1016/j.neuroimage.2018.03.064>, PubMed: 29604456
- Hawes, Z., Sokolowski, H. M., Ononye, C. B., & Ansari, D. (2019). Neural underpinnings of numerical and spatial cognition: An fMRI meta-analysis of brain regions associated with symbolic number, arithmetic, and mental rotation. *Neuroscience & Biobehavioral Reviews*, *103*, 316–336. <https://doi.org/10.1016/j.neubiorev.2019.05.007>, PubMed: 31082407
- Holloway, I. D., Price, G. R., & Ansari, D. (2010). Common and segregated neural pathways for the processing of symbolic and nonsymbolic numerical magnitude: An fMRI study. *Neuroimage*, *49*, 1006–1017. <https://doi.org/10.1016/j.neuroimage.2009.07.071>, PubMed: 19666127
- Houdé, O., Rossi, S., Lubin, A., & Joliot, M. (2010). Mapping numerical processing, reading, and executive functions in the developing brain: An fMRI meta-analysis of 52 studies including 842 children. *Developmental Science*, *13*, 876–885. <https://doi.org/10.1111/j.1467-7687.2009.00938.x>, PubMed: 20977558
- Ischebeck, A., Zamarian, L., Siedentopf, C., Koppelstätter, F., Benke, T., Felber, S., et al. (2006). How specifically do we learn? Imaging the learning of multiplication and subtraction. *Neuroimage*, *30*, 1365–1375. <https://doi.org/10.1016/j.neuroimage.2005.11.016>, PubMed: 16413795
- Jeffreys, H. (1961). *The theory of probability* (3rd ed.). Oxford University Press.
- Jeon, H.-A., Kuhl, U., & Friederici, A. D. (2019). Mathematical expertise modulates the architecture of dorsal and cortico-thalamic white matter tracts. *Scientific Reports*, *9*, 1–11. <https://doi.org/10.1038/s41598-019-43400-6>, PubMed: 31048754
- Jolles, D., Supekar, K., Richardson, J., Tenison, C., Ashkenazi, S., Rosenberg-Lee, M., et al. (2016). Reconfiguration of parietal circuits with cognitive tutoring in elementary school children. *Cortex*, *83*, 231–245. <https://doi.org/10.1016/j.cortex.2016.08.004>, PubMed: 27618765
- Jovanovic, V., Fishbein, A. R., de la Mothe, L., Lee, K.-F., & Miller, C. T. (2022). Behavioral context affects social signal representations within single primate prefrontal cortex neurons. *Neuron*, *110*, 1318–1326. <https://doi.org/10.1016/j.neuron.2022.01.020>, PubMed: 35108498
- Kanjilja, S., Lane, C., Feigenson, L., & Bedny, M. (2016). Absence of visual experience modifies the neural basis of numerical thinking. *Proceedings of the National Academy of Sciences, U.S.A.*, *113*, 11172–11177. <https://doi.org/10.1073/pnas.1524982113>, PubMed: 27638209
- Kaufmann, L., Wood, G., Rubinsten, O., & Henik, A. (2011). Meta-analyses of developmental fMRI studies investigating typical and atypical trajectories of number processing and calculation. *Developmental Neuropsychology*, *36*, 763–787. <https://doi.org/10.1080/87565641.2010.549884>, PubMed: 21761997
- Kersey, A. J., Wakim, K.-M., Li, R., & Cantlon, J. F. (2019). Developing, mature, and unique functions of the child's brain in reading and mathematics. *Developmental Cognitive Neuroscience*, *39*, 100684. <https://doi.org/10.1016/j.dcn.2019.100684>, PubMed: 31398551
- Klessinger, N., Szczerbinski, M., & Varley, R. (2007). Algebra in a man with severe aphasia. *Neuropsychologia*, *45*, 1642–1648. <https://doi.org/10.1016/j.neuropsychologia.2007.01.005>, PubMed: 17306848

- Lerner, Y., Scherf, K. S., Katkov, M., Hasson, U., & Behrmann, M. (2021). Changes in cortical coherence supporting complex visual and social processing in adolescence. *Journal of Cognitive Neuroscience*, *33*, 2215–2230. [https://doi.org/10.1162/jocn\\_a\\_01756](https://doi.org/10.1162/jocn_a_01756), PubMed: 34272958
- Maruyama, M., Pallier, C., Jobert, A., Sigman, M., & Dehaene, S. (2012). The cortical representation of simple mathematical expressions. *Neuroimage*, *61*, 1444–1460. <https://doi.org/10.1016/j.neuroimage.2012.04.020>, PubMed: 22521479
- Matejko, A. A., & Ansari, D. (2021). Shared neural circuits for visuospatial working memory and arithmetic in children and adults. *Journal of Cognitive Neuroscience*, *33*, 1003–1019. [https://doi.org/10.1162/jocn\\_a\\_01695](https://doi.org/10.1162/jocn_a_01695), PubMed: 33656397
- Monti, M. M., Parsons, L. M., & Osherson, D. N. (2012). Thought beyond language: Neural dissociation of algebra and natural language. *Psychological Science*, *23*, 914–922. <https://doi.org/10.1177/0956797612437427>, PubMed: 22760883
- Nastase, S. A., Gazzola, V., Hasson, U., & Keysers, C. (2019). Measuring shared responses across subjects using intersubject correlation. *Social Cognitive and Affective Neuroscience*, *14*, 667–685. <https://doi.org/10.1093/scan/nsz037>, PubMed: 31099394
- O'Boyle, M. W., Cunnington, R., Silk, T. J., Vaughan, D., Jackson, G., Syngeniotis, A., et al. (2005). Mathematically gifted male adolescents activate a unique brain network during mental rotation. *Cognitive Brain Research*, *25*, 583–587. <https://doi.org/10.1016/j.cogbrainres.2005.08.004>, PubMed: 16150579
- Park, J., Hebrank, A., Polk, T. A., & Park, D. C. (2012). Neural dissociation of number from letter recognition and its relationship to parietal numerical processing. *Journal of Cognitive Neuroscience*, *24*, 39–50. [https://doi.org/10.1162/jocn\\_a\\_00085](https://doi.org/10.1162/jocn_a_00085), PubMed: 21736455
- Peters, L., & De Smedt, B. (2018). Arithmetic in the developing brain: A review of brain imaging studies. *Developmental Cognitive Neuroscience*, *30*, 265–279. <https://doi.org/10.1016/j.dcn.2017.05.002>, PubMed: 28566139
- Pinel, P., Thirion, B., Meriaux, S., Jobert, A., Serres, J., Le Bihan, D., et al. (2007). Fast reproducible identification and large-scale databasing of individual functional cognitive networks. *BMC Neuroscience*, *8*, 91. <https://doi.org/10.1186/1471-2202-8-91>, PubMed: 17973998
- Pinheiro-Chagas, P., Daitch, A., Parvizi, J., & Dehaene, S. (2018). Brain mechanisms of arithmetic: A crucial role for ventral temporal cortex. *Journal of Cognitive Neuroscience*, *30*, 1757–1772. [https://doi.org/10.1162/jocn\\_a\\_01319](https://doi.org/10.1162/jocn_a_01319), PubMed: 30063177
- Prescott, J., Gavrilescu, M., Cunnington, R., O'Boyle, M. W., & Egan, G. F. (2010). Enhanced brain connectivity in math-gifted adolescents: An fMRI study using mental rotation. *Cognitive Neuroscience*, *1*, 277–288. <https://doi.org/10.1080/17588928.2010.506951>, PubMed: 24168381
- Price, A. R., Bonner, M. F., Peelle, J. E., & Grossman, M. (2015). Converging evidence for the neuroanatomic basis of combinatorial semantics in the angular gyrus. *Journal of Neuroscience*, *35*, 3276–3284. <https://doi.org/10.1523/JNEUROSCI.3446-14.2015>, PubMed: 25698762
- Price, G. R., Holloway, I., Räsänen, P., Vesterinen, M., & Ansari, D. (2007). Impaired parietal magnitude processing in developmental dyscalculia. *Current Biology*, *17*, R1042–R1043. <https://doi.org/10.1016/j.cub.2007.10.013>, PubMed: 18088583
- Price, G. R., Mazzocco, M. M. M., & Ansari, D. (2013). Why mental arithmetic counts: Brain activation during single digit arithmetic predicts high school math scores. *Journal of Neuroscience*, *33*, 156–163. <https://doi.org/10.1523/JNEUROSCI.2936-12.2013>, PubMed: 23283330
- Richardson, H., Lisandrelli, G., Riobueno-Naylor, A., & Saxe, R. (2018). Development of the social brain from age three to twelve years. *Nature Communications*, *9*, 1027. <https://doi.org/10.1038/s41467-018-03399-2>, PubMed: 29531321
- Rivera, S. M., Reiss, A. L., Eckert, M. A., & Menon, V. (2005). Developmental changes in mental arithmetic: Evidence for increased functional specialization in the left inferior parietal cortex. *Cerebral Cortex*, *15*, 1779–1790. <https://doi.org/10.1093/cercor/bhi055>, PubMed: 15716474
- Rouder, J. N., Speckman, P. L., Sun, D., Morey, R. D., & Iverson, G. (2009). Bayesian t tests for accepting and rejecting the null hypothesis. *Psychonomic Bulletin & Review*, *16*, 225–237. <https://doi.org/10.3758/PBR.16.2.225>, PubMed: 19293088
- Sanchez-Alonso, S., & Aslin, R. N. (2022). Towards a model of language neurobiology in early development. *Brain and Language*, *224*, 105047. <https://doi.org/10.1016/j.bandl.2021.105047>, PubMed: 34894429
- Schönbrodt, F. D., Wagenmakers, E.-J., Zehetleitner, M., & Perugini, M. (2017). Sequential hypothesis testing with Bayes factors: Efficiently testing mean differences. *Psychological Methods*, *22*, 322–339. <https://doi.org/10.1037/met0000061>, PubMed: 26651986
- Seghier, M. L. (2013). The angular gyrus: Multiple functions and multiple subdivisions. *Neuroscientist*, *19*, 43–61. <https://doi.org/10.1177/1073858412440596>, PubMed: 22547530
- Shum, J., Hermes, D., Foster, B. L., Dastjerdi, M., Rangarajan, V., Winawer, J., et al. (2013). A brain area for visual numerals. *Journal of Neuroscience*, *33*, 6709–6715. <https://doi.org/10.1523/JNEUROSCI.4558-12.2013>, PubMed: 23595729
- Simon, O., Mangin, J.-F., Cohen, L., Le Bihan, D., & Dehaene, S. (2002). Topographical layout of hand, eye, calculation, and language-related areas in the human parietal lobe. *Neuron*, *33*, 475–487. [https://doi.org/10.1016/S0896-6273\(02\)00575-5](https://doi.org/10.1016/S0896-6273(02)00575-5), PubMed: 11832233
- Skagenholt, M., Träff, U., Västfjäll, D., & Skagerlund, K. (2018). Examining the triple code model in numerical cognition: An fMRI study. *PLoS One*, *13*, e0199247. <https://doi.org/10.1371/journal.pone.0199247>, PubMed: 29953456
- Soltanlou, M., Coldea, A., Artemenko, C., Ehli, A.-C., Fallgatter, A. J., Nuerk, H.-C., et al. (2019). No difference in the neural underpinnings of number and letter copying in children: Bayesian analysis of functional near-infrared spectroscopy data. *Mind, Brain, and Education*, *13*, 313–325. <https://doi.org/10.1111/mbe.12225>
- Soltanlou, M., Sitnikova, M. A., Nuerk, H.-C., & Dresler, T. (2018). Applications of functional near-infrared spectroscopy (fNIRS) in studying cognitive development: The case of mathematics and language. *Frontiers in Psychology*, *9*, 277. <https://doi.org/10.3389/fpsyg.2018.00277>, PubMed: 29666589
- Uddin, L. Q., & Menon, V. (2009). The anterior insula in autism: Under-connected and under-examined. *Neuroscience & Biobehavioral Reviews*, *33*, 1198–1203. <https://doi.org/10.1016/j.neubiorev.2009.06.002>, PubMed: 19538989
- Vanderwal, T., Eilbott, J., & Castellanos, F. X. (2019). Movies in the magnet: Naturalistic paradigms in developmental functional neuroimaging. *Developmental Cognitive Neuroscience*, *36*, 100600. <https://doi.org/10.1016/j.dcn.2018.10.004>, PubMed: 30551970
- Vogel, S. E., Goffin, C., & Ansari, D. (2015). Developmental specialization of the left parietal cortex for the semantic representation of Arabic numerals: An fMR-adaptation study. *Developmental Cognitive Neuroscience*, *12*, 61–73. <https://doi.org/10.1016/j.dcn.2014.12.001>, PubMed: 25555264
- Williams, M. N., Bääth, R. A., & Philipp, M. C. (2017). Using Bayes factors to test hypotheses in developmental research. *Research in Human Development*, *14*, 321–337. <https://doi.org/10.1080/15427609.2017.1370964>
- Yeo, D. J., Pollack, C., Merkle, R., Ansari, D., & Price, G. R. (2020). The “inferior temporal numeral area” distinguishes numerals from other character categories during passive

- viewing: A representational similarity analysis. *Neuroimage*, 214, 116716. <https://doi.org/10.1016/j.neuroimage.2020.116716>, PubMed: 32151762
- Yeo, D. J., Wilkey, E. D., & Price, G. R. (2017). The search for the number form area: A functional neuroimaging meta-analysis. *Neuroscience & Biobehavioral Reviews*. <https://doi.org/10.1016/j.neubiorev.2017.04.027>, PubMed: 28467892
- Zamarian, L., Ischebeck, A., & Delazer, M. (2009). Neuroscience of learning arithmetic—Evidence from brain imaging studies. *Neuroscience & Biobehavioral Reviews*, 33, 909–925. <https://doi.org/10.1016/j.neubiorev.2009.03.005>, PubMed: 19428500
- Zhang, H., Chen, C., & Zhou, X. (2012). Neural correlates of numbers and mathematical terms. *Neuroimage*, 60, 230–240. <https://doi.org/10.1016/j.neuroimage.2011.12.006>, PubMed: 22202882
- Zhou, X., Li, M., Li, L., Zhang, Y., Cui, J., Liu, J., et al. (2018). The semantic system is involved in mathematical problem solving. *Neuroimage*, 166, 360–370. <https://doi.org/10.1016/j.neuroimage.2017.11.017>, PubMed: 29129671