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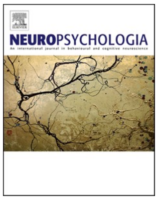

Connectome-based predictive modeling indicates dissociable neurocognitive mechanisms for numerical order and magnitude processing in children

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ABSTRACT

Symbolic numbers contain information about their relative numerical cardinal magnitude (e.g., $\mathbf{2} < 3$) and ordinal placement in the count-list (e.g., 1, **2**, 3). Previous research has primarily investigated magnitude discrimination skills and their predictive capacity for math achievement, whereas numerical ordering has been less systematically explored. At approximately 10–12 years of age, numerical order processing skills have been observed to surpass cardinal magnitude discrimination skills as the key predictor of arithmetic ability. The neurocognitive mechanisms underlying this shift remain unclear. To this end, we investigated children's (ages 10–12) neural correlates of numerical order and magnitude discrimination, as well as task-based functional connectomes and their predictive capacity for numeracy-related behavioral outcomes. Results indicated that number discrimination uniquely relied on bilateral temporoparietal correlates, whereas order processing recruited the bilateral IPS, cerebellum, and left premotor cortex. Connectome-based models were not cross-predictive for numerical order and magnitude, suggesting two dissociable mechanisms jointly supported by visuospatial working memory. Neural correlates of learning and memory were predictive of age and arithmetic ability, only for the ordinal task-connectome, indicating that the numerical order mechanism may undergo a developmental shift, dissociating it from mechanisms supporting cardinal number processing.

1. Introduction

An elementary knowledge of mathematics and a basic level of numerical competence is required for life in modern society, enabling one to live within economic means and to correctly assess numerical information featured in, for instance, transit schedules and price tags at the grocery store. Over the past 25 years, research has fruitfully advanced our understanding of the developmental factors underlying number processing abilities in children and adults, and how these mechanisms support the further development of mathematical skills (Cohen Kadosh and Dowker, 2015). Research in the field of numerical cognition has thus far primarily focused on numerical cardinality (i.e., quantity), whereas cognitive mechanisms underlying the ordinal aspect of number (i.e., sequential positional value) have been less systematically investigated. For instance, the number "2" has the cardinal property of being numerically greater than "1", while also being the third element in a descending sequence featuring the numbers "4-3-2-1". Such ordinal number processing skills have been found to significantly surpass cardinal magnitude discrimination skills as the strongest predictor of children's arithmetic ability during the later years of elementary school (i.e., ages 10–12; Lyons et al., 2014). Contrary to the prevalent view of developmental dyscalculia (a deficit specific to the domain of numerical processing) as resulting from a singular cardinal number processing deficit (e.g., Wilson and Dehaene, 2007; Butterworth et al., 2011), these results suggest that cardinal and ordinal number processing are based on separable neurocognitive mechanisms. Rubinsten and Sury (2011) have, accordingly, proposed a dual-systems model of number processing, arguing for two domain-specific core systems that work together but independently recruit distinct cognitive resources. Although language abilities have been argued to act as a bridge between the numerical

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magnitude and order systems when either mechanism is deficient, the nature and dissimilarity of the neurocognitive mechanisms supporting numerical order and cardinality processing in children remains unclear. To this end, the purpose of the current study was to explore potential mechanistic differences in how the brains of typically developing children, in the critical developmental period where numerical order appears to emerge as the key predictor of mathematics achievement (i.e., ages 10–12), process cardinal and ordinal numerical judgement tasks. Although ordinal number processing abilities are present as early as eleven months of age (e.g., Brannon, 2002), we reasoned that their increased role in arithmetic skill development for middle-school-aged children should render them more readily distinguishable from cardinal number discrimination abilities.

A cross-validated brain–behavior correlation approach (*connectome-based predictive modeling*; Shen et al., 2017) was chosen to investigate if functional whole-brain connectomes (i.e., functional network connectivity), acquired during task performance, could successfully predict scores on separately administered individual cognitive-behavioral outcome measures. Here, we included both domain-specific (i.e., number processing, arithmetic) and domain-general (i.e., language, working memory) abilities. The use of connectome-based predictive modeling served two key purposes: allowing for the identification of cognitive abilities that contribute either jointly or separately to cardinal and ordinal number processing, and–crucially–to determine whether the task-specific functional connectomes were cross-predictive for the two tasks. That is, if the cognitive mechanisms supporting cardinal and ordinal number processing are similar (i.e., dependent on a single system), we would expect the functional connectome associated with either number processing task to be similarly accurate in predicting performance for both cardinal and ordinal number judgements. Conversely, if the dual-systems model (Rubinsten and Sury, 2011) correctly predicts that the processing of numerical order and cardinality depends on separate systems, the functional connectomes associated with either task should only reliably predict performance within the same task. This would, for instance, entail that the functional connectome acquired during the cardinal number discrimination task (e.g., determining which number is greater: 2 or 6) only predicts performance on the same behavioral task administered outside the MRI scanner, but would not be predictive of performance for the ordinal task (see Fig. 1). In this vein, we also expected to observe that the degree of overlap in whole-brain neural activity (i.e., standard task-based univariate contrast analyses) would be higher if the two tasks were supported by the same (i.e., cardinal) system, whereas separate systems would entail less neural overlap.

The hypothesized separate systems for cardinal and ordinal numerical cognition are supported by both neurocognitive and behavioral research in adults (e.g., Franklin and Jonides, 2009; Lyons and Beilock, 2013; Attout et al., 2014; Knops and Willmes, 2014). Prior work by Lyons and Beilock (2013) investigated the neural correlates of numerical cardinal magnitude and order processing in adults. No overlapping neural activity was identified for the conjunction of symbolic cardinal and ordinal number processing (i.e., [Ordinal > Control] ∩ [Cardinal > Control]), suggesting that the two tasks depend on qualitatively different mechanisms. When contrasted against an ordinal luminance control task (i.e., judging whether three symbols were ordered according to brightness), the symbolic ordinal number task only produced activations in the following areas of the premotor cortex: the pre-supplemental motor area (pre-SMA), and left dorsal and ventral premotor cortex. Notably, no activity was found in the right anterior intraparietal sulcus (IPS), a region consistently activated during number discrimination tasks and argued to map domain-specific numerical input (e.g., Arabic numbers and number words) onto a common amodal representation of numerical magnitude (e.g., Dehaene, 2003; Cohen Kadosh et al., 2008; Arsalidou and Taylor, 2011). However, Lyons and Beilock (2013) found the right IPS to be active during both a symbolic and nonsymbolic (i.e., determining which of two arrays contains a larger quantity of dots) cardinal number processing task, as well as during a nonsymbolic ordinal task (e.g., determining whether a set of dots become more numerous in an ascending left-to-right order). This latter result is of particular interest, as it aligns with behavioral data indicating that judgments of nonsymbolic ordinality appear to leverage cardinal number processing mechanisms, rather than those implicated in its symbolic ordinal counterpart. Cardinal discrimination tasks are subject to a reliable distance effect (Moyer and Landauer, 1967), eliciting longer response times for judgments of small compared to large-distance number pairs (e.g., 1 or 2 versus 3 or 7). Symbolic (but not nonsymbolic) numerical ordering tasks instead result in the so-called *reversed distance effect*, where response times are shorter when judging small-distance triplets (e.g., 1-2-3) as opposed to larger distances (e.g., 1-3-5). Whereas the standard distance effect suggests the use of an item–item comparison mechanism (Vos et al., 2017), the reversed distance effect aligns with the associative chaining model, arguing that ordered sequences are processed through inter-item associations where each digit serves as a trigger for the following digit (Lewandowsky and Murdock, 1989; Caplan, 2015). The reversed distance effect has been observed to be weaker for descending compared to ascending sequences, consistent with a facilitated retrieval of rote-learned ascending sequences (i.e., the verbal count-list) from long-term memory (Sasanguie et al., 2017; Vos et al., 2017). Beyond the associative chaining mechanism, recent research has begun to argue for a role of other cognitive

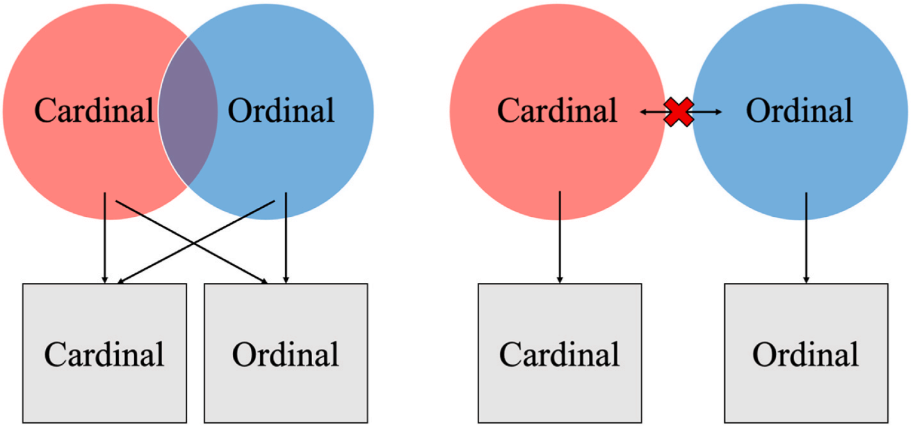

Fig. 1. Overview of predicted mechanisms for numerical cardinality and ordinality. Left: overlapping (or shared) neurocognitive systems for cardinal and ordinal processing entail similar predictability of corresponding behavioral-level outcome measures. Right: separable systems for cardinal and ordinal processing do not afford cross-predictive capacity of behavioral-level outcome measures.

mechanisms relevant to ordinal number processing, such as visuospatial representations and serial-order working memory (e.g., Attout et al., 2014; Lyons et al., 2016; Rubinsten, 2016). These mechanisms may not be unique to ordinality, considering that a visuospatial mental number line–representing numerosities as ascending from left to right (e.g., Dehaene et al., 1993; Göbel et al., 2011)–has been argued to support both ordinal and cardinal number processing (Franklin and Jonides, 2009; Kucian et al., 2011; Morsanyi et al., 2017).

A limited amount of research on numerical order processing in children (e.g., Kaufmann et al., 2009; Kucian et al., 2011; McCaskey et al., 2017; Matejko et al., 2019; Sommerauer et al., 2020) indicates that, earlier in ontogeny, the IPS may serve as a common neural correlate of both ordinal and cardinal numerical cognition. In other words, it may be the case that neurodevelopmental maturation effects around the ages of 10–12 serve to separate and specialize the cognitive mechanisms required for numerical order and magnitude processing, as indicated by their different contributions to continued mathematics achievement (Lyons et al., 2014). In typically developing 10-year-old children, the right IPS responds uniformly to both symbolic numerical and non-numerical (i.e., physical size) ordinal tasks (Kaufmann et al., 2009), not only suggesting neural overlap with cardinal number processing but also a domain-general ordinal processing mechanism. The authors note that both types of stimuli inherently feature both cardinal and ordinal cues, making it difficult to disentangle the relative contribution of each system. It is therefore important, as in the current study, to explicitly compare the neural activity elicited by separate cardinal and ordinal number tasks to establish whether such domain-general IPS activity is attributable to numerical cognition or task design, stimulus properties, and demands.

Results from longitudinal neuroimaging research on ordinal number processing in children, over the course of approximately four years (ages 8–11), has indicated bilateral IPS activity at both baseline and follow-up (McCaskey et al., 2017). Typically developing children also demonstrated, at follow-up, activity associated with the ordinal number processing task in the following regions: the bilateral caudate nucleus, hippocampus, and intraparietal sulcus, the left thalamus and cerebellum. This pattern of results, notwithstanding bilateral IPS activity, resembles the left-lateralized motor circuit identified by Lyons and Beilock (2013) for adult symbolic ordinal processing. Notably, the caudate nucleus and thalamus make up key regions in the corticostriatal circuit, with functional projection to the hippocampus as well as higher cortical regions, such as the pre-SMA and the premotor cortex (Grahn et al., 2008; Haber, 2016). This corticostriatal and left premotor cortex network is indicative of associative and sensorimotor goal-directed processing (Grahn et al., 2008), possibly aligned with visuomotor associations related to the count-list (Lyons and Beilock, 2013). In prior work resembling the current study, Sommerauer et al. (2020) leveraged neural activity and behavioral measures derived from symbolic ordinal and cardinal number processing tasks in children (ages 7.5–10.25) to indicate that the association between numerical cardinality and arithmetic ability is fully mediated by symbolic ordinal number processing ability. An age-dependent activation increase in the left IPS was found to be exclusively correlated with numerical ordering ability. This result stands in contrast to the absence of IPS activity for symbolic numerical ordering in adults (Lyons and Beilock, 2013), but does identify a similar lack of overlap in recruitment of neurocognitive mechanisms for ordinal and cardinal numerical cognition. These results beg the question: is the age-dependent increase in left IPS activity for numerical ordering a fleeting phenomenon (ages 7–10), subsiding over the course of maturation as the cardinal and ordinal mechanisms appear to diverge (i.e., ages 10–12; cf. Lyons et al., 2014)? Is it rather the case that the region assumes the role of a numerical ordering mechanism built upon the amodal number identification system (approximate number system; e.g., Dehaene et al., 2003) for cardinal number discrimination?

Based on the reviewed research, we hypothesized that cardinal and ordinal number processing would be supported by two distinctly separable neurocognitive systems in 10–12-year-old children. In line with the hypothesized distinction between numerical order and cardinality processing systems, we expected four main observable outcomes: (1) a lack of cross-predictability for task-based functional connectomes of either number task onto behavioral outcome measures associated with the opposite task; (2) distinct prediction performance for the two tasks onto non-numerical cognitive abilities (e.g., language ability, working memory) that may be differently or independently recruited; (3) a lack of overlapping neural activity for the two tasks given the need for different mechanisms supported by different neural correlates; and (4) that the neurocognitive system leveraged by ordinal number processing uniquely predicts arithmetic ability (cf. Lyons et al., 2014; Sommerauer et al., 2020). The use of connectome-based predictive modeling furthermore allows for the identification of key neural network nodes that differentiate the two systems, which may provide further insight into the potential mechanistic differences in numerical ordinality and cardinality processing.

2. Methods

2.1. Participants

Thirty-seven ($N = 37$) children (ages 10–12, *Mean age* = 11.41, *SD* = 0.55, 12 girls and 25 boys) participated in the study. Written informed consent was obtained from a legal guardian prior to participation, and children were asked to verbally affirm their desire to participate during each session. Each participant initially performed a behavioral testing session, before completing the fMRI scanning session conducted on a separate day at the Center for Medical Imaging and Visualization (CMIV), Linköping University. All participants were healthy, had no evidence of neurological illness, and had normal or corrected-to-normal vision. No participants had self-reported or formally documented mathematical difficulties. The study was approved by the Regional Ethical Review Board in Linköping, Sweden (study approval reference: 2018/513–32). The families were not paid for their participation.

2.2. Behavioral measures

Measures collected outside the MRI scanner (split-half reliability described in parentheses) included participant age; arithmetic calculation ability ($r_{sh} = 0.74$), arithmetic fact retrieval (addition, subtraction, and multiplication; $r_{sh} = 0.99$), and arithmetic equation scores ($r_{sh} = 0.82$); response times for the symbolic cardinal number discrimination ($r_{sh} = 0.95$), nonsymbolic magnitude discrimination ($r_{sh} = 0.95$), and symbolic ordinal number ($r_{sh} = 0.96$), alphabet ($r_{sh} = 0.95$), and nonsymbolic line segment processing ($r_{sh} = 0.97$) tasks; verbal ($r_{sh} = 0.89$) and visuospatial working memory ($r_{sh} = 0.97$) scores; and a measure of reading ability ($r_{sh} = 0.97$). See Table 1 for an overview of descriptive statistics and correlations between measures. In the interest of space, behavioral tasks are described in the Supplementary Materials.

2.3. Neuroimaging tasks

All participants performed an hour-long mock scanner practice session to familiarize them with the MRI scanner. To ensure task comprehension, participants completed three trials of each task until full accuracy was reached.

The fMRI scanning session lasted for 62 min. Three Echo Planar Imaging (EPI) BOLD sequence runs were administered, each featuring six tasks (for an overview of tasks beyond the scope of this paper, see Skagenholt et al., 2021). An alternating blocked design with a fixed task order was used to minimize the elapsed time between instances of recurring similar tasks (cf. Henson, 2007). A 12s resting period was administered between task blocks. Each of the three EPI runs were split into two halves, with the first half consisting only of "easy" trials (as defined by the standard and reversed distance effects) and the second

Table 1
Descriptive statistics and correlations (r_s) for behavioral measures of interest.

Condition	*M*	*SD*	2	3	4	5	6	7	8	9	10	11	12
1. Age	11.41	0.55	−.014	.284	−.026	**−.432****	−.133	−.180	−.069	**−.378***	−.239	−.249	.063
2. Arithmetic calculations	9.44	2.05	–	.217	**.431****	−.024	−.078	.023	−.086	−.041	.200	**.385***	.256
3. Arithmetic fluency	76.19	20.67		–	**.542****	**−.386***	−.216	**−.566****	**−.433****	**−.476****	.134	.026	**.690****
4. Arithmetic equations	12.81	2.42			–	.017	.083	−.155	.029	−.078	.095	**.413***	**.597****
5. Cardinal processing[a]	737.18	130.62				–	**.347***	**.540****	**.392***	**.656****	.138	.263	−.071
6. Nonsymbolic magnitude[b]	1211.85	420.86					–	.306	.163	.318	−.083	−.046	−.098
7. Ordinal: number[c]	2586.64	1017.69						–	**.645****	**.707****	.075	.276	−.197
8. Ordinal: alphabet[d]	4849.03	1453.40							–	**.554****	−.189	.202	−.076
9. Ordinal: nonsymbolic[e]	1645.58	529.24								–	.002	.150	−.105
10. Verbal WM (hits)	21.64	6.93									–	.248	.273
11. Visuospatial WM (hits)	14.14	8.42										–	.152
12. Reading ability (score)	11.67	3.73											–

Measures a-e indicate response times in milliseconds (both ordered and mixed trials for ordinal processing tasks). WM: Working memory. Significant correlations in bold: *$p < .05$, **$p < .01$.

half consisting only of "difficult" trials. For the cardinal number discrimination task, this entails far-distance trials (e.g., 3 vs 7) for the first half of a run, whereas the other half consisted of near-distance trials (e.g., 4 vs 5). The ordinal number processing task, given the reversed distance effect, had the opposite structure: near-distance triplets (e.g., 1-2-3) in the first half of a run and far-distance triplets (e.g., 7-5-1) in the other half. Each block within a run featured 14 trials, resulting in 84 trials per task (i.e., 14 trials × 2 distances × 3 runs) in total. Each individual trial lasted for 4000 ms, including a 500 ms fixation cue, 2000 ms stimulus presentation, and a 1500 ms response cue. Participants were instructed to respond during the response cue (question mark), using one of two buttons placed under their right index and middle fingers (Lumia response pad; Cedrus Corporation, San Pedro, CA, USA). Stimulus presentation and response registration was performed using SuperLab 5 (Cedrus Corporation, San Pedro, CA, USA). Stimuli were presented through a pair of VisuaStimDigital video goggles (Resonance Technology Inc., Northridge, CA, USA). See Fig. 2 for a graphical overview of the experimental paradigm.

2.3.1. *Symbolic cardinal number discrimination task*

Two Arabic digits were presented across the horizontal plane, requiring participants to select the numerically larger digit by pressing the corresponding index (for left) or middle finger (for right) button on the response pad. Numerical distances were far (4–5; e.g., 3 vs 7) for the first block in each run and near (1–2; e.g., 4 vs 5) for the second block in each run.

2.3.2. *Symbolic ordinal number processing task*

Three Arabic digits were presented across the horizontal plane. The task was to determine whether the three digits were presented in a correctly ascending or descending order, regardless of numerical distance (e.g., 1-2-3 or 9-7-5). Half of all trials were regarded as incorrect, where the numerical triplet was neither an ascending nor descending sequence (i.e., mixed-order; 1-5-3). Participants used the middle finger (right) response pad button to indicate a correct triplet sequence and the index (left) response pad button to indicate an incorrect triplet sequence. Two numerical distances were used to account for far (2–3; e.g., 2-4-6) and near (1; e.g., 5-4-3) trials, alternated for each block in a run.

2.3.3. *Letter case discrimination (control) task*

To control for task-irrelevant activity associated with the symbolic cardinal number discrimination task, participants were presented with a superficially similar task featuring two alphabetical (one uppercase and one lowercase) letters presented across the horizontal plane (e.g., t vs J). The purpose of this task was to select the uppercase letter, using the corresponding response pad button for the left or right-hand side.

2.3.4. *Symbolic congruity comparison (control) task*

To control for task-irrelevant activity associated with the symbolic ordinal number processing task, participants were presented with three symbols across the horizontal plane and asked to determine whether all three were identical. Half of all trials were congruent, meaning that all three symbols were the same (e.g., A-A-A), whereas the other half of

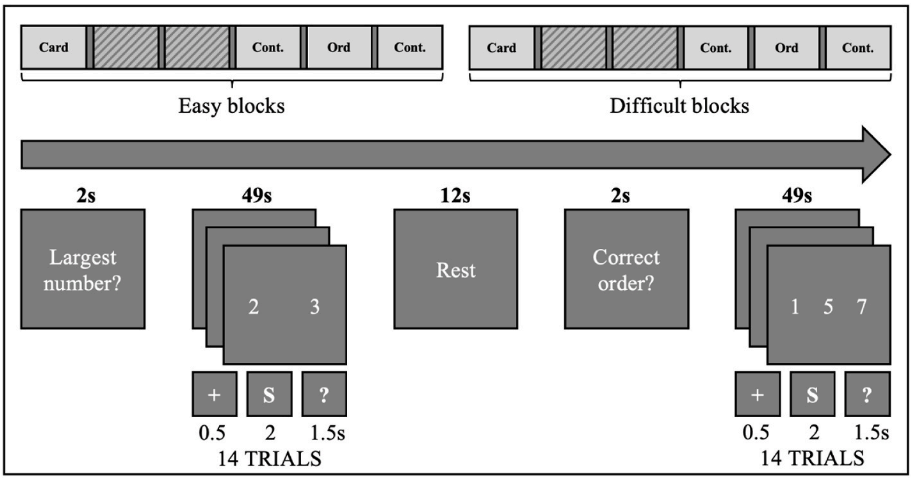

Fig. 2. Overview of the fMRI paradigm. Top row indicates a full EPI run, split into two halves featuring "easy" and "difficult" trial blocks, respectively. Card: cardinal. Ord: ordinal. Cont: control tasks. Unrelated task blocks (dashed lines) are reported in Skagenholt et al. (2021). Symbols below trial examples indicate fixation (+), stimulus presentation (S), and response cue (?).

trials were incongruent (e.g., 2-B-2). For congruent trials, participants were requested to answer using the middle finger (right) response pad button, and the index finger (left) for incongruent trials. As for the corresponding experimental task, the response requirement and visual presentation was identical, but the control stimuli had no internal order as not to subtract activity unique to ordinal processing. Numerical and alphabetical stimuli were used, both separately (e.g., A-A-A; 2-2-2) and combined within trials (e.g., Y–Y-7). Different letters or numbers were never used within a trial to avoid suggesting an underlying ordinal sequence.

2.4. *fMRI data acquisition*

Neuroimaging data were acquired at the Center for Medical Imaging and Visualization (CMIV), Linköping University. A Siemens Magnetom Prisma 3.0 T MRI scanner was used, fitted with a twenty-channel head coil. A T1-weighted pulse sequence (208 slices, thickness = 0.9 mm^3, TR = 2300 ms, TE = 2.36 ms, flip = 8°, GRAPPA multi-band acceleration = factor 3) was used to acquire high-resolution structural scans prior to experimental task administration. Whole-brain functional task-based scans were acquired using a T2*-weighted BOLD-sensitive (Blood-Oxygen-Level-Dependent) ascending Echo Planar Imaging (EPI) pulse sequence (48 slices, thickness = 3.0 mm^3, TR = 1340 ms, TE = 30 ms, flip = 69°, slice acceleration = factor 2).

2.5. *fMRI data preprocessing*

All neuroimaging data were preprocessed using the default pipeline in the CONN functional connectivity toolbox version 20.b (Whitfield-Gabrieli and Nieto-Castanon, 2012) for SPM12 (Wellcome Department of Cognitive Neurology, London, UK). Performed preprocessing steps included functional realignment and unwarping, outlier identification (intermediate setting: framewise displacement >0.9 mm or global BOLD signal changes >5 *SD*), direct segmentation and normalization into standard MNI space, and functional smoothing with a 6 mm full-width-at-half-maximum (FWHM) Gaussian kernel. No slice-timing correction was performed. All data were denoised using default CONN parameters: band-pass filtering between 0.008 and 0.09 Hz and linear detrending. No despiking was performed on the denoised data. Following preprocessing, two participants were excluded as more than 20% of overall volumes were flagged as outliers, resulting in a final sample of $N = 37$ participants as described above.

2.6. *fMRI data analysis*

Near and far-distance trials of each experimental task were collapsed into single Cardinal and Ordinal conditions, for two reasons: as a means of increasing power (by treating all 84 trials per task as a whole) and because we were primarily interested in exploring mechanistic differences regardless of numerical distance, which was used as a means of counterbalancing the trials. Distance effects are however accounted for in the behavioral data. Probabilistic cytoarchitectonic mapping was performed using the SPM Anatomy Toolbox (Eickhoff et al., 2005).

2.6.1. *GLM analysis of BOLD activation*

General linear model (GLM) analysis was performed using SPM12. Data preprocessed in the CONN toolbox were imported, including individual movement and outlier regressors generated during denoising. A whole-brain voxel-wise BOLD-analysis was performed for each subject individually (first-level; $p < .001$ uncorrected). Second-level analyses were performed with the Statistical Nonparametric Mapping (SnPM version 13.1.08; http://nisox.org/Software/SnPM13/) toolbox for SPM12. A cluster-forming threshold of $p < .001$ and a familywise error correction-threshold of $p < .05$ were used. No variance smoothing was applied given that the degrees of freedom in this sample exceeded the recommendations ($df < 20$) for such an approach. Each analysis was subject to 10,000 permutation tests. Cluster extent thresholds were calculated as the critical suprathreshold cluster size (STCS), with the minimum to maximum cluster extent ranging from 133 to 137 functional voxels.

Three analyses were performed. Two simple subtraction contrasts (i.e., [1 -1]) were used to subtract activity specific to cardinal number processing from activity elicited by the ordinal number processing task and vice versa. A conjunction (null) analysis was performed by subtracting activity specific to the matched control tasks from either experimental task, which resulted in two FWE-corrected [Task > Control] T-maps serving as input to SPM's ImCalc tool. The "min(i1,i2)" expression was used to determine the conjunction between the two tasks.

2.6.2. *Connectome-based predictive modeling*

ROI-based functional connectivity analysis was performed using the CONN toolbox, to extract the functional connectomes required for predictive modeling. Subject-specific whole-brain connectivity matrices based on the Shen 268 node parcellation atlas (268 × 268 ROI-to-ROI connections; Shen et al., 2013) were computed in a first-level analysis. Fisher *Z*-transformed whole-brain ROI-to-ROI connectivity matrices were then exported for all but one subject (who did not participate in behavioral testing) across both experimental conditions (resulting in two 268 × 268 × 36 connectivity matrices). Connectome-based predictive modeling (CPM; Shen et al., 2017) was used to investigate the association (Spearman's *rho* correlation) between task-based functional whole-brain connectivity patterns and the behavioral measures detailed in Table 1 (including separate measures of addition, subtraction, and multiplication fluency). This resulted in a total of 30 independent CPM analyses (i.e., 15 behavioral measures × 2 fcMRI RBC matrices). Partial correlation was used in order to provide an additional measure of control over effects associated with motion (mean framewise displacement per participant), which may otherwise confound functional connectivity analyses. A strict feature selection threshold of $p < .001$ was used for each task and behavioral measure, to reduce both the number of edges retained by the model and the overall computational load (cf. Gao et al., 2019). Such a strict feature selection threshold may increase the rate of false negative results, which were deemed preferable to false positives given the lack of a separate dataset for external validation. Leave-one-subject-out cross-validation was used iteratively, where each subject once constituted the test set whereas remaining participants ($n = 35$) made up the training set. Resulting connectivity matrices associated with each behavioral measure were permuted 1000 times to determine statistical significance. The connectivity viewer module featured in the Yale BioImage Suite (Papademetris et al., 2006) was used to visualize results and extract the top 5 highest-degree network nodes, as high-degree nodes are considered network hubs and exert strong influence on a network's function (e.g., Medaglia, 2017). We chose to report only the top 5 hub nodes, as opposed to the more common top 10 nodes (e.g., Wu et al., 2022; Ren et al., 2021), given the strict feature selection threshold and its impact on the remaining number of statistically significant edges associated with each node. That is, not all analyses resulted in ten nodes with one or more edges, which motivated the choice of five nodes for consistency.

3. Results

3.1. *Behavioral results*

For an overview of descriptive statistics and correlations between behavioral measures collected outside the MRI scanner, see Table 1. The response times (RTs) and accuracies for each of the tasks administered during the MRI scanning session were analyzed with two Bonferroni-corrected repeated-measures Analyses of Variance (ANOVA). See Table 2 for an overview of behavioral results. A statistically significant difference in response times, $F(1, 34) = 9.093$, $p = .005$, $\eta_p^2 = .211$, and

Table 2

Descriptive statistics for neuroimaging tasks (n = 35).

	Response Time (ms)		Accuracy	
Condition	*M*	*SD*	%	*SD*
Cardinal processing	566.74	90.75	99.51	0.97
Far-distance trials	575.41	96.96	99.66	1.03
Near-distance trials	557.65	98.21	99.38	1.73
Ordinal processing	613.74	112.68	93.61	6.43
Far-distance trials	618.99	114.81	94.75	6.05
Near-distance trials	609.23	121.34	92.77	9.89
Control: Letters	556.31	82.20	98.15	1.31
Control: Congruity	559.74	97.63	97.55	4.05

Data represents 35 out of 37 participants due to technical errors during acquisition.

accuracy, $F(1, 34) = 14.631, p < .001, \eta_p^2 = .301$, was identified. Refer to the Supplementary Materials for additional post-hoc tests.

It should be noted that response times for the cardinal ($r = 0.128$, $p = .462$) and ordinal ($r = 0.283$, $p = .099$) number processing tasks were not significantly correlated at the behavioral and neuroimaging levels. Such absent correlations are most parsimoniously explained by slight variations in the response procedures for the tasks when administered inside and outside the MRI scanner. While the tasks are in all respects equivalent in terms of stimulus content and procedure, the behavioral-level tasks allowed participants to respond while the stimuli were presented on screen. In the neuroimaging tasks, participants had to wait for 2 s following stimulus presentation before being granted a response window, meaning that these response times do not adequately capture purely stimulus-evoked (e.g., numerical distance) effects. In the neuroimaging tasks, the response times could rather be argued to reflect a general measure of psychomotor speed, given that participants have already decided on a given response alternative.

3.2. *Univariate GLM analyses*

3.2.1. *Conjunction analysis*

Overlapping BOLD activation for the two number processing tasks, subtracted by their respective control tasks, was identified in two clusters (all $p_{\text{FWE}} < .05$): the right lingual gyrus subdivision hOc2 ($T = 8.84$; MNI [10, −80, −6]; $k = 10291$ voxels), with local activation peaks in the fusiform gyrus subdivision hOc4v ($T = 8.81$; MNI [24, −68, −10]) and the calcarine gyrus subdivision hOc1 ($T = 7.64$; MNI [6, −84, 4]); as well as the left superior temporal gyrus subdivision PFcm ($T = 4.43$; MNI [−48, −34, 20]; $k = 165$ voxels), also featuring local activation peaks in subdivision PFop ($T = 4.28$; MNI [−60, −32, 20]) and the supramarginal gyrus subdivision PFt ($T = 4.04$; MNI [−52, −34, 30]). Critical STCS (cluster extent) was defined as 133 voxels, given that this value was consistent across both [Task > Control] analyses. In contrast to our hypothesis and the null result previously found by Lyons and Beilock (2013), the analysis thus indicates a degree of neural overlap for the two tasks. See Fig. 3.

3.2.2. *Symbolic ordinal number processing*

Activity unique to the ordinal number processing task was determined by subtracting activity elicited by the cardinal number processing task. Critical STCS (cluster extent) was defined as 135 voxels. Resulting activity was identified in the cerebellar vermis (lobules IX and I IV); left middle occipital gyrus, inferior and superior parietal lobule, precentral gyrus, and posterior-medial frontal cortex; as well as the right inferior occipital gyrus, angular gyrus (overlapping IPS subdivision hIP3), and superior parietal lobule. See Fig. 3 and Supplementary Table 1 for an overview of results.

3.2.3. *Symbolic cardinal number processing*

Activity unique to the cardinal number processing task was determined by subtracting activity elicited by the ordinal number processing task. Critical STCS (cluster extent) was defined as 137 voxels. Resulting activity was identified in the bilateral insula; right lingual gyrus, fusiform gyrus, supramarginal gyrus (subdivision PFop), postcentral gyrus, and inferior frontal gyrus (pars Triangularis); and the left superior occipital gyrus, middle temporal gyrus, as well as the left superior frontal gyrus. See Fig. 3 and Supplementary Table 1 for an overview of results.

3.3. *Connectome-based predictive modeling*

At the level of neural activity, overlap between the cardinal and ordinal number processing systems appears limited to the occipital lobe and left supramarginal gyrus. Although this outcome does not allow us to argue in favor of completely independent systems, the lack of overlapping IPS activity indicates that the two tasks are at least not fully supported by one and the same amodal cardinal number processing system. As a means of further teasing apart the mechanistic differences supporting the processing of numerical order and cardinality, connectome-based predictive modeling (CPM; Shen et al., 2017) was employed to investigate whether task-elicited whole-brain functional network connectivity was sufficiently distinct to predict different sets of behavioral outcome measures and, in particular, if the task-based connectomes exclusively predicted their behavioral-level equivalent outcome scores (i.e., ordinal–ordinal and cardinal–cardinal but no cross-prediction). The results detailed here pertain to the top 5 high-degree hub nodes (i.e., highly connected with other nodes) identified for each task and associated behavioral measure. *Permutation p*-values described below (as p_{perm}) indicate whether observed outcomes, compared to 1000 randomly shuffled associations between individual

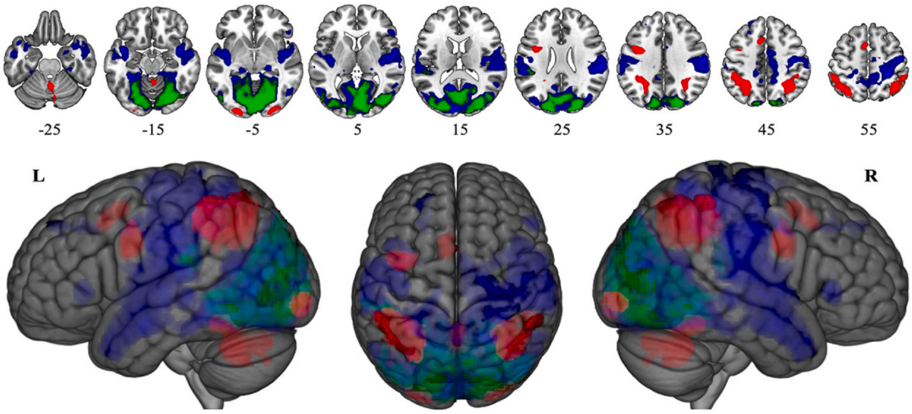

Fig. 3. Overview of GLM BOLD activation. Red clusters correspond to contrast [Ordinal > Cardinal], blue clusters to contrast [Cardinal > Ordinal], and green clusters to conjunction (null) between tasks (subtracted by matched control tasks). Slices (top) range from $z = -25$ to 55 in increments of 10.

connectomes and behavioral scores, were obtained with above-chance probability. For graphical representations of permutation testing results, see Supplementary Fig. 1. A graphical summary of results is presented in Fig. 4. See Fig. 5 for an overview of the top 5 high-degree nodes, for each task and successfully predicted behavioral outcome, and their respective patterns of functional connectivity that uniquely contribute to predictive capacity (see also Supplementary Tables 2 and 3 for an overview of hub nodes' associated connectivity patterns).

3.3.1. Symbolic ordinal number processing

Functional connectivity matrices elicited by the ordinal number processing task were observed to successfully predict participant age, arithmetic subtraction fluency score, mean response times associated with the ordinal number processing task (i.e., the task's behavioral-level equivalent), and visuospatial working memory scores. Notably, no cross-predictability was identified for cardinal number processing response times. See Table 3 and Figs. 4 and 5 for an overview of results.

Nodes of functional connectivity positively associated with higher participant age were observed in the right insula, caudate nucleus, and left cerebellum and hippocampus, $r_s = 0.46$, $p = .004$, $p_{perm} = .015$. Functional connectivity was positively associated with higher subtraction ability in the left hippocampus, parahippocampal gyrus, caudate nucleus, temporal pole, and right middle temporal gyrus, $r_s = 0.59$, $p < .001$, $p_{perm} = .001$. Mean response times associated with the behavioral ordinal number processing task could be successfully predicted by a negatively associated network, indicating that increased functional connectivity between the nodes was predictive of faster responses. This functional connectivity was elicited in the bilateral cerebellum, left middle frontal gyrus, and right superior frontal gyrus, $r_s = 0.38$, $p = .02$, $p_{perm} = .04$. Finally, the functional connectivity patterns elicited by the ordinal number processing task successfully predicted an increase in visuospatial working memory scores, meaning that connectivity was positively predictive of visuospatial working memory capacity, $r_s = 0.41$, $p = .01$, $p_{perm} = .048$. Predictive connectivity patterns were observed in the right parahippocampal gyrus, fusiform gyrus, left thalamus, and the interposed nucleus of the cerebellum.

3.3.2. Symbolic cardinal number processing

Functional connectomes elicited by the cardinal number processing task were observed to successfully predict negative associations with response times for the nonsymbolic magnitude discrimination task, as well as visuospatial working memory scores. Similar to the functional connectomes derived from the ordinal task, there was no cross-predictability between cardinal number processing at the neural level and numerical ordering task response times at the behavioral level. Together, these findings provide further support to the hypothesized dissociable systems for numerical ordinality and cardinality processing (cf. Rubinsten and Sury, 2011). See Table 4 and Figs. 4 and 5 for an overview of results.

Mean response times associated with the behavioral nonsymbolic magnitude discrimination task could successfully be predicted by a negatively associated network, indicating that increased functional connectivity between the nodes was predictive of faster responses. The connectome was not predictive of behavioral symbolic cardinal number discrimination response times, which is most likely due to the lack of a response time limit in the latter task. However, given both behavioral correlations between symbolic and nonsymbolic magnitude discrimination (see Table 1 and Fig. 4) as well as theoretical support for their interrelationship (e.g., Mundy and Gilmore, 2009), the nonsymbolic magnitude discrimination task can plausibly be seen as a proxy for symbolic cardinal number discrimination abilities. This interpretation is reinforced by the fact that response times for the behavioral nonsymbolic magnitude discrimination task were significantly correlated with the symbolic number discrimination task ($r_s = .347$, $p = .038$) but not with the (symbolic) ordinal number processing task ($r_s = 0.306$, $p = .069$), suggesting a meaningful distinction between the cognitive mechanisms for magnitude discrimination (i.e., distinguishing less versus more) and ordering regardless of stimulus format. That is, while symbolic and nonsymbolic discrimination tasks could rely on partially different processes, they appear more similar and likely reflect shared foundational cognitive mechanisms to a greater degree than with other numerical-cognitive tasks (e.g., ordering). Nevertheless, this outcome requires further attention in future replication and external validation attempts, given mixed findings in the literature regarding the relationship between symbolic and nonsymbolic number discrimination processes (e.g., Krajcsi et al., 2018).

Predictive connectivity was found in the left superior frontal gyrus, middle cingulate cortex, calcarine gyrus, and right middle frontal gyrus and cerebellum, $r_s = .40$, $p = .02$, $p_{perm} = .03$. Functional connectivity patterns elicited by the cardinal number processing task were also

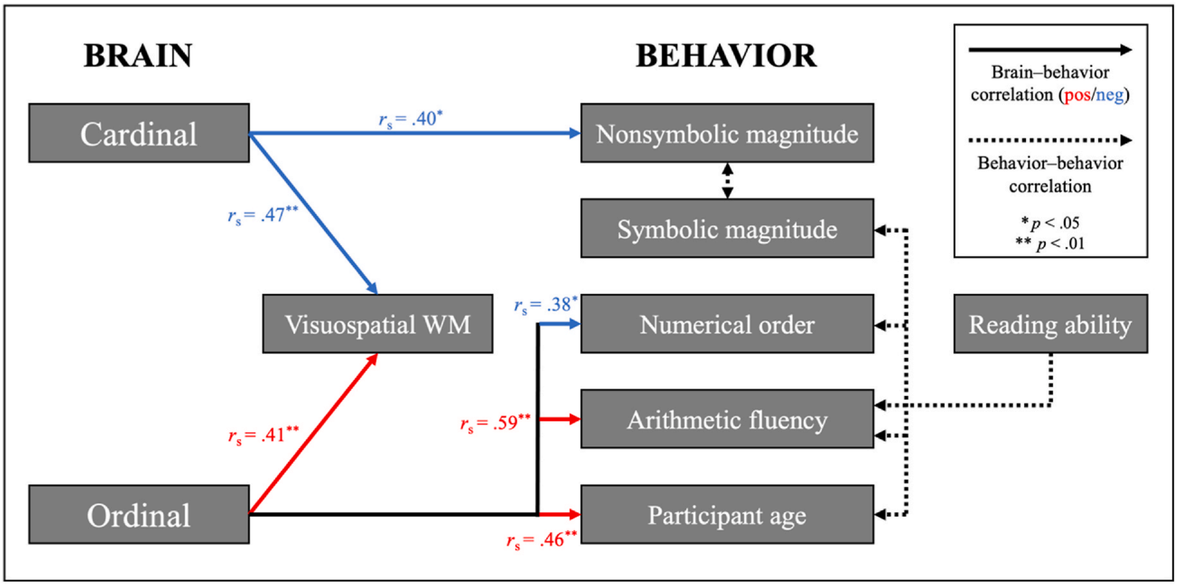

Fig. 4. Summary of brain–behavior analyses. See figure legend (top right) for details. Note that positive and negative brain–behavior correlations refer to networks positively and negatively correlated with outcome measures (e.g., increased functional connectivity in the cardinal connectome predicts faster response times for nonsymbolic magnitude processing), not positive or negative correlation coefficients (i.e., all r_s are positive).

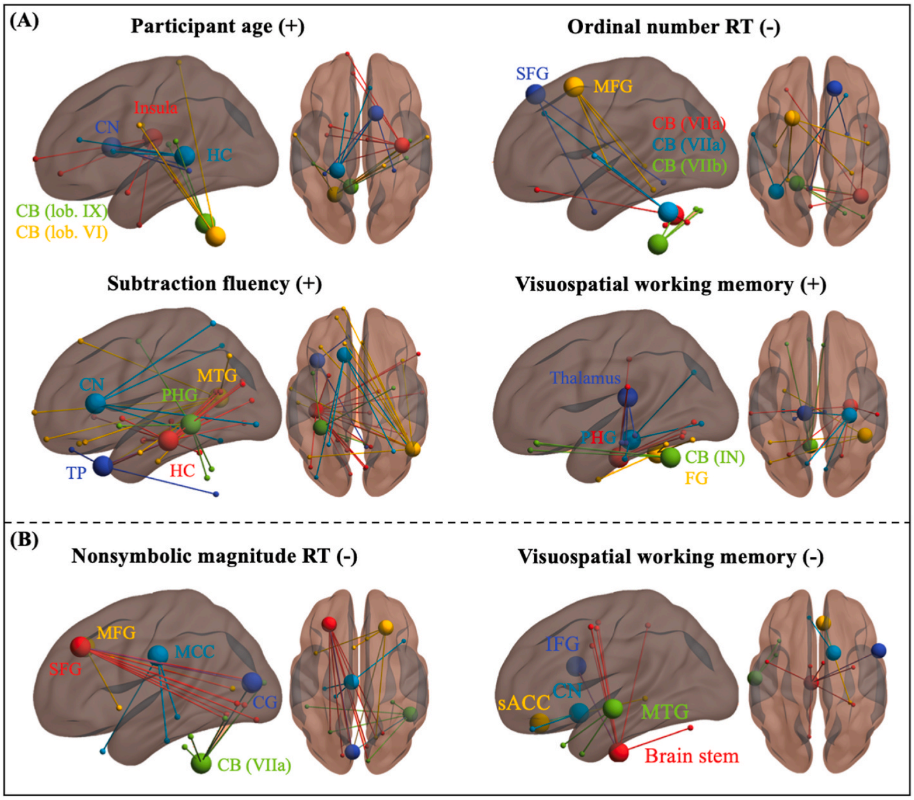

Fig. 5. Connectome-based predictive modeling of symbolic ordinal (A, above dashed line) and symbolic cardinal (B, below dashed line) number processing tasks. Titles (centered in bold) correspond to predicted behavioral measures and whether the functional connectivity network is positively (+) or negatively (−) associated. CN: caudate nucleus. HC: hippocampus. CB: cerebellum (lob: lobule; IN: interposed nucleus). SFG: superior frontal gyrus. MFG: middle frontal gyrus. TP: temporal pole. PHG: parahippocampal gyrus. MTG: middle temporal gyrus. FG: fusiform gyrus. MCC: middle cingulate cortex. CG: calcarine gyrus. sACC: anterior cingulate cortex (subgenual). IFG: inferior frontal gyrus.

negatively associated with visuospatial working memory capacity (i.e., increased connectivity predicted lower behavioral outcome scores). Nodes associated with this performance decrease were found in the left brainstem, middle temporal gyrus, and right rectal gyrus, caudate nucleus, and inferior frontal gyrus, $r_s = 0.47$, $p = .004$, $p_{perm} = .03$.

4. Discussion

The current study sought to investigate the neurocognitive mechanisms recruited by ordinal and cardinal number processing tasks, in 10–12-year-old children, to determine whether this point in ontogeny represents a separation of the mechanisms and a possible shift away from relying on a singular, amodal numerical representation system typically associated with numerical magnitude discrimination tasks (e.g., Dehaene et al., 2003). The chosen approach, a combination of univariate whole-brain contrast analyses and brain–behavior associations derived from functional connectivity, built on the premise that a greater dissimilarity of neurocognitive systems governing cardinality and ordinality would result in less overlap: both in terms of neural activity and in prediction of related cognitive-behavioral outcomes. We hypothesized that middle-school-aged children have reached a point in their neurocognitive development where the systems begin to dissociate, as previously shown for adults (e.g., Lyons and Beilock, 2013), which would manifest as: (1) a lack of cross-predictability; (2) distinct prediction performance for the two tasks onto non-numerical cognitive abilities (e.g., working memory, language); (3) a lack of overlapping neural activity for the two tasks; and (4) unique predictability of arithmetic ability from ordinal number processing (e.g., Lyons et al., 2014; Sommerauer et al., 2020).

4.1. A lack of cross-predictability for numerical ordinality and cardinality

In line with the hypothesis that numerical ordinality and cardinality processing depend on separate systems, the two tasks were not observed to reliably cross-predict between patterns of functional connectivity associated with one task (e.g., cardinal number processing) and the behavioral outcome score associated with the other task (e.g., ordinal number processing). Together with the limited but significant overlap between tasks at the neural activity level, this result indicates that the ordinal and cardinal number systems are at least separable and not indicative of a singular underlying processing mechanism. The results do not, however, allow us to claim that the systems are completely independent of one another. It has been argued that ordinal number processing tasks entail different solution strategies depending on whether the triplet is in a correctly ascending, descending, or mixed order. Dubinkina et al. (2021) found that three primary strategies are used during numerical order processing, one of which (“decomposition”) entails pairwise number comparisons akin to a standard number discrimination task (e.g., for the triplet 1-7-5: 1 < 7 and 7 > 5). Participants reported using the decomposition strategy primarily in non-ordered (i.e., mixed) trials, whereas ordered trials relied more on a memory retrieval strategy. These results indicate that mixed ordinal sequences may be processed differently than ordered sequences, potentially indicating the existence of separate subsystems for order processing, where mixed triplets in particular could depend on basic magnitude discrimination mechanisms. Furthermore, different numerical triplet distances may entail different executive function demands, given the argument that the reversed distance effect (i.e., faster responses to near-distance triplets) arises because less familiar sequences (e.g., 3-5-7) are inhibited to a greater extent than near-distance sequences (e.g., 1-2-3) are facilitated by memory (Gattas et al., 2021). While it is not possible to isolate correct and incorrect trials in the current neuroimaging data, due to the blocked fMRI design, a post-hoc analysis of the behavioral data (see the Supplementary Materials and Supplementary Table 4) indicated that (1) correctly ordered near-distance triplets (e.g., 1-2-3): were responded to significantly faster than non-ordered triplets (e.g., 3-1-2) and far-distance triplets (e.g., 2-4-6; 5-1-3), suggesting a possible facilitation effect of the count-list stored in memory (Dubinkina et al., 2021). No significant difference in response times was present for ordered and mixed far-distance triplets,

Table 3
Top 5 nodes associated with behavior in the ordinal functional connectivity network.

Behavioral measure	Network	Anatomical region [Node]	MNI (x,y, z)	Degree
Age	Positive	R Insula (OP3) [94]	36, −15, 18	6
		L Cerebellum lobule VI [250]	−23, −58, −49	4
		L Cerebellum lobule IX [237]	−9, −51, −40	3
		L Hippocampus [229]	−21, −37, 6	3
		R Caudate nucleus [121]	13, 13, 12	3
Subtraction fluency	Positive	L Hippocampus (CA1) [232]	−36, −25, −15	16
		R Middle temporal gyrus [50]	49, −59, 14	11
		L Parahippocampal gyrus [230]	−32, −40, −4	4
		L Caudate nucleus [257]	−11, 24, 10	4
		L Temporal pole [186]	−35, 19, −32	3
Ordinal: number	Negative	R Cerebellum (VIIa crusI) [113]	37, −57, −33	5
		L Middle frontal gyrus [164]	−23, 11, 54	4
		L Cerebellum lobule VIIIb [243]	−19, −46, −53	3
		L Cerebellum (VIIa crusI) [238]	−37, −53, −31	2
		R Superior frontal gyrus [12]	14, 37, 49	2
Visuospatial WM[a]	Positive	R Parahippocampal gyrus [96]	29, −20, −26	5
		R Fusiform gyrus (FG4) [71]	42, −46, −23	3
		Cereb. interposed nucleus [255]	−7, −55, −26	3
		R Parahippocampal gyrus [95]	28, −28, −14	3
		L Thalamus (temporal) [264]	−12, −26, 15	3

Degree corresponds to number of connections. Node (in brackets) indicates node number in the Shen et al. (2013) 268-node parcellation. Areas in parentheses correspond to closest cytoarchitectonic structures identified in SPM Anatomy Toolbox. Positive and negative networks indicate direction of association with behavioral scores. (a) WM: working memory. Cereb: cerebellum.

Table 4
Top 5 nodes associated with behavior in the cardinal functional connectivity network.

Behavioral measure	Network	Anatomical region [Node]	MNI (x,y, z)	Degree
Nonsymbolic[a]	Negative	L Superior frontal gyrus [146]	−27, 34, 36	8
		R Middle frontal gyrus [13]	24, 31, 36	5
		R Cerebellum (VIIa crusI) [107]	46, −47, −42	5
		L Middle cingulate cortex [224]	−7, −18, 30	3
		L Calcarine gyrus (hOc1) [215]	−6, −81, 12	3
Visuospatial WM[b]	Negative	L Brain stem [268]	−6, −19, −37	7
		R Rectal gyrus (ACC s32) [3]	5, 35, −17	2
		L Middle temporal gyrus [197]	−57, −15, −7	2
		R Caudate nucleus [125]	14, 8, −10	2
		R Inferior frontal gyrus (p. Op) [21]	55, 10, 22	1

Degree corresponds to number of connections. Node (in brackets) indicates node number in the Shen et al. (2013) 268-node parcellation. Areas in parentheses correspond to closest cytoarchitectonic structures identified in SPM Anatomy Toolbox. Positive and negative networks indicate direction of association with behavioral scores. (a) Mean response time of the behavioral nonsymbolic magnitude discrimination task. (b) WM: working memory. Note: "p. Op" refers to the pars Opercularis subdivision of the inferior frontal gyrus; ACC: anterior cingulate cortex.

which could indicate that ordered trials are similarly impeded by unfamiliarity as mixed trials (cf. Gattas et al., 2021). (2) All trials were positively correlated with inhibition capacity, suggesting consistent inhibitory responses across trial types. However, far-distance ordered trials were the only variation that did not significantly correlate with shifting ability, which may indicate a different processing strategy. Although there appear to be processing differences for different numerical ordering trials, it is noteworthy that the connectome-based predictive model still did not cross-predict between number tasks and correctly predicted performance within-task. A limitation of this study is nevertheless that the overarching measure of numerical ordering capacity may involve several sub-strategies, depending on trial type, that cannot be disentangled in the neuroimaging data. Future research should attempt to replicate these results using separate conditions for ordered and mixed trials, in order to distinguish whether the mechanistic separability observed in the current study remains or is impacted by the use of different strategies.

4.1.1. Ordinal number processing response times

The ordinal number processing connectome successfully predicted a negative association between functional connectivity and response times for the equivalent behavioral task. In other words, increased connectivity between the identified nodes was indicative of shorter response times. Although behavioral results indicated strong correlations between the three ordinal tasks (i.e., numerical, alphabetical, and nonsymbolic), CPM failed to indicate connectivity predictive of the remaining two behavioral-level tasks. In line with these results, recent research suggests a dissociation of neural mechanisms contributing to numerical order processing on the one hand and working memory as well as alphabetical order processing on the other (Attout et al., 2021). Numerical order may therefore feature unique properties conducive to the development of numerical and mathematical abilities. However, it is imperative that future research also includes non-numerical order tasks at the neuroimaging level, to investigate if a more domain-general ordering mechanism predicts mathematics abilities to a similar degree (e.g., Vos et al., 2017) as domain-specific numerical ordering alone.

The top five nodes of this negative network were found in the bilateral cerebellar lobule VIIa crus I; left cerebellar lobule VIIIb and middle frontal gyrus; and the right superior frontal gyrus. Connectivity associated with these hubs was primarily found in insular, hippocampal, prefrontal, and cerebellar nodes (see Supplementary Table 3). The DLPFC nodes (i.e., MFG, SFG) together with cerebellar lobule VIIa crus I constitute clear markers of the frontoparietal network, commonly associated with cognitive control and task difficulty (e.g., Brosnan and Wiegand, 2017). The negative correlation with response times indicates top-down modulation, facilitating the performance of numerical order judgment trials.

4.1.2. Nonsymbolic magnitude discrimination response times

The functional connectome derived from the symbolic cardinal number discrimination task was negatively predictive (i.e., increased connectivity implies faster responses) of response times associated with the behavioral-level nonsymbolic magnitude discrimination task. This outcome was unexpected, given the difference in representational format between the two tasks. A potential explanation is that the slight difference in response procedures (i.e., immediate and not time-constrained in the behavioral task versus delayed but time-limited in the neuroimaging task) may result in this outcome. The similarity in task presentation is thus greater between the behavioral nonsymbolic magnitude comparison task and the neuroimaging symbolic number comparison task, than the two symbolic tasks. This is because the behavioral nonsymbolic task features a time-limited response, akin to the symbolic neuroimaging task, and the subsequent item is presented regardless of participants' response once this time has elapsed. In contrast, the symbolic behavioral task remains visible until a response is given. If it were the case that the nonsymbolic and symbolic comparison tasks depend on fundamentally different processes, we would expect the correlation between these tasks to be no stronger than between the nonsymbolic comparison task and symbolic ordering task (featuring the same stimulus format and basic response procedures as the comparison task).

The top five nodes of the negative predictive network were identified in the left superior frontal and calcarine gyri, the middle cingulate cortex; and the right middle frontal gyrus as well as cerebellar lobule VIIa crus I. Like the network predictive of the symbolic ordinal number processing task, the identified hub nodes appear to similarly target the frontoparietal network (see Supplementary Tables 3–4), affording a similar interpretation of top-down modulation in service of improving task performance.

4.2. Distinct and overlapping neural activity for numerical order and cardinality

Shared activity for the cardinal and ordinal number processing tasks was identified in a large occipital lobe cluster spanning the V1–V4 subdivisions of the visual cortex, with local peaks in the fusiform and calcarine gyri, as well as in the left supramarginal gyrus. The ventral-temporal occipital cortex (particularly the fusiform gyrus) has been tied to numerical symbol recognition (e.g., Iuculano et al., 2018). Combined with the fact that a left-lateralized supramarginal gyrus cluster was the only other shared neural correlate across tasks, one interpretation is that the shared representational format (i.e., Arabic digits) requires both visual recognition in the early visual stream and a SMG-supported maintenance of quantity representations in working memory. Moreover, neural activity in the occipital cortex is modulated by the passive viewing of number symbols, indicative of visuospatial attention shifts consistent with leveraging the mental number line (Goffaux et al., 2012).

It is noteworthy that no additional clusters of shared activity were identified, given that previous research in adults (e.g., Franklin and Jonides, 2009) has minimally implicated the left IPS as a shared neural correlate of effortful (i.e., near-distance cardinal and far-distance order) number processing. Such results have not been replicated in 7–10-year-old children (Matejko et al., 2019), suggesting that the left IPS may become increasingly specialized to process numerical order over developmental time (e.g., Sommerauer et al., 2020).

4.2.1. Ordinal number processing

Activity associated with the ordinal task was identified in the cerebellar vermis, bilateral occipital lobe, bilateral inferior and superior parietal lobules (overlapping but not displaying peak clusters in the IPS), left precentral gyrus, and posterior medial-frontal cortex. Notwithstanding the pattern of bilateral parietal and occipital lobe activity, these results resemble adult-level symbolic ordinal number processing regions (Lyons and Beilock, 2013). It should be noted that the current study used a similar experimental paradigm as presented by Lyons and Beilock (2013), regarding both ascending and descending sequences as correct trials.

Mixed-order sequences may be processed in a cardinal rather than ordinal fashion (Matejko et al., 2019), which could explain the additional involvement of the bilateral IPS in the ordinal number task. However, this does not sufficiently explain why bilateral IPS involvement was unique to the ordinal task, given that the putative cardinal processing of mixed-order sequences should also exhibit similar activity in the symbolic cardinal number discrimination task. We propose two explanations. First, given that numerical order processing is a significantly more demanding task than cardinal number discrimination (evidenced by increased response times and decreased accuracy), activation of the central executive network including the IPS (e.g., Bressler and Menon, 2010) may indicate an increased reliance on working memory for the maintenance of sequences as opposed to single digits. This interpretation converges with previous research, as regions generally tied to sequential order processing (e.g., pre-SMA) and those implicated in retrieval from proceduralized count-lists (e.g., precentral gyrus) were jointly active with the IPS (cf. Lyons and Beilock, 2013). Further, the cerebellar vermis has been found to contribute to a working memory circuit tightly coupled with the central executive network (e.g., Seese, 2020; Habas, 2021) and demonstrates increased activity when tasks feature high executive demands (e.g., Küper et al., 2015). However, current results do not indicate whether a substantial increase in central executive demand could mask canonical number processing-elicited activity in the IPS. The second potential explanation concerns the role of the IPS in numerical cognition. It has been suggested that the IPS does not map numerical magnitude to an analog representation system (e.g., ANS), but rather tracks and processes ordinal associations between stimuli (Goffin, 2019). The left anterior IPS has been found to be active across alphabetical ordering, alphabetical short-term memory, and numerical order judgment tasks (Attout et al., 2014), illustrating the ordinal nature of numbers and alphabetical letters as well as their combined activation of the IPS under similar task demands. Hence, the exclusive IPS-adjacent activation for the current numerical order task may reflect the relatively higher salience of numerical ordinality in the triplet format (paired with an explicit order judgment task), masking the ordinal associations that may also occur when only two digits are presented. This may moreover explain the lack of overlap in IPS activity across the cardinal and ordinal tasks, as the cardinal control task (letter case discrimination) features alphabetical stimuli that could also subtract common, ordinality-elicited activity in the region. A previous study from our lab (Skagenholt et al., 2021), using the same letter case discrimination task, found that an "inverse" conjunction contrast (i.e., [Control > Number discrimination tasks]) resulted in bilateral IPS activity across both child and adult participants, possibly indicating a salient ordinal aspect in alphabetical letter stimuli trumping that of number pairs (cf. Previtali et al., 2009). Future research should investigate the role of the IPS in numerical magnitude and order processing, given conflicting findings indicating that letters did not elicit similar responses to numbers despite featuring similar ordinal relationships (Goffin et al., 2020).

4.2.2. Cardinal number processing

Activity elicited by the cardinal number discrimination task was identified in the bilateral insula; right lingual, fusiform, supramarginal (subdivision PFop), postcentral, and inferior frontal (pars Triangularis) gyri; as well as the left superior occipital, middle temporal, and superior frontal gyri. This activity pattern demonstrates a general concordance with previous accounts of a frontoparietal number network (e.g., Fias et al., 2013), barring the involvement of the IPS. It should also be noted that the predominantly temporoparietal pattern of activity has previously been associated with the default mode network, leveraged during basic rule-guided decision-making tasks (e.g., selecting a larger number) as opposed to delayed match-to-sample tasks (e.g., tracking spatial positions of multiple objects) that rather tax the frontoparietal network (Smallwood et al., 2021). This may entail that the lack of IPS activity is indicative of lesser visuospatial working memory demands, rather attributable to ordering and tracking of associations between more than two digits. Cardinal discrimination may sufficiently rely on basic, automatized schema-based ordering cues (e.g., "does 2 come before 3?") supported by the default mode network (e.g., Vatansever et al., 2017).

Although the left supramarginal gyrus was observed to be active across both tasks, in line with previous research indicating the region's importance for mental computation and symbolic number processing (e.g., Grabner et al., 2007; Park et al., 2014), it is interesting that the cardinal task further recruited the right SMG and IFG. While some studies have argued that the right SMG is a correlate of deficient number processing in children (e.g., Kaufmann et al., 2011), a recent meta-analysis (Faye et al., 2019) failed to find a consistent role for the region in numerical cognition. It is likely the case that the region does not contribute directly to number processing per se, but rather indirectly (together with the right IFG and insula) through numerical magnitude manipulation in visuospatial working memory (Menon, 2016). This pattern may therefore be indicative of qualitatively different visuospatial working memory mechanisms for cardinal and ordinal number processing. The ordinal aspect of number requires both domain-general sequence processing (in the pre-SMA; cf. Leek et al., 2016) and linguistically mediated retrieval from count-lists (in the left precentral and supramarginal gyri), together with mental number line mapping in the IPS. The cardinal aspect of number appears to consistently target nodes of the ventral attention network, attributed to bottom-up stimulus-driven attentional shifting as opposed to top-down goal-directed attention to stimulus features (e.g., Corbetta and Shulman, 2002). This interpretation holds weight given prior work in the fMRI adaptation paradigm, finding that number discrimination spontaneously takes place in the presence of numerical stimuli (e.g., Eger et al., 2003; Piazza et al., 2004; Holloway et al., 2013). Furthermore, this interpretation is in line with the distinction between the cardinal item–item comparison mechanism and ordinal associative chaining mechanism (e.g., Lewandowsky and Murdock, 1989). For ordinal number sequences, the stimulus-driven comparison mechanism in number discrimination would have to be extended to account for the inherent serial order of stimuli, directing top-down and goal-directed spatial attention to both the verbal count-list and the visuospatial mental number line. Recent research indicates that spatial attention is involved in serial retrieval from verbal working memory (Rasoulzadeh et al., 2021), with key nodes (e.g., parietal and premotor cortices, frontal eye fields) identified in accordance with the dorsal attention network. We find it plausible that visuospatial position markers, akin to the mental number line, could be deployed to create an integrated mental representation of both presented (i.e., visual number stimuli) and rehearsed (e.g., verbal count-list) numerical information in the IPS, precentral gyrus, and pMFC/pre-SMA (cf. Rasoulzadeh et al., 2021).

In summary, current results are indicative of a shared reliance on visuospatial working memory across the two number processing tasks, in accordance with the existence of a mental number line. However, the way in which this putatively shared neurocognitive process is deployed appears qualitatively different across tasks, where the ordinal aspect of number could be interpreted as requiring an integration of verbal and sequential knowledge in a more top-down, goal-directed fashion aligned with the dorsal attention network and IPS. Conversely, the cardinal aspect of number appears to rather be processed in a stimulus-driven manner (as evidenced primarily by increased reliance on the right SMG, IFG, and insula) consistent with the item–item comparison mechanism automatically elicited by numerical stimuli (e.g., Holloway et al., 2013).

4.3. Distinct prediction performance for ordinal and cardinal numerical cognition

The aim of this analysis was to identify whether task-based whole-brain connectivity profiles could be leveraged to predict outcomes of related cognitive-behavioral measures. Functional connectomes derived from the symbolic ordinal number processing task demonstrated statistically significant predictive abilities for participant age, subtraction fluency scores, and visuospatial working memory capacity. For connectomes derived from the symbolic cardinal number processing task, statistically significant predictions were obtained for visuospatial working memory capacity. These outcomes indicate that connectomes associated with numerical cardinality and ordinality distinctly predict different sets of behavioral outcome variables, save for a common reliance on visuospatial working memory. While the dual-systems model suggests that language constitutes a bridging ability between the two systems, the absence of predictability for reading scores may be due to the typically developing participant sample and the hypothesis that linguistic abilities primarily mediate performance of the quantity and order systems in deficient number processing (Rubinsten and Sury, 2011).

The identified network hubs are by no means exclusively predictive of behavioral outcomes, but rather constitute the five most reliable predictors. It is nevertheless surprising that the IPS, given its prominence in the numerical cognition literature, did not constitute one of these regions. We argue that individual differences in IPS connectivity, at least for this participant sample, may not be sufficiently varied to make the region a reliable predictor of behavioral outcomes over and above the other identified hub regions. A hypothetical interpretation is that the consistency of dorsolateral prefrontal cortex regions (i.e., SFG, MFG), for the predictability of both number processing tasks, could indicate that the degree of cognitive control (cf. Brosnan and Wiegand, 2017) demanded by the two tasks may serve as a more reliable predictor of behavioral performance. This interpretation appears reasonable given participants' near-ceiling accuracy across the number processing tasks, meaning that individual differences in performance are more likely to stem from domain-general factors as opposed to differences in correctly accessing and manipulating numerical quantity in the IPS. A means of testing this hypothesis in future research would be to recruit a more diverse sample, in terms of basic number processing ability, to investigate whether the IPS emerges as a reliable predictor.

4.3.1. Age

The fact that participant age could be successfully predicted during the performance of the ordinal number processing task is interesting for at least two reasons. The participant sample had a small variance in age ($SD = 0.55$ years), meaning that the model could successfully predict differences based on functional network connectivity on the order of months. This outcome aligns well with previous cross-sectional research, finding that ordinal number processing is a stronger predictor of math ability (particularly addition and subtraction) than number discrimination ability between, but not before, grades 5 and 6 (i.e., ages 10–11 to 11–12; Lyons et al., 2014). Seeing as the age-range of the current sample (10.25–12.34 years of age) overlaps with this potentially critical developmental period for ordinal number processing suggests that the model accurately represents an ontogenetically important shift in functional network connectivity. However, future longitudinal research is needed to investigate such developmental hypotheses further.

The top five functional nodes with the highest degrees, whose connectivity patterns can be interpreted as explaining the most amount of variance in support of predictive capacity, were: the right insula, the left cerebellar lobules VI and IX, the left hippocampus, and the right caudate nucleus (see Supplementary Tables 2–5 for an overview of hub node connectivity). Aligning with previous research by Supekar et al. (2013), the identified regions appear more congruent with neural correlates of learning and memory as opposed to canonical number processing areas. Hippocampal–basal ganglia and hippocampal–prefrontal circuits involved in skill development may thus undergo maturation effects (cf. Sussman et al., 2016) that facilitate ordinal number processing. Supekar et al. (2013) also found that functional connectivity of the cerebellum, beyond hippocampal circuits, had significant predictive power for arithmetic performance increases over an eight-week period of math tutoring in approximately 9-year-old children. In short, the effects of participant age differences identified in the ordinal functional connectome could be indicative of a maturation of cognitive flexibility and executive functioning that facilitates associative chaining as opposed to more cognitively taxing item–item comparisons, which in turn facilitates efficient numerical decisions through retrieval as opposed to explicit counting (Cho et al., 2012). This could be of explanatory value to the absence of age-dependent differences for the cardinal functional connectome, given that the task does not afford retrieval-based cues for efficient decision-making beyond the item–item comparison inherent to the task.

4.3.2. *Subtraction fluency*

The model was shown to successfully predict the outcome of subtraction fluency scores based on the functional connectome associated with the symbolic ordinal number processing task, as hypothesized. Notably, subtraction is argued to be the arithmetic operation least reliant on language (in contrast to e.g., multiplication tables) and therefore most clearly associated with numerical magnitude processing (Lee and Kang, 2002). Subtraction and addition operations prompt visuospatial attention shifts not observed for multiplication and division, suggesting their increased reliance on the mental number line (Li et al., 2018). The top 5 hub nodes associated with this predictive capacity were: the left hippocampus, right middle temporal gyrus, left parahippocampal gyrus, caudate nucleus, and temporal pole.

Key nodes predictive of subtraction fluency were observed to be in line with neural correlates of learning and memory. The predictive network consisted of a large number of edges (38 in total from the 5 key nodes), spanning canonical default mode (e.g., thalamus, PPC, temporal pole, IFG, AG); frontoparietal (e.g., right IFG, IPS, SFG); and visual (e.g., fusiform and lingual gyri) network nodes. This suggests that dynamic interactions between retrieval-based neural systems (such as the medial temporal lobe memory system; Menon, 2016) and canonical number processing areas (e.g., IPS, AG) are important for arithmetic abilities. The top nodes identified follow previous research indicative of the "gradual replacement of inefficient procedural strategies with direct retrieval of domain-relevant facts" (Menon, 2016, p. 8), associated with regions such as the hippocampus, parahippocampal gyrus, and medial temporal lobe. This interpretation aligns well with the role of the hippocampus in encoding and maintaining relations among stimulus items (Monti et al., 2015), uniting both arithmetic operations (tracking both numbers and operands) and ordinal number judgment tasks (tracking both numerical values and sequence) to a greater degree than the mere discrimination of two single digits. In this vein, a subset of the current sample was found to operate with near adult-level maturity in symbolic and nonsymbolic numerical discrimination tasks (Skagenholt et al., 2021), which motivates ordinal number processing being exclusively predictive of arithmetic outcomes given its importance for arithmetic development at this ontogenetic timepoint (Lyons et al., 2014).

A limitation of the current study is that only a numerical ordering task was administered in the neuroimaging experiment, meaning that we can only reliably demonstrate an association between connectomes derived from this specific task and behavioral arithmetic ability. Mixed results from prior research suggest, on the one hand, that arithmetic ability is predicted by non-numerical ordering task performance to a similar extent as numerical ordering (e.g., Vos et al., 2017). On the other hand, numerical ordering ability has been shown to independently predict arithmetic ability even after controlling for (domain-general) serial-order working memory ability (Attout and Majerus, 2017). In this vein, neurocognitive data indicates that numerical ordering is processed independently of a domain-general mechanism implicated in serial-order working memory and alphabetical ordering tasks (Attout et al., 2021), which aligns with the finding that CPM could not predict behavioral performance on non-numerical ordering tasks from the numerical order task connectome. Here, we do not attempt to argue for the domain-specificity of numerical ordering and its exclusive contributions to mathematics ability (i.e., a domain-general ordering mechanism could potentially demonstrate similar predictability), but rather demonstrate that numerical ordering appears to leverage mechanisms distinct to those of cardinal number discrimination, that in turn constitute stronger predictors of arithmetic ability. Future research should examine whether neural data gathered from other, non-numerical ordering tasks, is similarly predictive of arithmetic and general cognitive abilities.

4.3.3. *Visuospatial working memory*

As the only behavioral outcome measure successfully predicted by functional connectomes associated with both number processing tasks, the mental number line supported by visuospatial working memory appears to provide a general foundation for numerical magnitude and order processing (e.g., Morsanyi et al., 2017). This shared predictability across tasks is noteworthy due to the importance of visuospatial working memory for numerical and mathematical development (e.g., Ashkenazi et al., 2013; Fanari et al., 2019; Matejko and Ansari, 2021).

Directional differences (i.e., positive and negative associations) observed in the predictive networks is most parsimoniously explained as a result of developmental factors. At the behavioral level, participant age demonstrated a strong negative correlation ($r_s = -0.43$) with cardinal number discrimination response times, indicating that this period in ontogeny is subject to substantial gains in numerical magnitude discrimination ability. While both tasks are contingent on visuospatial working memory, this ontogenetic timepoint could reflect a level of maturity where such abilities are sufficiently developed for number discrimination but not ordering. The functional connectivity associated with number discrimination may therefore leverage visuospatial working memory capacities at near-ceiling levels, whereas identified negative associations are indicative of remaining inefficiencies that remain to be addressed with further maturation. In this vein, it has been argued that visuospatial working memory is employed to a greater extent for more novel numerical skills, such as ordinal number processing for the current age-group, and considerably less so for skills which children have already mastered (e.g., Allen et al., 2019).

5. Conclusions

The current study identified distinct neural correlates and functional connectomes of numerical order and magnitude processing in 10–12-year-old children, motivated by prior research indicating that numerical order overtakes numerical magnitude abilities as the key predictor of arithmetic ability at these ages (Lyons et al., 2014). While the two aspects of numerical cognition appear to minimally share a reliance on domain-general visuospatial working memory abilities, the whole-brain functional connectivity patterns elicited by numerical order processing were additionally predictive of arithmetic ability and participant age. These data are cross-sectional and do not allow strong developmental conclusions, but the ability to predict participant age from functional connectivity elicited by the ordering task may point to significant maturation effects that should be investigated in future longitudinal studies. Although the functional connectomes associated with both tasks were predictive of their respective outcome measures (i.e., behavioral ordinality and cardinality processing tasks), no cross-predictive ability was identified. This outcome suggests that numerical magnitude and order processing build upon dissociable neurocognitive mechanisms and lend further support to the hypothesis that these systems can be separately impaired (e.g., Rubinsten and Sury, 2011). In contrast to univariate analyses, connectome-based predictive modeling revealed large-scale interactions between subcortical, corticostriatal, and cerebellar networks with more neocortical (e.g., frontoparietal) networks canonically linked to numerical cognition. Moreover, regions commonly attributed to calculation, learning, and memory (e.g., hippocampus) as opposed to numerical discrimination abilities were consistently observed as predictive of behavioral outcomes. Identified predictive network hub nodes may constitute valuable biomarkers for future explorations of typically developing mathematical and numerical abilities. Future research should attempt to replicate these results using more appropriate numerical ordering tasks, given that the current study used both near and far-distance triplets in both ascending, descending, and mixed orders within the same task. Recent research indicates the presence of processing differences for different numerical distances, sequence orders, and for consecutive versus non-consecutive numbers (e.g., Dubinkina et al., 2021; Gattas et al., 2021), which may entail the use of different neurocognitive mechanisms. Future research could also fruitfully investigate whether connectomes derived from other ordered sequence tasks (e.g., letters, months, lines) predict behavioral outcomes (e.g., mathematics ability) similarly to numerical ordering, indicating a domain-general order mechanism (cf. Vos et al., 2017), or if numerical order depends on a more domain-specific cognitive mechanism (cf. Attout et al., 2021). To encourage future external validation, all connectome-based predictive modeling data have been made available at the Open Science Framework (https://osf.io/b8ax9/?view_only=4d1022e55e2841cb8ecb2c8da7c1bbc8).

Author contributions

Mikael Skagenholt: Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Data curation, Writing – Original draft, Writing – Review & Editing, Visualization. **Ian M. Lyons:** Writing – Review & Editing. **Kenny Skagerlund:** Conceptualization, Methodology, Validation, Investigation, Resources, Writing – Review & editing, Supervision, Project administration, Funding acquisition. **Ulf Träff:** Conceptualization, Methodology, Validation, Investigation, Resources, Writing – Review & editing, Supervision, Project administration, Funding acquisition.

Data availability

All relevant data for external validation can be found at the Open Science Framework: https://osf.io/b8ax9/?view_only=4d1022e55e2841cb8ecb2c8da7c1bbc8

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Appendix A. Supplementary data

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