

Neural Representations of Absolute and Relative Magnitudes in Symbolic and Nonsymbolic Formats

Parnika Bhatia ^{*}, Léa Longo, Hanna Chesnokova, Jérôme Prado^{*}

Lyon Neuroscience Research Center (CRNL), INSERM U1028 - CNRS UMR5292, University of Lyon, 69500 Bron, France

Address correspondence to Parnika Bhatia or Jérôme Prado, CRNL, 95 bd Pinel, 69675 Bron cedex, France. Email: parnika.bhatia@etu.univ-lyon1.fr (P.B.);

jerome.prado@univ-lyon1.fr (J.P.)

Humans differ from other animal species in their unique ability to use symbols to represent numerical information. This ability is thought to emerge from the “neural recycling” of mechanisms supporting nonsymbolic magnitudes in the intraparietal sulcus (IPS), a hypothesis that has been applied to both absolute magnitudes (e.g., whole numbers) and relative magnitudes (e.g., fractions). Yet, evidence for the neuronal recycling hypothesis is inconsistent for absolute magnitudes and scarce for relative magnitudes. Here, we investigated to what extent the neural representations of absolute and relative magnitudes in symbolic and nonsymbolic formats overlap in the IPS. In a functional magnetic resonance imaging (fMRI) adaptation design, 48 adult participants were sequentially presented with lines, whole numbers, line ratios, and fractions that varied (vs. not varied) in magnitudes. Univariate analyses showed that the extent to which IPS mechanisms associated with whole numbers relied on mechanisms associated with lines depended upon participants’ arithmetic fluency. Multivariate analyses revealed that the right IPS encoded differences in format (nonsymbolic vs. symbolic) across both absolute and relative magnitudes. Therefore, IPS activity associated with magnitude processing may depend on the presentation format (nonsymbolic vs. symbolic) more than it depends on the type of magnitude (absolute vs. relative), at least for most adult participants.

Key words: fMRI; fractions; intraparietal; math cognition; numbers.

Introduction

Humans possess the ability to represent magnitudes both nonsymbolically (e.g., ●●) and symbolically (e.g., two or 2). This ability is both shared and unique among other animals. On the one hand, infants and many animal species can estimate and discriminate nonsymbolic absolute magnitudes, suggesting that the human brain may be endowed with a nonsymbolic approximate number system (ANS) that is innate and evolutionarily old (Boysen and Capaldi 1993; Dehaene et al. 1998; Pica et al. 2004; Brannon 2005; Xu et al. 2005). On the other hand, the ability to represent absolute magnitudes as symbolic natural numbers is only found in humans and is largely believed to be a product of culture and language (Ansari 2008). Yet, it has long been proposed that this culturally developed ability is grounded in the evolutionarily old capacity to process nonsymbolic magnitudes (Dehaene et al. 2003; Ansari 2008). For instance, the “neural recycling” hypothesis argues that learning symbolic natural numbers relies on the co-option of brain mechanisms supporting nonsymbolic magnitude processing, which are largely thought to be located in the intraparietal sulcus (IPS) (Nieder 2016). In other words, it has been claimed that the same mechanisms of the IPS may represent both

nonsymbolic and symbolic magnitudes at an abstract level in adults (Dehaene and Cohen 2007) such that symbolic natural numbers may automatically activate the neural representations of absolute magnitudes in that region (Eger et al. 2003).

Symbolic mathematical skills, however, go largely beyond the ability to represent absolute magnitudes in humans. They also involve the ability to represent magnitudes in relation with one another, for instance, using fractions or decimals (i.e., rational numbers). Although the neuronal recycling theory was initially developed in the context of natural numbers, a similar proposal has recently emerged to explain the cultural acquisition of symbolic rational numbers (Lewis et al. 2015). Indeed, a growing body of evidence shows that infants and nonhuman primates are sensitive to ratios and relational quantities (Woodruff and Premack 1981; McCrink and Wynn 2007; Vallentin and Nieder 2008, 2010; Denison and Xu 2014; Drucker et al. 2016; Eckert et al. 2018; Tecwyn et al. 2017). This suggests the existence of an evolutionarily old nonsymbolic ratio processing system (RPS) akin to the ANS but tuned exclusively to relative quantities (Lewis et al. 2015). This cognitive system might provide the foundation for the acquisition of symbolic rational numbers (Lewis et al. 2015). Though the neural

basis of this RPS is less clear than that of the ANS, this line of thought suggests that overlapping brain regions may represent both nonsymbolic and symbolic ratios abstractly. In other words, symbolic rational numbers may automatically activate the neural representations of relative magnitudes.

To date, evidence that the acquisition of either natural or rational numbers relies on the recycling of brain pathways dedicated to the processing of nonsymbolic magnitudes remains equivocal. Overall, neuroimaging studies focusing on the processing of natural numbers have consistently found involvement of the IPS in both symbolic (Arabic digits or number words) and nonsymbolic (dot patterns) tasks (Nieder 2016; Sokolowski et al. 2017). However, studies that directly compared the neural substrates of symbolic and nonsymbolic natural number processing within the same participants show inconsistent results (Cohen Kadosh et al. 2007; Piazza et al. 2007; Eger et al. 2009; Cohen Kadosh et al. 2011; Damarla and Just 2013; Bulthé et al. 2014). For instance, in a seminal study using fMRI adaptation, Piazza et al. (2007) found that Arabic digits and dot patterns were represented in the same region of the IPS, thus supporting the neuronal recycling hypothesis. Some studies using multivariate analysis have also shown some degree of overlap between the brain mechanisms supporting symbolic and nonsymbolic magnitude processing (Eger et al. 2009). However, other studies concluded that Arabic numerals and dot patterns are supported by different neural populations in the IPS and surrounding brain regions (Cohen Kadosh et al. 2007; Cohen Kadosh et al. 2011; Bulthé et al. 2014). Overall, neuroimaging evidence is inconsistent regarding whether a natural number is represented abstractly or in a format-dependent manner in the human brain (Damarla and Just 2013; Ansari 2016; Wilkey and Ansari 2019).

Compared with the neuroimaging literature on the representations of natural numbers, few studies have investigated the neural representations and processing of rational numbers. Therefore, support for the idea that the neural substrates of the RPS may be “recycled” for the processing of symbolic fractions is scarce (Lewis et al. 2015; Mock et al. 2018). Nonetheless, the available studies suggest that the IPS is involved in the processing of both symbolic fractions (Ischebeck et al. 2009; Jacob and Nieder 2009b; DeWolf et al. 2016) and nonsymbolic line ratios (Jacob and Nieder 2009a) in adults. To the best of our knowledge, there is only one study comparing the neural bases of symbolic and nonsymbolic relative magnitude processing within the same participants (Mock et al. 2018, 2019). In that study, fMRI activity was measured while adult participants performed a magnitude comparison task in four formats, namely, fractions, dot patterns, decimals, and pie charts (Mock et al. 2018). Results point to not only overlapping activation between symbolic (e.g., fractions and decimals) and nonsymbolic (e.g., dot patterns and pie charts) proportions in the IPS but also to format-dependent activity in other brain

regions. To some extent, the format-independent activity found in the IPS supports the idea that there might be an abstract representation of relative magnitudes in the human brain. However, because this study used active tasks, it is unclear whether any overlapping neural activation is due to common processing of relative magnitudes or to a common reliance on response selection processes that also rely on the IPS (Göbel et al. 2004).

Here, we aimed to test whether the culturally developed ability to represent both absolute and relative magnitudes symbolically (e.g., using natural numbers and fractions) relies on the neural representations of absolute and relative magnitudes in a nonsymbolic format. Toward this aim, we adapted a passive blocked fMRI adaptation paradigm used in Girard et al. 2021 and Perachione et al. 2016 to investigate the neural representations of absolute and relative magnitudes in different formats while avoiding confounds due to active tasks. fMRI adaptation refers to the idea that repeatedly presenting a series of visual stimuli with a common property leads to a decrease in the activity of neurons that are sensitive to that property (Grill-Spector and Malach 2001). This sensitivity is captured by the “neural adaptation effect,” measured by comparing blocks of stimuli that differ from one another with respect to the property (i.e., no-adaptation blocks) to blocks of stimuli that do not (i.e., adaptation blocks). In the present study, participants were presented with adaptation and no-adaptation blocks of 1) nonsymbolic absolute magnitudes (lines), 2) symbolic absolute magnitudes (numbers), 3) nonsymbolic relative magnitudes (line ratios), and 4) symbolic relative magnitudes (fractions) (Fig. 1). Adaptation and no-adaptation blocks differed with respect to the numerical distance separating lines, numbers, line ratios, or fractions within a block such that stimuli were close in magnitude from one another in adaptation blocks and further apart in no-adaptation blocks.

We tested the neuronal recycling hypothesis of absolute and relative magnitudes using both univariate and multivariate methods. First, using univariate analyses, we aimed to identify the neural regions that may be sensitive to a change in numerical distance between stimuli across all participants, either with respect to their absolute magnitude (for lines and numbers) or relative magnitude (for line ratios and fractions). This should translate into a decrease of activity in adaptation compared to no-adaptation blocks in these regions (i.e., a neural adaptation effect). The neuronal recycling hypothesis assumes that processing symbolic stimuli (i.e., numbers and fractions) relies on neural mechanisms supporting nonsymbolic stimuli (i.e., lines and ratios). Thus, this hypothesis predicts that overlapping regions of the IPS may be associated with a neural adaptation effect for 1) numbers and lines and 2) fractions and ratios. Second, using multivariate analyses, we aimed to explore the relations between the patterns of activation associated with symbolic and nonsymbolic stimuli across magnitude types. Specifically, because the neuronal recycling

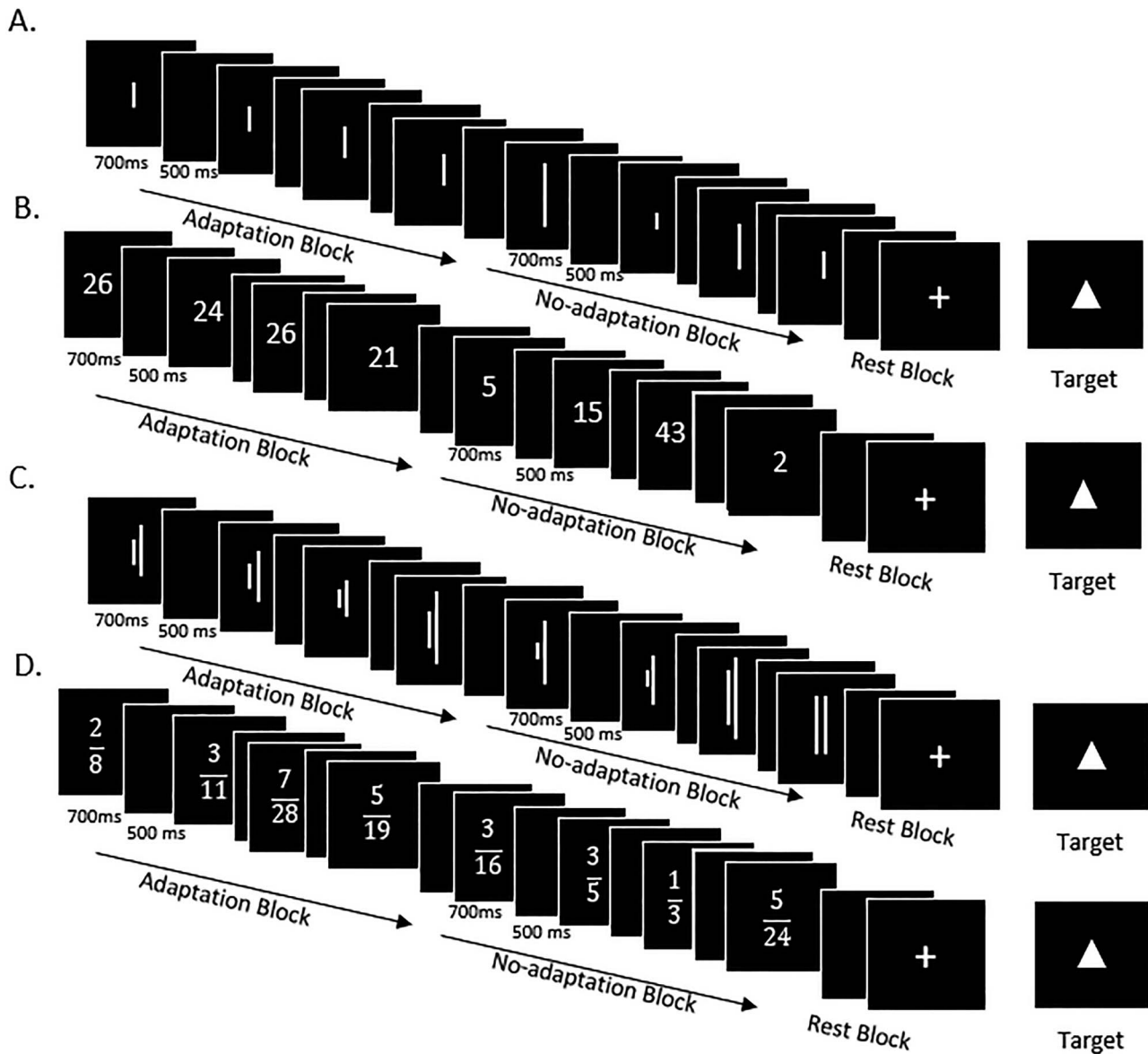


Figure 1. Experimental design. Participants were adapted to the sequential presentation of four types of stimuli that varied in format (nonsymbolic vs. symbolic) and magnitude type (absolute vs. relative): (A) adaptation to lines, (B) adaptation to numbers, (C) adaptation to line ratios, and (D) adaptation to fractions.

hypothesis assumes that similar IPS mechanisms process symbolic and nonsymbolic stimuli, it predicts that patterns of IPS activity may be similar between symbolic and nonsymbolic stimuli and are more likely to depend on the type of numerical magnitude (i.e., absolute vs. relative).

Material and Methods

Participants

Fifty-three right-handed adults participated in the experiment. Participants were mainly recruited through generic advertisements on social media (i.e., Facebook), mainly targeting university students in the Lyon area in France. Some participants were also recruited from prior studies at the imaging center at CERMEP. Five participants were excluded from the study because of

technical errors in the experimentation set-up ($n=4$) and contraindications to the MRI ($n=1$). Therefore, 48 adults (Mean age = 22.09, 34 female) were included in the main analyses. All participants were right handed and native French speakers with no history of neurological or psychiatric disorders. Participants gave written informed consent and were paid 80 euros for their participation. The study was approved by a national ethics committee (CPP- Strasbourg Est IV).

Psychometric Testing

Verbal intelligence quotient (IQ) and spatial IQ were estimated using the verbal reasoning and matrix reasoning subtest of WAIS-IV (Wechsler, 2008). Fluency in symbolic math was assessed using the Math Fluency section of the Woodcock-Johnson Test of Achievement (WJ-III) (Woodcock et al. 2001). In this test, participants have

to solve as many single-digit addition, subtraction, multiplication, and division problems as they can within 3 min. Participants also completed the Applied Problems subtest of the WJ-III. Unlike the Math Fluency subtest, this test is untimed and measures the ability to analyze basic numerical concepts and oral word problems. The test stops after six consecutive errors or when the last item is reached. To exclude participants with reading disabilities, their reading fluency was assessed with the Alouette-R test (Lefavrais 2005). This test requires participants to read a 265-word text aloud in 3 min and measures the number of words read correctly to evaluate the reading precision and speed. No other tests than those mentioned here were administered to the participants.

In-Scanner Task

Participants were presented with a passive blocked adaptation paradigm adapted from Girard et al. (2021) and Perrachione et al. (2016). In this paradigm, participants are passively presented with blocks of stimuli at the center of the screen. Here we presented four types of stimuli in four different runs of approximately 5 min: lines, numbers, line ratios, and fractions (Fig. 1). Numbers ranged from 1 to 62 ($\sim 1.72^\circ$ of visual angle), fractions ranged from $1/24$ to ~ 1 in magnitude ($\sim 3.45^\circ$ of visual angle), and lines ranged from 0.98 to 17.8 cm in length on a 37 cm screen (corresponded between ~ 0.69 and 12.24° of visual angle). All stimuli were shown in white on a black background. Within each run, participants were presented with adaptation and no-adaptation blocks (Fig. 1). Adaptation and no-adaptation blocks differed with respect to the numerical distance between the stimuli. Specifically, adaptation blocks consisted in the sequential presentation of eight quantities in a total of which four quantities were the same in magnitude and the other four quantities were relatively close. For instance, in the number adaptation block of 23, 26, 25, 26, 24, 26, 21, 26, four stimuli (e.g., 26) are identical and the other four stimuli have a minimum distance of 1 and a maximum distance of 5 between each other. Similarly, for fractions, adaptation to $1:4$ was composed of four exact equivalent fractions $2/8$, $1/4$, $4/16$, $7/28$ and the rest of the stimuli had the denominator changed by adding or subtracting 1 to the original fractions (i.e., $3/11$, $5/19$, $8/31$, $6/23$). Half of the stimuli for the adaptation block of fractions were constructed by small changes to the denominator (+1 or -1) to prevent the participant from reducing the fraction to its lowest form, thereby avoiding confounds due to calculation. No-adaptation blocks consisted in the sequential presentation of eight quantities that were relatively far from one another in magnitude (e.g., a minimum distance of 2 and a maximum distance of 55 between consecutive numbers in a block, and minimum magnitude of $1/24$ to maximum magnitude of $11/12$ for a block of fractions). The size of the individual line lengths and line ratios corresponded to those used for numbers and fractions. So, for line ratios, the length of the smaller line was calculated as the ratio of the longer

line length such that a fraction corresponding to $3/15$ would be a line ratio where the smaller line length is $3/15$ as long as the longer line length. Thus, the absolute line lengths did not vary with proportion. The shorter line was always on the left (i.e., corresponding to the numerator of a proper fraction) whereas the longer line was always on the right (i.e., corresponding to the denominator of a proper fraction). The complete list of stimuli can be found in Supplementary Table 1.

Experimental Timeline

In each adaptation and no-adaptation block, stimuli remained on the screen for 700 ms, with a 500 ms interstimulus interval (for a total block duration of 9.6 s). Ten adaptation blocks and 10 no-adaptation blocks were presented along with 10 blocks of visual fixation (duration = 9.6 s) in each run. Block presentation was pseudo-randomized such that two blocks of the same type could not follow each other. Participants were instructed to passively observe the stimuli in the scanner. However, 10 target stimuli (a triangle) randomly appeared in each run (outside of the blocks). Participants were asked to press a button every time this target appeared. This allowed us to ensure that participants paid attention to the stimuli. The task was presented using Psychopy (Peirce et al. 2019).

fMRI Data Acquisition

Images were collected with a Siemens Prisma 3 T MRI scanner (Siemens Healthcare, Erlangen, Germany) at the CERMEP Imagerie du vivant in Lyon, France. The blood oxygen level-dependent (BOLD) signal was measured with a susceptibility-weighted, single-shot echo planar imaging (EPI) sequence. Imaging parameters were as follows: TR = 2000 ms, TE = 24 ms, flip angle = 80° , matrix size = 128×120 , field of view = 220×206 mm, slice thickness = 3 mm (0.48 mm gap), number of slices = 32. A high-resolution T1-weighted whole-brain anatomical volume was also collected for each participant. Parameters were as follows: TR = 3500 ms, TE = 2.24 ms, flip angle = 8° , matrix size = 256×256 , field of view = 224×224 mm, slice thickness = 0.9 mm, number of slices = 192.

fMRI Data Preprocessing

fMRI data analysis was performed using SPM12 (<http://www.fil.ion.ucl.ac.uk/spm>, Wellcome Department of Cognitive Neurology). The first three images of each run were discarded to allow for T1 equilibration effects. Functional images were corrected for slice acquisition delays and spatially realigned to the first image of the first run to correct for head movements. Realigned images were smoothed with a Gaussian filter equal to twice the voxel size ($4 \times 4 \times 7$ mm full-width at half maximum). Using ArtRepair (https://www.nitrc.org/projects/art_repair/), functional volumes with a global mean intensity greater than three standard

deviations from the average of the run or a volume-to-volume motion greater than 2 mm were identified as outliers and substituted by the interpolation of the two nearest nonrepaired volumes (Romeo et al. 2018). Finally, functional images were normalized into the standard Montreal Neurological Institute (MNI) space. This was done in two steps. First, after coregistration with the functional data, the structural image was segmented into gray matter, white matter, and cerebrospinal fluid by a unified segmentation algorithm (Ashburner and Friston 2005). Second, the functional data were normalized to the MNI space by the normalization parameters estimated during unified segmentation (normalized voxel size, $2 \times 2 \times 3.5 \text{ mm}^3$).

Univariate Analyses

For each participant and each run, a general linear model analysis was conducted on brain activity associated with adaptation and no-adaptation blocks. Blocks were modeled as epochs with onsets time-locked to the beginning of each block and a duration of 9.6 s per block. All epochs were convolved with a canonical hemodynamic response function. The time-series data were high-pass filtered (1/128 Hz), and serial correlations were corrected using an auto-regressive AR (1) model. The neural adaptation effect was measured by subtracting activity associated with adaptation blocks from activity associated with no-adaptation blocks. These subject-specific contrasts were then submitted to the second level for group-level random effect analyses. Clusters were considered significant at a family-wise error (FWE)-corrected threshold of $P < 0.05$ (using a cluster-defining threshold of $P < 0.005$, uncorrected).

Multivariate Analyses

In addition to the main univariate analysis, we also used the CosmoMVPA toolbox (<https://www.cosmomvpa.org/>) to perform a representation similarity analysis (RSA) assessing the similarity and dissimilarity of neural activation patterns associated with different magnitude types (absolute vs. relative) and presentation formats (symbolic vs. nonsymbolic). This analysis was conducted on the four beta maps corresponding to the contrasts of lines versus fixation, numbers versus fixation, line ratios versus fixation, and fractions versus fixation (collapsing across adaptation and no-adaptation blocks). First, we created two 4×4 theoretical representation dissimilarity matrices (RDMs) corresponding to 1) the expected dissimilarity between absolute and relative magnitudes (and expected similarity between symbolic and nonsymbolic stimuli) and 2) the expected dissimilarity between symbolic and nonsymbolic stimuli (and expected similarity between absolute and relative magnitudes). In the absolute versus relative RDM (see Fig. 4A), all stimuli of the same magnitude type (numbers–numbers, numbers–lines, fractions–fractions, and fractions–line ratios) had a dissimilarity coefficient of 0 whereas all stimuli of a different magnitude type

(numbers–fractions, numbers–line ratios, fractions–lines, and lines–line ratios) had a dissimilarity coefficient of 1. In the symbolic versus nonsymbolic RDM (see Fig. 5A), all stimuli of the same format (numbers–numbers, numbers–fractions, lines–lines, and lines–line ratios) had a dissimilarity coefficient of 0, whereas all stimuli of a different format (numbers–lines, numbers–line ratios, lines–fractions, and line ratios–fractions) had a dissimilarity coefficient of 1. Second, we extracted brain activity from the four contrasts (i.e., lines vs. fixation, numbers vs. fixation, line ratios vs. fixation, and fractions vs. fixation) using spherical searchlights (1.4 cc, i.e., 100 voxels) at every voxel in the brain. A 4×4 neural RDM was constructed for each searchlight, in which each cell represented 1 minus the Pearson correlation between the voxel-wise beta value for each pair of contrasts. The Pearson correlation between the neural RDM and each theoretical RDM was then calculated for each searchlight and converted to a Z value using a Fisher transform. The Fisher-transformed correlation coefficient for each searchlight was systematically associated with the central voxel of that searchlight. Fisher-transformed correlation maps were then submitted to second-level one-sample t-tests across all participants to identify voxels for which the correlation between the theoretical and neural DSMs was greater than 0. Clusters were considered significant at a FWE-corrected threshold of $P < 0.05$ (using a cluster-defining threshold of $P < 0.005$, uncorrected).

Data and Software Availability

The task as well as all individual behavioral and MRI data are publicly available via Zenodo at <http://doi.org/10.5281/zenodo.5566914>. The general and custom scripts used to analyze fMRI data are available at <https://github.com/BBL-lab/BBL-batch-system>. The software used to overlay functional images on brain anatomy (HiBoP) is available at <https://github.com/hbp-HiBoP/HiBoP>.

Results

Psychometric Testing and In-Scanner Performance

Standardized verbal IQ ranged from 85 to 140 (mean = 117.29), while standardized spatial IQ ranged from 70 to 120 (mean = 94.68). Thus, participants' IQ was in the normal to the superior range. The number of arithmetic problems correctly solved in 3 min in the Math Fluency subtest ranged from 47 to 160 (mean = 114.25), suggesting a substantial variability in arithmetic fluency among participants. The untimed Applied problems subtest indicated less variability, with scores ranging from 39 to 61 (mean = 49.06). Finally, participants' reading precision scores ranged from 90.18 to 100 (mean = 98.28), and reading speed ranged from 336.69 to 787.11 (mean = 551.198)—the optimal cut-off for dyslexia

Table 1. Brain regions showing an effect of neural adaptation across all participants (univariate analyses)

Anatomical location	Cluster level $P_{FWE-corrected}$	Cluster size (cc)	MNI coordinates			t-score
			x	y	z	
Line adaptation task						
L. inferior occipital gyrus	0.000	28.55	-32	-90	-4	5.89
L. intraparietal sulcus	—	—	-34	-50	51	3.33
R. inferior occipital gyrus	0.000	21.01	40	-84	-12	5.48
R. intraparietal sulcus	—	—	30	-58	55	3.99
R. thalamus	0.019	2.13	10	-16	13	5.44
R. supplementary motor area	0.000	6.27	2	12	66	5.16
R. hippocampus	0.004	2.74	22	-20	-12	4.81
L. caudate	0.026	2.0	-14	-2	13	4.37
R. precentral gyrus	0.033	1.9	-44	4	52	4.33
R. precentral gyrus	0.003	2.85	54	-2	44	4.31
L. posterior cingulate	0.025	2.01	-6	-42	16	4.31
Number adaptation task						
L. occipital fusiform gyrus	0.004	2.81	-26	-90	-12	4.46
Line ratio adaptation task						
No suprathreshold cluster						
Fraction adaptation task						
No suprathreshold cluster						

Note: L: left; R: right; MNI: Montreal Neurological Institute; FWE-corr: Family-wise error corrected.

is a reading precision score above 87 or reading speed above 402.26 (Cavalli et al. 2018).

To make sure participants were attentive to the stimuli in the scanner, a target detection task was inserted in all four tasks. Participants had to press a button when they saw a triangle during the task. Average performance on detection of the target for the different runs was 95.3% (SD = 0.152) for fraction, 92.7% (SD = 0.186) for numbers, 91.4% (SD = 0.208) for line ratios, and 92.4% (SD = 0.194) for lines. There was no difference in target detection between the four tasks (all $t < 1.9$, all $P > 0.06$) indicating that participants paid equal attention to the stimuli in the tasks. The response to target stimuli was not correlated with math fluency and applied problem skills (all $r > -0.24$, all $P > 0.10$).

Univariate Analyses

For each stimulus type (lines, numbers, line ratios, and fractions), brain activity associated with adaptation blocks was subtracted from activity associated with no-adaptation blocks to identify brain regions showing a neural adaptation effect across all participants. For lines, a neural adaptation effect was observed in the bilateral IPS as well as in a wider network of brain regions encompassing the precentral and occipital cortices (see Table 1 and Fig. 2A). For numbers, the only region showing a significant neural adaptation effect was located in the left fusiform gyrus (see Table 1 and Fig. 2B). No significant adaptation effect was observed in any brain region for either fractions or line ratios.

Contrary to our assumptions, lines were the only stimuli associated with a significant neural adaptation effect in the IPS across all participants. Therefore, we did not find any evidence that common neural mechanisms in the IPS may process both symbolic and nonsymbolic stimuli. However, there was relatively large variability

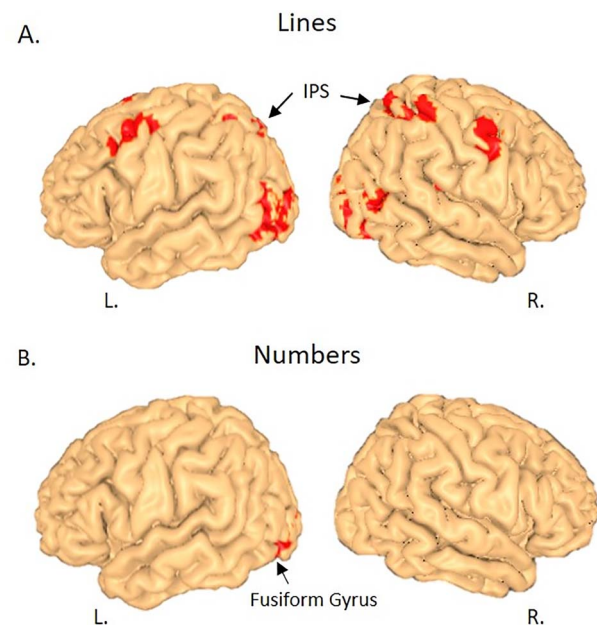


Figure 2. Neural adaptation effects across all participants (univariate analyses): (A) brain regions showing a neural adaptation effect for lines and (B) brain regions showing a neural adaptation effect for numbers.

in participants' fluency with symbolic math (as suggested by the Math Fluency subtest, see above). It is thus possible that the neural adaptation effect for symbolic stimuli may depend on participants' levels of fluency. This is consistent with the results of our previous study using a similar paradigm in which we found a positive correlation between neural adaptation to numbers and math fluency scores (Girard et al. 2021). In other words, because our paradigm is passive, magnitudes of symbolic stimuli such as numbers and fractions may only be automatically processed by the most fluent participants.

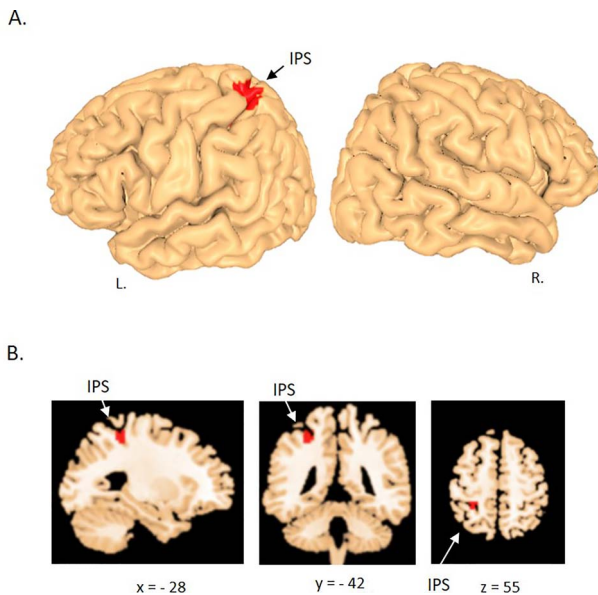


Figure 3. Relation between arithmetic fluency and neural adaptation effects (univariate analyses): (A) brain region showing a positive relation between arithmetic fluency and neural adaptation effect for numbers and (B) brain region showing both a positive relation between arithmetic fluency and neural adaptation effect for numbers and a neural adaptation effect for lines across all participants (conjunction analysis).

To examine this possibility, we regressed neural adaptation effects on participants' math fluency scores across the whole brain. We did not find any positive relation between math fluency and neural adaptation effect for fractions, lines, or line ratios. For numbers, however, the neural adaptation effect increased with math fluency in a region of the left IPS (see Fig. 3A). Critically, a conjunction analysis revealed that this region overlapped with the region showing an overall neural adaptation effect across all participants for lines (center of mass: $x = -28$, $y = -42$, $z = 55$, the volume of overlap = 70 mm^3) (see Fig. 3B). Thus, increased math fluency was linked to an enhanced neural adaptation effect for numbers in the same left IPS region that exhibited a neural adaptation effect across all participants for lines.

Multivariate Analyses

As described above, the univariate analyses only provided limited evidence for common brain mechanisms in the IPS processing nonsymbolic and symbolic magnitudes. We then turned to multivariate analyses (RSA) to test whether patterns of IPS activity may depend on the type of numerical magnitude (and be similar between nonsymbolic and symbolic stimuli) or on the presentation format (and be similar between absolute and relative magnitudes). This was done by evaluating the degree of (1) dissimilarity between patterns of activation associated with absolute and relative magnitudes (and similarity between nonsymbolic and symbolic stimuli) (see Figs 2 and 4A) dissimilarity between patterns of activation associated with symbolic and nonsymbolic stimuli (and similarity between absolute and relative magnitudes) (see Fig. 5A). On the one hand, as shown

in Figure 4B and Table 2, a limited brain system distinguished between absolute and relative magnitudes while representing similarly nonsymbolic and symbolic magnitudes. This system was composed of the right occipital cortex and left rostro-lateral prefrontal cortex. Critically, this system did not include the IPS. On the other hand, as shown in Figure 5B and Table 2, a larger brain system distinguished between symbolic and nonsymbolic format while representing similarly absolute and relative magnitudes. This system encompassed the bilateral occipital and middle temporal cortices, but also included the right IPS. Overall, these results suggest that patterns of IPS activity depend on the presentation format (nonsymbolic vs. symbolic) more so than they depend on the type of magnitudes (absolute vs. relative).

Discussion

In the present study, we used univariate and multivariate analyses to test the neuronal recycling hypothesis of absolute and relative magnitudes. Participants passively attended to numerical stimuli in the scanner, presented as symbolic fractions, nonsymbolic line ratios, symbolic numbers, and nonsymbolic lines. Each of these stimuli was presented in adaptation and no-adaptation blocks, wherein the numerical quantity presented was near and far in magnitude (respectively). In the following, we will first discuss the result of the univariate analyses (comparing the difference in activity between no-adaptation and adaptation blocks, or neural adaptation effect, for the four stimuli). We will then discuss the findings of multivariate analyses.

Univariate Analyses Provide Limited Evidence for Neuronal Recycling of Absolute Magnitudes

In line with the neuronal recycling hypothesis of both absolute and relative magnitudes, we predicted that symbolic and nonsymbolic magnitudes would rely on overlapping brain mechanisms in the IPS. This would have translated into neural adaptation effects in similar regions of the IPS for symbolic and nonsymbolic magnitudes, thus suggesting an abstract representation of magnitudes in the IPS. Across all participants, we found a neural adaptation effect for nonsymbolic absolute magnitudes (i.e., lines) in a relatively wide network of brain areas encompassing the bilateral IPS, the occipital, the supplementary motor area, and the precentral cortices. These results (particularly concerning the recruitment of occipitoparietal areas) are in line with prior passive viewing paradigms investigating the representation of nonsymbolic absolute magnitudes (Pinel et al. 2004; Ansari and Dhital 2006; Roggeman et al. 2011; Demeyere et al. 2014). In fact, a recent meta-analysis revealed that nonsymbolic magnitude processing was associated with consistent activations in the bilateral parietal cortex and occipital gyri across studies (Sokolowski et al. 2017). A recent study using a magnitude comparison task involving both dot patterns and lines of different

A. Absolute versus Relative Model



B.

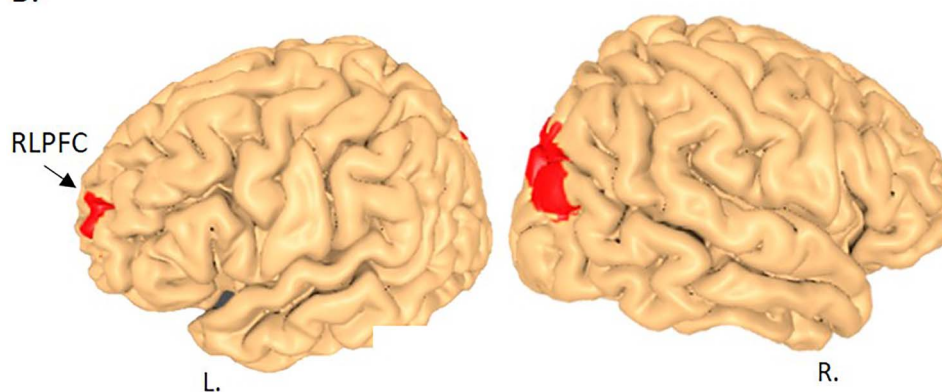


Figure 4. Results of the representational similarity analysis for the absolute versus relative model (multivariate analysis). (A) Hypothesized model for the RSA, the matrix represents a dissimilarity matrix where red denotes dissimilar items (0) and yellow denotes similar items (1). (B) Brain regions representing differently absolute and relative magnitudes while representing similarly nonsymbolic and symbolic magnitudes.

Table 2. Brain regions identified in representational similarity analysis (multivariate analyses)

Anatomical location	Cluster level $P_{FWE-corrected}$	Cluster size (cc)	MNI coordinates			t-score
			x	y	z	
Symbolic versus nonsymbolic						
L. inferior occipital gyrus	0.00	91.44	-34	-84	-4	8.18
L. supramarginal gyrus	0.012	1.51	-50	-38	34	4.76
L. postcentral gyrus	0.00	4.11	-30	-30	66	4.72
R. superior parietal lobule	0.00	7.91	26	-46	58	4.60
R. intraparietal sulcus	—	—	30	-58	55	2.75
Absolute versus relative						
L. superior occipital gyrus	0.00	3.09	-10	-90	27	4.74
L. lingual gyrus	0.009	1.61	-28	-62	-1	4.36
L. superior frontal gyrus	0.046	1.21	-24	60	13	3.74
L. middle frontal gyrus	—	—	-28	48	13	3.74
R. middle occipital gyrus	0.00	7.15	38	-84	20	5.29

Note: L: left; R: right; MNI: Montreal Neurological Institute; FWE-corr: Family-wise error corrected.

lengths also revealed overlapping activations for these conditions in the bilateral parietal and occipital cortices (Borghesani et al. 2019). Overall, the fact that the IPS exhibits a neural adaptation effect for lines in our study is consistent with a long line of studies pointing to the IPS as a major locus for the representation of nonsymbolic absolute magnitudes in the human brain (Nieder 2016).

In contrast to our predictions, however, we failed to find any neural adaptation effect for symbolic absolute magnitudes (i.e., numbers) in the IPS. Instead, a neural adaptation effect was found in the left fusiform gyrus, which may reflect the visual processing of numerals (e.g., Holloway et al. 2013). Indeed, it has long been posited that there may exist dedicated neural mechanisms for

A. Symbolic versus Non-symbolic Model

	Number	Line	Fraction	Line Ratio
Number	Yellow	Red	Yellow	Red
Line	Red	Yellow	Red	Yellow
Fraction	Yellow	Red	Yellow	Red
Line Ratio	Red	Yellow	Red	Yellow

B.

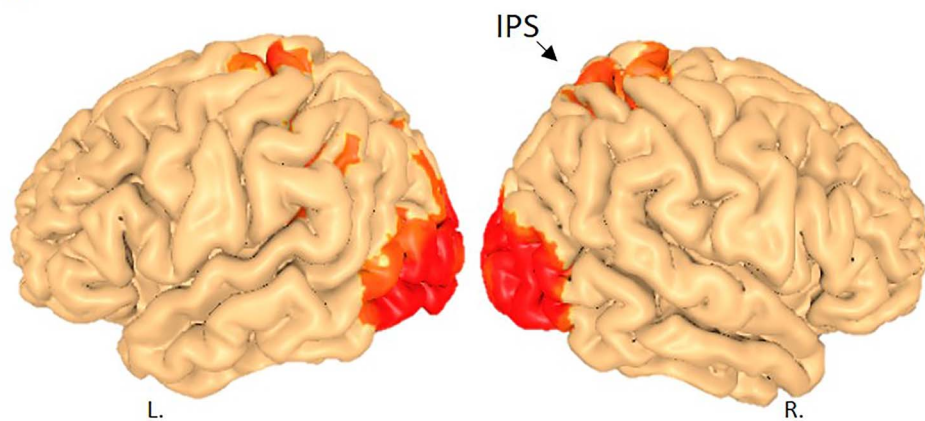


Figure 5. Results of the representational similarity analysis for the symbolic versus nonsymbolic model (multivariate analysis). (A) Hypothesized model for the RSA, the matrix represents a dissimilarity matrix where red denotes dissimilar items (0) and yellow denotes similar items (1). (B) Brain regions representing differently nonsymbolic and symbolic magnitudes while representing similarly absolute and relative magnitudes.

processing the visual aspect of symbolic numbers. For example, the Triple Code Model assumes that number processing involves a wide network of specialized neural regions associated with the semantic and analog but also visual properties of numbers (Dehaene 1992). In line with this proposal, recent studies suggest that the fusiform gyrus may house a “number form area,” which might be responsible for the visual recognition of Arabic numerals (Amalric and Dehaene 2016; Grotheer et al. 2016; Yeo et al. 2017; Vatansever et al. 2020). Our findings might add to this body of evidence suggesting an automatic activation of the fusiform gyrus in response to the passive presentation of Arabic numerals in adults.

The lack of IPS activation, however, is in contrast to the majority of literature on the role of left-lateralized IPS in the development of symbolic magnitude processing (Vogel et al. 2015). It is important to note that, in contrast to most previous studies, our adaptation paradigm is passive and therefore captures an automatic representation of numerical magnitude from the viewing of symbolic stimuli. This is critical because the IPS is also involved in response selection (Göbel et al. 2004; Cappelletti et al. 2010). Previous studies using active tasks (e.g., number

comparison tasks, in which participants select the largest number; Ansari et al. 2005; Cohen Kadosh et al. 2005; Lyons and Ansari 2009; Holloway and Ansari 2010) may have thus confounded magnitude-related activity in the IPS with response demands. In other words, access to magnitudes from symbolic stimuli may not be as automatic as often argued. In fact, our study provides some evidence that this access may depend on participants’ fluency with symbolic math. Indeed, we found that neural adaptation for numbers in the IPS increased with arithmetic fluency. This result was consistent with a prior study performed on children using digits (Girard et al. 2021). Similar to findings reported here, Girard et al. (2021) did not find a digit adaptation effect in the IPS but did report IPS activity in children with higher arithmetic fluency. Together with that study, our findings suggest that participants with higher levels of mathematics fluency might be more able to automatically access numerical magnitudes than participants with lower levels of mathematics fluency. Interestingly, the IPS cluster in which this relation was found overlapped with the cluster showing a neural adaptation for lines across all participants. Therefore, it might be that

individuals with higher levels of math fluency are able to better recruit and recycle the IPS pathways involved in nonsymbolic magnitude processing for symbolic magnitude tasks, thereby creating stronger links between the two magnitude formats (but see [Schwartz et al. 2021](#)).

Univariate Analyses Fail to Capture Automatic Processing of Relative Magnitudes

Contrary to our expectations, we did not observe any neural adaptation effect for fractions and line ratios. Although research on relative magnitudes is limited, these findings conflict with prior studies that also used adaptation tasks ([Jacob and Nieder 2009a, 2009b](#)). A major difference between our study and that of [Jacob and Nieder \(2009b\)](#) is that the stimuli used here were more complex, mostly because all 10 adaptation blocks corresponded to different ratios (e.g., 1:5, 2:3, 2:5, 1:4, 3:5, 2:9). In contrast, [Jacob and Nieder \(2009b\)](#) used only one simple adapting ratio of 1:6 for symbolic fractions with a higher repetition frequency of the stimuli. This leaves open the possibility that during that task participants were able to explicitly compute the magnitude of these simple fractions. However, we think that this was near to impossible in the task used here because each adaptation block for a specific adapting ratio (there were 10 adapting ratios in total) included only eight fraction stimuli. Therefore, as compared to the prior study, we argue that the task used in the current study was better controlled for confounds related to the calculation of the magnitude (though we cannot exclude that at least some participants might have performed calculations even in our task). In any case, the lack of neural adaptation effect for fractions in the current study suggests a lack of automatic processing of the relative magnitudes of symbolic fractions, at least for participants who are not expert in mathematics (it remains possible that such automaticity might be found in participants with higher mathematical skills than in the current sample). The lack of adaptation effect for line ratios also highlights the absence of automatic processing for nonsymbolic relative magnitudes. Although behavioral studies in children, typically achieving adults, and adults with mathematical difficulties indicate access to proportional information when comparing and estimating nonsymbolic line ratios ([Lewis et al. 2015; Bhatia et al. 2020](#)), research on the neural representation of line ratios is scarce ([Jacob and Nieder 2009a](#)). It is possible that the contradictory results may have been due to the differences in the task design. For example, the task in the current study used a greater variety of ratios (e.g., 1:3, 1:4, 1:5, 2:3, 2:5, 3:5, 2:9, 3:7, 1:6, 2:7) than in prior studies (e.g., [Jacob and Nieder 2009b](#)). Future experiments varying the complexity of ratios while controlling for calculation and estimation strategies are needed to identify the source of inconsistencies between studies. In any case, it is difficult from the lack of neural adaptation effect for fractions and line ratios in the present study to

evaluate the neuronal recycling hypothesis of relative magnitudes.

Multivariate Analyses Do not Provide Evidence for Neuronal Recycling of Magnitudes in the IPS

To provide further evidence for the neuronal recycling hypothesis, we complemented univariate analyses with searchlight RSA. This allowed us to explore the relations between the patterns of activation associated with symbolic and nonsymbolic stimuli across magnitude types. Specifically, if similar IPS mechanisms process symbolic and nonsymbolic stimuli, we reasoned that patterns of IPS activity may depend on the type of numerical magnitude (i.e., absolute vs. relative) more so than they may depend on the presentation format (i.e., nonsymbolic vs. symbolic). In contrast to this hypothesis, RSA revealed differences between neural representations of absolute and relative magnitudes (across presentation formats) in the left rostro-lateral prefrontal cortex (RLPFC) and the right occipital cortices but not in the IPS. That is, we did not find any evidence that patterns of activity were similar between symbolic and nonsymbolic stimuli in the IPS (and only depended on the type of numerical magnitude). Interestingly, several studies have suggested that the RLPFC may support relational comparisons and integrating relational information ([Krawczyk 2012](#)). Specifically, relative magnitudes such as fractions cannot be understood without relating the two components (numerator and denominator) to each other. Similarly, for line ratios, the correct magnitude cannot be determined unless the magnitude of the two lines are thought in relation to each other. In line with this claim, recent studies have highlighted the role of relational thinking in processing fractions and rational numbers ([DeWolf et al. 2015; Kalra et al. 2020](#)). Therefore, our finding might provide initial evidence linking relational reasoning and relative magnitude processing at the neural level.

Not only did we not find evidence that the IPS represented similarly nonsymbolic and symbolic magnitudes (while distinguishing between absolute and relative magnitudes) we also found evidence that a cluster of the right IPS represented differently nonsymbolic and symbolic magnitudes (while representing similarly absolute and relative magnitudes). This cluster was part of a larger occipital-parietotemporal network distinguishing between nonsymbolic and symbolic magnitudes. Therefore, multivariate results suggest that patterns of activity in several brain regions depend on the presentation format (nonsymbolic vs. symbolic) more so than they depend on the type of magnitudes (absolute vs. relative). Although some studies have found evidence for overlapping activity between nonsymbolic and symbolic stimuli, these findings are consistent with a stream of recent evidence suggesting that nonsymbolic and symbolic magnitudes rely on separate neural resources ([Cohen Kadosh et al. 2007, 2011](#)). A recent study using MVPA decoding also found distinguishable neural patterns of dots and digits in occipital, parietal, frontal, and temporal areas ([Bulthé et al. 2014](#)). A growing body of evidence

on hemispheric specialization within the parietal lobes also challenges the idea that a single system processes numbers abstractly. That is, the left IPS is often shown to be involved in processing symbolic numbers (Vogel et al. 2015) whereas the right IPS is more often found to be activated during nonsymbolic number processing, indicating different regions within the parietal lobe for both notations (Cantlon et al. 2006; Holloway and Ansari 2010). Furthermore, a developmental meta-analysis focused on symbolic and nonsymbolic number processing in children also showed the influence of the notation of numbers on the neural activation patterns within and outside the parietal areas (Kaufmann et al. 2011). Therefore, the multivariate results reaffirm the growing body of literature suggesting that separate neural regions process both symbolic and non-symbolic magnitudes.

Conclusion

In conclusion, the current study shows limited support for the neuronal recycling hypothesis. On the one hand, consistent with the hypothesis, univariate analyses do show some overlap between the brain regions supporting nonsymbolic and symbolic absolute magnitudes. However, this overlap was limited to absolute (not relative) magnitudes and dependent upon the degree of symbolic math fluency of participants. That is, we found an increase in the adaptation effect for numbers (not fractions) as a function of math fluency in a region of the left IPS that supports the representation of nonsymbolic absolute magnitudes. Thus, individuals with higher levels of math fluency might be able to better recruit and recycle the IPS pathways involved in nonsymbolic magnitude processing for symbolic tasks. On the other hand, inconsistent with the neuronal recycling hypothesis, univariate and multivariate analyses do not provide any evidence that similar IPS brain regions support both nonsymbolic and symbolic magnitudes across all participants. Instead, we found a region of the right IPS encoding differences in format (nonsymbolic vs. symbolic) across both absolute and relative magnitudes. Therefore, our study suggests that IPS activity depends on the presentation format (nonsymbolic vs. symbolic) more than it depends on the type of magnitude (absolute vs. relative) for most participants.

Notes

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Supplementary Material

Supplementary material can be found at *Cerebral Cortex* online.

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