



HAL
open science

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

Parnika Bhatia, Léa Longo, Hanna Chesnokova, Jérôme Prado

► **To cite this version:**

Parnika Bhatia, Léa Longo, Hanna Chesnokova, Jérôme Prado. Neural Representations of Absolute and Relative Magnitudes in Symbolic and Nonsymbolic Formats. *Cerebral Cortex*, In press, 10.1093/cercor/bhab513 . hal-03750178

HAL Id: hal-03750178

<https://hal.science/hal-03750178>

Submitted on 11 Aug 2022

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1
2
3 **Neural representations of absolute and relative magnitudes in symbolic and non-**
4 **symbolic formats**
5
6
7
8
9

10 Parnika Bhatia¹, Léa Longo¹, Hanna Chesnokova¹, & Jérôme Prado¹
11
12
13

14 ¹ Lyon Neuroscience Research Center (CRNL), INSERM U1028 - CNRS UMR5292,
15 University of Lyon, 69500 Bron, France.
16
17
18
19
20
21
22
23

24 **Corresponding Authors:**
25
26

27 P. Bhatia (parnika.bhatia@etu.univ-lyon1.fr) or J. Prado (jerome.prado@univ-
28 lyon1.fr), CRNL, 95 bd Pinel, 69675 Bron cedex, France.
29
30
31
32
33

34 **Brief Running Title:** neural representations of magnitudes
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

Abstract

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 non-symbolic 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 non-symbolic formats overlap in the IPS. In an fMRI adaptation design, forty-eight adult participants were sequentially presented with lines, whole numbers, line ratios, and fractions that varied (versus 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 (non-symbolic versus symbolic) across both absolute and relative magnitudes. Therefore, IPS activity associated with magnitude processing may depend on the presentation format (non-symbolic versus symbolic) more than it depends on the type of magnitude (absolute versus relative), at least for most adult participants.

Keywords

fMRI, numbers, fractions, math cognition, intraparietal

1
2
3
4
5
6 Humans possess the ability to represent magnitudes both non-symbolically (e.g.,
7
8 ••) and symbolically (e.g., two or 2). This ability is both shared and unique among other
9
10 animals. On the one hand, infants and many animal species can estimate and discriminate
11
12 non-symbolic absolute magnitudes, suggesting that the human brain may be endowed
13
14 with a non-symbolic Approximate Number System (ANS) that is innate and evolutionarily
15
16 old (Barth, La Mont, Lipton, & Spelke, 2005; Boysen & Capaldi, 1993; Brannon, 2005;
17
18 Dehaene, Dehaene-Lambertz, & Cohen, 1998; Dehaene, 1997; Pica, Lemer, Izard, &
19
20 Dehaene, 2004; Xu, Spelke, & Goddard, 2005). On the other hand, the ability to represent
21
22 absolute magnitudes as symbolic natural numbers is only found in humans and is largely
23
24 believed to be a product of culture and language (Ansari, 2008). Yet, it has long been
25
26 proposed that this culturally developed ability is grounded in the evolutionarily old capacity
27
28 to process non-symbolic magnitudes (Dehaene et al., 2003; Ansari, 2008). For instance,
29
30 the 'neuronal recycling' hypothesis argues that learning symbolic natural numbers relies
31
32 on the co-option of brain mechanisms supporting non-symbolic magnitude processing,
33
34 which are largely thought to be located in the intra-parietal sulcus (IPS) (Nieder, 2016). In
35
36 other words, it has been claimed that the same mechanisms of the IPS may represent
37
38 both non-symbolic and symbolic magnitudes at an abstract level in adults (Dehaene &
39
40 Cohen, 2007), such that symbolic natural numbers may automatically activate the neural
41
42 representations of absolute magnitudes in that region (Eger, Sterzer, Russ, Giraud, &
43
44 Kleinschmidt, 2003).
45
46
47
48
49
50
51
52

53 Symbolic mathematical skills, however, go largely beyond the ability to represent
54
55 absolute magnitudes in humans. They also involve the ability to represent magnitudes in
56
57
58
59
60

1
2
3 relation with one another, for instance using fractions or decimals (i.e., rational numbers).
4
5 Although the neuronal recycling theory was initially developed in the context of natural
6
7 numbers, a similar proposal has recently emerged to explain the cultural acquisition of
8
9 symbolic rational numbers (Lewis, Matthews, & Hubbard, 2016). Indeed, a growing body
10
11 of evidence shows that infants and non-human primates are sensitive to ratios and
12
13 relational quantities (Drucker et al., 2016; Eckert et al., 2018; Tecwyn et al., 2017; Vallentin
14
15 & Nieder, 2008, 2010; Woodruff & Premack, 1981; Denison & Xu, 2014; McCrink & Wynn.,
16
17 2007). This suggests the existence of an evolutionary old non-symbolic Ratio Processing
18
19 System (RPS) akin to the ANS but tuned exclusively to relative quantities (Lewis,
20
21 Matthews, & Hubbard, 2016). This cognitive system might provide the foundation for the
22
23 acquisition of symbolic rational numbers (Lewis, Matthews, & Hubbard, 2016). Though the
24
25 neural basis of this RPS is less clear than that of the ANS, this line of thought suggests
26
27 that overlapping brain regions may represent both non-symbolic and symbolic ratios
28
29 abstractly. In other words, symbolic rational numbers may automatically activate the
30
31 neural representations of relative magnitudes.
32
33
34
35
36
37

38 To date, evidence that the acquisition of either natural or rational numbers relies
39
40 on the recycling of brain pathways dedicated to the processing of non-symbolic
41
42 magnitudes remains equivocal. Overall, neuroimaging studies focusing on the processing
43
44 of natural numbers have consistently found involvement of the IPS in both symbolic
45
46 (Arabic digits or number words) and non-symbolic (dot patterns) tasks (Neider, 2016;
47
48 Sokolowski, Fias, Mousa, & Ansari, 2017). However, studies that directly compared the
49
50 neural substrates of symbolic and non-symbolic natural number processing within the
51
52 same participants show inconsistent results (Cohen Kadosh, Cohen Kadosh, Kaas, Henik,
53
54
55
56
57
58
59
60

1
2
3 & Goebel, 2007; Cohen Kadosh, Bahrami, Walsh, Butterworth, Popescu, & Price, 2011;
4
5 Damarla & Just, 2013; Bulthé, De Smedt, & Op de Beeck, 2014; Eger, Michel, Thirion,
6
7 Amadon, Dehaene, Kleinsch-midth, 2009; Piazza et al., 2007). For instance, in a seminal
8
9 study using fMRI adaptation, Piazza et al. (2007) found that Arabic digits and dot patterns
10
11 were represented in the same region of the IPS, supporting the neuronal recycling
12
13 hypothesis. Some studies using multivariate analysis have also shown some degree of
14
15 overlap between the brain mechanisms supporting symbolic and non-symbolic magnitude
16
17 processing (Eger et al., 2009). However, other studies concluded that Arabic numerals
18
19 and dot patterns are supported by different neural populations in the IPS and surrounding
20
21 brain regions (Bulthe, De Smedt, & Op de Beeck, 2013; Cohen Kadosh, Cohen Kadosh,
22
23 Kaas, Henik, & Goebel, 2007; Cohen Kadosh, Bahrami, Walsh, Butterworth, Popescu, &
24
25 Price, 2011). Overall, neuroimaging evidence is inconsistent regarding whether a natural
26
27 number is represented abstractly or in a format-dependent manner in the human brain
28
29 (Ansari, 2016; Damarla & Just, 2013; Wilkey & Ansari, 2019).
30
31
32
33
34
35

36 Compared to the neuroimaging literature on the representations of natural
37
38 numbers, few studies have investigated the neural representations and processing of
39
40 rational numbers. Therefore, support for the idea that the neural substrates of the RPS
41
42 may be 'recycled' for the processing of symbolic fractions is scarce (Lewis, Matthews, &
43
44 Hubbard, 2016; Mock et al., 2018). Nonetheless, the available studies suggest that the
45
46 IPS is involved in the processing of both symbolic fractions (DeWolf et al., 2016; Jacob &
47
48 Neider, 2009b; Ischebeck, Schocke, & Delazer, 2009) and non-symbolic line ratios (Jacob
49
50 & Neider, 2009a) in adults. To our knowledge, there is only one study comparing the
51
52 neural bases of symbolic and non-symbolic relative magnitude processing within the same
53
54
55
56
57
58
59
60

1
2
3 participants (Mock et al., 2018, 2019). In that study, fMRI activity was measured while
4
5 adult participants performed a magnitude comparison task in four formats (fractions, dot
6
7 patterns, decimals, and pie charts) (Mock et al., 2018). Results point to overlapping
8
9 activation between symbolic (e.g., fractions and decimals) and non-symbolic (e.g., dot
10
11 patterns and pie charts) proportions in the IPS, but also to format-dependent activity in
12
13 other brain regions. To some extent, the format-independent activity found in the IPS
14
15 supports the idea that there might be an abstract representation of relative magnitudes in
16
17 the human brain. However, because this study used active tasks, it is unclear whether any
18
19 overlapping neural activation is due to common processing of relative magnitudes or to a
20
21 common reliance on response selection processes that also rely on the IPS (Göbel,
22
23 Johansen-Berg, Behrens, & Rushworth, 2004).
24
25
26
27
28

29 Here, we aimed to test whether the culturally developed ability to represent both
30
31 absolute and relative magnitudes symbolically (e.g., using natural numbers and fractions)
32
33 relies on the neural representations of absolute and relative magnitudes in a non-symbolic
34
35 format. To this aim, we adapted a passive blocked fMRI adaptation paradigm used in
36
37 Girard et al., 2021 and Perrachione et al., 2016 to investigate the neural representations
38
39 of absolute and relative magnitudes in different formats, while avoiding confounds due to
40
41 active tasks. FMRI adaptation refers to the idea that repeatedly presenting a series of
42
43 visual stimuli with a common property leads to a decrease in the activity of neurons that
44
45 are sensitive to that property (Grill-Spector and Malach, 2001). This sensitivity is captured
46
47 by the *neural adaptation effect*, measured by comparing blocks of stimuli that differ from
48
49 one another with respect to the property (i.e., no-adaptation blocks) to blocks of stimuli
50
51 that do not (i.e., adaptation blocks). In the present study, participants were presented with
52
53
54
55
56
57
58
59
60

adaptation and no-adaptation blocks of (1) non-symbolic absolute magnitudes (lines), (2) symbolic absolute magnitudes (numbers), (3) non-symbolic relative magnitudes (line ratios), and (4) symbolic relative magnitudes (fractions) (**Figure 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.

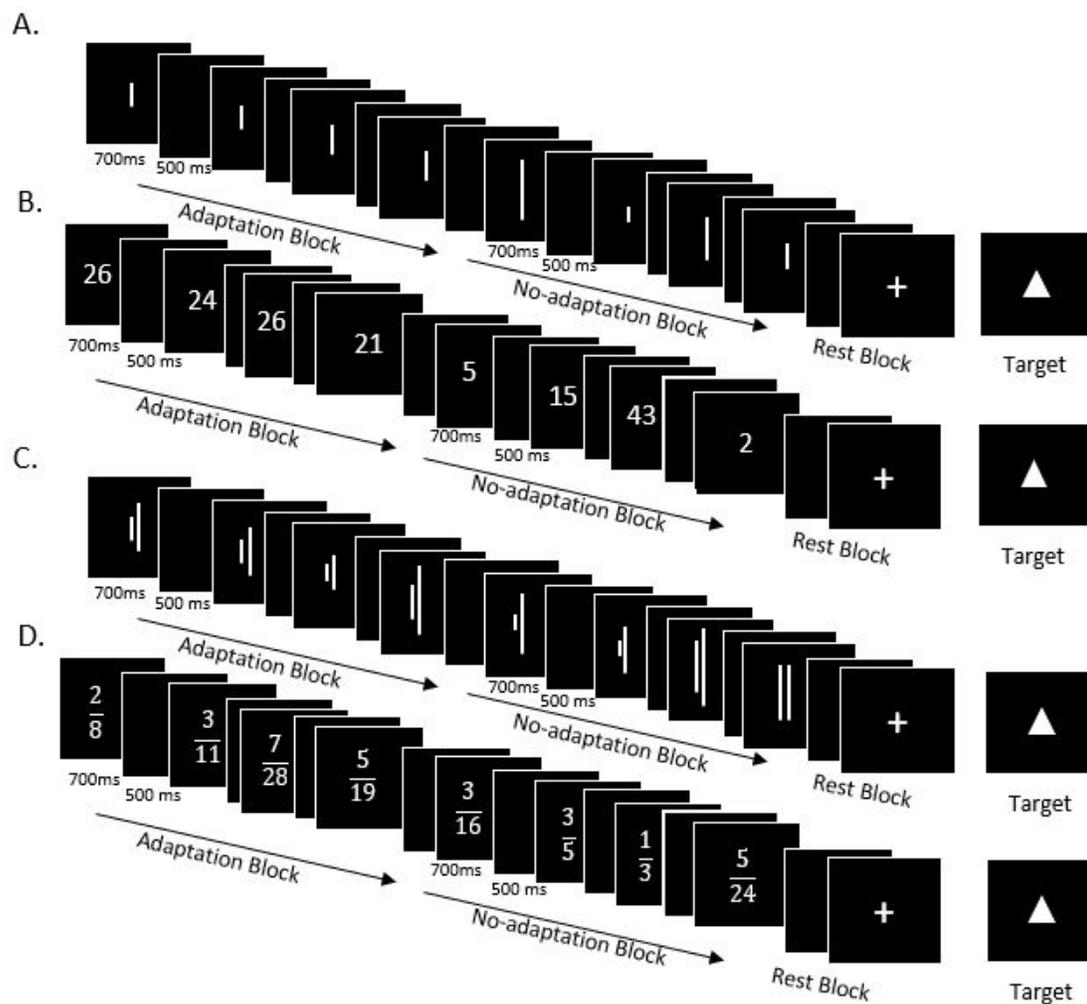


Figure 1: Experimental design. Participants were adapted to the sequential presentation of four types of stimuli that varied in format (non-symbolic versus symbolic) and magnitude type

1
2
3 (absolute versus relative). A. Adaptation to lines. B. Adaptation to numbers. C. Adaptation to
4 line ratios. D. Adaptation to fractions.
5
6
7
8
9

10 We tested the neuronal recycling hypothesis of absolute and relative magnitudes
11 using both univariate and multivariate methods. First, using univariate analyses, we aimed
12 to identify the neural regions that may be sensitive to a change in numerical distance
13 between stimuli across all participants, either with respect to their absolute magnitude (for
14 lines and numbers) or relative magnitude (for line ratios and fractions). This should
15 translate into a decrease of activity in adaptation compared to no-adaptation blocks in
16 these regions (i.e., a neural adaptation effect). The neuronal recycling hypothesis
17 assumes that processing symbolic stimuli (i.e., numbers and fractions) relies on neural
18 mechanisms supporting non-symbolic stimuli (i.e., lines and ratios). Thus, this hypothesis
19 predicts that overlapping regions of the IPS may be associated with a neural adaptation
20 effect for (1) numbers and lines and (2) fractions and ratios. Second, using multivariate
21 analyses, we aimed to explore the relations between the patterns of activation associated
22 with symbolic and non-symbolic stimuli across magnitude types. Specifically, because the
23 neuronal recycling hypothesis assumes that similar IPS mechanisms process symbolic
24 and non-symbolic stimuli, it predicts that patterns of IPS activity may be similar between
25 symbolic and non-symbolic stimuli and are more likely to depend on the type of numerical
26 magnitude (i.e., absolute versus relative).
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49

50 **Material and methods**

51 *Participants*

52
53
54
55
56
57
58
59
60

1
2
3 Fifty-three right-handed adults participated in the experiment. Participants were
4
5 mainly recruited through generic advertisements on social media (i.e., Facebook), mainly
6
7 targeting university students in the Lyon area, France. Some participants were also
8
9 recruited from prior studies at the CERMEP imaging center. Five participants were
10
11 excluded from the study because of technical errors in the experimentation set-up (n=4)
12
13 and contraindications to the MRI (n=1). Therefore, 48 adults (*Mean age* = 22.09, 34
14
15 *females*) were included in the main analyses. All participants were right-handed and native
16
17 French speakers with no history of neurological or psychiatric disorders. Participants gave
18
19 written informed consent and were paid 80 euros for their participation. The study was
20
21 approved by a national ethics committee (CPP- Strasbourg Est IV).
22
23
24
25

26 27 *Psychometric testing* 28 29

30 Verbal IQ and spatial IQ were estimated using the verbal reasoning and matrix
31
32 reasoning subtest of the WAIS-IV (Wechsler, 2008). Fluency in symbolic math was
33
34 assessed using the Math Fluency of the Woodcock-Johnson Test of Achievement (WJ-III)
35
36 (Woodcock, Mather, McGrew, & Wendling, 2001). In this test, participants have to solve
37
38 as many single-digit addition, subtraction, multiplication, and division problems as they
39
40 can within 3 min. Participants also completed the Applied Problems subtest of the WJ-III.
41
42 Unlike the Math Fluency subtest, this test is un-timed and measures the ability to analyze
43
44 basic numerical concepts and oral word problems. The test stops after 6 consecutive
45
46 errors or when the last item is reached. To exclude participants with reading disabilities,
47
48 their reading fluency was assessed with the Alouette-R test (Lefavrais, 1967). This test
49
50 requires participants to read a 265-word text aloud in 3 minutes and measures the number
51
52
53
54
55
56
57
58
59
60

1
2
3 of words read correctly to evaluate the reading precision and speed. No other tests than
4
5 those mentioned here were administered to participants.
6
7

8 *In-scanner task* 9

10
11 Participants were presented with a passive blocked adaptation paradigm adapted
12 from Girard et al., 2021 and Perrachione et al., 2016. In this paradigm, participants are
13 passively presented with blocks of stimuli at the center of the screen. Here we presented
14 four types of stimuli in four different runs of approximately 5 min: lines, numbers, line
15 ratios, and fractions (**Figure 1**). Numbers ranged from 1 to 62 ($\sim 1.72^\circ$ of visual angle),
16 fractions ranged from $\frac{1}{24}$ to ~ 1 in magnitude ($\sim 3.45^\circ$ of visual angle), and lines ranged
17 from 0.98 to 17.8 cm in length on a 37 cm screen (corresponded to $\sim 0.69 - 12.24^\circ$ of
18 visual angle). All stimuli were shown in white on a black background. Within each run,
19 participants were presented with adaptation and no-adaptation blocks (**Figure 1**).
20
21 Adaptation and no-adaptation blocks differed with respect to the numerical distance
22 between the stimuli. Specifically, adaptation blocks consisted in the sequential
23 presentation of 8 quantities in a total of which 4 quantities were the same in magnitude
24 and the other 4 quantities were relatively close. For instance, in the number adaptation
25 block of 23, 26, 25, 26, 24, 26, 21, 26, four stimuli (e.g., 26) are identical and the other
26 four stimuli have a minimum distance of 1 and a maximum distance of 5 between each
27 other. Similarly, for fractions, adaptation to 1:4 was composed of four exact equivalent
28 fractions $\frac{2}{8}$, $\frac{1}{4}$, $\frac{4}{16}$, $\frac{7}{28}$ and the rest of the stimuli had the denominator changed by
29 adding or subtracting 1 to the original fractions (i.e., $\frac{3}{11}$, $\frac{5}{19}$, $\frac{8}{31}$, $\frac{6}{23}$). Half of the
30 stimuli for the adaptation block of fractions were constructed by small changes to the
31 denominator (+1 or -1) to prevent the participant from reducing the fraction to its lowest
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

1
2
3 form, thereby avoiding confounds due to calculation. No-adaptation blocks consisted in
4 the sequential presentation of 8 quantities that were relatively far from one another in
5 magnitude (e.g., a minimum distance of 2 and a maximum distance of 55 between
6 consecutive numbers in a block, and minimum magnitude of 1/24 to maximum magnitude
7 of 11/12 for a block of fractions). The size of the individual line lengths and line ratios
8 corresponded to those used for numbers and fractions. So, for line ratios, the length of the
9 smaller line was calculated as the ratio of the longer line length such that a fraction
10 corresponding to $\frac{3}{15}$ would be a line ratio where the smaller line length is $\frac{3}{15}$ as long as the
11 longer line length. Thus, the absolute line lengths did not vary with proportion. The shorter
12 line was always on the left (i.e., corresponding to the numerator of a proper fraction) while
13 the longer line was always on the right (i.e., corresponding to the denominator of a proper
14 fraction). The complete list of stimuli can be found in **Supplementary Table 1**.

31 32 Experimental timeline

33
34
35 In each adaptation and no-adaptation block, stimuli remained on the screen for 700
36 ms, with a 500 ms inter-stimulus interval (for a total block duration of 9.6 seconds). Ten
37 adaptation blocks and ten no-adaptation blocks were presented along with ten blocks of
38 visual fixation (duration = 9.6 seconds) in each run. Block presentation was pseudo-
39 randomized such that 2 blocks of the same type could not follow each other. Participants
40 were instructed to passively observe the stimuli in the scanner. However, 10 target stimuli
41 (a triangle) randomly appeared in each run (outside of the blocks). Participants were asked
42 to press a button every time this target appeared. this allowed us to ensure that
43 participants paid attention to the stimuli. The task was presented using Psychopy (Peirce
44 et al., 2019).

fMRI Data Acquisition

Images were collected with a Siemens Prisma 3T MRI scanner (Siemens Healthcare, Erlangen, Germany) at the CERMEP Imagerie du vivant in Lyon, France. The BOLD signal was measured with a susceptibility-weighted single-shot 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, London, UK). The first 3 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 equals to twice the voxel size (4 × 4 × 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 3 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 2 nearest non-repaired volumes (Romeo et al., 2018). Finally, functional images were normalized into the standard Montreal Neurological Institute (MNI)

1
2
3 space. This was done in two steps. First, after coregistration with the functional data, the
4 structural image was segmented into grey matter, white matter, and cerebrospinal fluid by
5 using a unified segmentation algorithm (Ashburner and Friston, 2005). Second, the
6 functional data were normalized to the MNI space by using the normalization parameters
7 estimated during unified segmentation (normalized voxel size, $2 \times 2 \times 3.5 \text{ mm}^3$).
8
9
10
11
12
13

14 15 Univariate analyses

16
17
18 For each participant and each run, a general linear model analysis was conducted
19 on brain activity associated with adaptation and no-adaptation blocks. Blocks were
20 modeled as epochs with onsets time-locked to the beginning of each block and a duration
21 of 9.6 sec per block. All epochs were convolved with a canonical hemodynamic response
22 function. The time-series data were high-pass filtered (1/128Hz), and serial correlations
23 were corrected using an auto-regressive AR (1) model. The neural adaptation effect was
24 measured by subtracting activity associated with adaptation blocks from activity
25 associated with no-adaptation blocks. These subject-specific contrasts were then
26 submitted to the second level for group-level random effect analyses. Clusters were
27 considered significant at a FWE-corrected threshold of $p < .05$ (using a cluster-defining
28 threshold of $p < .005$, uncorrected).
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43

44 45 Multivariate analyses

46
47
48 In addition to the main univariate analysis, we also used the CosmoMVPA toolbox
49 (<https://www.cosmomvpa.org/>) to perform a representation similarity analysis (RSA)
50 assessing the similarity and dissimilarity of neural activation patterns associated with
51 different magnitude types (absolute versus relative) and presentation formats (symbolic
52
53
54
55
56
57
58
59
60

1
2
3 versus non-symbolic). This analysis was conducted on the four beta maps corresponding
4
5 to the contrasts of lines versus fixation, numbers versus fixation, line ratios versus fixation,
6
7 and fractions versus fixation (collapsing across adaptation and no-adaptation blocks).
8
9 First, we created two 4x4 theoretical representation dissimilarity matrices (RDMs),
10
11 corresponding to (1) the expected dissimilarity between absolute and relative magnitudes
12
13 (and expected similarity between symbolic and non-symbolic stimuli) and (2) the expected
14
15 dissimilarity between symbolic and non-symbolic stimuli (and expected similarity between
16
17 absolute and relative magnitudes). In the *absolute versus relative* RDM (see **Figure. 4A**),
18
19 all stimuli of the same magnitude type (numbers - numbers, numbers - lines, fractions -
20
21 fractions, fractions - line ratios) had a dissimilarity coefficient of 0, whereas all stimuli of a
22
23 different magnitude type (numbers - fractions, numbers - line ratios, fractions - lines, lines
24
25 - line ratios) had a dissimilarity coefficient of 1. In the *symbolic versus non-symbolic* RDM
26
27 (see **Figure. 5A**), all stimuli of the same format (numbers - numbers, numbers - fractions,
28
29 lines - lines, lines - line ratios) had a dissimilarity coefficient of 0, whereas all stimuli of a
30
31 different format (numbers - lines, numbers - line ratios, lines - fractions, line ratios -
32
33 fractions) had a dissimilarity coefficient of 1. Second, we extracted brain activity from the
34
35 four contrasts (i.e., lines versus fixation, numbers versus fixation, line ratios versus
36
37 fixation, and fractions versus fixation) using spherical searchlights (1.4 cc, i.e., 100 voxels)
38
39 at every voxel in the brain. A 4x4 neural RDM was constructed for each searchlight, which
40
41 each cell representing 1 minus the Pearson correlation between the voxel-wise beta value
42
43 for each pair of contrasts. The Pearson correlation between the neural RDM and each
44
45 theoretical RDM was then calculated for each searchlight and converted to a z value using
46
47 a Fisher transform. The Fisher-transformed correlation coefficient for each searchlight was
48
49 systematically associated with the central voxel of that searchlight. Fisher-transformed
50
51
52
53
54
55
56
57
58
59
60

1
2
3 correlation maps were then submitted to second-level one-sample t-tests across all
4 participants to identify voxels for which the correlation between the theoretical and neural
5 DSMs was greater than 0. Clusters were considered significant at a FWE-corrected
6 threshold of $p < .05$ (using a cluster-defining threshold of $p < .005$, uncorrected).
7
8
9

10 11 12 13 Data and software availability

14
15
16 The task as well as all individual behavioral and MRI data are publicly available via
17 Zenodo at <http://doi.org/10.5281/zenodo.5566914>. The general and custom scripts used
18 to analyze fMRI data are available at <https://github.com/BBL-lab/BBL-batch-system>. The
19 software used to overlay functional images on brain anatomy (HiBoP) is available at
20 <https://github.com/hbp-HiBoP/HiBoP>
21
22
23
24
25
26
27

28 Results

29 30 31 Psychometric testing and in-scanner performance

32
33
34 Standardized verbal IQ ranged from 85 to 140 ($mean = 117.29$), while standardized
35 spatial IQ ranged from 70 to 120 ($mean = 94.68$). Thus, participants' IQ was in the normal
36 to the superior range. The number of arithmetic problems correctly solved in 3 min in the
37 Math fluency subtest ranged from 47 to 160 ($mean = 114.25$), suggesting a substantial
38 variability in arithmetic fluency among participants. The untimed Applied problems subtest
39 indicated less variability, with scores ranging from 39 to 61 ($mean = 49.06$). Finally,
40 participants' reading precision scores ranged from 90.18 to 100 ($mean = 98.28$), and
41 reading speed ranged from 336.69 to 787.11 ($mean = 551.198$) (the optimal cut-off for
42 dyslexia is a reading precision score above 87 or reading speed above 402.26; Cavalli et
43 al., 2018).
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

1
2
3 To make sure participants were attentive to the stimuli in the scanner, a target
4 detection task was inserted in all four tasks. Participants had to press a button when they
5 saw a triangle during the task. Average performance on detection of the target for the
6 different runs was 95.3% ($SD = 0.152$) for fraction, 92.7% ($SD = 0.186$) for numbers,
7 91.4% ($SD = 0.208$) for line ratios, and 92.4% ($SD = 0.194$) for lines. There was no
8 difference in target detection between the four tasks (*all t's* < 1.9, *all p's* > 0.06), indicating
9 that participants paid equal attention to the stimuli in the tasks. The response to target
10 stimuli was not correlated with math fluency and applied problem skills (*all r's* > - 0.24, *all*
11 *p's* > 0.10).
12
13
14
15
16
17
18
19
20
21
22
23

24 Univariate analyses

25
26
27 For each stimulus type (lines, numbers, line ratios, and fractions), brain activity
28 associated with adaptation blocks was subtracted from activity associated with no-
29 adaptation blocks to identify brain regions showing a neural adaptation effect across all
30 participants. For lines, a neural adaptation effect was observed in the bilateral IPS as well
31 as in a wider network of brain regions encompassing the precentral and occipital cortices
32 (see **Table 1** and **Figure 2A**). For numbers, the only region showing a significant neural
33 adaptation effect was located in the left fusiform gyrus (see **Table 1** and **Figure 2B**). No
34 significant adaptation effect was observed in any brain region for either fractions or line
35 ratios.
36
37
38
39
40
41
42
43
44
45
46
47
48

49 Contrary to our assumptions, lines were the only stimuli associated with a
50 significant neural adaptation effect in the IPS across all participants. Therefore, we did not
51 find any evidence that common neural mechanisms in the IPS may process both symbolic
52
53
54
55
56
57
58
59
60

1
2
3 and non-symbolic stimuli. However, there was relatively large variability in participants'
4 fluency with symbolic math (as suggested by the Math fluency subtest, see above). It is
5 thus possible that the neural adaptation effect for symbolic stimuli may depend on
6 participants' levels of fluency. This would be consistent with the results of our previous
7 study using a similar paradigm, in which we found a positive correlation between neural
8 adaptation to numbers and Math fluency scores (Girard et al., 2021). In other words,
9 because our paradigm is passive, magnitudes of symbolic stimuli such as numbers and
10 fractions may only be automatically processed by the most fluent participants. To examine
11 this possibility, we regressed neural adaptation effects on participants' Math fluency
12 scores across the whole brain. We did not find any positive relation between math fluency
13 and neural adaptation effect for fractions, lines, or line ratios. For numbers, however, the
14 neural adaptation effect increased with math fluency in a region of the left IPS (see **Figure.**
15 **3A**). Critically, a conjunction analysis revealed that this region overlapped with the region
16 showing an overall neural adaptation effect across all participants for lines (center of mass:
17 $x=-28$, $y=-42$, $z=55$, the volume of overlap = 70mm^3) (see **Figure. 3B**). Thus, increased
18 math fluency was linked to an enhanced neural adaptation effect for numbers in the same
19 left IPS region that exhibited a neural adaptation effect across all participants for lines.
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

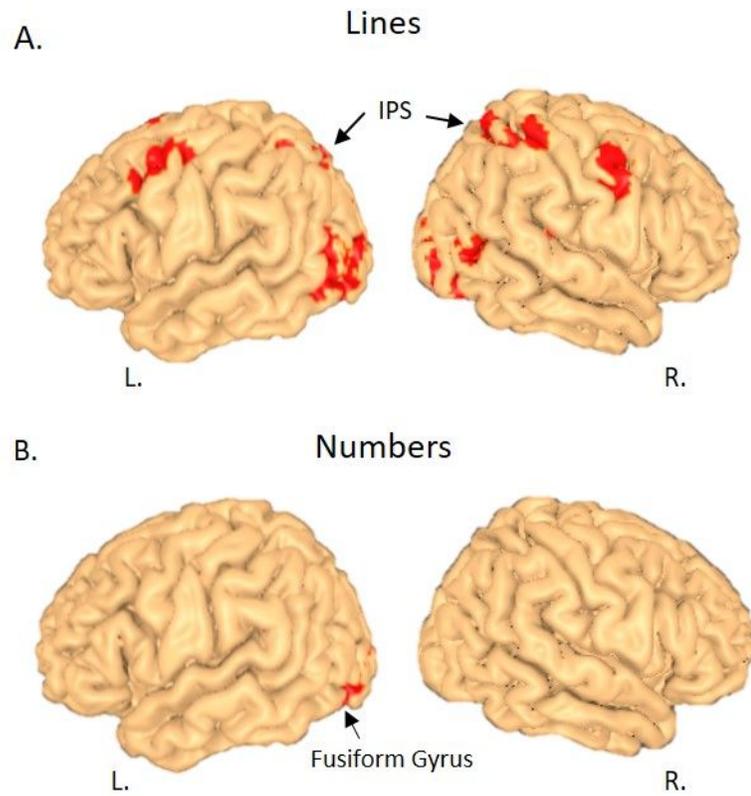
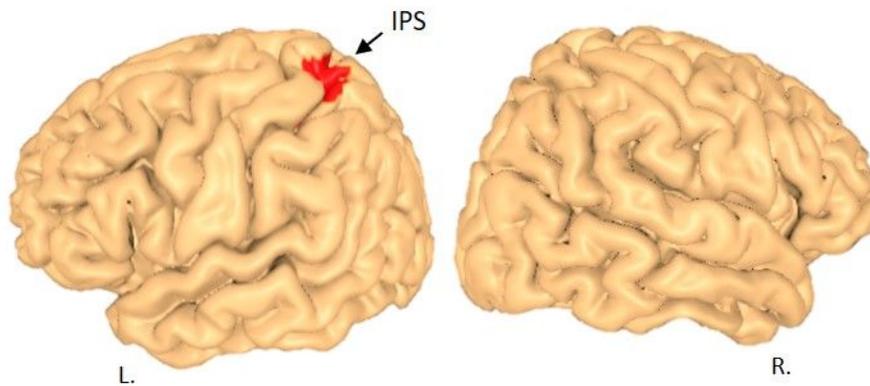


Figure 2: Neural adaptation effects across all participants (univariate analyses). A. Brain regions showing a neural adaptation effect for lines. B. Brain regions showing a neural adaptation effect for numbers.

A.



B.

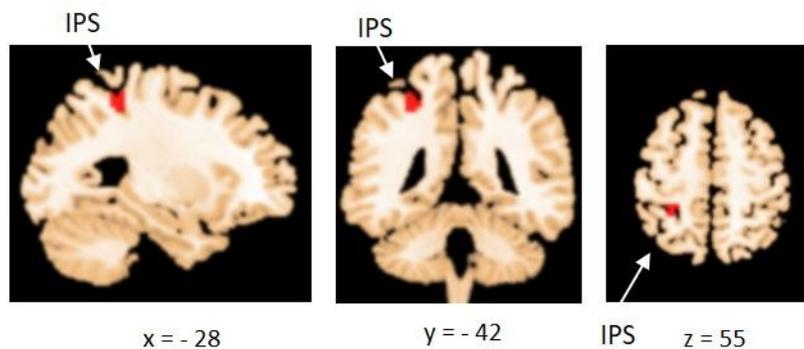


Figure 3: Relation between arithmetic fluency and neural adaptation effects (univariate analyses). A. Brain region showing a positive relation between arithmetic fluency and neural adaptation effect for numbers. B. Brain region showing both a positive relation between arithmetic fluency and neural adaptation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

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

Anatomical Location	Cluster level $P_{\text{FWE-corrected}}$	Cluster size (cc)	MNI coordinates			t-score
			x	y	z	
			<i>Line adaptation task</i>			
L. Inferior Occipital Gyrus	.000	28.55	-32	-90	-4	5.89
L. Intraparietal Sulcus	-	-	-34	-50	51	3.33
R. Inferior Occipital Gyrus	.000	21.01	40	-84	-12	5.48
R. Intraparietal Sulcus	-	-	30	-58	55	3.99
R. Thalamus	.019	2.13	10	-16	13	5.44
R. Supplementary Motor area	.000	6.27	2	12	66	5.16
R. Hippocampus	.004	2.74	22	-20	-12	4.81
L. Caudate	.026	2.0	-14	-2	13	4.37
R. Precentral Gyrus	.033	1.9	-44	4	52	4.33
R. Precentral Gyrus	.003	2.85	54	-2	44	4.31
L. Posterior Cingulate	.025	2.01	-6	-42	16	4.31
<i>Number adaptation task</i>						
L. Occipital Fusiform Gyrus	.004	2.81	-26	-90	-12	4.46
<i>Line Ratio adaptation task</i>						
No suprathreshold cluster						
<i>Fraction adaptation task</i>						
No suprathreshold cluster						

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

Multivariate analyses

As described above, the univariate analyses only provided limited evidence for common brain mechanisms in the IPS processing non-symbolic 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 non-symbolic 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 non-symbolic and symbolic stimuli) (see **Figure 4A**) and (2) dissimilarity between patterns of activation associated with symbolic and non-symbolic stimuli (and similarity between absolute and relative magnitudes) (see **Figure 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 non-symbolic 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 non-symbolic 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 (non-symbolic versus symbolic) more so than they depend on the type of magnitudes (absolute versus relative).

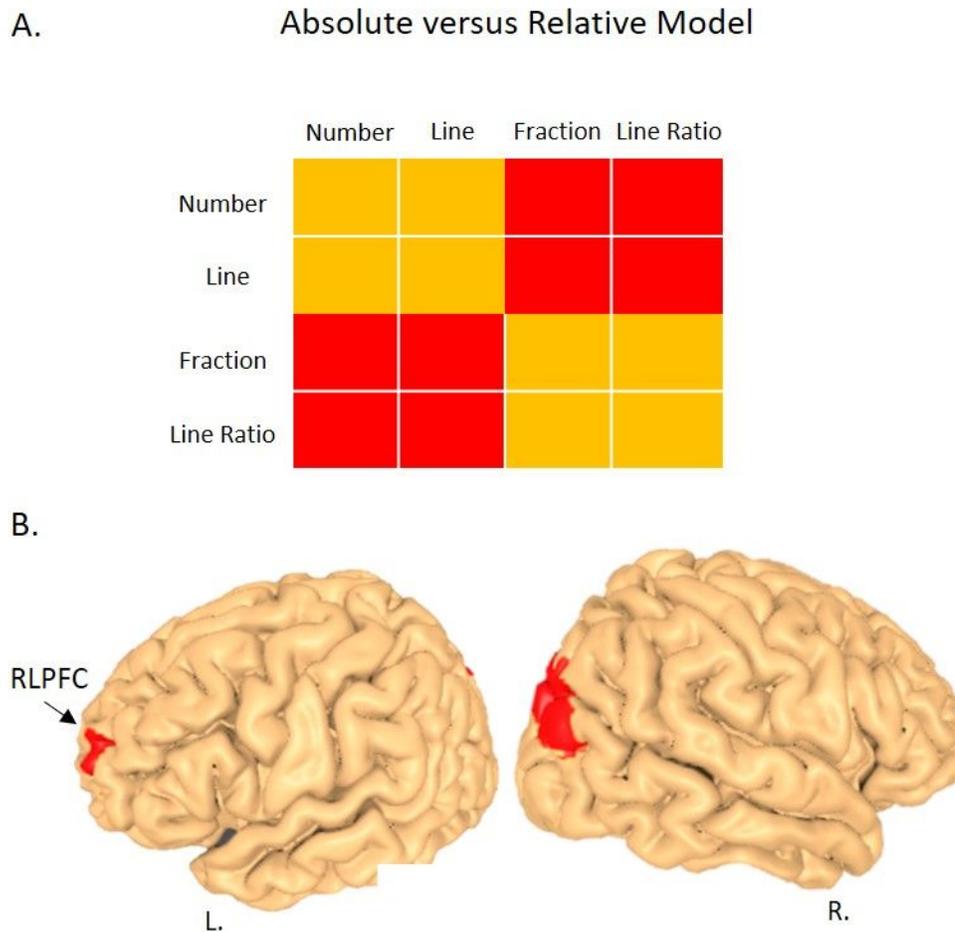


Figure 4: Results of the Representational Similarity Analysis for the Absolute versus Relative model (multivariate analysis). A. Hypothesized Model for the RSA, the matrix represents a dissimilarity matrix where red denotes dissimilar items (0) and yellow denotes similar items (1). B. Brain regions representing differently absolute and relative magnitudes while representing similarly non-symbolic and symbolic magnitudes.

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.

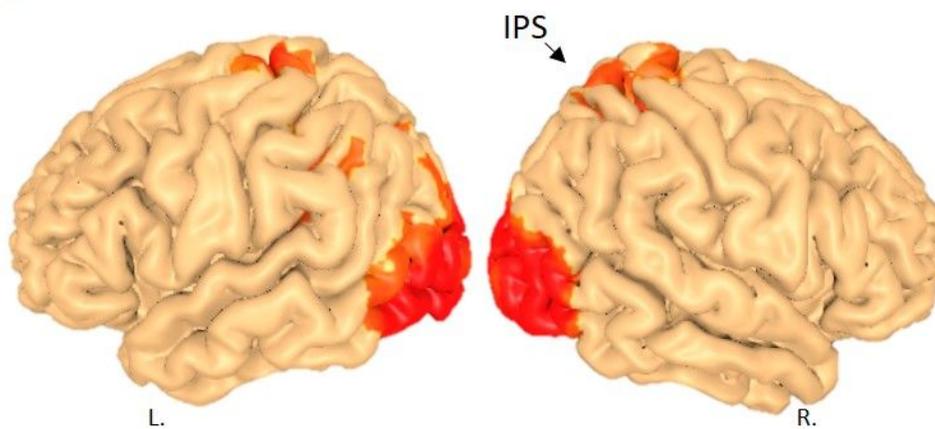


Figure 5: Results of the Representational Similarity Analysis for the Symbolic versus Non-symbolic model (multivariate analysis). A. Hypothesized Model for the RSA, the matrix represents a dissimilarity matrix where red denotes dissimilar items (0) and yellow denotes similar items (1). B. Brain regions representing differently non-symbolic and symbolic magnitudes while representing similarly absolute and relative magnitudes.

Table 2: Brain regions identified in Representational Similarity Analysis (multivariate analyses)

Anatomical Location	Cluster level $P_{\text{FWE-corrected}}$	Cluster size (cc)	MNI coordinates			t-score
			x	y	z	
<i>Symbolic versus Non-symbolic</i>						
L. Inferior Occipital Gyrus	.00	91.44	-34	-84	-4	8.18
L. Supramarginal Gyrus	.012	1.51	-50	-38	34	4.76
L. Postcentral Gyrus	.00	4.11	-30	-30	66	4.72
R. Superior Parietal Lobule	.00	7.91	26	-46	58	4.60
R. Intra-parietal sulcus	-	-	30	-58	55	2.75
<i>Absolute versus Relative</i>						
L. Superior Occipital Gyrus	.00	3.09	-10	-90	27	4.74
L. Lingual Gyrus	.009	1.61	-28	-62	-1	4.36
L. Superior Frontal Gyrus	.046	1.21	-24	60	13	3.74
L. Middle Frontal Gyrus	-	-	-28	48	13	3.74
R. Middle Occipital Gyrus	.00	7.15	38	-84	20	5.29

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

Discussion

In the present study, we used univariate and multivariate analyses to test the neuronal recycling hypothesis of absolute and relative magnitudes. Participants passively

1
2
3 attended to numerical stimuli in the scanner, presented as symbolic fractions, non-
4 symbolic line ratios, symbolic numbers, and non-symbolic lines. Each of these stimuli was
5 presented in adaptation and no-adaptation blocks, wherein the numerical quantity
6 presented was near and far in magnitude (respectively). In the following, we will first
7 discuss the result of the univariate analyses (comparing the difference in activity between
8 no-adaptation and adaptation blocks, or neural adaptation effect, for the four stimuli). We
9 will then discuss the findings of multivariate analyses.
10
11
12
13
14
15
16
17
18
19

20 *Univariate analyses provide limited evidence for neuronal recycling of absolute*
21 *magnitudes*
22
23
24

25 In line with the neuronal recycling hypothesis of both absolute and relative
26 magnitudes, we predicted that symbolic and non-symbolic magnitudes would rely on
27 overlapping brain mechanisms in the IPS. This would have translated into neural
28 adaptation effects in similar regions of the IPS for symbolic and non-symbolic magnitudes,
29 suggesting an abstract representation of magnitudes in the IPS. Across all participants,
30 we found a neural adaptation effect for non-symbolic absolute magnitudes (i.e., lines) in a
31 relatively wide network of brain areas encompassing the bilateral IPS, the occipital, the
32 supplementary motor area, and the precentral cortices. These results (particularly
33 concerning the recruitment of occipito-parietal areas) are in line with prior passive viewing
34 paradigms investigating the representation of non-symbolic absolute magnitudes (Ansari
35 & Dhital., 2006; Demeyere, Rotshtein, & Humphreys, 2014; Pinel et al., 2004; Roggeman
36 et al., 2011). In fact, a recent meta-analysis revealed that non-symbolic magnitude
37 processing was associated with consistent activations in the bilateral parietal cortex and
38 occipital gyri across studies (Sokolowski et al., 2017). A recent study using a magnitude
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

1
2
3 comparison task involving both dot patterns and lines of different lengths also revealed
4
5 overlapping activations for these conditions in the bilateral parietal and occipital cortices
6
7 (Borghesani et al., 2019). Overall, the fact that the IPS exhibits a neural adaptation effect
8
9 for lines in our study is consistent with a long line of studies pointing to the IPS as a major
10
11 locus for the representation of non-symbolic absolute magnitudes in the human brain
12
13 (Nieder, 2016).
14
15

16
17 In contrast to our predictions, however, we failed to find any neural adaptation effect
18
19 for symbolic absolute magnitudes (i.e., numbers) in the IPS. Instead, a neural adaptation
20
21 effect was found in the left fusiform gyrus, which may reflect the visual processing of
22
23 numerals (e.g., Holloway et al., 2013). Indeed, it has long been posited that there may
24
25 exist dedicated neural mechanisms for processing the visual aspect of symbolic numbers.
26
27 For example, the Triple Code Model assumes that number processing involves a wide
28
29 network of specialized neural regions associated with the semantic, analog, but also visual
30
31 properties of numbers (Dehaene, 1992). In line with this proposal, recent studies suggest
32
33 that the fusiform gyrus may house a “number form area”, which might be responsible for
34
35 the visual recognition of the Arabic numerals (Amalric & Dehaene, 2016; Grotheer et al.,
36
37 2016; Vatansever et al., 2020; Yeo et al., 2017). Our findings might add to this body of
38
39 evidence, suggesting an automatic activation of the fusiform gyrus in response to the
40
41 passive presentation of Arabic numerals in adults.
42
43
44
45
46
47

48 The lack of IPS activation, however, is in contrast to the majority of literature on the
49
50 role of left-lateralized IPS in the development of symbolic magnitude processing (Vogel,
51
52 Goffin, & Ansari, 2014). It is important to note that, in contrast to most previous studies,
53
54 our adaptation paradigm is passive and therefore captures an automatic representation of
55
56
57
58
59
60

1
2
3 numerical magnitude from the viewing of symbolic stimuli. This is critical because the IPS
4 is also involved in response selection (Cappelletti et al., 2010; Göbel et al., 2004).
5
6
7 Previous studies using active tasks (e.g., number comparison tasks, in which participants
8 select the largest number; Ansari et al., 2005; Cohen Kadosh et al., 2005; Lyons & Ansari,
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

numerical magnitude from the viewing of symbolic stimuli. This is critical because the IPS is also involved in response selection (Cappelletti et al., 2010; Göbel et al., 2004). 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 & Ansari, 2009; Holloway & 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 and colleagues (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 non-symbolic 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. While research on relative magnitudes is limited, these findings

1
2
3 conflict with prior studies that also used adaptation tasks (Jacob & Nieder, 2009 a, b). A
4 major difference between our study and that of Jacob & Nieder (2009) is that the stimuli
5 used here were more complex, mostly because all of the ten adaptation blocks
6 corresponded to different ratios (e.g. 1:5, 2:3, 2:5, 1:4, 3:5, 2:9). Contrarily, Jacob & Nieder
7 (2009) used only one simple adapting ratio of 1:6 for symbolic fractions with a higher
8 repetition frequency of the stimuli (Jacob & Nieder, 2009). This leaves open the possibility
9 that during that task participants were able to explicitly compute the magnitude of these
10 simple fractions. However, we think that this was near to impossible in the task used here
11 because each adaptation block for a specific adapting ratio (there were 10 adapting ratios
12 in total) included only eight fraction stimuli. Therefore, as compared to the prior study, we
13 argue that the task used in the current study was better controlled for confounds related
14 to the calculation of the magnitude (though we cannot exclude that at least some
15 participants might have performed calculations even in our task). In any case, the lack of
16 neural adaptation effect for fractions in the current study suggests a lack of automatic
17 processing of the relative magnitudes of symbolic fractions, at least for participants who
18 are not expert in mathematics (it remains possible that such automaticity might be found
19 in participants with higher mathematical skills than in the current sample). The lack of
20 adaptation effect for line ratios also highlights the absence of automatic processing for
21 non-symbolic relative magnitudes. While behavioral studies in children, typically achieving
22 adults and adults with mathematics difficulty indicate access to proportional information
23 when comparing and estimating non-symbolic line ratios (Matthews, Lewis, & Hubbard,
24 2015; Bhatia et al., 2020), research on the neural representation of line ratios is scarce
25 (Jacob & Nieder, 2009a). It is possible that the contradictory results may have been due
26 to the differences in the task design. For example, the task in the current study used a

1
2
3 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
4
5 studies (e.g., Jacob & Nieder, 2009b). Future experiments varying the complexity of ratios
6
7 while controlling for calculation and estimation strategies are needed to identify the source
8
9 of inconsistencies between studies. In any case, it is difficult from the lack of neural
10
11 adaptation effect for fractions and line ratios in the present study to evaluate the neuronal
12
13 recycling hypothesis of relative magnitudes.
14
15

16
17
18 *Multivariate analyses do not provide evidence for neuronal recycling of magnitudes in the*
19
20 *IPS*
21
22

23 To provide further evidence for the neuronal recycling hypothesis, we
24
25 complemented univariate analyses with searchlight RSA. This allowed us to explore the
26
27 relations between the patterns of activation associated with symbolic and non-symbolic
28
29 stimuli across magnitude types. Specifically, if similar IPS mechanisms process symbolic
30
31 and non-symbolic stimuli, we reasoned that patterns of IPS activity may depend on the
32
33 type of numerical magnitude (i.e., absolute versus relative) more so than they may depend
34
35 on the presentation format (i.e., non-symbolic versus symbolic). In contrast to this
36
37 hypothesis, RSA revealed differences between neural representations of absolute and
38
39 relative magnitudes (across presentation formats) in the left rostro lateral prefrontal cortex
40
41 (RLPFC) and the right occipital cortices, but not in the IPS. That is, we did not find any
42
43 evidence that patterns of activity were similar between symbolic and non-symbolic stimuli
44
45 in the IPS (and only depended on the type of numerical magnitude). Interestingly, several
46
47 studies have suggested that the RLPFC may support relational comparisons and
48
49 integrating relational information (Krawczyk, 2012). Specifically, relative magnitudes such
50
51 as fractions cannot be understood without relating the two components (numerator and
52
53
54
55
56
57
58
59
60

1
2
3 denominator) to each other. Similarly, for line ratios, the correct magnitude cannot be
4
5 determined unless the magnitude of the two lines are thought in relation to each other. In
6
7 line with this claim, recent studies have highlighted the role of relational thinking in
8
9 processing fractions and rational numbers (Dewolf et al., 2015; Kalra et al., 2020).
10
11 Therefore, our finding might provide initial evidence linking relational reasoning and
12
13 relative magnitude processing at the neural level.
14
15

16
17 Not only did we not find evidence that the IPS represented similarly non-symbolic
18
19 and symbolic magnitudes (while distinguishing between absolute and relative
20
21 magnitudes), we found evidence that a cluster of the right IPS represented differently non-
22
23 symbolic and symbolic magnitudes (while representing similarly absolute and relative
24
25 magnitudes). This cluster was part of a larger occipital-parieto-temporal network
26
27 distinguishing between non-symbolic and symbolic magnitudes. Therefore, multivariate
28
29 results suggest that patterns of activity in several brain regions depend on the presentation
30
31 format (non-symbolic versus symbolic) more so than they depend on the type of
32
33 magnitudes (absolute versus relative). Although some studies have found evidence for
34
35 overlapping activity between non-symbolic and symbolic stimuli, these findings are
36
37 consistent with a stream of recent evidence suggesting that non-symbolic and symbolic
38
39 magnitudes rely on separate neural resources (Cohen Kadosh and Walsh, 2009; Cohen
40
41 Kadosh et al., 2011 ; Roi Cohen Kadosh et al., 2007). A recent study using MVPA
42
43 decoding also found distinguishable neural patterns of dots and digits in occipital, parietal,
44
45 frontal, and temporal areas (Bluthé et al., 2014). A growing body of evidence on
46
47 hemispheric specialization within the parietal lobes also challenges the idea that a single
48
49 system processes numbers abstractly. That is, the left IPS is often shown to be involved
50
51
52
53
54
55
56
57
58
59
60

1
2
3 in processing symbolic numbers (Vogel et al., 2014) while the right IPS is more often found
4
5 to be activated during non-symbolic number processing, indicating different regions within
6
7 the parietal lobe for both notations (Cantlon et al., 2006; Holloway & Ansari, 2010).
8
9 Furthermore, a developmental meta-analysis focused on symbolic and non-symbolic
10
11 number processing in children also showed the influence of the notation of numbers on
12
13 the neural activation patterns within and outside the parietal areas (Kaufman et al., 2011).
14
15 Therefore, the multivariate results reaffirm the growing body of literature suggesting that
16
17 separate neural regions process both symbolic and non-symbolic magnitudes.
18
19
20
21

22 **Conclusion**

23
24
25 In conclusion, the current study shows limited support for the neuronal recycling
26
27 hypothesis. On the one hand, consistent with the hypothesis, univariate analyses do show
28
29 some overlap between the brain regions supporting non-symbolic and symbolic absolute
30
31 magnitudes. However, this overlap was limited to absolute (not relative) magnitudes and
32
33 dependent upon the degree of symbolic math fluency of participants. That is, we found an
34
35 increase in the adaptation effect for numbers (not fractions) as a function of math fluency
36
37 in a region of the left IPS that supports the representation of non-symbolic absolute
38
39 magnitudes. Thus, individuals with higher levels of math fluency might be able to better
40
41 recruit and recycle the IPS pathways involved in non-symbolic magnitude processing for
42
43 symbolic tasks. On the other hand, inconsistent with the neuronal recycling hypothesis,
44
45 univariate and multivariate analyses do not provide any evidence that similar IPS brain
46
47 regions support both non-symbolic and symbolic magnitudes across all participants.
48
49 Instead, we found a region of the right IPS encoding differences in format (non-symbolic
50
51 versus symbolic) across both absolute and relative magnitudes. Therefore, our study
52
53
54
55
56
57
58
59
60

1
2
3 suggests that IPS activity depends on the presentation format (non-symbolic versus
4 symbolic) more than it depends on the type of magnitude (absolute versus relative) for
5
6 most participants.
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

Acknowledgements:

We thank Franck Lambertson and Danielle Ibarrola at the CERMEP imaging centre for their help in data collection.

Funding:

This work was supported by the Région Auvergne-Rhône-Alpes- Pack Ambition Recherche 2017 under grant number 1701098001.

References

- Amalric, M., and Dehaene, S. (2016). Origins of the brain networks for advanced mathematics in expert mathematicians. *Proc. Natl. Acad. Sci. U.S.A.* 113, 4909–4917. doi: 10.1073/PNAS.1603205113
- Ansari, D. (2008). Effects of development and enculturation on number representation in the brain. *Nature reviews neuroscience*, 9(4), 278-291.
- Ansari, D., & Dhital, B. (2006). Age-related changes in the activation of the intraparietal sulcus during nonsymbolic magnitude processing: an event-related functional magnetic resonance imaging study. *Journal of cognitive neuroscience*, 18(11), 1820-1828.
- Ashburner, J., & Friston, K. J. (2005). Unified segmentation. *Neuroimage*, 26(3), 839-851.
- Barth, H., La Mont, K., Lipton, J., Dehaene, S., Kanwisher, N., & Spelke, E. (2006). Non-symbolic arithmetic in adults and young children. *Cognition*, 98(3), 199-222.
- Boysen, S. T., & Capaldi, Ô. C. EJ (1993). The development of numerical competence: animal and human models.
- Borghesani, V., de Hevia, M. D., Viarouge, A., Pinheiro-Chagas, P., Eger, E., & Piazza, M. (2019). Processing number and length in the parietal cortex: Sharing resources, not a common code. *Cortex*, 114, 17-27.
- Brannon, E. M. (2005). What animals know about numbers. *Handbook of mathematical cognition*, 381, 85-107.
- Cohen Kadosh R, Cohen Kadosh K, Kaas A, Henik A, Goebel R. 2007. Notation-Dependent and- Independent Representations of Numbers in the Parietal Lobes. *Neuron*. 53(2):307–314.

- 1
2
3 Cohen Kadosh R, Bahrami B, Walsh V, Butterworth B, Popescu T, Price CJ. 2011.
4 Specialization in the human brain: the case of numbers. *Front Hum Neurosci.*
5 5(July):62. doi:10.3389/fnhum.2011.00062.
6
7
8
9 Dehaene, S., Dehaene-Lambertz, G., & Cohen, L. (1998). Abstract representations of
10 numbers in the animal and human brain. *Trends in neurosciences*, 21(8), 355-361.
11
12
13 Demeyere, N., Rotshtein, P., & Humphreys, G. W. (2014). Common and dissociated
14 mechanisms for estimating large and small dot arrays: Value-specific fMRI
15 adaptation. *Human brain mapping*, 35(8), 3988-4001.
16
17
18
19 Damarla SR, Just MA. 2013. Decoding the representation of numerical values from brain
20 activation patterns. *Hum Brain Mapp.* 34(10):2624–34. doi:10.1002/hbm.22087
21
22
23 Bulthé, J., De Smedt, B., & de Beeck, H. O. (2014). Format-dependent representations of
24 symbolic and non-symbolic numbers in the human cortex as revealed by multi-
25 voxel pattern analyses. *NeuroImage*, 87, 311-322.
26
27
28
29 Kadosh, R. C., Kadosh, K. C., Kaas, A., Henik, A., & Goebel, R. (2007). Notation-
30 dependent and-independent representations of numbers in the parietal
31 lobes. *Neuron*, 53(2), 307-314.
32
33
34
35 DeWolf, M., Chiang, J. N., Bassok, M., Holyoak, K. J., & Monti, M. M. (2016). Neural
36 representations of magnitude for natural and rational numbers. *NeuroImage*, 141,
37 304–312. <https://doi.org/10.1016/j.neuroimage.2016.07.052>
38
39
40
41 DeWolf, M., Bassok, M., & Holyoak, K. J. (2015). Conceptual structure and the procedural
42 affordances of rational numbers: Relational reasoning with fractions and decimals.
43 *Journal of Experimental Psychology: General*, 144(1), 127–150.
44 <https://doi.org/10.1037/xge0000034>
45
46
47
48
49 Drucker, C. B., Rossa, M. A., & Brannon, E. M. (2016). Comparison of discrete ratios by
50 rhesus macaques (*Macaca mulatta*). *Animal cognition*, 19(1), 75-89.
51
52
53
54
55
56
57
58
59
60

- 1
2
3 Eckert, J., Call, J., Hermes, J., Herrmann, E., & Rakoczy, H. (2018). Intuitive statistical
4 inferences in chimpanzees and humans follow Weber's law. *Cognition*, *180*, 99-
5 107.
6
7
8
9 Eger, E., Sterzer, P., Russ, M. O., Giraud, A. L., & Kleinschmidt, A. (2003). A supramodal
10 number representation in human intraparietal cortex. *Neuron*, *37*(4), 719-726.
11
12
13 Eger E, Michel V, Thirion B, Amadon A, Dehaene S, Kleinschmidt A (2009): Deciphering
14 cortical number coding from human brain activity patterns. *Curr Biol* 19:1608–1615
15
16
17 Girard, C., Bastelica, T., Léone, J., Epinat-Duclos, J., Longo, L., & Prado, J. Nurturing the
18 mathematical brain: Home numeracy practices are associated with children's
19 neural responses to Arabic numerals, *Psychological Science*, in press.
20
21
22
23 Göbel, S. M., Johansen-Berg, H., Behrens, T., & Rushworth, M. F. (2004). Response-
24 selection-related parietal activation during number comparison. *Journal of*
25 *Cognitive Neuroscience*, *16*(9), 1536-1551.
26
27
28
29 Grill-Spector, K., & Malach, R. (2001). fMR-adaptation: a tool for studying the functional
30 properties of human cortical neurons. *Acta psychologica*, *107*(1-3), 293-321.
31
32
33
34 Holloway, I. D., Battista, C., Vogel, S. E., & Ansari, D. (2013). Semantic and Perceptual
35 Processing of Number Symbols: Evidence from a Cross-linguistic fMRI Adaptation
36 Study. *Journal of Cognitive Neuroscience*, *25*(3), 388–400.
37 https://doi.org/10.1162/jocn_a_00323
38
39
40
41 Ischebeck, A., Schocke, M., & Delazer, M. (2009). The processing and representation of
42 fractions within the brain. *NeuroImage*, *47*(1), 403–413.
43 <https://doi.org/10.1016/j.neuroimage.2009.03.041>
44
45
46
47 Cohen Kadosh, R., Bahrami, B., Walsh, V., Butterworth, B., Popescu, T., & Price, C. J.
48 (2011). Specialization in the human brain: the case of numbers. *Frontiers in*
49 *Human Neuroscience*, *5*, 62.
50
51
52
53 Jacob, S. N., & Nieder, A. (2009). Tuning to non-symbolic proportions in the human
54 frontoparietal cortex: Representation of proportions in the human brain. *European*
55
56
57
58
59
60

1
2
3 *Journal of Neuroscience*, 30(7), 1432–1442. <https://doi.org/10.1111/j.1460-9568.2009.06932.x>

4
5
6
7 Jacob, S. N., & Nieder, A. (2009). Notation-Independent Representation of Fractions in
8 the Human Parietal Cortex. *Journal of Neuroscience*, 29(14), 4652–4657.
9 <https://doi.org/10.1523/JNEUROSCI.0651-09.2009>

10
11
12
13 Kalra, P. B., Hubbard, E. M., & Matthews, P. G. (2019). Taking the Relational Structure of
14 Fractions Seriously: Relational Reasoning Predicts Fraction Knowledge in
15 Elementary School Children [Preprint]. PsyArXiv.
16 <https://doi.org/10.31234/osf.io/u3m4q>

17
18
19
20
21 Krawczyk, D. C. (2012). The cognition and neuroscience of relational reasoning. *Brain*
22 *research*, 1428, 13-23.

23
24
25 Lewis, M. R., Matthews, P. G., & Hubbard, E. M. (2016). Neurocognitive architectures and
26 the nonsymbolic foundations of fractions understanding. In *Development of*
27 *mathematical cognition* (pp. 141-164). Academic Press.

28
29
30
31 Lefavrais, P. (1967). Test de l'Alouette.

32
33
34 McCrink, K., & Wynn, K. (2007). Ratio abstraction by 6-month-old infants. *Psychological*
35 *science*, 18(8), 740-745.

36
37
38 Mock, J., Huber, S., Bloechle, J., Dietrich, J. F., Bahnmueller, J., Rennig, J., Klein, E., &
39 Moeller, K. (2018). Magnitude processing of symbolic and non-symbolic
40 proportions: An fMRI study. *Behavioral and Brain Functions*, 14(1).
41 <https://doi.org/10.1186/s12993-018-0141-z>

42
43
44
45
46 Mock, J., Huber, S., Bloechle, J., Bahnmueller, J., Moeller, K., & Klein, E. (2019).
47 Processing symbolic and non-symbolic proportions: Domain-specific numerical
48 and domain-general processes in intraparietal cortex. *Brain Research*, 1714, 133–
49 146. <https://doi.org/10.1016/j.brainres.2019.02.029>

50
51
52
53 Nieder, A. (2016). The neuronal code for number. *Nature Reviews Neuroscience*, 17(6),
54 366-382.

- 1
2
3 Piazza M, Pinel P, Le Bihan D, Dehaene S. 2007. A magnitude code common to
4 numerosities and number symbols in human intraparietal cortex. *Neuron*.
5 53(2):293–305. doi:10.1016/j.neuron.2006.11.022.
6
7
8
9 Pica, P., Lemer, C., Izard, V., & Dehaene, S. (2004). Exact and approximate arithmetic in
10 an Amazonian indigene group. *Science*, 306(5695), 499-503.
11
12
13 Peirce, J., Gray, J. R., Simpson, S., MacAskill, M., Höchenberger, R., Sogo, H., ... &
14 Lindeløv, J. K. (2019). PsychoPy2: Experiments in behavior made easy. *Behavior*
15 *research methods*, 51(1), 195-203.
16
17
18
19 Perrachione, T. K., Del Tufo, S. N., Winter, R., Murtagh, J., Cyr, A., Chang, P., ... &
20 Gabrieli, J. D. (2016). Dysfunction of rapid neural adaptation in
21 dyslexia. *Neuron*, 92(6), 1383-1397.
22
23
24
25 Roggeman, C., Santens, S., Fias, W., & Verguts, T. (2011). Stages of nonsymbolic
26 number processing in occipitoparietal cortex disentangled by fMRI
27 adaptation. *Journal of Neuroscience*, 31(19), 7168-7173.
28
29
30
31 Schwartz, F., Zhang, Y., Chang, H., Karraker, S., Kang, J. B., & Menon, V. (2021). Neural
32 representational similarity between symbolic and non-symbolic quantities predicts
33 arithmetic skills in childhood but not adolescence. *Developmental Science*,
34 desc.13123. <https://doi.org/10.1111/desc.13123>
35
36
37
38
39 Simon, O., Mangin, J. F., Cohen, L., Le Bihan, D., & Dehaene, S. (2002). Topographical
40 layout of hand, eye, calculation, and language-related areas in the human parietal
41 lobe. *Neuron*, 33(3), 475-487.
42
43
44
45 Starrfelt, R., & Gerlach, C. (2007). The visual what for area: words and pictures in the left
46 fusiform gyrus. *Neuroimage*, 35(1), 334-342.
47
48
49 Sokolowski, H. M., Fias, W., Mousa, A., & Ansari, D. (2017). Common and distinct brain
50 regions in both parietal and frontal cortex support symbolic and nonsymbolic
51 number processing in humans: A functional neuroimaging meta-
52 analysis. *Neuroimage*, 146, 376-394.
53
54
55
56
57
58
59
60

- 1
2
3 Tecwyn, E. C., Denison, S., Messer, E. J., & Buchsbaum, D. (2017). Intuitive probabilistic
4 inference in capuchin monkeys. *Animal cognition*, 20(2), 243-256.
5
6
7 Vallentin, D., & Nieder, A. (2008). Behavioral and prefrontal representation of spatial
8 proportions in the monkey. *Current Biology*, 18(18), 1420-1425.
9
10
11 Vatansever, G., Üstün, S., Ayyıldız, N., and Çiçek, M. (2020). Developmental alterations
12 of the numerical processing networks in the brain. *Brain Cogn.* 141:105551. doi:
13 10.1016/j.bandc.2020.105551
14
15
16
17 Vogel, S. E., Goffin, C., & Ansari, D. (2015). Developmental specialization of the left
18 parietal cortex for the semantic representation of Arabic numerals: An fMR-
19 adaptation study. *Developmental Cognitive Neuroscience*, 12, 61-73.
20
21
22
23 Woo, C. W., Krishnan, A., & Wager, T. D. (2014). Cluster-extent based thresholding in
24 fMRI analyses: pitfalls and recommendations. *Neuroimage*, 91, 412-419.
25
26
27
28 Woodcock, R. W., Mather, N., McGrew, K. S., & Wendling, B. J. (2001). Woodcock-
29 Johnson III tests of cognitive abilities.
30
31
32 Woodruff, G., & Premack, D. (1981). Primate mathematical concepts in the chimpanzee:
33 proportionality and numerosity. *Nature*, 293(5833), 568-570.
34
35
36
37 Wilkey, E. D., & Ansari, D. (2019). Challenging the neurobiological link between number
38 sense and symbolic numerical abilities. *Ann. NY Acad. Sci*, 40, 1-23.
39
40
41 Xu, F., Spelke, E. S., & Goddard, S. (2005). Number sense in human
42 infants. *Developmental science*, 8(1), 88-101.
43
44
45 Yeo, D. J., Wilkey, E. D., and Price, G. R. (2017). The search for the number form area: a
46 functional neuroimaging meta-analysis. *Neurosci. Biobehav. Rev.* 78, 145–160.
47 doi: 10.1016/j.neubiorev.2017.04.027
48
49
50
51
52
53
54
55
56
57
58
59
60

Supplementary Table 1. Stimuli used for Relative and Absolute Magnitudes

Block	Relative Magnitude
No-Adapt	$\frac{2}{6}, \frac{3}{7}, \frac{11}{32}, \frac{9}{17}, \frac{7}{9}, \frac{2}{7}, \frac{11}{70}, \frac{5}{48}$
No-Adapt	$\frac{2}{4}, \frac{12}{15}, \frac{6}{17}, \frac{16}{26}, \frac{2}{15}, \frac{16}{54}, \frac{13}{28}, \frac{5}{6}$
Adapt_1:3	$\frac{1}{3}, \frac{4}{12}, \frac{6}{19}, \frac{3}{9}, \frac{8}{25}, \frac{2}{7}, \frac{5}{15}, \frac{7}{22}$
No Adapt	$\frac{14}{15}, \frac{11}{32}, \frac{1}{8}, \frac{13}{27}, \frac{34}{62}, \frac{7}{26}, \frac{12}{39}, \frac{7}{11}$
No Adapt	$\frac{15}{19}, \frac{1}{4}, \frac{14}{35}, \frac{8}{13}, \frac{12}{31}, \frac{5}{18}, \frac{3}{23}, \frac{8}{10}$

Adapt_1:6	$\frac{2}{12}, \frac{1}{6}, \frac{8}{48}, \frac{6}{36}, \frac{4}{24}, \frac{3}{17}, \frac{5}{29}, \frac{7}{41}$
Adapt_1:5	$\frac{1}{5}, \frac{3}{15}, \frac{5}{26}, \frac{8}{40}, \frac{2}{11}, \frac{6}{30}, \frac{4}{21}, \frac{7}{35}$
No Adapt	$\frac{3}{5}, \frac{15}{19}, \frac{7}{14}, \frac{8}{62}, \frac{4}{21}, \frac{9}{19}, \frac{45}{68}, \frac{4}{37}$
Adapt_2:3	$\frac{8}{12}, \frac{6}{9}, \frac{2}{3}, \frac{10}{16}, \frac{4}{7}, \frac{12}{18}, \frac{14}{22}, \frac{16}{24}$
Adapt_2:5	$\frac{4}{10}, \frac{8}{19}, \frac{14}{35}, \frac{6}{15}, \frac{2}{5}, \frac{12}{29}, \frac{10}{25}, \frac{16}{39}$
Adapt_3:5	$\frac{3}{5}, \frac{6}{10}, \frac{15}{25}, \frac{18}{31}, \frac{9}{16}, \frac{12}{21}, \frac{24}{40}, \frac{21}{35}$

No Adapt	$\frac{1}{3}, \frac{21}{67}, \frac{5}{24}, \frac{3}{16}, \frac{24}{54}, \frac{5}{8}, \frac{3}{5}, \frac{1}{8}$
Adapt_2:9	$\frac{2}{9}, \frac{4}{18}, \frac{8}{35}, \frac{6}{26}, \frac{10}{45}, \frac{12}{54}, \frac{14}{63}, \frac{16}{71}$
No Adapt	$\frac{8}{9}, \frac{11}{14}, \frac{3}{8}, \frac{14}{41}, \frac{2}{5}, \frac{21}{33}, \frac{2}{3}, \frac{8}{19}$
Adapt_3:7	$\frac{18}{41}, \frac{6}{14}, \frac{3}{7}, \frac{9}{20}, \frac{12}{28}, \frac{15}{34}, \frac{21}{49}, \frac{24}{55}$
Adapt_1:4	$\frac{2}{8}, \frac{3}{11}, \frac{5}{19}, \frac{8}{31}, \frac{1}{4}, \frac{6}{23}, \frac{4}{16}, \frac{7}{28}$

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

No Adapt	$\frac{4}{9}, \frac{16}{18}, \frac{15}{35}, \frac{2}{6}, \frac{13}{31}, \frac{8}{9}, \frac{12}{34}, \frac{11}{27}$
Adapt_2:7	$\frac{2}{7}, \frac{4}{14}, \frac{6}{22}, \frac{8}{28}, \frac{10}{35}, \frac{12}{43}, \frac{14}{49}, \frac{16}{57}$
No Adapt	$\frac{21}{66}, \frac{3}{4}, \frac{2}{26}, \frac{13}{23}, \frac{5}{5}, \frac{9}{11}, \frac{7}{17}, \frac{14}{36}$
No Adapt	$\frac{5}{9}, \frac{15}{29}, \frac{14}{31}, \frac{3}{8}, \frac{2}{16}, \frac{34}{62}, \frac{11}{12}, \frac{1}{24}$

Block	Absolute Magnitudes
Adapt	8, 6, 8, 10, 8, 7, 8, 9
Adapt	23, 26, 25, 26, 24, 26, 21, 26
Adapt	11, 14, 16, 11, 12, 11, 17, 11
Adapt	33, 31, 36, 31, 32, 31, 35, 31
Adapt	6, 5, 4, 6, 3, 6, 7, 6
Adapt	23, 25, 26, 23, 23, 24, 23, 27
Adapt	53, 52, 55, 52, 54, 52, 56, 52
Adapt	9, 8, 5, 9, 7, 9, 11, 9
Adapt	3, 5, 3, 4, 3, 6, 3, 2
Adapt	16, 17, 15, 16, 16, 13, 16, 11
No Adapt	5, 14, 33, 2, 9, 17, 6, 10
No Adapt	19, 4, 35, 44, 6, 18, 3, 10
No Adapt	3, 10, 32, 6, 15, 8, 25, 9
No Adapt	2, 13, 7, 14, 20, 11, 25, 39
No Adapt	8, 29, 17, 54, 16, 9, 36, 5
No-Adapt	32, 6, 18, 3, 17, 7, 22, 11
No-Adapt	4, 18, 22, 5, 34, 9, 7, 62
No-Adapt	1, 14, 7, 28, 4, 40, 16, 37
No-Adapt	36, 18, 2, 6, 16, 35, 8, 21
No-Adapt	1, 16, 25, 18, 9, 4, 33, 2