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Characterizing the neural coding of symbolic quantities

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ABSTRACT

How the brain encodes abstract numerical symbols is a fundamental question in philosophy and cognitive neuroscience alike. Here we probe the nature of symbolic number representation in the brain by characterizing the neural similarity space for symbolic quantities in regions sensitive to their semantic content. In parietal and occipital regions, the similarity space of number symbols was positively predicted by the lexical frequency of numerals in parietal and occipital areas, and was unrelated to numerical ratio. These results are more consistent with a categorical, frequency-based account of symbolic quantity encoding. In contrast, the similarity space of analog quantities was positively predicted by ratio in prefrontal, parietal and occipital regions. We thus provide an explanation for why previous work has indicated that symbolic and analog quantities are distinct: number symbols operate primarily like discrete categories sensitive to input frequency, while analog quantities operate more like approximate perceptual magnitudes. In addition, we find substantial evidence for related patterns of activity across formats in prefrontal, parietal and occipital regions. Crucially however, between-format relations were not specific to individual quantities, indicating common processing as opposed to common representation. Moreover, evidence for between-format processing was strongest for quantities that could be represented as exact, discrete values in both systems (quantities in the 'subitizing' range: 1–4). In sum, converging evidence presented here indicates that symbolic quantities are coded in the brain as discrete categories sensitive to input frequency and largely independent of approximate, analog quantities.

Introduction

How the brain represents discrete, symbolic forms and the relationship between these representations to approximate, analog (continuous, perceptually grounded) forms are long-standing questions in the cognitive and neural sciences (e.g., Peirce, 1955; Harnad, 1990). Views on these questions are manifold, though they can perhaps be broadly distilled into two general perspectives. From one perspective, symbolic representational systems fundamentally derive their meaning and structure from an analog counterpart, with the former thus being firmly ‘grounded in’ or ‘embodied by’ the latter (e.g., Varela et al., 1991; Pulvermüller, 2013). In general, this more extensional view of symbolic representation places emphasis on understanding the organizational structure of analog representations and the mechanisms that link them to their corresponding symbolic forms. The second perspective posits that true symbolic systems are primarily determined by the relations between the symbols within the system, perhaps even at the expense of weakened links to analog perceptual grounding (e.g., Deacon, 1997). From this perspective, the primary challenge is in mapping the (often largely independent) associative relations between symbols that uniquely define a given symbolic system.

In the current paper, we take up the challenges posed by both perspectives in a domain where the symbolic/analog debate is especially salient: how the brain represents symbolic numbers. Specifically, we use representational similarity analyses (RSA) to characterize the neural similarity space of the set of single-digit Indo-Arabic numbers. We thus tested how different properties predicted this neural similarity space, and how this pattern of results aligned with the two theoretical views of symbolic representation outlined above. We also computed the neural similarity space of the same set of quantities presented as approximate, analog magnitudes. This allowed us to compare whether the same properties predict symbolic and analog similarity spaces in order to test whether quantities in the two formats are organized in parallel fashion. Furthermore, we assessed the manner and extent to which the neural patterns elicited by symbolic and analog quantities may be directly related. Does the neural pattern elicited by ●●● strongly predict that

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elicited by ‘3’, as suggested by a perceptually grounded view of symbolic representation; or are the patterns largely unrelated, indicating weakened symbolic-analog links, as suggested by a more relational or association-based view of symbolic representation?

Humans have the capacity to represent and manipulate quantities (cardinal values) in both symbolic form (Indo-Arabic numerals) and analog form (as in concrete sets of dots or objects; note that analog quantities are sometimes referred to as ‘nonsymbolic’ quantities) (Buckley & Gilman, 1974). Views on quantity representation broadly mirror the two perspectives outlined above, with some emphasizing a close, extensional link between symbolic and analog quantity systems; for instance: “When we learn number symbols, we simply attach their arbitrary shapes to the relevant nonsymbolic quantity representations” (Dehaene, 2008). Indeed, over the last several decades, it is perhaps fair to say this was the more dominant view among researchers in the field of numerical cognition, with the general sentiment echoed many times over (e.g., Dehaene, 1997, 2008; Feigenson et al., 2004, 2013; Lyons and Ansari, 2009; Nieder and Dehaene, 2009; Piazza et al., 2007). Meanwhile, others have suggested that numerical symbols are chiefly defined by their associations with other numerical symbols; for instance: “Symbolic reference is crucially a link between sign-sign relations, not between individual sign-object relations” (Nieder, 2009). And in a recent proposal, Núñez (2017) made the property ‘is relational’ a minimal defining criterion of symbolic numbers. Some support for this view has emerged in that symbolic representations of quantity appear to be largely distinct (and possibly even independent) from analog representations of quantity (e.g., Bulthé et al., 2014, 2015; Cohen Kadosh et al., 2011; Damarla and Just, 2013; Lyons et al., 2012, 2015a; for a comprehensive review, see Knops, 2017). Comparatively very little evidence has revealed precisely how number symbols are associated with one another, however, especially at the neural level.

Numerical similarity spaces: characterizing within-format quantity-quantity relations

There is strong evidence that analog representation of quantity is driven by overlapping neural tuning curves whose width increase with the quantity being represented (larger quantities have wider tuning curves, roughly in keeping with Weber's law; e.g., Piazza et al., 2004; Nieder, 2005; Merten and Nieder, 2009). This means that the neural similarity space of analog quantities should be strongly predicted by numerical ratio: the pattern of neural responses for two quantities whose ratio is close to 1 (e.g., 8:9) will be more similar than two quantities whose ratio is further from 1 (e.g., 1:2). This is precisely what Lyons et al. (2015a) found. On the other hand, the properties determining the neural similarity space of symbolic numbers remains largely unknown. Indeed, what evidence we have strongly suggests that similarity space of symbolic quantities does not follow this same ratio-dependent pattern that analog quantities do (Lyons et al., 2015a). However, this is essentially a negative statement, leaving largely unanswered the question: what properties *do* predict the neural similarity space of symbolic quantities?

One possibility is that symbolic quantities operate less as approximate distributions in the form of tuning curves, but more as truly *discrete* (if still ordered) categories (Núñez, 2017). If so, then – in contrast to approximate, analog quantities – the symbolic similarity space should be largely insensitive to numerical ratio due to minimally overlapping representations of even adjacent quantities. Another potential source of neural similarity is relative *frequency* – specifically, frequency of co-occurrence. Perhaps crucial, then, is the fact that smaller symbolic quantities in the form of number words and written numerals are encountered more frequently in the lexicon than are larger symbolic quantities (Dehaene and Mehler, 1992). When we learn to count, we usually start with smaller quantities (Wynn, 1990), and thus ordinal relations between smaller quantities are rehearsed more frequently than those between larger quantities (Lyons and Ansari, 2015). Thus, not only do we encounter 3 and 4 more often than 7 and 8, we encounter 3 and 4 *together* more often than we do 7 and 8. A frequency-based account would predict higher similarity for higher joint frequency (a positive relation between frequency and similarity). By extension, this view also predicts smaller quantities should show greater neural similarity to one another than larger quantities – e.g., greater similarity between 3 and 4 than between 7 and 8. Note that this stands in opposition to analog quantities, where wider tuning curves for larger quantities would predict greater similarity between larger quantities, as discussed above. Taken together with the (hypothesized) lack of relation between symbolic similarity and the numerical ratio between two number symbols, such a pattern of results would be consistent with the notion that symbolic quantities operate more like distinct categories that are sensitive to the relative frequency with which they are encountered. Said pattern of results would also dovetail with the heavy emphasis placed on the associative nature of symbolic representation by some theorists (Deacon, 1997; Nieder, 2009; Núñez, 2017).

Relations between symbolic and nonsymbolic quantities

A second key question that arises when attempting to describe how the brain encodes number symbols concerns the extent to which symbolic and analog quantities are directly related to one another, in that the neural pattern for a quantity or set of quantities in one format may be related to the neural pattern seen for quantities in the other format. Note that this question is independent of the preceding discussion about within-system similarity spaces: while the within-system relations between quantities may follow different organizing principles, there may nevertheless be important links between systems. For instance, branches of the same company might operate in different countries with radically different political and social organization. There are multiple ways to think about direct links between symbolic and analog quantity systems, however, which make different predictions with respect to neural similarity. Perhaps the most straightforward view focuses on the representational level, by proposing that a general neural pattern (‘three-ness’) might be shared across two different systems (symbolic and analog). Dehaene's quote above (“When we learn number symbols, we simply attach their arbitrary shapes to the relevant nonsymbolic quantity representations,” Dehaene, 2008) perhaps most succinctly characterizes this view. This representation-based view predicts that the neural similarity between formats should be particularly high when looking at the *same quantity* (e.g., the similarity between ‘3’ and ●●● should be higher than the similarity between ‘3’ and ●, ●●, ●●●●, and so on).

An alternative view is that quantities may be *processed* via a common mechanism, but that this mechanism is largely agnostic to the *specific* quantity in question. For instance, general attentional or working memory mechanisms might be agnostic to the type of numerical input, processing all such quantities in a similar fashion. As such, the direct relations between systems (in terms of patterns of neural activity) may not be quantity specific. The relation between ‘3’ and ●●● may be no different than the relations between ‘3’ and ●, ‘3’ and ●●, ‘3’ and ●●●●, and so on. However, this view would nevertheless still predict that between-format similarity should overall be positive (greater than 0).

The role of subitizing

A third important point to consider is the specific set of quantities in question. A prominent theory of children's numerical development posits that early acquisition of number symbols is bootstrapped from nonverbal (nonsymbolic) quantity processing, but specifically for the limited range of small quantities that the visual system is capable of representing discretely – i.e., those in the ‘subitizing’ range, 1–4 (Le Corre and Carey, 2007; Carey, 2011; Carey et al., 2017). Moreover, behavioral evidence demonstrating estrangement between symbolic and analog quantity processing is significantly weaker for quantities within the subitizing range (Lyons et al., 2012). Thus, in assessing similarity in neural patterns between symbolic and analog quantities, it may be critical to consider whether the quantities in question are within the subitizing range or not. In particular, one might predict common representation (quantity-specific similarity) may be higher within versus outside the subitizing range. Alternatively, nonsymbolic quantities within the subitizing range can be processed in exact, discrete fashion (Trick and Pylyshyn, 1994; Revkin et al., 2008). Hence, one might instead predict common processing within a general mechanism such as short-term memory or visual attention that is specific to subitizable quantities, but agnostic with respect to the specific quantity therein. This view would predict between-format similarity to be particularly strong for quantities within the subitizing range, but in a manner that does not distinguish between whether the two inputs indicate the same quantity (the neural pattern for ‘3’ is equally related to that of ●●, ●●● and ●●●●).

Current study

In the present study we sought to characterize the nature of symbolic number representation in the brain. Specifically, we adopted a representational similarity analysis (RSA) approach (using human fMRI data) in which one computes the similarity of spatially distributed activity patterns between two conditions in a given section of cortex (Kriegeskorte et al., 2008). This approach allows one to assess the relative similarity in cortical processing for a large set of conditions by mapping the ‘similarity space’ that defines the pairwise relations between all conditions in the set. This similarity space can then be tested against predictions based on various assumptions or models (Davis and Poldrack, 2013).

Here, we sought to characterize the relational structure of symbolic quantities by assessing (1) which numerical properties (such as ratio and frequency, Fig. 1b–c) predict the neural similarity space elicited by processing individual[1] number symbols (Fig. 1a, region outlined in blue). We also assessed (2) whether these properties parallel those of analog quantities (Fig. 1a, region outlined in red), and (3) whether the similarity space within one format predicts that of the other (Fig. 1a, region outlined in green/turquoise). Furthermore, (4) we tested for direct relations between the same quantity in different formats by assessing how the neural pattern for a given quantity in one format relates to the same quantity in the other format (common representation, e.g., ‘3’ to ●●●; Fig. 1a, turquoise diagonal). We also tested (5) for more general common processing between systems – i.e., a consistent relation between neural patterns but in a quantity-agnostic manner (e.g., ‘3’ relates equally to ●, ●●, ●●●, ●●●●, etc.; Fig. 1a, off-diagonal section outlined in green). We also assessed (6) whether the degree of between-format similarity depends on whether the quantities in question can be represented discretely (i.e., within the ‘subitizing’ range, 1–4; Fig. 1a, pink/purple and yellow/orange outlines). Finally, to narrow functional interpretation of the RSA results, we examined the above in all regions that showed systematic sensitivity to relative quantity.

Methods

Participants

Participants were 33 right-handed neurologically normal University of Chicago students (16 female, mean age = 20.03yrs).

Procedure

All procedures were approved for use with human subjects by the University of Chicago Institutional Review Board (IRB). The data analyzed here were taken from a larger data collection project (Lyons and Beilock, 2013; Lyons et al., 2015a) spanning multiple scanning sessions; results here are not reported elsewhere and address a unique set of hypotheses. The data reported here were from 6 functional runs from the same scanning session. The high-resolution anatomical scan was acquired halfway through the functional runs; this allowed participants a brief rest and reduced the maximum amount of spatial discrepancy between the anatomical and functional runs.

Task and stimuli

During scanning, participants completed 6 runs of a delayed match-to-sample (DMS) task adapted from single-cell studies with monkeys that have been successful in detailing numerical tuning curves for individual neurons (see Nieder, 2005, Fig. 2c; see also Lyons et al., 2015a, Fig. 2). In the current version, participants first saw a quantity for 500msec followed by a jittered delay (1.5–5.5sec). A second quantity was then presented for 500 msec, after which the screen went blank for 2500msec or until the participant responded. Fixation time between response on a given trial and the initial stimulus onset for the subsequent trial was also jittered (1.9–8.4sec). Participants' task was to determine if the two quantities were numerically equal or different by pressing one of two buttons with their two index fingers. Which button meant same or different was randomized across participants. The two numbers were numerically equal on 50% of trials (match); the second number was greater than the first on 25% of trials (nonmatch) and less than the first on 25% of trials (nonmatch). For numerals, font style was randomized for symbolic trials to reduce the efficacy of visual pattern-matching. Note that the short presentation time of both stimuli reduced the likelihood that participants counted the dots in the dot-arrays. Continuous parameters (dot-size, array contour, density, aggregate area) were balanced across analog trials, such that each parameter was correlated with quantity on half the trials, and anti-correlated on the remaining half. This was intended to reduce the efficacy of relying on any one parameter to compare quantities in the analog task.

The quantities to be held in mind during the delay period (between the first and second quantities) were the integers 1–9. Participants saw eighteen trials for each quantity; in nine of these trials, quantities were presented as numerals (symbolic format); in the other nine, quantities were presented as dot-arrays (analog format). The second stimulus always matched the first in terms of format. Trial order (including quantity and format) was randomized across participants. To increase the precision of our estimate for a given voxel's activity for a given quantity, activity across the nine trials (for each participant) was averaged together. Our focus was on activity during the first stimulus and the delay before the onset of the second stimulus, as this allowed for a measure of neural activity during representation of a single quantity, independent of activation related to preparation and execution of a specific motor response. Activity during the second stimulus and response was modeled as a covariate of no interest to remove response-related variance according to the duration of the response (which optimizes model fit and implicitly controls for trial-by-trial variability in response times[2]; Grinband et al., 2008; Yarkoni et al., 2009; Motes et al., 2017).

MRI analysis

Acquisition and preprocessing

Data were collected on a 3T Philips Achieva scanner using an 8-channel Philips SENSE head-coil. 36 descending interleaved slices were collected at a TR of 2sec (TE = 25 msec), with a slice-thickness of 3.0 mm (0.25 mm skip), an in-plane resolution of 2.875 × 2.875 mm (80 × 80 matrix), and a flip-angle of 80°. Prior to analysis, time-series were

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[1] Neural patterns were estimated when participants were processing only one quantity at a given time and prior to the onset of response demands.

[2] This approach causes some variability in run duration, though said variability here was minor: range = 142 to 156 TRs, mean = 143.2, median = 143, sd = 1.18; 96% of all runs fell between 142 and 147 TRs. Results did not differ if the 4% of runs with 148 or more TRs were omitted.

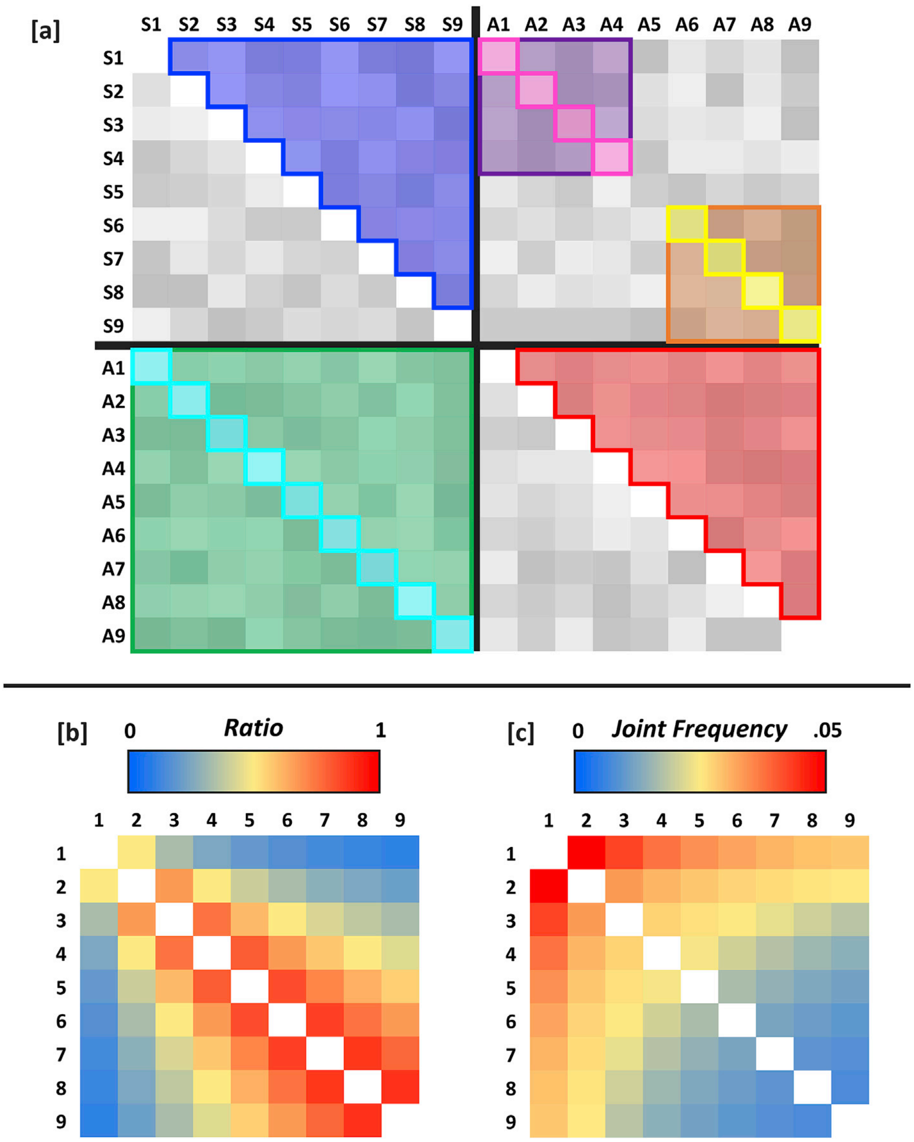

Fig. 1. **[a]** gives a sample similarity matrix with subsections highlighted to indicate which analyses they were used in. Blue: Symbolic within-format analyses; Red: Analog within-format analyses; Green: different-quantity between-format similarity; Turquoise: same-quantity between-format similarity; Purple: between-format similarity for small quantities (pink indicates same-quantity); Orange: between-format similarity for large quantities (yellow indicates same-quantity). Each cell indicates the correlation between each pair of quantities in the indicated format(s). 'S' indicates Symbolic; 'A' indicates Analog; the number indicates quantity. The variations in shading simulate variations in similarity values; they are not real data. Note that the overall matrix is symmetrical over the main diagonal; hence it is arbitrary whether one extracts data from the upper or lower triangle. Fig. 1 **[b]** and **[c]** show predicted similarity matrices for Ratio and Frequency, respectively.

corrected for slice-timing and subject motion, and then subjected to a high-pass temporal filter (GLM Fourier basis set). No spatial smoothing was used. Data were next submitted to a random-effects GLM (Friston et al., 1994) convolved using a standard 2-gamma HRF model. Preprocessing and whole-brain RFX univariate analyses were conducted using BrainVoyager 20.4); ROI-based analyses (univariate and RSA) were conducted using Matlab.

Regions of interest (ROIs)

One of the central goals of this study was to characterize the respective neural similarity spaces for symbolic and analog quantities (via RSA), within regions that demonstrate systematic sensitivity to relative quantity. ROIs were identified in three steps. First, we identified regions that showed a significant main effect of quantity via a whole-brain univariate ANOVA [2(Format: symbolic, analog) × 9(Quantity: 1–9)]. RSA operates by computing correlations over voxels within an ROI, so ensuring a reasonable minimum number of voxels (i.e., a minimum number of observations) per ROI is important for ensuring meaningful correlation estimates. For this reason, the statistical map was thresholded voxelwise at $p < .005$, and subsequently cluster-level corrected for multiple-comparisons using a Monte-Carlo simulation procedure (Forman et al., 1995) at $\alpha < .01$. The slightly more liberal voxelwise and more conservative cluster-level thresholds emphasized larger ROIs; however, all ROIs that survived this threshold also survived the more conventional (Cunningham and Koscik, 2017; Slotnick, 2017) threshold of $p < .001$, $\alpha < .05$. Second, we split very large ROIs into smaller, anatomically more sensible smaller ROIs. While overly small ROI sizes are problematic for RSA as noted above, overly large ROIs that span substantially different sections of cortex can also prove difficult to interpret. To balance this concern, very large bilateral ROIs spanning intraparietal, occipital and ventral-posterior temporal cortices were split into 5 sub-clusters in each hemisphere using a standard k-means clustering algorithm (Lloyd, 1982; as implemented via the kmeans function in Matlab using squared Euclidean distance). Importantly, only anatomical coordinate information was used for clustering purposes so that clustering was independent of specific functional activity patterns. This broke the superclusters into IPSa, IPSp, POJ, OCCp, and TOJv (see Fig. 2 for abbreviations). In addition, a large midline prefrontal region clearly spanning ACCdp and PreSMA were split into 2 sub-clusters using the same approach.

Recall that the primary purpose of the ROI-identification process was to ensure RSA results obtained in regions that demonstrated systematic sensitivity to relative quantity. Therefore, third, within each resulting ROI, we verified that each ROI showed a significant linear contrast effect

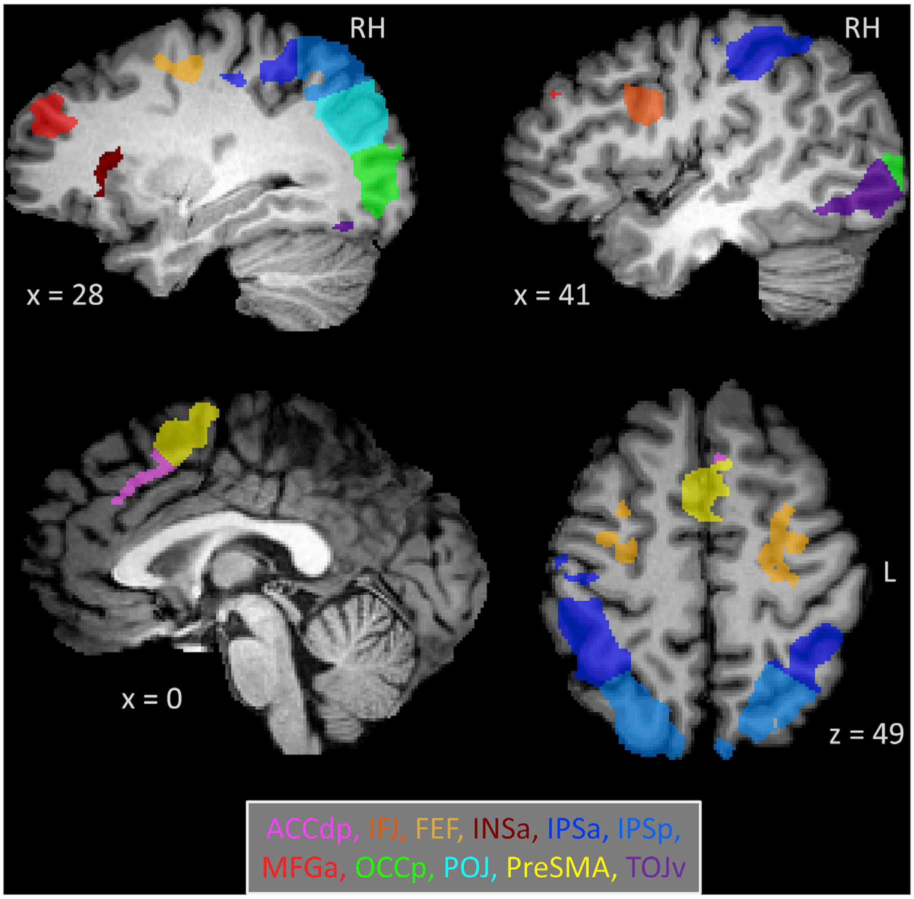

Fig. 2. Visualizes regions that showed a significant main effect of Quantity at the whole-brain level. These regions also comprised the ROIs that were used for subsequent ROI-based analyses. See Table 1 for region details. Abbreviations: ACCdp: dorso-posterior anterior cingulate cortex, FEF: frontal eye-fields, IFJ: inferior frontal junction, INSa: anterior insula, IPSa: anterior intraparietal sulcus, IPSp: posterior intraparietal sulcus, MFGa: anterior middle frontal gyrus, OCCp: posterior occipital cortex, POJ: parietal-occipital junction, PreSMA: pre-supplementary motor area, TOJv: ventral temporal-occipital junction.

in both formats.[3] A main effect with 9 levels might be driven by any number of patterns, so this step provided crucial verification that modulation of activity by quantity followed a systematic pattern, such that activity increased (or decreased) as a function of input quantity. This step also served as a kind of manipulation check in that it helped guard against the notion – especially in the case of symbolic quantities – that participants may have solved the behavioral portion of the task via simple pattern matching. Systematic modulation of activity as a function of the symbolic quantity represented strongly suggests participants were indeed processing the semantic content of the numerical symbols. Furthermore, assessing a linear trend is made all the more important by the fact that, in the current case, 'baseline' (a beta of 0) corresponds to average activity across all runs (for that subject in that voxel). In the case of a linear trend with increasing quantities, higher quantities will, by necessity, show activity 'above baseline' and lower quantities will show activity 'below baseline'. Hence, for current purposes, a linear contrast was seen as the more informative criterion, rather than, say, contrasting mean activity across all quantities against 0 (baseline).

When reporting all ROI-based results (both univariate and RSA), we provide two statistical thresholds – the more traditional $p < .05$, and a more stringent threshold of $p < .0027$. This latter value was determined by correcting for multiple comparisons using the Dunn-Šidák (1967) method assuming 19 comparisons (for the 19 ROIs revealed in the univariate analyses – see Table 1 in the Results below). Note that this correction is intended for situations where one's focus is on whether any *single* result may have been the result of chance. The .0027 threshold is thus likely overly conservative in the present case (i.e., we would not necessarily advise discounting every result that fails to pass this stricter threshold) because we are concerned here more with the overall pattern of results (e.g., do the majority of parietal regions show pattern X versus pattern Y) rather than with the significance of a single region in isolation. Nevertheless, we provide information about this more conservative threshold as it provides greater context for interpreting the strength of the various effects. Finally, to maximize generalizability, critical statistics are reported as effect-sizes (Cohen's *d*) wherever possible.

Representational similarity analysis (RSA)

In the present study, for each voxel in each participant, we extracted 19 different values from the RFX GLM. These were activity levels for the symbolic and analog quantities 1–9, and a measure of baseline activity (average activity for that subject and that voxel[4]). In all RSA analyses, baseline activity was included as a covariate (hence, all RSA results reported here are based on partial-correlations). This is because adjacent voxels will share vascular, neural, and imaging elements (e.g., field strength) that may create the appearance of very high correlations across voxels due largely to sources unrelated to the functional elements of interest here (numerical processing). Covarying out baseline activity is a

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[3] One might remark that the primary focus of this study is on symbolic quantities, so ROIs should not require sensitivity to quantity for analog quantities as well. Thus, it is important to note that there were no regions outside of the set considered in Fig. 2 that showed a significant main effect of quantity for just symbolic quantities.

[4] These may be understood as deflections from the global mean (across all voxels and all subjects) specific to that voxel and that subject, which are a natural consequence of treating individual voxels independently and each subject as a random influence under the assumptions of the whole-brain, random-effects GLM (Friston et al., 1994). In this way, the 'baseline' vector for each subject across voxels controls for idiosyncratic – but potentially systematic – correlations in activity between voxels that may have little to do with the activity evoked by the stimuli of interest.

Table 1

Anatomical details for regions showing a main effect of quantity. Coordinates are centers of gravity. The number of voxels for each region is given in terms of functional voxels (3 mm on a side, 27 mm^3). See Fig. 2 for abbreviations and region visualization.

ROI	Tal. Coordinates			Voxels	ROI	Tal. Coordinates			Voxels
	x	y	z			x	y	z	
RIPSa	36.9	−36.1	46.2	251	ACCdp	3.9	15.6	39.2	94
LIPSa	−33.5	−39.4	45.7	125	PreSMA	0.1	5.5	51.5	105
RIPSp	21.0	−64.4	46.8	310	RINSa	30.6	19.9	8.0	33
LIPSp	−19.3	−62.1	49.3	204	RMFGa	28.8	41.9	27.1	84
RPOJ	28.5	−71.9	26.8	202	LMFGa	−25.6	42.9	29.8	17
LPOJ	−23.9	−74.1	26.6	206	RIFJ	45.7	5.8	27.5	110
ROCCp	27.9	−80.1	4.9	247	LIFJ	−43.6	−1.1	34.6	51
LOCCp	−25.8	−83.0	1.2	254	RFEF	25.9	−5.1	48.2	54
RTOJv	41.4	−66.2	−3.8	145	LFEF	−25.1	−10.1	51.4	66
LTOJv	−38.9	−69.4	−2.6	145					

statistical means of reducing the influence of those elements of no interest (Lyons et al., 2015a). Within each ROI, a partial-r was computed for each pair of quantities. The resulting matrix of r-values thus mapped the 'similarity spaces' defining symbolic ~ symbolic, analog ~ analog and between-format (symbolic ~ analog) coding (see Fig. 1a). This was done separately for each of the 33 subjects. Because r-values are non-normally distributed, r-values were next transformed using Fisher's z-transformation: $z = \text{arctanh}(r)$. All relevant statistics were then computed using these z-values as inputs. Results are reported in figures as effect-sizes (d), with traditional statistical thresholds also indicated. Means and standard errors for these z-values can be found in Supplementary Information (Tables S1–S7). Voxelwise data for all 19 ROIs can be found at https://osf.io/d645p/.

Predictive properties

The two main properties we used to predict pairwise neural similarity for symbolic and analog quantities were Ratio and Frequency. Ratio was defined as the ratio between two quantities, where $Ratio = \frac{\min(n_1,n_2)}{\max(n_1,n_2)}$.

To estimate joint frequency, one can start with frequency estimates of individual numbers. We took these from Benford's law: $p = \log_{10}(n+1) - \log_{10}(n)$, which describes the probability of encountering written (Indo-Arabic) digits as they appear in the left-most position of a given number (Benford, 1938). The lattermost assumption is introduced to account for the fact that larger written numbers tend to be rounded to the nearest decade, century, etc., and rounded values follow frequency patterns that closely mirror those seen for singleton digits (1, 2, …9). For data that nicely conform to Benford's law from more modern lexical corpi (including the rounding assumption), as well as a detailed treatment and discussion of the source of Benford's law, see Dehaene and Mehler (1992). In short, Benford's law gives one the probability of encountering a given digit, which decreases in a power-law manner as quantity increases. One can then estimate joint frequency by multiplying the probabilities of two quantities together. Fig. 1c illustrates the joint frequency matrix for 1–9. This matrix can then be vectorized and used to predict pairwise similarity values, just as with Ratio.[5]

Two additional numerical properties are commonly assessed in the literature: numerical Size and Distance, where $Size = \text{mean}(n_1, n_2)$, and $Distance = \text{abs}(n_1 - n_2)$. It is important to note that Size is strongly negatively correlated with Frequency ($r = -.84$ for quantities 1–9), as is Distance with Ratio ($r = -.84$ for quantities 1–9). For this reason, while we include results for Size and Distance in Supplementary Information (Figures S1-S3, Tables S6-S7), we would expect results to be highly similar (just reversed) for Frequency and Size, and for Ratio and Distance. This is indeed the case, though careful scrutiny reveals slightly higher overall (absolute) fit in most regions for Frequency relative to Size, and for Ratio relative to distance, indicating that indeed Frequency and Ratio may be the optimal means of characterizing categorical and tuning-curve-based quantity coding, respectively.

Results

Regions responsive to quantity (univariate results)

We identified regions that were systematically sensitive to relative quantity in both symbolic and analog formats. First, using a whole-brain approach, we identified regions that showed a main effect of quantity in a 2(Format: symbolic, analog) × 9(Quantity: 1–9) ANOVA at the whole-brain level ($p < .005$, $\alpha < .01$). Second, within each ROI, we then verified that this main effect was characterized by a significant linear contrast effect for each format separately. In this way, we ensured that a given ROI showed linearly increasing activity as quantity increased, and that this effect was present for both symbolic and analog formats.

Regions showing a whole-brain main-effect of quantity are shown in Fig. 2; regions are colored to reflect the delineations described in the Methods section, and match the ROI-specific color-scheme used in the remaining figures showing univariate and RSA results (Figs. 3–8). Region details are summarized in Table 1. Though not of immediate relevance given the main goals of this paper, it is perhaps interesting that only one region showed a significant Format × Quantity interaction at the whole-brain level: left PreSMA (Talairach: −6, 12, 46; 27 voxels). Perhaps most remarkable is the relative dearth of regions showing an interaction, especially given 9 levels of Quantity in the model. This suggests that, for the majority of the brain, wherever one finds modulation of activity based on quantity for one format, one is likely to find similar modulation for the other format as well.

ROI verification

Because a main effect with multiple levels (nine, in the case of quantity) may be driven by a wide range of patterns, within each of the ROIs identified in the previous section (Fig. 2, Table 1), we tested for a significant linear contrast effect of quantity. This pattern would indicate systematic sensitivity to quantity with neural responses increasing (or possibly decreasing) with increasing quantity. To ensure that each ROI was sensitive to quantity in both formats (symbolic and analog), we assessed linear contrast effects in each format separately. ROI analyses were conducted by averaging activity estimates for each condition across all voxels in the ROI for each participant, with statistics computed across subjects ($N = 33$). Linear contrast results are given in Table 2. Mean activity values along with linear trend-lines are plotted in Fig. 3.

As can be seen in Table 2, there was a significant linear contrast effect

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[5] Frequency and Ratio predictors were correlated at −.41, though this degree of collinearity is not extreme by most accounts: The variance inflation factor (VIF) associated with these two vectors is 1.21, which is well within the acceptable range of VIF<10 (Kutner et al., 2004), and even the more conservative range of VIF<5 (Sheather, 2009). Furthermore, our primary theoretical interest was less with comparing Frequency and Ratio than with comparing the relative fits across formats (comparing symbolic fit against analog fit for, say, Frequency).

Table 2
Linear contrast results for each ROI, given as effect-sizes (Cohen's *d*). Values significant at $p < .0027$ are in bold.

ROI	Symbolic		Analog		ROI	Symbolic		Analog	
	d	*p*	*d*	*p*		*d*	*p*	*d*	*p*
RIPSa	**.580**	**3E-04**	**.713**	**2E-06**	ACCdp	**.553**	**7E-04**	**.772**	**9E-08**
LIPSa	**.534**	**.001**	**.656**	**2E-05**	PreSMA	.487	.004	**.721**	**1E-06**
RIPSp	**.588**	**3E-04**	**.764**	**1E-07**	RINSa	**.558**	**6E-04**	**.677**	**1E-05**
LIPSp	**.556**	**6E-04**	**.710**	**3E-06**	RMFGa	**.630**	**6E-05**	**.597**	**2E-04**
RPOJ	**.649**	**3E-05**	**.695**	**5E-06**	LMFGa	**.583**	**3E-04**	**.556**	**6E-04**
LPOJ	**.577**	**4E-04**	**.658**	**2E-05**	RIFJ	**.596**	**2E-04**	**.736**	**7E-07**
ROCCp	**.640**	**5E-05**	**.670**	**1E-05**	LIFJ	.458	.006	**.725**	**1E-06**
LOCCp	**.644**	**4E-05**	**.748**	**4E-07**	RFEF	.452	.007	**.721**	**1E-06**
RTOJv	**.699**	**4E-06**	**.591**	**2E-04**	LFEF	**.641**	**4E-05**	**.708**	**3E-06**
LTOJv	**.712**	**2E-06**	**.578**	**3E-04**					

for all regions and in both formats. Indeed, contrast effects were highly significant $p < .0027$ in all regions with the exception of LIFJ, PreSMA and RFEF for symbols ($ps = .004$, .006 and .007, respectively). Fig. 3 shows that all trends were in the positive direction. While overall greater activity tended to be observed for analog quantities, the positive linear trend nevertheless held for both formats with roughly similar slopes across formats. In sum, ROI verification demonstrated that all 19 ROIs were indeed sensitive to quantity in both formats such that relative activity was modulated via a positive deflection as the input quantity increased. Focusing on these regions thus simplifies our functional interpretation of the subsequent RSA results: the patterns of neural coding we observe there can be said to obtain in regions thus known to be sensitive to relative differences in quantity. In the next sections, we turn to RSA to characterize the similarity spaces for symbolic and analog quantities.

Characterizing symbolic and analog similarity spaces

In this section, we sought to characterize the similarity spaces of symbolic and analog quantities by computing the correlations between neural activity patterns (in a given ROI) for each pair of quantities in our stimulus set (1–9). In the first section (Within-Format Encoding), we focus on characterizing the properties that best define Symbolic and Analog similarity spaces, respectively. In the subsequent sections, we focus on characterizing how the different formats relate to one another: (1) how do the *similarity spaces* of symbolic and analog quantities relate to one another; and (2) how do the neural patterns *for specific quantities* relate to one another between formats? Note that due to space constraints, the following sections report statistical results directly pertinent to the hypotheses being tested; complete correlation matrices for all 19 ROIs are provided in Supplementary Information. For each analysis, corresponding means and standard errors (across subjects) can also be found in Supplementary Information (Tables S1–S5). Complete voxelwise data for all 19 ROIs can be found found at https://osf.io/d645p/.

Within-Format Encoding

Within each format, we assessed whether the neural similarity space was predicted by numerical Ratio and/or Frequency. Moreover, we were particularly interested in the direction (sign) of these predictions: does neural similarity increase as Ratio gets closer or further from one; does neural similarity increase as Frequency increases or decreases? Recall that an overlapping-tuning-curves account predicts similarity should increase as Ratio gets closer to one. A categorical, frequency-based account predicts similarity should be largely insensitive to Ratio and that it should increase as Frequency increases. The similarity matrices predicted by Ratio and Frequency are given in Fig. 1b–c.

For each format and in each region, we computed the pairwise similarity matrix (a canned example is given in Fig. 1a). Similarity matrices are symmetrical around the main diagonal, so we took either the upper or lower triangle [outlined in blue (symbolic) and red (analog) in Fig. 1a], vectorized and Fisher *z*-transformed it, and then computed the degree to which Ratio and Frequency each predicted this vector of similarities. The results was 33 *r*-values (one for each subject), which were *z*-transformed and then compared against 0 using a one-sample *t*-test across subjects ($N = 33$). This was done separately for all 19 ROIs from the previous section that were shown to be linearly responsive to relative quantity.

Ratio. Results are shown in Fig. 4 (see also Table S-1). Analog similarity space was strongly positively predicted by Ratio in the majority of regions. All 10 posterior regions, including all IPS regions, showed significant effects of Ratio, as did 6 of the 9 prefrontal regions (excepting RINSa and bilateral MFGa). By contrast, Ratio largely failed to predict Symbolic similarity space, with the lone exception a weak[6] negative effect in LIPSp. Fig. 4b shows that Ratio was a significantly stronger positive predictor of Analog relative to Symbolic encoding in the clear majority of regions (15 of 19, the probability of which occurring by chance is 9.8E-17). In sum, results were more consistent with an overlapping-tuning-curves account for Analog quantity encoding, such that pairs of quantities with Ratio closer to 1 tended to show more similar neural processing. Results for symbolic quantities, on the other hand, were more consistent with a categorical account of quantity encoding in which tuning curves do not vary as a function of quantity.

Frequency. Results are shown in Fig. 5 (see also Table S-2). For symbolic similarity space, a significant positive effect was found in 7 of the 10 posterior regions. The probability of finding an effect in 7 of 19 regions (at $p < .05$) by chance is 2.3E-05; the probability of finding a significant effect in 7 of the 10 posterior regions by chance is 8.2E-09. Note that a positive effect here implies that quantities which are expected to co-occur more frequently show a higher degree of neural similarity. For Symbols then, results are consistent with the view that symbolic quantities are encoded in a manner sensitive to lexical Frequency. In contrast, the majority (14 of 19 at $p < .05$, with a joint probability of 5.6E-15) of regions showed a significant *negative* effect for Analog quantities. As joint Frequency is strongly inversely related to numerical size, and because analog tuning curves increase in width as quantity increases, we see this latter result as simply further converging evidence that Analog quantities are encoded according to the tuning-curves account (for evidence highly consistent with this interpretation, see Supplementary Information where we explicitly modeled numerical Size). Fig. 5b shows that Symbolic similarity space was more positively (or less negatively in some cases) fit by Frequency in the majority of regions (14 of 19 overall, $p = 5.6E\text{-}15$, and in 10 of 10 posterior regions). In sum, results were more consistent with the view that Symbolic quantities are encoded according to the relative (joint) frequencies with which they are encountered.

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[6] The effect was significant only at the more liberal threshold of .05. The probability of 1 or more significant effects at this threshold with 19 comparisons (ROIs) by chance is .623.

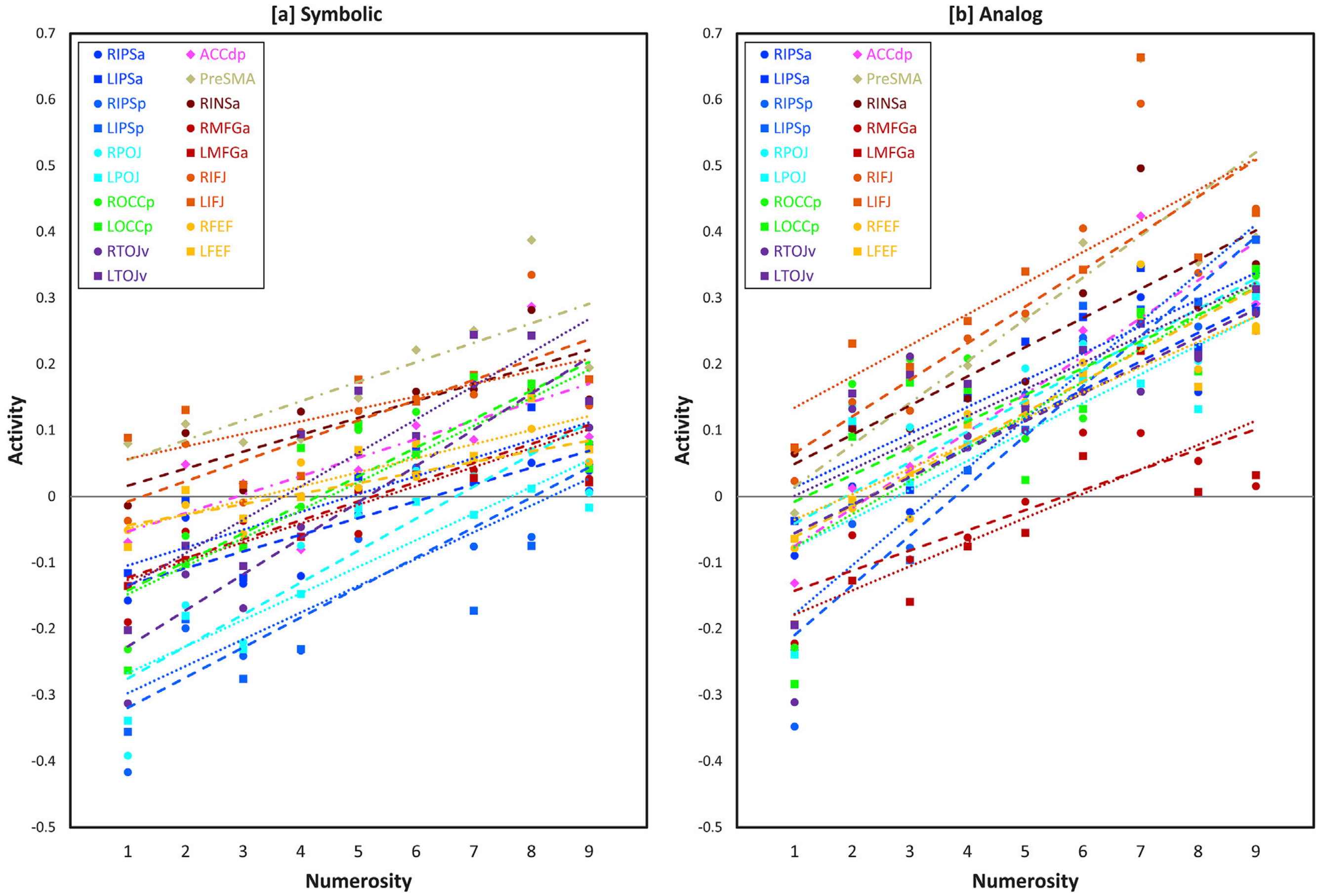

Fig. 3. Shows mean activity values and linear trend-lines for each ROI in response to **[a]** Symbolic and **[b]** Analog quantities. ROIs are color-coded in the same manner as Fig. 2 (see also Fig. 2 for abbreviations). Dashed-lines: right-hemisphere, dotted-lines: left-hemisphere; dash-dot-lines: mid-line regions.

Analog quantities are encoded in a manner inversely related to frequency, which is likely a reflection of the greater influence of broader tuning curves for larger quantities.

Correspondence between symbolic and analog similarity spaces

In the previous section, we saw that, even though a range of brain regions show sensitivity to relative quantity in both symbolic and analog formats, the underlying similarity spaces for each format appear to be organized according to different properties. Symbolic quantities are encoded more as discrete categories and Analog quantities are encoded with respect to approximate tuning curves. This suggests that the similarity spaces characterizing each format are qualitatively different from one another. However, another test of this assertion would be to simply correlate these similarity spaces with one another. In a given region, the similarity matrix of one format might be positively correlated with the other, suggesting a structural-level link between the two formats in that region. The matrices may be uncorrelated, suggesting independent structures. Or, if a negative relation were observed, this would suggest the two formats are structurally related, but in an opposing manner. To assess this, for each region and each subject, we vectorized and z-transformed the blue and red portions of the similarity matrices in Fig. 1a, computed the correlation between these z-transformed matrices, and then tested whether the (z-transformed) average correlation (across subjects, $N = 33$) was different from 0 (and if so, in which direction).

Results are shown in Fig. 6 (see also Table S-3). Significant *negative* effects were found in RIPSp and LPOJ, along with a lone positive effect in RIFJ. That said, none of these effects passed the more stringent ($p < .0027$) threshold. The probability that 1 of 19 effects would show a positive effect by chance at $p < .05$ is .623; the probability that two effects would show a negative effect by chance at $p < .05$ by chance is .245. Thus, it is perhaps most accurate to state that the overall pattern of results supports the view that, in regions sensitive to relative quantity, the relational structures for symbolic and analog quantities are largely independent of one another.

Between-format encoding

A key question concerns the extent to which Symbolic and Analog quantities are directly related, in that they may share common patterns of distributed neural activity. From the univariate analyses, we saw that all 19 brain regions showed systematic sensitivity to relative quantity in both formats. However, subsequent RSA analyses demonstrated that the nature of Symbolic and Analog coding is substantially different, and the last section showed that the similarity spaces of the two formats are largely unrelated to one another. Thus, Symbolic and Analog numbers appear to operate in distinct ways, but that does not preclude individual quantities from different formats from sharing common neural representation and/or processing. Moreover, common representation/processing may depend on whether the quantities are within or outside the subitizing range.

Relations between neural patterns for symbolic and analog quantities. To test for relations between neural patterns across formats, we examined the cross-format section of the similarity matrix in Fig. 1a (outlined in green and turquoise). The cells on the off-diagonal section of the between-format matrix shaded green indicate the correlation between the *different quantities* in different formats (e.g., between ‘3’ and ●, ‘3’ and

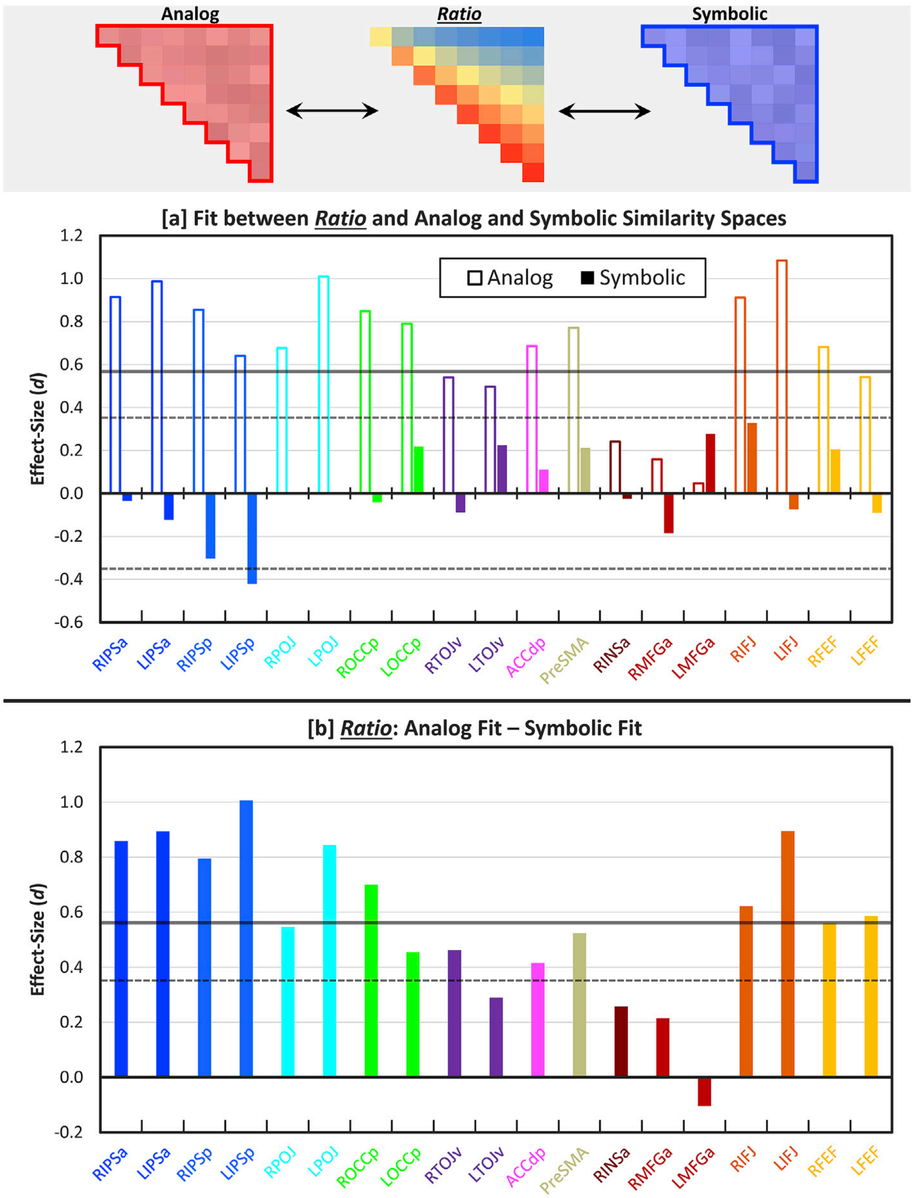

Fig. 4. Shows the degree to which numerical *Ratio* predicts the neural similarity spaces for Symbolic and Analog quantities **[a]**. The difference between fits across formats (Analog – Symbolic) is shown in **[b]**. Results are given as effect-sizes (Cohen's *d*). Horizontal grey lines indicate statistical significance given the current sample size ($N = 33$); dashed lines denote $p < .05$, and solid lines denote $p < .0027$.

●●, ‘3’ and ●●●●, and so on). The cells in this section are thus seen as indicative of more general between-format *processing*. The cells on the main diagonal of the between-format matrix that are shaded turquoise indicate the correlation between the *same quantity* in different formats (e.g., ‘3’ and ●●●). The cells in this section are potentially (to the extent that they show higher average similarity than the off-diagonal – green – cells) indicative of quantity-specific cross-format *representation*.

In each region and participant, same-quantity (average of turquoise cells in Fig. 1a) and different-quantity (average of green cells in Fig. 1a) correlations were *z*-transformed and tested against 0 across participants ($N = 33$). The results of this analysis are given in Fig. 7a (see also Table S-4).

The a priori criterion for a given region to demonstrate at least generic between-format similarity was significant cross-format similarity for both different-quantity and same-quantity correlations – because common processing across formats should be agnostic as to whether the quantities are the same or different. Results showed strong evidence in favor of generic between-format similarity in the majority of regions, including 9 of the 10 posterior regions and 6 of the 9 frontal regions. Thus, even though we saw in previous sections that the relational structures of Symbolic and Analog numbers are largely independent of one another, the two formats clearly show evidence of common neural processing across a range of brain areas, including key parietal regions. The next question, then, is whether we see evidence that this between-format similarity also implies quantity-specific *representation*.

To test for quantity-specific between-format representation, we asked whether a given region showed significantly greater same-quantity than different-quantity similarity (significantly higher outlined than solid bars in Fig. 7a). The results of this contrast are shown in Fig. 7b. There was weak[7] evidence for common same-quantity between-format representation in IPSp and POJ; however, effects only reached significance in the

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[7] Neither effect obtained at the more stringent (corrected for multiple-comparisons) threshold and the probability of obtaining 2 of 19 significant effects at p < .05 is .245.

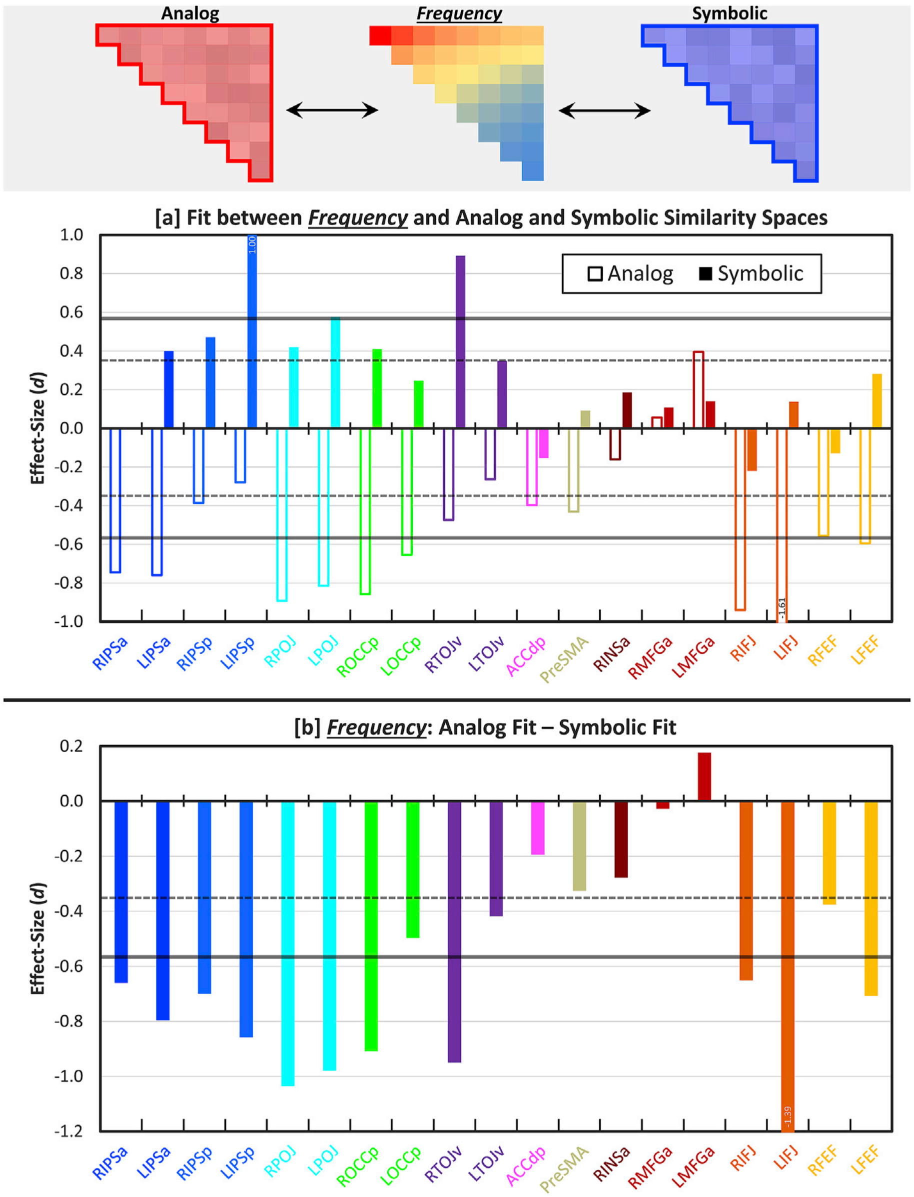

Fig. 5. Shows the degree to which lexical *Frequency* predicts the neural similarity spaces for Symbolic and Analog quantities **[a]**. The difference between fits across formats (Analog – Symbolic) is shown in **[b]**. Results are given as effect-sizes (Cohen's *d*). Horizontal grey lines indicate statistical significance given the current sample size ($N = 33$); dashed lines denote $p < .05$, and solid lines denote $p < .0027$.

right hemisphere, and even that was at the lower $p < .05$ threshold. Or to put it another way, 17 of the 19 regions showed no significant evidence in favor of same-quantity between-format representation (with strong contrary evidence in RMFGa). Thus, while there is perhaps some evidence for same-quantity between-format representation in posterior parietal areas, this is not nearly as strong as that demonstrating more general between-format *processing*.

In sum, results provide strong evidence for general between-format *processing* across a wide range of areas. However, the preponderance of evidence clearly showed that the neural commonalities between symbolic and analog quantities are *not* quantity-specific – i.e., not indicative of a common, abstract representation that transcends formats.

The role of subitizing in between-format similarity. Here we assessed whether the strength of between-format similarity depends on whether quantities can be represented *discretely* in both formats – i.e., whether quantities are within (1–4) or beyond (6–9) the subitizing range. Though the previous section showed an overall lack of support for same-quantity cross-format processing in the previous section, we first checked for an interaction by dividing the cross-format (green) matrix into Small (1–4) and Large (6–9) regions (purple and orange sections in Fig. 1a), as well as by Same/Different-quantities as in the previous section (from Fig. 1a: small-same = pink, small-different = purple, large-same = yellow, large-different = orange). Data were then entered into a 2 (Type: same, different) × 2(Size: large, small) ANOVA ($N = 33$). Only LFEF showed a significant ($p = .024$) interaction. However, this effect was driven by greater different-than same-quantity similarity for small quantities ($p = .007$), and no difference for large quantities ($p = .575$). Moreover, the familywise probability of a single significant interaction effect at $p < .05$ is .623. Furthermore, none of the 19 regions showed significantly ($p < .05$) greater similarity for same-relative to different-quantity processing when we looked separately at either small quantities (1–4, pink versus purple sections of Fig. 1a) or large quantities (6–9, yellow versus orange sections of Fig. 1a). Hence, we simplified subsequent analyses of the effect of Size on between-format similarity by collapsing across same- and different-quantity neural similarity estimates. Small (average of

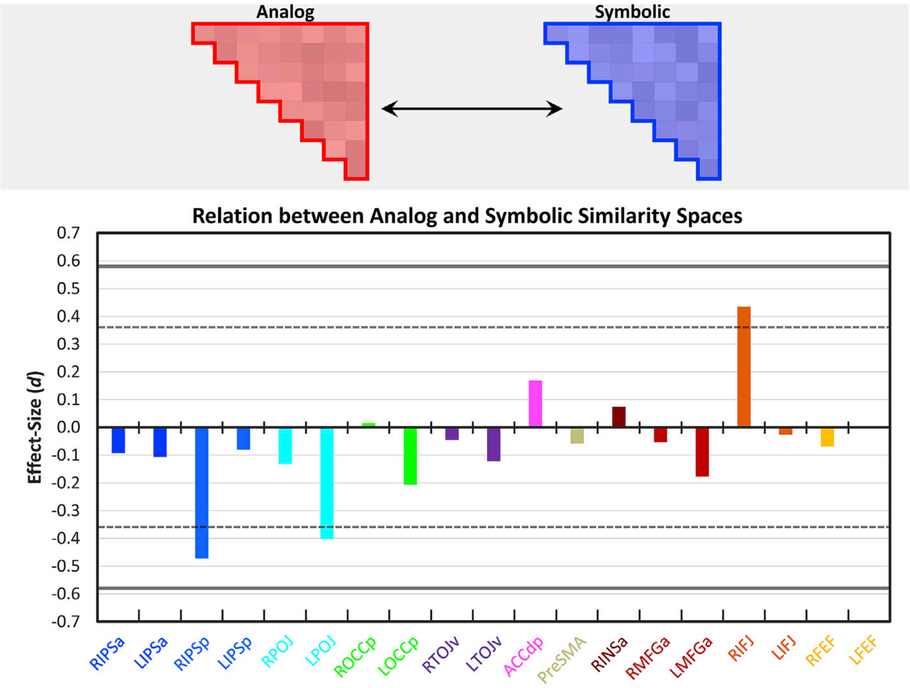

Fig. 6. Shows the degree to which the neural similarity spaces for Symbolic and Analog quantities related to one another. Results are given as effect-sizes (Cohen's *d*). Horizontal grey lines indicate statistical significance given the current sample size ($N = 33$); dashed lines denote $p < .05$, and solid lines denote $p < .0027$.

purple and pink regions in Fig. 1a) and Large (average of orange and yellow regions in Fig. 1a) correlations were *z*-transformed and tested against 0. Results are shown in Fig. 8a as effect-sizes (see also Table S-5).

For subitizable quantities, there was very strong evidence of general between-format similarity: significant effects were seen in 19 of 19 ROIs, including highly significant effects in 10 of 10 posterior and 7 of 9 frontal regions. By contrast, regions showing significant general between-format similarity for large quantities were notably fewer, with significant effects in 12 of 19 regions (including only 1 of the 4 IPS regions) and highly significant effects in just 7 of 19 regions.

To formally test whether between-format similarity was significantly greater for subitizable relative to large quantities, we contrasted large- and small-quantity similarity values (Large – Small). Results are shown in Fig. 8b. Between-format similarity was significantly greater for small quantities (negative contrast effects) in all 6 parietal regions (IPS and POJ), with highly significant effects in all 3 right-hemisphere regions. There was a general trend toward greater small than large similarity in the other regions, though this obtained significance only in ROCCp. No regions showed a significant effect in the opposite direction (Large > Small).

In sum, we see that similarity in between-format neural processing is overall enhanced for quantities within the subitizing range, an effect that was particularly strong in parietal regions. This pattern of results is consistent with the notion that between-format neural processing is enhanced when quantities can be represented discretely in both formats. Notably, however, even within the subitizing range, we did not find evidence indicating a common, abstract *representation* that transcends formats. Instead, results were more consistent with the notion that between-format *processing* of subitizable quantities is enhanced in a more general manner, in that it is agnostic with respect to the specific quantity or format of the input so long as the quantities fall within that range.

Discussion

We assessed how the brain processes discrete, symbolic representations and approximate, analog (continuous, perceptually grounded) representations – as well as the potential interrelations between the two – in the numerical domain. From a univariate perspective, brain areas that showed systematic (linear) sensitivity to relative quantity in one format did so in the other. Within these regions, however, representational similarity analysis (RSA) of patterns of neural activity showed qualitative differences in the neural coding of quantity between formats. On the one hand, the structure of the similarity space for analog quantities was well predicted by ratio (higher similarity when ratios were closer to 1), which is consistent with an overlapping tuning-curves account of analog quantity representation. On the other hand, the structure of the similarity space for symbolic quantities was unrelated to ratio in most areas and positively related to frequency (higher similarity for pairs of quantities with higher joint frequency) in a range of posterior areas, including the IPS. Results in these areas are thus consistent with a categorical, frequency-based account of symbolic quantity representation. Moreover, the neural similarity spaces for the two formats were largely independent of one another, which is all the more striking given that all regions under consideration showed sensitivity to relative quantity in both formats. In other words, a wide range of frontal and posterior regions – not just the IPS – code for both symbolic and nonsymbolic relative quantity, but the quantity-to-quantity relations that define the relational structure of each system is fundamentally different. Analysis of the link between symbolic and analog quantities showed strong evidence for between-format neural similarity in a range of regions across frontal, parietal and occipital cortices. However, this similarity was qualified in two important ways. First, it was primarily *not* quantity-specific, indicating similarity in general (input-agnostic) processing as opposed to similarity of representation. Second, between-format similarity tended to be strongest for quantities within the subitizing range (1–4), a result that was particularly strong in parietal areas, including the IPS. This latter finding is highly consistent with the view that symbolic and analog quantity processing is linked most strongly within the range of quantities that can be processed discretely in both systems.

As part of the broader question about the nature of symbolic representation, a detailed mapping of the inter-relations between symbolic and analog quantities in the brain presents both a challenge and a major opportunity. In particular, it can address several key questions posed by competing perspectives on the nature of symbolic representation in the

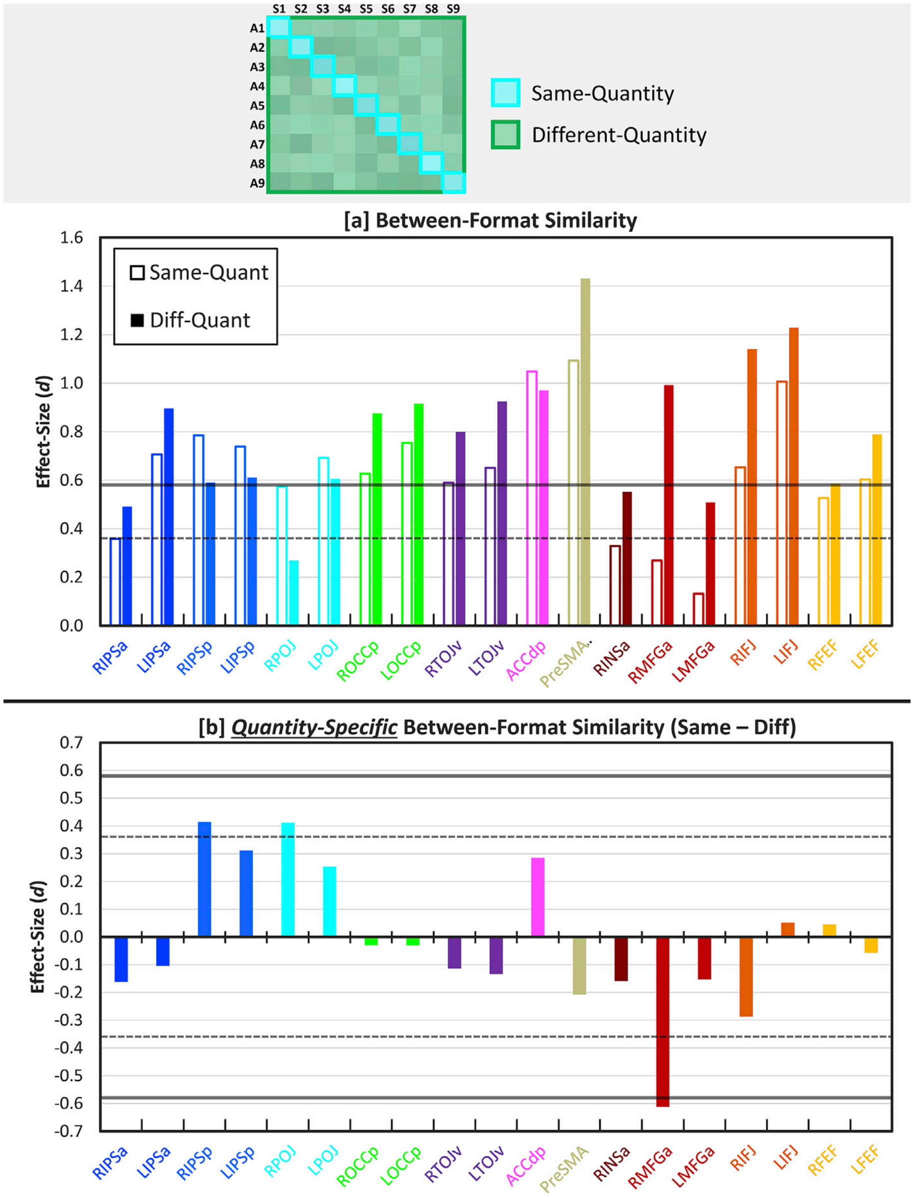

Fig. 7. Shows neural similarity between formats **[a]** for same-quantities (e.g., '3' and ●●●) and different-quantities (e.g., '3' and ●●), and **[b]** the difference between the two. Results are given as effect-sizes (Cohen's *d*). Horizontal grey lines indicate statistical significance given the current sample size ($N = 33$); dashed lines denote $p < .05$, and solid lines denote $p < .0027$.

brain. One such question concerns the properties that define the respective neural similarity spaces of symbolic and analog quantities, and in particular whether those of symbolic quantities retain a similar structure as that of their analog counterparts.

For analog quantities, the vast majority (16 of 19) brain regions that showed sensitivity to relative quantity were also characterized by neural similarity spaces that were closely aligned with numerical ratio: the closer ratio was to 1, the higher the degree of neural similarity between to analog quantities. This is precisely the pattern predicted by an account of quantity encoding characterized by analog (approximate, probabilistic) neural tuning, wherein the imprecision of this tuning and overlap between neighboring quantities increase systematically as the quantities in question increase (e.g., Piazza et al., 2004; Nieder, 2005; Merten and Nieder, 2009; Lyons et al., 2015a; Castaldi et al., 2016). We are by no means the first to present evidence of this for analog, nonverbal (nonsymbolic) quantity inputs (for a review, see Knops, 2017). However, much of the previous work has focused on the IPS (e.g., Piazza et al., 2004; Lyons et al., 2015a; though see also Harvey and Dumoulin, 2017). Here, we show that this pattern obtains not just in the IPS, but in a range of other posterior and prefrontal regions (Fig. 4).

By contrast, in these same brain regions, the neural similarity space for symbolic quantities was unrelated to ratio in 18 of 19 regions, with the lone exception in fact an *inverse* relation in LIPSp. This result is consistent with recent work showing that the presence of behavioral ratio effects (worse performance as ratio approaches 1) for symbolic quantities is far less reliable at the individual level than that for analog (nonsymbolic) quantities (Lyons et al., 2015b). Recall that the strong ratio effect for analog quantities is predicted because of numerical tuning curves that systematically widen (and thus increase to a greater to degree) as quantity increases. If, on the other hand, symbolic quantities are represented more as discrete categories, then their respective 'tuning curves' should be equally precise across quantities; this in turn implies the structure of symbolic similarity space should be unrelated to ratio, which is precisely what we found. Thus, our data are more consistent with the idea that symbolic quantities are represented in the brain not in a probabilistic, analog manner, but instead as discrete categories.

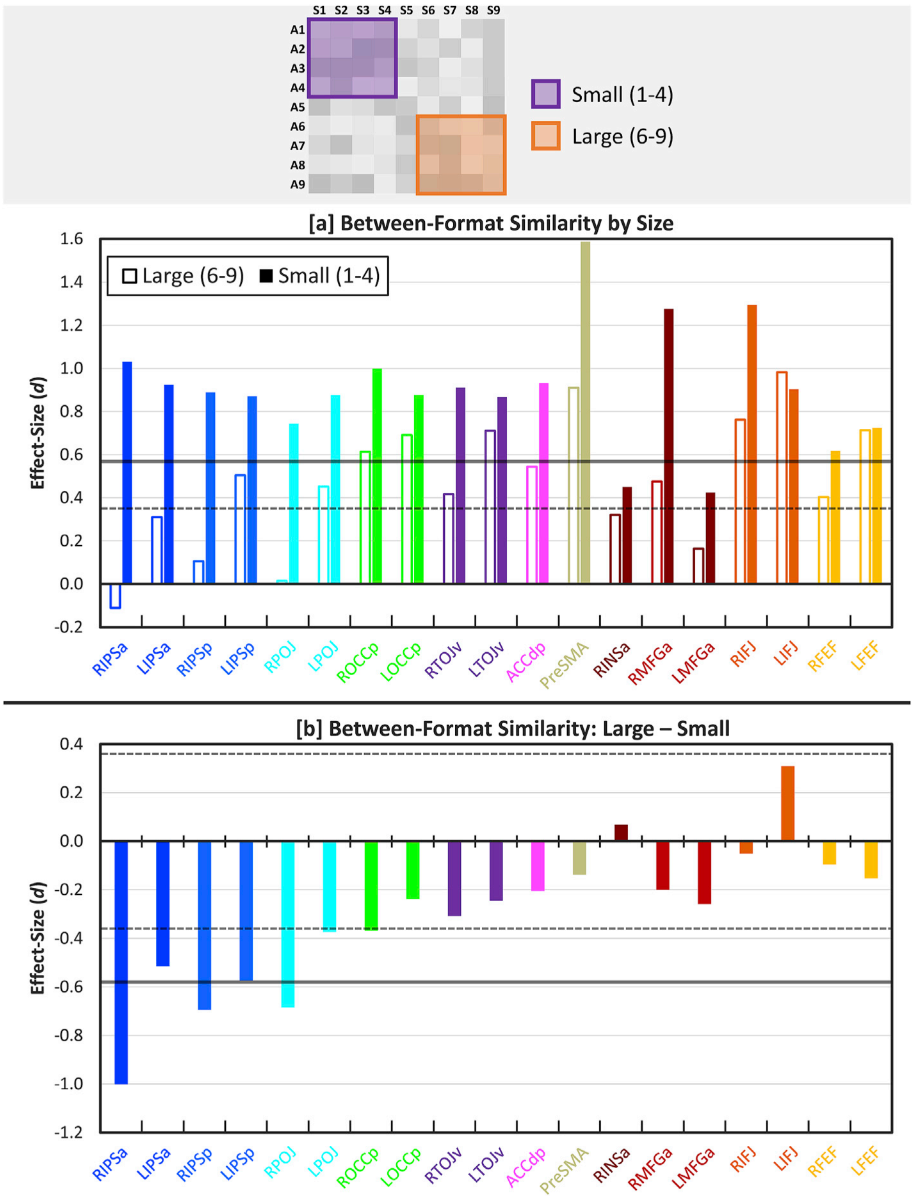

Fig. 8. Shows cross-format neural similarity **[a]** for small (1–4) and large (6–9) quantities, and **[b]** the difference between the two. Results are given as effect-sizes (Cohen's *d*). Horizontal grey lines indicate statistical significance given the current sample size ($N = 33$); dashed lines denote $p < .05$, and solid lines denote $p < .0027$. Note that values here ignore whether similarity values are same- or different-quantity; see Fig. 7 and main text for details.

Furthermore, for symbolic quantities, the majority (7 of 10) of posterior regions, including 3 of the 4 IPS regions showed a positive relation with lexical frequency (Fig. 5a). As frequency and numerical size are inversely related, this implies that neural similarity between *smaller* symbolic quantities was higher than that between larger quantities (see Supplementary Information for an analysis directly confirming this prediction using Size as a predictor of similarity). Crucially, this pattern of results is literally the opposite of was seen for analog quantities. What might explain this result for symbolic quantities, especially if – as we discussed in the previous paragraph – evidence is more consistent with the notion that symbolic quantities operate more as discrete categories? Verguts et al. (2005) in fact developed a model of exact number representation, wherein quantities operated as discrete (i.e., exact) categories. Crucially, they found that size effects emerged only when the models were trained such that they ‘encountered’ different numbers with varying frequency. This frequency reflected the relative frequency with which quantities are encountered in lexical corpi, with smaller quantities encountered most often, and frequency then falling off with increasing quantity as a power-law function (Dehaene and Mehler, 1992). Thus, frequency may play a key role in shaping symbolic quantity representation. In particular, when we learn to count, we usually start with smaller quantities (Wynn, 1990), and thus ordinal relations between smaller quantities are rehearsed more frequently than those between larger quantities (Lyons and Ansari, 2015). The relations between smaller quantities – primarily due to more practice and higher rates of co-occurrence – should therefore be stronger than those between larger quantities. Our results are consistent with this view. Interestingly, this pattern was restricted to posterior regions, suggesting a degree of regional specificity. That said, though a relation with frequency was found in canonical ‘number’ regions such as the IPS, this effect was also seen in right inferior temporal and occipital regions (RTOJv, ROCCp), regions previously associated with recognition of complex visual shapes such as written numbers (Shum et al., 2013; Grotheer et al., 2016a; b). It may thus be possible that the associative structure of symbolic quantities – especially as it reflects frequency of exposure – is present even in the ventral visual processing stream, an interpretation consistent with work by Daitch et al. (2016) showing a link between ventral temporal and lateral parietal cortex during processing of numerals in an arithmetic context. In sum, evidence suggests that symbolic quantities operate more as discrete categories whose relational structure is determined more by associative frequency – at least in posterior and parietal brain regions.

Another key question about the nature of symbolic and analog quantities is whether the within-format similarity spaces that define each format parallel one another or are largely independent. The fact that each seems to be defined by different properties – per the discussion above – suggests these spaces are in fact distinct. On the other hand, one might suggest that both symbolic and analog quantities operate according to a tuning-curves model, with the curves just substantially narrower overall for symbolic quantities (see, e.g., Eger et al., 2009). Indeed, the lack of relation we see here between symbolic similarity space and ratio (Fig. 4a) would still fit this alternative view, as we might simply lack the fine-grained resolution and/or statistical power to detect these very narrow tuning curves. However, it is difficult to see how a tuning-curves account could explain the positive relation seen here in the majority of parietal and posterior regions between frequency and symbolic similarity space. Recall that this relation implies *higher* similarity for *smaller* quantities (an implication directly confirmed in Supplementary Information). Perhaps a tuning-curves account could accommodate this result by positing *wider* tuning-curves for smaller quantities; but we would argue that such a model would be a sufficiently radical departure from standard tuning-curve-based models to warrant a qualitative distinction be made. Hence, it is important to emphasize here that we are arguing for a qualitative division between symbolic and nonsymbolic quantity encoding, as a categorical, frequency-based account – in the case of symbols – is most consistent with the full body of data presented here.

Further evidence consistent with this view indicated that symbolic and analog similarity spaces were largely unrelated, suggesting the existence of two independent systems for representing quantities (Fig. 6). Only 1 of the 19 regions sensitive to relative quantity showed a positive relation (RIFJ), and even then only at the lower significance threshold ($p = .05$), the probability of which occurring by chance is .623. Two parietal regions (RIPSp, LPOJ) in fact showed a *negative* relation between symbolic and analog similarity spaces, suggesting directly opposing associative structures, though these effects also failed to reach the higher significance threshold, so caution may be warranted in interpreting these effects as well. Regardless, the overwhelming majority of evidence (18 of the 19 regions)[8] indicated that the neural similarity spaces that define symbolic and analog coding of quantity are either independent or in direct opposition to one another. These results are perhaps all the more remarkable because each of these regions showed systematic sensitivity to relative quantity in both formats. Though each of these regions may be modulated by both symbolic and nonsymbolic quantity, the underlying manner in which they code for relations between quantities – the underlying associative structure – is fundamentally different.

A third key question about the nature of symbolic and analog quantities concerns the manner in which symbolic and analog quantity systems may be directly linked in terms of correlated distributed patterns of neural activity. Results indicated strong support (significant effects in 15 of 19 regions) for common cross-format processing (Fig. 7a). How can it be that symbolic and analog quantities comprise different similarity spaces, but nevertheless show significant between-format similarity? One important point is that we found very little evidence[9] that this similarity was quantity-specific, which argues against the notion of a common representation underlying a given quantity in each format (e.g., a common sense of 'three-ness' underlying both '3' and ●●●). This general lack of evidence for common representation is also broadly consistent with previous behavioral and neural evidence (Roggeman et al., 2007; Lyons et al., 2012, 2015a; Bulthé et al., 2014, 2015). Instead, this input-agnostic between-format processing is perhaps more indicative of the fact that other general processes, such as working memory, attention, calculation, etc., operate over numerical inputs regardless of format (symbolic or analog).

This result may also help explain certain behavioral results that seem to show a link between symbolic and analog quantity processing. For instance, Park and Brannon (2013, 2014) showed that training individuals to do basic arithmetic using analog quantities transferred to gains in symbolic arithmetic performance. However, training aimed at improving the representational precision of specific analog quantities via an analog quantity comparison task did not. This perhaps indicates that the key to transfer was alignment in processing (arithmetic), rather than quantity representation, a distinction that may have implications for future design of training regimes that rely on transfer between analog and symbolic systems. In a similar vein, common processing might help explain why in the univariate analyses (Fig. 3) we saw similar sensitivity to relative quantity for symbolic and analog quantities in a wide range of brain areas. Recall that while participants were completing a numerical matching task, our analysis focused on the portion of the time-series in which participants simply held a given quantity in mind – which may be seen as essentially maintenance in working memory (Miyake and Shah, 1999). Hence, it may be that the information processing that allows quantities to be maintained in working memory is similar regardless of whether the quantities are symbolic or analog. At a broader level, this notion is consistent with the view that numerical cognition is not modular in nature: it is subject to and interacts with many other neurocognitive functions throughout the brain. For instance, based on our results, we would predict that symbolic and analog quantities would interact with – i.e., be processed by – other cognitive control functions such as inhibition and updating in a similar manner (Miyake et al., 2000). However, it is important to acknowledge that we did not include non-numerical stimuli here, so further work is needed to test the precise extent to which our results are indeed 'input-agnostic'.

We should also emphasize we do not believe that our results as a whole can be explained away as 'just' a working memory effect. Results discussed above clearly show the similarity spaces of symbolic and analog quantities are determined by different – sometimes even antithetical – properties, these spaces are largely independent of one another, and we find only minimal evidence for quantity-specific cross-format processing. These results would be hard to reconcile with a purely working memory based account. Instead, we believe that symbolic and analog quantities comprise distinct numerical systems characterized by distinct relational properties; however, quantities from these two systems nevertheless *can* interact in similar ways with other cognitive processes – calculation, working memory, inhibition, long-term memory storage, etc.

An important caveat is that similar processing of symbolic and analog quantities is stronger (especially in the IPS) when the analog quantities in question can be processed in discrete fashion (that is, they are within the subitizing range, 1–4). Large analog quantities may diverge more dramatically from their symbolic counterparts in that the former will tend to be processed in an ever-increasingly approximate fashion (i.e., as quantity increases further and further beyond the subitizing range), whereas large symbolic quantities continue to be processed in discrete, categorical fashion. By contrast, small analog quantities (1–4) can be subitized and so processed in discrete fashion, thereby lending themselves to processing mechanisms more similar to those utilized for

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[8] 16 of these regions showed a null effect, so to combat inference from the null, we checked Bayes factors quantifying evidence for the null over the alternative (B_{01}): B_{01} values for all 16 regions were between 3 and 10, indicating moderate evidence *in favor of* the null.

[9] 2 of 19 regions showed a significant effect at $p < .05$, the familywise probability of which is .243. 1 region showed a strong *reverse* effect (even at the familywise corrected rate). Of the remaining 16 regions, 4 showed anecdotal evidence in favor of the null (B_{01} between 1 and 3), and 12 regions showed moderate evidence in favor of the null (B_{01} between 3 and 10). Or to put it another way, 13 of the 19 regions (68%) showed moderate to strong evidence *against* the notion that between-format similarity was specific to representation of individual quantities, and evidence for the remaining 6 regions did not pass a statistical threshold sufficient to warrant rejection of the null.

symbolic quantities. This interpretation dovetails nicely with the view put forth by Susan Carey (Carey, 2004, 2011) of how children first acquire cardinal understanding of number words – that is, the numerical meaning of what are likely the first number symbols (number words) that children learn. This view posits that children first learn to map the meaning of number words to the cardinality of sets of concrete (nonsymbolic) items, but exclusively within the subitizing range (Le Corre and Carey, 2007), because only within this range can nonsymbolic quantities be represented in exact, discrete fashion (Trick and Pylyshyn, 1994; Revkin et al., 2008). Until children learn to count beyond the subitizing range (which succeeds acquisition of symbol-cardinality mappings within the subitizing range; Le Corre and Carey, 2007), nonsymbolic quantities outside this range can be processed only in approximate, analog fashion (Carey et al., 2017). This analog aspect of larger quantities appears to be largely an anathema to the discrete, categorical nature of symbolic quantity representation, which thus argues against the view that our understanding of larger symbolic quantities is fundamentally grounded in our understanding of larger analog quantities. Perhaps instead, symbolic quantities come to assume an associative structure that quickly outpaces their analog counterparts in terms of complexity, scope and abstraction (Peirce, 1955; Deacon, 1997; Nieder, 2009; Lyons, 2015; Núñez, 2017).

Conclusion

Taken together, our results show that symbolic quantities operate more like symbolic systems as they have been conceptualized by thinkers such as Peirce (1955), Deacon (1997), and Núñez (2017), in that number symbols are primarily defined by relations between the symbols within the system, perhaps even at the expense of weakened links to their perceptual analog counterparts. Our results are less consistent with the view that symbolic quantities are firmly 'grounded in' or 'embodied by' their analog counterparts (e.g., Varela et al., 1991; Pulvermüller, 2013; Dehaene, 1997, 2008; Feigenson et al., 2004, 2013; Lyons and Ansari, 2009; Nieder and Dehaene, 2009; Piazza et al., 2007). That said, while our data are clearly more consistent with the view that symbolic and analog quantities comprise distinct numerical systems characterized by distinct relational properties, they also show that quantities from these two systems may nevertheless interact via more general neurocognitive processes. Though numerical symbols are of course only one type of symbolic representation, our results may nevertheless contribute to answering the deeper question of how the brain processes discrete, symbolic inputs and approximate, analog (continuous, perceptually grounded) inputs, as well as the potential interrelations between these two forms.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.neuroimage.2018.05.062.

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