Neural representations of magnitude for natural and rational numbers

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ABSTRACT

Humans have developed multiple symbolic representations for numbers, including natural numbers (positive integers) as well as rational numbers (both fractions and decimals). Despite a considerable body of behavioral and neuroimaging research, it is currently unknown whether different notations map onto a single, fully abstract, magnitude code, or whether separate representations exist for specific number types (e.g., natural versus rational) or number representations (e.g., base-10 versus fractions). We address this question by comparing brain metabolic response during a magnitude comparison task involving (on different trials) integers, decimals, and fractions. Univariate and multivariate analyses revealed that the strength and pattern of activation for fractions differed systematically, within the intraparietal sulcus, from that of both decimals and integers, while the latter two number representations appeared virtually indistinguishable. These results demonstrate that the two major notations formats for rational numbers, fractions and decimals, evoke distinct neural representations of magnitude, with decimals representations being more closely linked to those of integers than to those of magnitude-equivalent fractions. Our findings thus suggest that number representation (base-10 versus fractions) is an important organizational principle for the neural substrate underlying mathematical cognition.

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Introduction

Representations of symbolic number types

Humans are unique in having developed symbolic notations for numbers. Given that a primary function of numbers is to convey magnitude values, it is important to understand the mental and neural representations of numerical magnitudes. The goal of the current study was to address the question of how different symbolic notations (natural numbers, fractions, and decimals) map onto magnitude codes. Specifically, we sought to determine whether different notations map onto a single, fully abstract, magnitude code, or whether separate representations exist for specific number types (e.g., natural versus rational) or number representations (e.g., base-10 versus fractions).

Numerous studies of numerical magnitude comparisons have yielded a *symbolic distance effect*: comparisons of numbers that are closer in magnitude (e.g., 7 vs. 8) are slower and more error prone than comparisons of numbers that are farther apart (e.g., 2 vs. 8; Moyer and Landauer, 1967; Holyoak, 1978). A similar distance effect is observed in children (Barth et al., 2005; Brannon, 2002). Rhesus monkeys

display a distance effect for numerosity comparisons; moreover, they are capable of learning shapes (Arabic numerals) corresponding to small numerosities (1–4 dots), such that the shapes acquire neural representations overlapping those of the corresponding perceptual numerosities (Diester and Nieder, 2007).

The distance effect and other phenomena have been interpreted as indications that numerical magnitudes (at least for integers) are associated with an analog magnitude representation akin to a mental number line (Dehaene and Changeux, 1993; Gallistel, 1993; Opfer and Siegler, 2012). Neuroimaging studies with both adults and children have implicated the intraparietal sulcus (IPS) as the central area for representing and comparing symbolic integer magnitudes (and also non-symbolic magnitudes) (Dehaene et al., 2003; Nieder and Dehaene, 2009; Piazza et al., 2007; Pinel et al., 2001). Further, IPS activation is inversely related to the numerical distance between two numbers being compared (Cohen Kadosh et al., 2005; Kaufmann et al., 2005), consistent with the behavioral distance effect.

While the representation of whole-number magnitude has received considerable attention, far less is known about the representation of other symbolic number types, such as the rational numbers (fractions and decimals). Some have argued that the representation of magnitude in general is entirely abstract, and that all symbolic and non-symbolic magnitudes can be represented using a single mental (and neural) number line (Eger et al., 2003; Naccache and Dehaene, 2001; Siegler

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et al., 2011). However, studies investigating this topic have as yet failed to reach a consensus. Previous behavioral research has mainly focused on the extent to which fractions are represented holistically. This work has focused on the issue of whether the overall (holistic) magnitude of a fraction is accessed automatically, like an integer (Kallai and Tzelgov, 2009; Meert et al., 2010a, 2010b; Schneider and Siegler, 2010; Sprute and Temple, 2011). Evidence for holistic magnitude representation come from studies examining the distance effect during fraction comparisons. Many studies (e.g. Schneider and Siegler, 2010) have found that adults show a distance effect when representing fractions during comparisons. However, other studies have shown that depending on the stimuli and availability of various shortcut strategies, adults may represent only the whole-number components of the fraction and not its holistic magnitude (e.g. Bonato et al., 2007; Fazio et al., 2015).

Moreover, other work has shown that even when a distance effect is found for fraction comparisons, the size and scale of the effect is entirely different for fractions relative to either integers or decimals. DeWolf et al. (2014) had adults compare fractions, matched decimals (rounded to three digits) and integers (created by multiplying the equivalent decimal by 1000 to obtain a three-digit integer). Comparisons for all three number types yielded reliable distance effects, based on the holistic magnitudes of the numbers being compared. Importantly, however, response times and error rates for the fraction comparisons were much higher than for comparisons of either decimals or integers, with the latter number types showing no differences in response times or errors. Moreover, the distance effect was much more pronounced for fractions, with response times averaging between 2 and 8 s for far versus near number pairs. In contrast, response times for integers and decimals overlapped with one another, and generally were no longer than 2 s. This dramatic difference in the scale of the distance effect across number types suggests that the magnitude information associated with fractions may be less precise than that associated with integers or decimals, and that the process of accessing magnitudes is more effortful and less automatic for fractions than for either integer or decimal formats.

Using fMRI to investigate magnitude representation

Behavioral research investigating rational number magnitudes suggests there are important differences between magnitude processing for fractions relative to other number types. Although neuroimaging methods, and functional magnetic resonance imaging (fMRI) in particular, have been employed to assess the neural substrates of numerical magnitude representation (e.g., Darmla and Just, 2013), numerical symbols representations (see Ansari, 2016) and algebra (e.g., Monti et al., 2012), there is no consensus regarding the interpretation of the behavioral differences observed between fractions and other number types. The present study applied neuroimaging methods to assess the relationships among the neural representations of magnitude for different symbolic formats. If the representation of magnitude is entirely abstract, then the neural representations of a fraction and its magnitude-equivalent decimal (e.g., 2/5 vs. 0.40) in the IPS might be expected to be identical. In contrast, if fractions and decimals are processed very differently (as some behavioral studies suggest), then the neural codes for the different notations may differ. To date, these alternative predictions remain untested. In fact, only two studies have ever probed the neural representations underlying the processing of fractional numbers (Ishebeck et al., 2009; Jacob and Nieder, 2009a), and neither of these assessed the neural representations underlying decimal numbers, or the relationship between neural representations of magnitude across different formats for rational numbers.

A few other studies have examined how neural representations of magnitude differ as a function of notation by comparing neural responses to whole numbers versus their verbal equivalents (e.g., "12" versus "twelve"). Some studies have found that IPS activation was notation-independent (Eger et al., 2003; Naccache and Dehaene, 2001), whereas other studies suggest there may be both notation-specific and notation-independent areas (Bluthe et al., 2015; Cohen Kadosh et al., 2007; Darmla and Just, 2013). However, these studies all compared a single mathematical notation (whole numbers) versus natural language (number names). No work has been done to investigate the question of whether alternative mathematical formats, such as fractions versus decimals, evoke similar or distinct neural representations of magnitude.

As noted above, only two studies have investigated the representation of symbolic fraction magnitudes using fMRI. Jacob and Nieder (2009a) used an adaptation paradigm to test symbolic fraction magnitudes (single and multi-digit fractions). Recovery in the BOLD signal after habituation was observed in the frontoparietal cortex, and specifically the IPS. The pattern of signal recovery was the same after presentation of either a new symbolic fraction (e.g., "1/2") or a new fraction written as a word (e.g., "half"), suggesting that fractions and their verbal equivalents recruit the same or overlapping neural areas.

The second study that investigated symbolic fraction notation with fMRI used a magnitude comparison paradigm, rather than an adaptation paradigm. Ishebeck et al. (2009) had adult participants perform a simple magnitude comparison task with fractions, in which participants saw two fractions simultaneously on the screen and pressed a button to indicate which was larger in numerical magnitude. The stimuli included different types of fraction pairs, some with common components, in order to enable a variety of potential strategies during the comparison process. The results showed that activity in the right IPS was inversely correlated with the distance between the two fractions based on their holistic magnitude difference, and not with the distances between any component parts. Ischebeck et al. interpreted their fMRI results as supporting the hypothesis that (despite an opportunity to use componential strategies) fraction comparisons were performed using holistic magnitudes.

However, neither Ishebeck et al. (2009) nor Jacob and Nieder (2009a) directly compared processing of fractions with that of other symbolic formats. Although previous work indicates that magnitude representations for fractions involve roughly the same general neural area (the IPS) as do magnitude representations for symbolic integers (and non-symbolic numerosities; see Jacob and Nieder, 2009b; Jacob et al., 2012), the extent to which processing and representation of magnitude is the same or different for fractions relative to other number types has not been examined. Furthermore, the more general question of whether different symbolic formats for numbers evoke the same or different abstract magnitude representations remains unanswered.

The present study

In the present experiment, we employ univariate and multivariate analysis of fMRI data to compare, in a within-subject design, the neural representations of magnitude across different symbolic notations (integers, decimals, and fractions). We hypothesized that, consistent with previous research, all of the number types would activate the IPS. The main questions concerned possible differences between the number types. If all number types activate the same abstract neural representation (based on relative rather than absolute magnitude, to take account of the scale difference between integers and rational numbers), then no differences among the number types would be expected. A second possibility is that neural activation of integers will differ from that of rational numbers (either fractions or decimals), both because the latter are more complex and because the overall magnitude scale differs. A third possibility, based on the behavioral findings of DeWolf et al. (2014), is that fractions will evoke a neural signature distinct from that of either magnitude-equivalent decimals or integers, whereas the latter two number types will evoke similar activation patterns.

Methods

Participants

Sixteen participants (12 female, mean age 21 years) with no documented history of neurological disorders were recruited at the University of California, Los Angeles (UCLA) through a flyer distributed in the Psychology department. Participants signed informed consent prior to the experimental session, and were paid $30 for their participation in the 1-hour study, in compliance with the procedures accepted by the local institutional review board (IRB).

Stimuli

Stimuli consisted of pairs of numbers in one of three possible symbolic types: fractions (e.g., 1/2, 3/4), decimals (e.g., 0.50, 0.75) or integers (e.g., 50, 75). Table 1 lists the complete set of pairs for each number type. Within each pair, numbers were always of the same type. In order to control for the number of digits on the screen across symbolic types, only single-digit fractions, double-digit decimals, and double-digit whole numbers were presented. Thus, instances of the three symbolic number types were always constructed from exactly two digits. All of the fraction comparison pairs were comprised of fractions that did not have any common components. This constraint served to minimize the use of shortcut strategies, thereby encouraging participants to access the holistic magnitude of each individual fraction. Magnitude-equivalent decimals were created by dividing out the

Table 1
List of the stimuli used for each of the fraction, decimal, and integer comparisons. Each pair was shown twice in each order.

Fraction pairs		Decimal pairs		Integer pairs	
1/9	3/7	.11	.43	11	43
1/8	3/7	.13	.43	13	43
1/8	4/9	.13	.44	13	44
1/7	3/8	.14	.38	14	38
1/6	2/7	.17	.29	17	29
1/5	3/8	.20	.38	20	38
1/5	7/8	.20	.88	20	88
2/9	4/7	.22	.57	22	57
1/4	2/7	.25	.29	25	29
1/4	5/7	.25	.71	25	71
2/7	5/8	.29	.63	29	63
1/3	2/7	.33	.29	33	29
1/3	3/4	.33	.75	33	75
3/8	2/7	.38	.29	38	29
2/5	5/9	.40	.56	40	56
3/7	2/9	.43	.22	43	22
3/7	5/9	.43	.56	43	56
4/9	1/7	.44	.14	44	14
4/9	2/3	.44	.67	44	67
1/2	2/5	.50	.40	50	40
1/2	2/3	.50	.67	50	67
5/9	6/7	.56	.86	56	86
4/7	1/4	.57	.25	57	25
4/7	3/4	.57	.75	57	75
3/5	2/9	.60	.22	60	22
3/5	5/8	.60	.63	60	63
5/8	1/9	.63	.11	63	11
2/3	1/8	.67	.13	67	13
2/3	4/7	.67	.57	67	57
5/7	4/9	.71	.44	71	44
5/7	7/8	.71	.88	71	88
7/9	1/3	.78	.33	78	33
4/5	1/9	.80	.11	80	11
4/5	7/8	.80	.88	80	88
5/6	1/5	.83	.17	83	17
5/6	7/9	.83	.78	83	78
6/7	2/5	.86	.40	86	40
6/7	3/5	.86	.60	86	60
8/9	2/5	.89	.40	89	40
8/9	3/4	.89	.75	89	75

corresponding fraction and rounding the result to two decimal places.[1] Integers were created by multiplying the matched decimal by 100 to create a two-digit number.

A total of 40 unique comparison pairs were generated for each number type. Because the numbers in the comparisons were shown sequentially, rather than simultaneously, each pair was shown twice, once in each order. Accordingly, there were a total of 80 trials for each of the three number types.

Behavioral task

Participants were given instructions before entering the scanning room, after performing a routine safety check. Participants were told that they would see a series of numbers presented sequentially in pairs. Each trial started with a fixation cross, at the middle of the screen, for 0.5 s followed by a brief blank screen jittered for 0.1–0.2 s. The first number was then presented for 1.5 s followed by a brief blank screen, which was jittered for 2–7 s, and then a second number (see Fig. 1). Participants controlled the length of presentation of the second number by pressing a button to indicate whether the second number was larger or smaller than the first number. They were instructed to try to go as fast as possible without sacrificing accuracy.

The 240 total trials (80 per symbolic type) were evenly distributed across four runs. Allocation of pairs across the four runs and order of presentation within each run was determined randomly for each participant.

fMRI data acquisition

Data were acquired on a 3 Tesla Siemens Tim Trio Magnetic Resonance Imaging (MRI) scanner at the Staglin IMHRO Center for Cognitive Neuroscience at UCLA. Structural data were acquired using a T1-weighted sequence (MP RAGE, TR = 1900 ms, TE = 2.26 ms, voxel size 1 mm^3 isovoxel). Blood oxygenation level dependent (BOLD) functional data were acquired with a T2-weighted Gradient Recall Echo sequence (TR = 2000 ms, TE = 30 ms, 32 interleaved slices, voxel size $3 \times 3 \times 4$ mm, Flip Angle = 78°). Overall, individual runs lasted an average of 566 s (min = 492 s, max = 756 s).

fMRI data-analysis procedures

Data preprocessing
Data analysis was carried out using FSL (Smith et al., 2004). Prior to analysis, data underwent a series of conventional preprocessing steps including motion correction (Jenkinson et al., 2002), slice-timing correction (using Fourier-space time-series phase-shifting), spatial smoothing using a Gaussian kernel of 5 mm full-width half-max, and high-pass temporal filtering (Gaussian-weighted least-squares straight line fitting, with sigma = 50 s). Data from each individual run were analyzed employing a univariate general linear model approach (Monti, 2011) with pre-whitening correction for autocorrelation (Woolrich et al., 2001).

Univariate analysis
For each run of each participant, a univariate GLM analysis was conducted with three regressors of interest marking the onset time and duration of the presentation of the *first number* of each pair, separately for each notation type (fractions, decimals, and integers). These analyses completely avoid any confounding with problem difficulty: because

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[1] Behavioral work (DeWolf et al., 2014) has shown that decimals are processed in a similar fashion regardless of whether the stimulus set uses a fixed number of digits without a leading zero (e.g., .75), or includes numbers with leading zeros (e.g., 0.75) or additional digits after the decimal (e.g., .750). In the present study we used only 2-digit decimals without leading zeros in order to equate the number of constituent digits across the three number types.
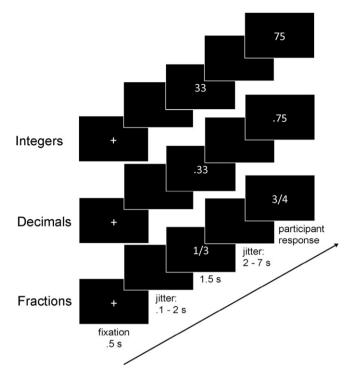
Fig. 1. Trial procedure for each of the number type conditions (integers, decimals, fractions).

the second number is yet to be presented, the comparison process cannot yet be initiated. A number of additional regressors modeled the second number presentation, cue periods, and motion (first and second derivatives, and their difference). Data from the presentation of the second number was not analyzed further because it was confounded with movement (from pressing the response button) and cognitive processes relating to the comparison task (cf., Todd et al., 2013). For each run we computed seven contrasts. These were based on the data collected during the presentation of the first number in a comparison pair. These included the simple effects of each notation type (fraction vs. baseline, decimal vs. baseline and integer vs. baseline), as well as the pairwise differences between them (fractions > decimals; fractions > integers; integers > decimals; and decimals > integers). Prior to group analysis, individual statistical maps were transformed into MNI template space via a 2-step procedure concatenating a boundary-based co-registration to align functional data to single-subject anatomical data and a 12° of freedom linear co-registration to align single-subject anatomical data to the MNI template. Data from individual runs were aggregated using a mixed-effects model (i.e., employing both the within- and between-subject variance), using automatic outlier detection. Z (Gaussianised t) statistic images were thresholded using a cluster correction of $Z > 2.3$ and a (corrected) cluster significance threshold of $p = 0.05$.

In order to avoid reverse subtractions (Morcom and Fletcher, 2007), for each A > B contrast (e.g., fractions > decimals), we employed a "greater-than-zero-sum" masking procedure. In this approach, analysis is restricted to voxels for which the sum of the Z statistic associated with task A (compared to fixation; Z_A) and the Z statistic associated with task B (compared to fixation; Z_B) resulted in a number greater than zero (i.e., $(Z_A + Z_B) > 0$). In other words, for a voxel to be included in the contrast analysis, either Z_A and Z_B have to both be positive values (in which case it is not possible to have reverse subtractions), or Z_A had to be more positive than Z_B was negative, thereby preventing the possibility of a brain activation resulting from a weakly positive Z_A coupled with a strongly negative Z_B. This latter point is particularly important since it highlights the advantage of our approach over the more conventional $Z_A > 0$ masking which, indeed, would return an activation in the case

where a weakly positive Z_A (e.g., $Z_A = 0.01$) were associated with a sufficiently negative Z_B. Furthermore, our approach also has the advantage of not excluding voxels in which Z_A might be strongly positive while Z_B is (weakly) negative, unlike a $Z_B > 0$ masking procedure.

MVPA analysis

The input to the multivariate pattern analysis (MVPA) was a set of volumes of regression coefficients (i.e., "beta" values) marking the magnitude of activation, for each voxel, in each trial (per participant). These trial-wise "patterns of activations" were obtained by employing the iterative Least Squares – Separate approach (LS-S; Mumford et al., 2012) in which a separate GLM is run (here, using FILM with local autocorrelation; Woolrich et al., 2001) for each trial. The patterns of activation were then concatenated across time to construct a subject-wise "beta-series" of activation magnitude per trial per voxel (Rissman et al., 2004).

Representational Similarity Analysis (RSA) was run on the beta-series of activation magnitudes, in MATLAB using the RSA toolbox (Nili et al., 2014). RSA characterizes the representation in a brain region by a representational dissimilarity matrix (RDM), and compares the empirical matrix with a model. An RDM is a square symmetric matrix, with each entry referring to the dissimilarity between the activity patterns associated with two trials (e.g., entry (1, 2) would represent the dissimilarity between activity patterns of trial 1 and trial 2 for a given participant). Each element of the RDM is calculated as 1 minus the Spearman correlation between the beta-series for each pair of trials. Models were manually generated to reflect idealized RDMs expected if the group of voxels was indeed modulating its activity with respect to the manipulation (see models in Fig. 2). The Number Type Model (Fig. 2a) was designed to test the overall ability to distinguish between each of the three number types. We then compared each of the pairwise number-type combinations to attempt to distinguish between each number type. The assumption behind the model RDMs was that a group of voxels sensitive to an experimental condition would display lower dissimilarity for same-condition trials as opposed to different-condition trials.

The RSA was performed with a searchlight approach (searchlight radius: 6 mm or 2 voxels; cf. Kriegeskorte et al., 2006) within an anatomical mask of the IPS as defined by the Jülich Histological Atlas (available in FSL; Choi et al., 2006; Scheperjans et al., 2008). Within each searchlight sphere, a Spearman coefficient was computed between the empirical and model RDMs, yielding a single second-order similarity value per voxel, which reflected the resemblance of searchlight sphere activity with the hypothesized model. These coefficients were registered to the standard template, with the same 2-step procedure employed for univariate single-subject statistical parametric maps, and assessed for significance ($\rho > 0$) using FSL's randomize with threshold-free cluster enhancement (corrected $p < 0.05$) (Smith and Nichols, 2009; Winkler et al., 2014).

Results

Behavioral results

Mean accuracy on the magnitude comparison task for each number type was obtained by averaging over all participants. A one-way repeated measures ANOVA revealed a significant effect of number type ($F(2, 30) = 23.23$, $MSE = 0.002$, $p < 0.001$), with fractions having lower accuracy than decimals (fractions: 84% vs. decimals: 92%, $t(15) = 6.72$, $p < 0.001$) and integers (91%, $t(15) = 4.82$, $p < 0.001$). There was no difference in accuracy between decimals and integers ($t(15) = 0.69$, $p = 0.50$).

Mean response times (RTs) for correct trials were averaged for each number type across participants. A one-way repeated measures ANOVA revealed a significant effect of number type ($F(2, 30) = 24.34$, $MSE = 0.09$, $p < 0.001$), with fractions being compared more slowly than either decimals (fractions: 1.91 s vs. decimals: 1.30 s, $t(15) = 5.22$, $p < 0.001$)
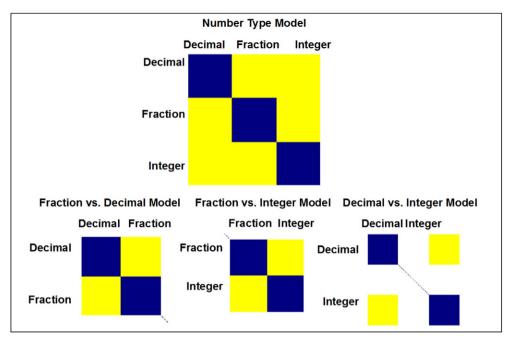
Fig. 2. Ideal models generated for the RSA searchlight MVPA. Each matrix represents a dissimilarity matrix where yellow (1) denotes completely dissimilar items and blue (0) denotes maximally similar items.

or integers (1.24 s, $t(15) = 5.19, p < 0.001$). There was no significant difference in response time between decimals and integers ($t(15) = 1.15$, $p = 0.27$).

In order to assess the distance effect, average accuracies and response times were calculated for each trial across participants for fraction, decimal, and integer conditions. Regression analyses across individual items were conducted for accuracies and response times based on a logarithmic distance measure, log(|first number − second number|), which we will abbreviate as "log Dist" (see DeWolf et al., 2014; Hinrichs et al., 1981). Log Dist significantly predicted accuracy outcomes for fractions ($\beta = -0.65, t(37) = 26.91, p < 0.001$) but not for decimals ($\beta = 0.02, t(37) = 0.12, p = 0.90$) or integers ($\beta = 0.23$, $t(37) = 1.44, p = 0.16$). The lack of a distance effect in accuracy for decimals and integers likely reflects the fact that accuracy for these number types was near ceiling. Accordingly, we focused more closely on distance effects based on RTs for correct responses. Fig. 3 shows the
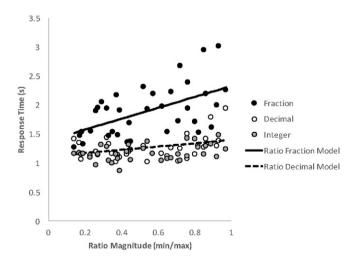

Fig. 3. Average correct response times for each trial across participants for fractions, decimals, and integers. Fitted lines represent predictions derived from LogDist models for Fractions and Decimals. (Because predictions of the Integer model were nearly identical to those of the Decimal model, the Integer model is excluded here for simplicity.)

average RT for each trial across participants for fractions, decimals, and integers. Log Dist significantly predicted RT outcomes for each of the number types (fractions: $\beta = -0.64, t(37) = 5.01, p < 0.001$; decimals: $\beta = -0.33, t(37) = 2.16, p = 0.04$; integers: $\beta = -0.33, t(37) = 2.12, p = 0.04$). These results replicate the pattern of distance effects observed by DeWolf et al. (2014), including (as evidenced by the much larger beta coefficient for fractions) a more pronounced distance effect for fractions than for either of the other two number types.
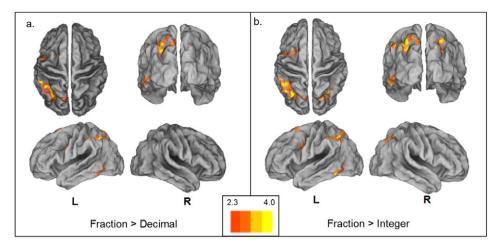
fMRI results

Univariate analyses

The contrast of fractions versus decimals resulted in extensive activations within and around the left horizontal segment of the intraparietal sulcus, spanning inferior (Brodmann Area [BA] 40) and superior (BA 7) parietal lobuli, as well as the junction of the intraparietal and intraoccipital sulci. Additional left hemispheric activations were detected in frontal cortex, centered around the precentral gyrus (BA 6) together with smaller foci within the superior (BA 6) and middle (BA 9) frontal gyri, and in temporal cortex, spanning the most caudal segments of the inferior and middle temporal gyri (BA 37). Finally, right lateralized activations were observed in the cerebellum, with foci in Crus I and Lobules VI and VIIB (see Fig. 4a and Table 2 for complete list of local maxima).

The contrast of fractions versus integers resulted in extensive activations in bilateral parietal cortex (with L > R), centered within and around the horizontal segment of the intraparietal sulci, spanning inferior (BA 40) and superior (BA 7) parietal lobuli.[2] Similarly to the contrast of fractions versus decimals, left lateralized activations were also obtained in frontal cortices, mostly within the precentral gyrus (BA

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[2] The analyses comparing fractions to decimals and fractions to integers revealed hemispheric differences, with the latter comparison resulting in bilateral parietal activations and the former resulting in left lateralized activations only. However, these differences were mainly attributable to the non-linear nature of the thresholding procedure. Inspection of uncorrected statistical parametric maps resulting from the fractions-minus-decimals contrast revealed clusters of above-threshold voxels (i.e., individual Z > 2.3); however, these were too small to survive the cluster-extent thresholding. These sub-threshold activations explain why no difference was apparent when directly comparing decimals and integers.

Fig. 4. Results of the univariate analysis for (a) comparison of fraction and decimal activation and (b) comparison of fraction and integer activation, from dorsal, posterior, and lateral views. Red areas represent significant differences in activations. The color scale represents z-values for significant activations.

6) together with foci across superior (BA 6, 8) and middle (BA 8) frontal gyri, and in the caudal section of temporal cortex, in the inferior and middle temporal gyri (BA 37). Finally, right hemispheric activations were again observed in the cerebellum, with foci in Crus I and II, and Lobule VI (see Fig. 4b and Table 3 for a complete list of local maxima).

Direct comparison of the decimal and integer conditions, in both directions (i.e., decimals > integers; integers > decimals), failed to reveal any significant activation.

Multivariate analyses

Because MVPA requires an equal number of trials across all conditions, one participant was excluded from this analysis because she did not finish one of the runs due to a computer error (missed two trials).

Table 2
Local maxima for the fractions > decimals univariate contrast (abbrev.: hIPS: horizontal segment of the intraparietal sulcus; IOS: intraoccipital sulcus; L: left; R: Right).

MNI coordinates			Hem	Region label (BA)	Z
x	y	z			
Parietal					
−42	−48	48	L	Inferior parietal lobule (hIPS; 40)	4.30
−30	−58	44	L	Superior parietal lobule (hIPS; 7)	3.93
−54	−38	48	L	Inferior parietal lobule (40)	3.91
−28	−70	38	L	Occipito-parietal junction (hIPS/IOS;40/7)	3.75
−28	−76	54	L	Superior parietal lobule (hIPS; 7)	3.71
−34	−50	42	L	Inferior parietal lobule (hIPS; 40)	3.71
Frontal					
−56	14	24	L	Precentral gyrus/inferior frontal gyrus (6/44)	3.77
−50	6	32	L	Precentral gyrus (6)	3.65
−22	6	70	L	Superior frontal gyrus (6)	3.27
−30	2	62	L	Precentral gyrus/superior frontal gyrus (6)	3.25
−34	2	28	L	Precentral gyrus/inferior frontal gyrus (6/44)	3.18
−36	2	62	L	Precentral gyrus/superior frontal gyrus (6)	3.16
−54	8	46	L	Precentral gyrus (6)	2.93
−40	−4	56	L	Precentral gyrus (6)	2.93
−28	−8	58	L	Precentral gyrus (6)	2.91
−18	12	66	L	Superior frontal gyrus (6)	2.85
−50	26	28	L	Inferior frontal gyrus/middle frontal gyrus (44/9)	2.70
−44	−4	30	L	Precentral gyrus (6)	2.68
Temporal					
−50	−56	-22	L	Inferior temporal gyrus (37)	3.18
−56	−56	-14	L	Inferior temporal gyrus (37)	3.13
-48	−64	-4	L	Inferior temporal gyrus (37)	3.03
−50	−60	0	L	Middle temporal gyrus (37)	2.84
−48	−56	0	L	Middle temporal gyrus (37)	2.60
Cerebellum					
38	−56	−32	R	Crus I	3.88
38	−60	−40	R	Crus I	3.41
28	−76	−50	R	Lobule VIIB	3.19
32	−72	−26	R	Crus I	3.13
44	−66	−30	R	Crus I	2.86
26	−60	−34	R	Lobule VI	2.86

Table 3
Local maxima for the fractions > integers univariate contrast (abbrev.: hIPS: horizontal segment of the intraparietal sulcus; L: left; R: Right).

MNI coordinates			Hem	Region label (BA)	Z
x	y	z			
Parietal					
−28	−62	46	L	Superior parietal lobule (hIPS; 7)	4.71
−30	−74	54	L	Superior parietal lobule (hIPS; 7)	4.39
−30	−70	54	L	Superior parietal lobule (7)	4.21
−48	−50	52	L	Inferior parietal lobule (40)	3.99
−48	−48	48	L	Inferior parietal lobule (40)	3.98
−40	−46	46	L	Inferior parietal lobule (hIPS; 40)	3.82
32	−68	48	R	Inferior parietal lobule (40)	3.82
30	−60	50	R	Superior parietal lobule (hIPS; 7)	3.74
28	−64	50	R	Inferior parietal lobule (40)	3.69
24	−68	48	R	Superior parietal lobule (7)	3.58
42	−54	58	R	Superior parietal lobule (7)	3.40
22	−72	50	R	Superior parietal lobule (7)	3.33
Frontal					
−50	10	28	L	Precentral gyrus (6)	3.88
−52	12	24	L	Precentral gyrus (6)	3.78
−52	10	36	L	Precentral gyrus (6)	3.62
−24	16	54	L	Superior frontal gyrus (8)	3.62
−36	4	28	L	Precentral gyrus (6)	3.51
−24	12	58	L	Middle frontal gyrus (8)	3.51
−46	6	34	L	Precentral gyrus (6)	3.41
−36	2	62	L	Precentral gyrus (6)	3.37
−52	2	42	L	Precentral gyrus (6)	3.34
−18	12	64	L	Superior Frontal gyrus (6)	2.97
−24	8	46	L	Middle frontal gyrus (8)	2.82
−24	14	66	L	Superior frontal gyrus (8)	2.78
Temporal					
−50	−56	−10	L	Inferior temporal gyrus (37)	3.76
−54	−54	−14	L	Inferior temporal gyrus (37)	3.65
−42	−60	−6	L	Inferior temporal gyrus (37)	3.08
−56	−64	−10	L	Inferior temporal gyrus (37)	2.98
−48	−64	−4	L	Inferior temporal gyrus (37)	2.96
−48	−48	−14	L	Inferior temporal gyrus (20/37)	2.76
Cerebellum					
38	−56	−30	R	Crus I	3.87
36	−64	−44	R	Crus II	3.25
40	−60	−38	R	Crus I	3.24
20	−66	−26	R	Lobule VI	3.21
38	−58	−42	R	Crus II	3.18
32	−72	−26	R	Crus I	3.18

Fig. 5 shows the areas within the IPS that yielded significant activations for each of the four models. The Number Type model (distinguishing between the three number types) shows a broad set of bilateral activations. Mirroring the results of the univariate analysis, the Fraction vs. Decimal model shows mostly left-lateralized IPS activation, whereas the Fraction vs. Integer model shows bilateral IPS activation. Unlike the results of the univariate analysis, the Decimal vs. Integer model yielded a small number (~3) of significant voxels that distinguished between decimals and integers. While this is a small area, it points to a possible pattern difference in the encoding of decimals and integers beyond what the univariate analysis revealed.

Discussion

Fraction magnitudes are neutrally distinct from decimals and integers

The central goal of the present study was to distinguish between possible models of neural representation for different symbolic number formats. The behavioral results showed that each of the number types elicited a reliable distance effect on correct RT. The presence of a distance effect suggests that all number types were processed holistically. However, the neuroimaging results showed that magnitudes evoked distinct neural patterns that distinguished the number types. Critically, the design allowed us to examine the neural response to an individual number presented in isolation, prior to the point at which a comparison with a second number could begin. Results of both a univariate analysis and MVPA indicate that while fractions, decimals, and integers all activate areas of the IPS, fractions yield a distinct pattern of activation associated with a unique subarea of the IPS. In contrast, decimals and integers yielded very similar and overlapping patterns, with MVPA identifying only a very small set of voxels that distinguished the latter two number types. Particularly in light of the differences identified in

the univariate analysis, it seems very likely that processing an individual fraction (even when a comparison is not possible) endogenously triggers a greater number of cognitive processes, or a greater cognitive load, as compared to the other two number formats. These results suggest that while neural representations, across notations, all elicit activation within the intraparietal sulcus, neural representation appear to be sensitive to number representation (notably, base-10 numbers versus fractions), but not to number type (natural versus rational).

To our knowledge, the present neuroimaging study is the first to compare fractions with both decimals and integers. The two previous studies (Ishebeck et al., 2009; Jacob and Nieder, 2009a) that investigated the representation of fraction magnitudes using fMRI had assumed that because fractions activate the IPS (as do integers), and because fraction activation was modulated by a distance effect based on holistic magnitude, the brain represents proportional (fraction) magnitudes in the same way that it does absolute (integer) magnitudes. However, by making direct comparisons among all three number types, the present study was able to clearly dissociate magnitude activations for fractions as compared to those for either integers or decimals.

Isolating magnitude representations for individual numbers

An important methodological innovation of the present study is its use of a design based on sequential presentation of individual numbers in a magnitude comparison task. Compared to passive observation of numbers, the magnitude comparison task strongly guides participants to access holistic magnitude representations for individual numbers. Moreover, the behavioral results from the comparison task fully replicated previous work comparing performance with the three number types (DeWolf et al., 2014). Comparisons were less accurate and slower for pairs of fractions than for pairs of decimals or integers. A distance effect was obtained for all number types, but was most pronounced for
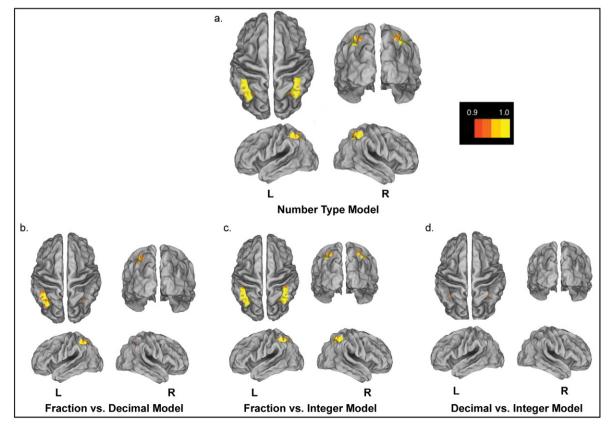

Fig. 5. Results of the multivoxel pattern analysis (MVPA) from dorsal, posterior, and lateral views for each of the four hypothesized models (see Fig. 2). The color scale represents 1 - *p*-values (e.g., 0.95 to 1 would be significant). Note: The searchlight analysis was restricted to the IPS, which was selected as a region of interest.

fractions. Our behavioral results thus confirm that participants in our neuroimaging paradigm were performing magnitude comparisons in essentially the same way as has been observed in previous behavioral studies.

At the same time, the sequential nature of the present design allowed us to decouple the process of *accessing* a magnitude representation for an individual number from the process of magnitude *comparison*. Our fMRI analyses focused solely on the initial 1.5 s period when a single number was displayed. During this period participants were motivated to access the magnitude of the presented number, but were unable to initiate a comparison because the second number in the pair had not yet appeared. Previous neuroimaging studies with fractions recorded neural signals during the comparison process itself. In contrast, our findings provide a clear picture of the neural activity underlying access to the magnitude of a single individual number, isolated from the additional activity that would be triggered by comparing two magnitudes.

What is special about fraction magnitudes?

We considered three hypotheses about the relation between magnitude representations for different symbolic notations. (1) All notations might evoke some universal, fully abstract magnitude code; (2) the magnitude code might differ between natural numbers (integers) and the more complex rational numbers (fractions and decimals); or (3) the magnitude code for fractions might differ from that for the base-10 notations (decimals and integers). Our findings clearly support the third of these hypotheses. To the best of our knowledge, no previous study has shown such a strong dissociation between the neural patterns elicited by alternative notations for the same magnitude. Even though 2/5 and 0.40 express the same magnitude, the brain processes the two symbols very differently. In contrast, the magnitude representations for a decimal (0.40) and an integer expressing a magnitude 100 times larger (40) are very similar. Importantly, the latter result implies that the neural code for numerical magnitude is on a scale that is fundamentally relative rather than absolute. Thus base-10 notations evoke similar activation patterns based on their relative magnitudes, whereas the bipartite fraction notation is processed very differently from either.

Future directions

The present study lays the groundwork for further exploration of the differences among neural representations evoked by different symbolic number types. Behavioral evidence points to a major conceptual distinction between fractions and decimals, with the former being selectively used to code the magnitudes of *discrete* entities (which can be counted), and the latter selectively used to code the magnitudes of *continuous* quantities (which can be either estimated or measured by imposing arbitrary units; see Rapp et al., 2015). In addition, it is important to examine neural processing in mathematical tasks other than those that focus on magnitudes. Whereas fractions are disadvantaged relative to decimals in magnitude comparison tasks, fractions convey reliable advantages in a variety of reasoning tasks. Because of their bipartite structure, fractions have a much more natural correspondence to relational concepts based on ratios of countable sets (DeWolf et al., 2015a). The relational aspects of fraction representations appear to make fraction understanding a critical bridge to learning algebra (DeWolf et al., 2015b), which depends critically on grasping the concept of a variable (understood to represent a quantity of unknown magnitude). The "isolation" technique introduced in the present paper (imaging activity evoked by an individual number as the participant prepares for a specific mathematical task performed immediately afterwards) might usefully be extended to compare the neural patterns evoked by the same symbol (e.g., a fraction) in preparation for tasks that require different types of information (e.g., magnitudes or relational concepts).

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