Brief Communications

Notation-Independent Representation of Fractions in the Human Parietal Cortex

Simon N. Jacob and Andreas Nieder

Department of Animal Physiology, Institute of Neurobiology, University of Tübingen, 72076 Tübingen, Germany

Although the concept of whole numbers is intuitive and well suited for counting and ordering, it is with the invention of fractions that the number system gained precision and flexibility. Absolute magnitude is encoded by single neurons that discharge maximally to specific numbers. However, it is unknown how the ratio of two numbers is represented, whether by processing numerator and denominator in separation, or by extending the analog magnitude code to relative quantity. Using functional MRI adaptation, we now show that populations of neurons in human fronto-parietal cortex are tuned to preferred fractions, generalizing across the format of presentation. After blood oxygen level-dependent signal adaptation to constant fractions, signal recovery to deviant fractions was modulated parametrically as a function of numerical distance between the deviant and adaptation fraction. The distance effect was invariant to changes in notation from number to word fractions and strongest in the anterior intraparietal sulcus, a key region for the processing of whole numbers. These findings demonstrate that the human brain uses the same analog magnitude code to represent both absolute and relative quantity. Our results have implications for mathematical education, which may be tailored to better harness our ability to access automatically a composite quantitative measure.

Introduction

The ability to encode magnitude, regardless of modality and format of presentation, is a prerequisite for the development of arithmetic and mathematics (Dehaene, 1997). The emergence of language and with it the invention of symbols has transformed the phylogenetically ancient approximate representation of absolute magnitude to allow for a highly precise rendition of number. The introduction of fractions, the ratio of two integers, constituted another major conceptual step, broadening the range and flexibility of the magnitude system beyond the limits immanent to whole numbers. Although much is known about the cerebral processing of absolute quantity (numerosity and integers) in a fronto-parietal network with the intraparietal sulcus (IPS) as key node (Nieder, 2005), there are currently no data describing how the human brain processes fractions. It thus also remains elusive whether connections exist between the neuronal code for absolute and relative magnitude.

There is recent evidence that, both ontogenetically and phylogenetically, proportions are not new mental constructs but are given intuitively. On the behavioral level, infants were reported to be able to discern two ratios sufficiently far apart, long before being introduced to the concept of proportionality during schooling (McCrink and Wynn, 2007). Similarly, monkeys have

been shown to process the relation of two line lengths (Vallentin and Nieder, 2008). The same study also reported that this ratio is encoded by single neurons in the macaque prefrontal cortex that discharge maximally to preferred proportions. Tuning to magnitude ratios shows that the primate brain is capable of representing relative quantity as an abstract category, using the same coding scheme as described for absolute number (Nieder et al., 2002; Nieder and Miller, 2003). This suggests a biological precursor onto which symbolic fractions may map [neuronal recycling hypothesis (Dehaene and Cohen, 2007)] and begs the question whether the human brain can indeed process fractions automatically or, alternatively, accesses numerator and denominator in separation.

We designed a functional MRI (fMRI) adaptation (fMRA) experiment to study how fractions are represented and whether they exploit the nonverbal core system of magnitude. The neurophysiological phenomenon of adaptation is based on the observation that repetitive presentation of invariant sensory features entails a decrease in activity [read out as change in spike rate or blood oxygen level-dependent (BOLD) signal] in the neurons sensitive to this property (Li et al., 1993; Miller and Desimone, 1994; Sobotka and Ringo, 1996; Grill-Spector et al., 1999; Grill-Spector and Malach, 2001). This finding is thought to indicate automatic processing of the dimension of interest.

Using a protocol modified from well established fMRA experiments on the cortical location and mechanisms of the representation of absolute number (Piazza et al., 2004; Ansari et al., 2006; Cantlon et al., 2006; Cohen Kadosh et al., 2007; Piazza et al., 2007), we confronted healthy subjects with a visual stream of fractions. After an adaptation phase, we included deviants in the sequence at irregular intervals that differed parametrically in numerical distance from the adaptation fraction (Fig. 1A). To en-

A

Adaptation Deviants { Fraction numerals (experiment 1) / Fraction words (experiment 2)

2:12 5:30 1:6 8:48   5:6 or 10:12   5:6 or 10:12   2:6 or 4:12   2:6 or 4:12   4:6 or 8:12   4:6 or 8:12   3:6 or 6:12   3:6 or 6:12

6:36 4:24 3:18 10:60   halb ("one half") or nach ("after")   sechstel ("one sixth") or zwischen ("between")   drittel ("one third") or entlang ("along")   viertel ("one fourth") or während ("during")

|1:6| ... |1:6| ... |1:6| ... |1:6| ... |1:6| ... |1:6| ... |1:6| ... |1:6| ... |1:6| |1:6| ... |1:6| ... |1:6| ...

39.6 s   3.6 - 13.2 s   Time

B

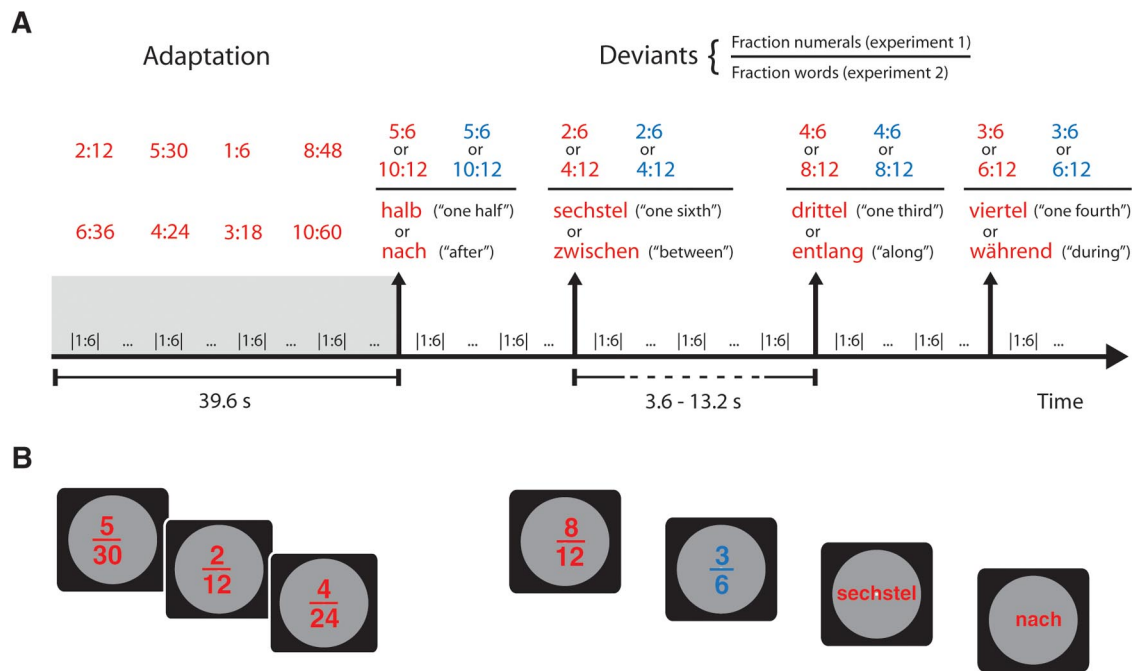5/30   2/12   4/24   8/12   3/6   sechstel   nach

Figure 1. Experimental protocol. ***A***, In both experiments, subjects were adapted to |1:6|. Adaptation stimuli included a wide range of numerators and denominators. After adaptation, stimuli deviating in proportion (deviants) were intermingled with the adaptation stimuli at irregular intervals. Two distinct notations were used for the deviants. In the first experiment, deviants were |2:6|, |3:6|, |4:6|, and |5:6| (fraction numerals). They were presented with denominators 6 or 12 (using the numerators of the adaptation phase) and colored red or blue (three-factorial design). In the second experiment, deviants were the German words for one-sixth, one-fourth, one-third, and one-half (fraction words). The terms for between, during, along, and after were used as controls. ***B***, Example images for both experiments.

sure that fractions were represented independently of absolute numbers, a wide range of numerators and denominators was used for the adaptation stimuli while maintaining constant the actual fraction (|1:6|). We also varied the notation of the deviants using numerals (i.e., |3:6|) and words (i.e., *halb*, German for "one-half") in two experiments (Fig. 1*A*; example stimuli in Fig. 1*B*).

Materials and Methods

Participants
Twelve healthy right-handed volunteers (ages 21–29) participated in the study after the local ethics committee approved all experiments. Fourteen different subjects (right handed, ages 22–42) were recruited for the control adaptation experiment.

Experimental protocol
Stimulus presentation in the MRI scanner was controlled with Presentation (Neurobehavioral Systems). All stimuli comprised a large gray background circle subtending 9.2° of visual angle to focus the subjects' attention and a central white fixation spot. Stimuli were presented for 500 ms followed by the blank background circle and fixation point for an additional 700 ms (interstimulus interval, 1.2 s). In both protocols (fraction numeral or fraction word deviants), subjects were adapted to |1:6|. Each experiment opened with an adaptation phase, during which 33 stimuli were presented without intervening deviants. For the remainder of the experiment, deviant stimuli were randomly interspersed among the adaptation images, separated by 3–11 stimuli (interdeviant time, 3.6–13.2 s). The first deviant was chosen to signal a maximal change in the dimension of interest. It occurred directly after the adaptation phase. In each experiment, a total of 360 stimuli were presented, of which 48 were deviants. Each protocol was repeated once. The sequence of experimental runs was the same for all subjects. To ensure that intentional response selection did not confound the results, subjects were not given any explicit task but merely instructed to fixate and attend to the features of the visual display.

Stimulus design
Fraction numerals. Adaptation fractions were 1:6, 2:12, 3:18, 4:24, 5:30, 6:36, 8:48, and 10:60 in red color for the main experiments. In the experiment controlling for calculation, adaptation stimuli were derived from the original fractions by small changes to the denominator in both directions for a total of 24 different fractions: 1:5, 1:6, 1:7, 2:11, 2:12, 2:13, 3:17, 3:18, 3:19, 4:22, 4:24, 4:26, 5:28, 5:30, 5:32, 6:34, 6:36, 6:38, 8:45, 8:48, 8:51, 10:56, 10:60, and 10:64. Deviants were |2:6|, |3:6|, |4:6|, and |5:6|. Each deviant fraction was presented equally often with denominator 6 or 12, colored red or blue (equiluminant). For all adaptation and deviant stimuli, individual numerals were presented in sans serif font, point sizes varied randomly between 40 and 50. The bar was centered on the fixation spot but allowed to vary by 0.8° along the *x*-axis.

Fraction words and control words. All stimuli were considered deviants. Fraction word deviants were the German words for "one-sixth," "one-fourth," "one-third," and "one-half" (*sechstel*, *viertel*, *drittel*, *halb*, respectively). Control word deviants were the German terms for "between," "during," "along," and "after," matched for word length (*zwischen*, *während*, *entlang*, *nach*, respectively). All words were presented in lowercase red sans serif font, point sizes varied randomly between 21 and 26. Stimuli were centered on the fixation spot but allowed to vary by 0.8° along the *x*-axis.

Image acquisition
T2*-weighted functional images [repetition time (TR), 2.4 s; echo time (TE), 37 ms] sensitive to the BOLD contrast were acquired in gradient echo-planar-imaging sequences on a 3T Siemens Tim Trio scanner (Siemens). Thirty-six slices with a 0.5 mm gap were acquired in descending order at 3 × 3 × 3 mm isotropic resolution [flip angle, 90°; field of view (FOV), 192 mm; image matrix, 64 × 64]. Anatomical scans used the three-dimensional gradient-echo T1-weighted Siemens MPRAGE sequence [TI (inversion time) 1.1 s; TR, 2.3 s; TE, 2.92 ms] acquiring 176 slices in the sagittal plane at 1 × 1 × 1 mm isotropic resolution (flip angle, 8°; FOV, 256 mm; image matrix, 256 × 256).

Data analysis

Functional images were analyzed with SPM5 (Wellcome Department of Imaging Neuroscience, London, UK). The first three scans were discarded to allow for equilibration of T1 magnetization. The remaining volumes were unwarped with the FieldMap toolbox, corrected for motion, slice-time corrected, normalized to the Montreal Neurological Institute (MNI) standard space, smoothed with an isotropic Gaussian kernel of 8 mm, and high-pass filtered (320 s). In the general linear model framework, time and dispersion derivatives were added to the hemodynamic response function model. For the fraction numeral deviants, separate regressors were used for numerical distance, denominator and color in a three-factorial design [factors distance (four levels) and denominator/color (two levels)]. For the word deviants, there were regressors for fraction word and control word deviants (four levels each). A regressor decreasing linearly during the adaptation period approximated BOLD signal adaptation. The distance effect was modeled by a (linear) parametric regressor spanning all four levels of distance with greater signal recovery for the numerically distant compared with the closer deviants. Realignment parameters were included as regressors of no interest. Contrasts identifying voxels with significant adaptation and other main effects were entered in a second-level random effects analysis. The adaptation regressor was orthogonal to the event condition regressors, meaning they accounted for independent components of the BOLD signal variance. Thus, there was no selection bias by using the adaptation regressor for further analysis of the effect of numerical distance. To ensure comparability to previous studies of magnitude processing (Piazza et al., 2004, 2007; Cantlon et al., 2006), thresholds for statistical inference were set at $p < 0.01$ uncorrected at the voxel level, corrected for multiple comparisons at the cluster level to $p < 0.05$ with a cluster extent of 30 voxels. Conjunction analysis testing for joint activation in both experiments was performed by calculating minimum t statistics for the two distance effects. The result was thresholded at $p < 0.05$ with a cluster size of 30 voxels to account for the conservative test of the conjunction null (as opposed to the global null). Student's paired t test with one-tailed distributions was used for statistics.

Results

In the first experiment, both the adaptation and deviant stimuli were fractions expressed with numerals ("fraction numerals") (Fig. 1*A*). |1:6| was used for adaptation. Deviants were |2:6|, |3:6|, |4:6|, and |5:6|, with denominator 6 or 12. The deviants' only novel property was proportion; both the numerator and denominator had been part of the adaptation fractions. Similarly, the absolute difference between numerator and denominator did not inform about the specific proportion and fell within the range covered in the adaptation phase. All stimuli were colored in red, except for half of the deviants, which were presented in blue color to control for possible non-numerical effects, such as capturing of attention caused by changes in the visual display of the deviants. The experiment, therefore, conformed to a three-factorial design with deviant fraction (|2:6|, |3:6|, |4:6|, or |5:6|), denominator (6 or 12), and color (blue or red) as main factors.

The BOLD signal in several brain regions decreased systematically during the adaptation phase. These areas included bilateral parietal cortex, precentral cortex, prefrontal cortex, the anterior cingulate cortex, and infero-temporal cortex. The strongest effects were observed in parietal cortex, spanning the whole length of the IPS from the postcentral sulcus to the posterior superior parietal lobule (SPL) (in anterior–posterior direction) (Fig. 2*A*).

To discern areas involved in processing non-numerical features from those representing the quantitative aspect of the stimuli, we identified voxels sensitive to changes in stimulus color. In addition to activation in bilateral infero-temporal cortex, prefrontal cortex, the posterior cingulate cortex, and the precuneus, significant voxels in the parietal cortex were restricted to the posterior regions of the SPL (Fig. 2*B*). This structure has frequently
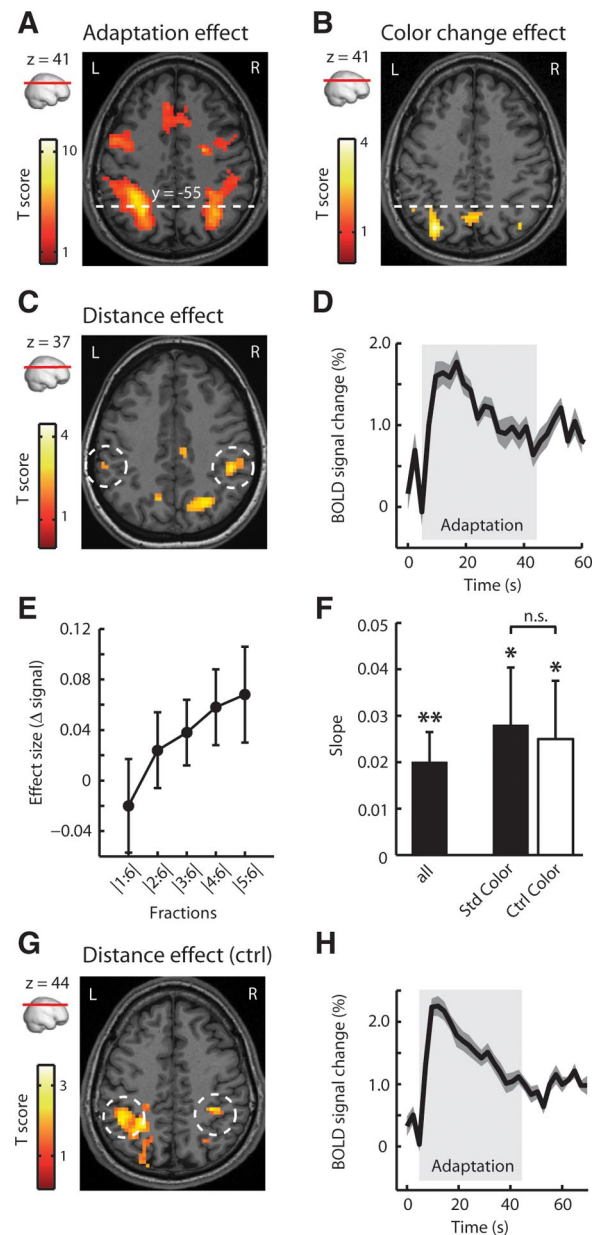

Figure 2. Tuning to fractions in the anterior parietal cortex. *A*, Cortical areas with a systematic BOLD signal decrease during the adaptation phase. *B*, Voxels sensitive to color changes were restricted to the posterior parietal cortex. *C*, BOLD signal distance effect for fraction numerals (stronger recovery to numerically more distant stimuli) was present also in the anterior parietal cortex (dashed circles). *D*, BOLD signal time course extracted from the anterior parietal cortex defined by the adaptation contrast (anterior to a coronal plane at $y = -55$; *A*), averaged over hemispheres and subjects. *E*, Percentage signal change in the same areas plotted as a function of presented fraction. *F*, Averaged slope of linear fits to individual subjects' deviant data points averaged over all stimuli (left) as well as for standard color and control color deviants separately (right). *G*, *H*, Same analysis as in *C* and *D* for the control adaptation experiment. L, Left; R, right; **$p < 0.01$, *$p < 0.05$; n.s., not significant.

been implicated in allocating attention (bottom-up) and is activated by unspecific stimulus novelty (Dehaene et al., 2003; Gur et al., 2007). Similarly, an effect of deviant denominator (6 vs 12) was present in primary visual cortex and a small region in right posterior-most parietal cortex only; no effect of deviant denominator was observed in the IPS (data not shown).

When testing for stronger activation to numerically distant deviants compared with stimuli closer to the adaptation proportion (distance effect), the only regions surviving the threshold

were bilateral parietal cortex and a small area in the middle cingulate. Notably, parietal activation included a well defined region in bilateral anterior IPS that overlapped entirely with the anterior parietal regions seen in the adaptation phase but did not share any voxels with the areas responsive to color and denominator changes (Fig. 2C, dashed circles). A coronal plane at $y = -55$ (MNI coordinates) provided perfect separation of the anterior and posterior parietal clusters. Interestingly, in a meta-analysis of fMRI studies on magnitude processing (Dehaene et al., 2003), this plane discriminated well between anterior number-specific regions and posterior novelty areas in the SPL.

The BOLD signal time course in the anterior IPS (defined by the adaptation contrast anterior to the coronal plane, $y = -55$, averaged over subjects and hemispheres) showed a marked increase from rest following introduction of the first stimulus and then decreased constantly during the adaptation phase. There was a clear rebound after presentation of the first fraction deviant (Fig. 2D).

We plotted the signal change associated with each deviant in the anterior IPS as a function of numerical distance from the adaptation stimulus (averaged over subjects, hemispheres, and denominators) (Fig. 2E). Recovery from adaptation increased significantly during presentation of more distant deviant fractions, i.e., the slopes of linear fits to individual subjects' graphs (deviant data points only) were larger than zero ($p = 0.0047$; t test; $n = 12$) (Fig. 2F, left). Importantly, recovery for standard and control color deviants was equal, showing that BOLD response to salient novel colors did not exceed that for standard stimuli ($p > 0.88$) (Fig. 2F, right). In summary, BOLD signal recovery in anterior IPS, a region mostly insensitive to general stimulus novelty, was a function of numerical distance between deviant and adaptation proportion.

To exclude that subjects were rapidly calculating the exact equality over the presented fractions, whereby our results would reflect adaptation to constant absolute quantity instead of number ratios, we performed a control experiment. Fourteen new, naive subjects were adapted to approximately 1:6. Adaptation stimuli were derived from the original fractions by small variations of the denominator (see Materials and Methods) and thus no longer comprised an identical fraction with numerator and denominator multiplied by the same integer. Even when exact calculation was made impossible, we observed a strong distance effect in bilateral anterior IPS (Fig. 2G) with robust BOLD signal adaptation in this region (Fig. 2H).

To determine whether the observed coding of fractions was independent of the specific symbolic notation, we next presented the deviant stimuli in written verbal form (while the adaptation fractions remained numerals) using the German words *sechstel*, *viertel*, *drittel*, and *halb* for one-sixth, one-fourth, one-third, and one-half, respectively ("fraction words"). As controls for confounding effects caused by the transition from numerals to words, we included the German terms *zwischen*, *während*, *entlang*, and *nach* for between, during, along, and after, respectively, matched for word length with the fraction words (Fig. 1A). By changing the notation with perceptually very different stimuli, we aimed to clearly discern novelty processing from true representation of proportionality.

In good agreement with our previous results, a robust distance effect for fraction words was observed in posterior, and importantly, anterior parietal regions that overlapped with the adaptation areas found for fraction numerals (Fig. 3A,B, dashed circles). An effect of numerical distance was also present in the anterior cingulate and left precentral cortex. The same areas were
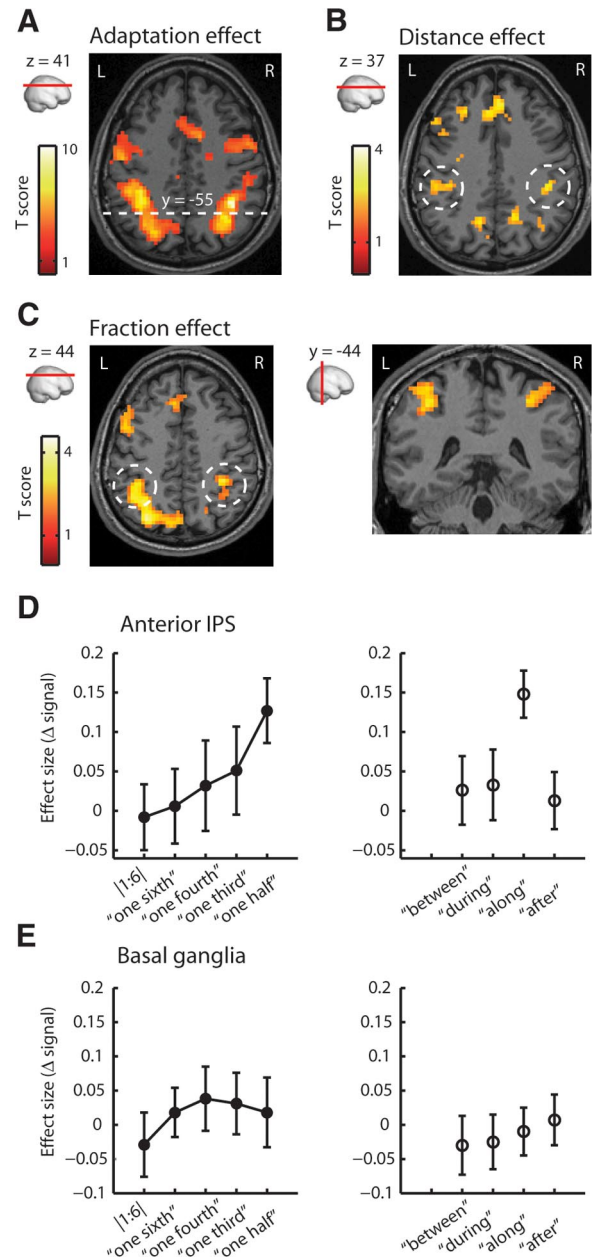

Figure 3. Notation-independent encoding of fractions in the anterior parietal cortex. **A**, Cortical areas with a systematic BOLD signal decrease during the adaptation phase. **B**, Voxels with a significant BOLD signal distance effect for fraction words include the anterior parietal cortex (dashed circles). **C**, Greater signal recovery to fraction words compared with control words in the same areas. **D**, Percentage signal change in the anterior parietal cortex defined as described in Figure 2 for the fraction words (left) and control words, matched for word length (right). **E**, Same analysis for the striatum. L, Left; R, right.

active when we directly contrasted the fraction words with the control words (Fig. 3C). BOLD signal recovery extracted from the anterior parietal adaptation areas (anterior to the coronal plane, $y = -55$) increased as the fraction word deviant became more remote from the adaptation stimulus (fraction numeral) (Fig. 3D). Notably, after adaptation to |1:6|, there was no difference in BOLD signal recovery between |1:6| and one-sixth in the anterior IPS ($p = 0.84$; t test; $n = 12$), supporting a notation-independent representation of fractions (Fig. 3D, left panel). The same analysis for the control words, matched with fraction words for word length, failed to show a parametric modulation of BOLD signal.
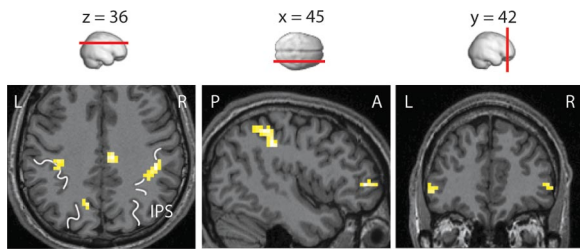
Figure 4. Frontoparietal representation of fractions across notations. Conjunction analysis searching for regions with a BOLD signal distance effect in both experiments identified the bilateral IPS and prefrontal cortex. IPS marked in white.

This emphasizes that the BOLD signal rebound observed for fraction words indeed reflected a numerical distance effect for fractions and was not merely attributable to presentation of novel stimulus material. The control data points showed no recovery from adaptation ($p > 0.23$; t test; $n = 12$), with the exception of the word along (German *entlang*) (Fig. 3D, right panel). We speculate that the semantic association with spatial extent inherent to this word might have caused the disproportionate recovery.

Moreover, we verified that BOLD signal recovery was not related to the number word fragments "six," "four," and "three" contained in the deviant fraction words, which would have resulted in the greatest signal change to one-sixth. To that aim, we conducted a full-brain search for an inverted distance effect, i.e., largest BOLD signal recovery to one-sixth (data not shown). No voxels reached the significance threshold, demonstrating that subjects had correctly perceived the deviants as fractions and not absolute numbers.

To ascertain that the distance effect was attributable to automatic semantic processing of magnitudes and therefore specific to the IPS, we plotted the same data extracted from the striatum, a region that had adapted strongly and is sensitive to changes in stimulus saliency (Zink et al., 2006). Unlike in parietal cortex, signal recovery was comparable across deviants, and there was a small BOLD signal recovery associated with changes from fraction numerals to fraction words (Fig. 3E, left panel). As in the IPS, there was no difference among control words in the striatum (Fig. 3E, right panel). When plotting the individual subjects' effect size to fraction word deviants as a function of numerical distance, only the slopes of the linear fits to the IPS data were significantly positive (t test, $n = 12$; fractions: IPS 0.038 ± 0.017, $p = 0.027$; striatum -0.007 ± 0.017, $p = 0.34$; controls: IPS 0.008 ± 0.015, $p = 0.31$; striatum 0.010 ± 0.008, $p = 0.12$). This region of interest analysis confirms the previous whole-brain analyses of the distance effect (Figs. 2C, 3B), demonstrating that the neural circuitry to represent fractions resides in the IPS.

Finally, in a conjunction analysis, the predominant brain regions with neuronal populations activated by fraction changes in both formats were the IPS and the prefrontal cortex (the latter had not survived the threshold in the previous analyses) (Fig. 4). Significant voxels were observed in bilateral prefrontal cortex and especially the fundus of the IPS bilaterally, extending from the posterior margin of the postcentral sulcus to the horizontal segment of the IPS. A small cluster was also present in the right cingulate cortex.

Discussion
Our experiments show that neuronal populations in the human parietal cortex surrounding the anterior and horizontal IPS are tuned to preferred fractions, regardless of the format of presentation. The observed parametric modulation of BOLD signal re-

covery with numerical distance from the adaptation stimulus indicates that the composite, derived ratio of numbers is represented automatically by an analog magnitude code.

Several arguments emphasize that unspecific effects of stimulus novelty did not confound our results. First, salient color and notation changes strongly violated the subjects' expectancy but failed to elicit BOLD signal changes in the anterior IPS, which was exclusively sensitive to novel fractions. This finding is in good agreement with previous observations that allocating attention activates the posterior SPL only (Dehaene et al., 2003; Gur et al., 2007). Second, the analyzed areas in anterior IPS partially overlap with the regions reported by a meta-analysis of fMRI studies that are considered dedicated to the processing of magnitudes (Dehaene et al., 2003). Third, tuning to fractions was replicated with two distinct notations, suggesting that symbolic ratios are represented as an abstract magnitude category in the human brain.

We can exclude that subjects performed a simple division for each fraction to create a real number, in which case our findings would reflect processing of absolute numbers instead of proportions. Adaptation to approximately 1:6 with fractions that were not merely derived by multiplying the numerator and denominator with the same integer produced results identical to the previous experiments. Since fractions were no longer identical, subjects were prevented from calculating the exact equality for the stimuli given the rapid succession of stimuli with tight time constraints. In addition, such a strategy was hardly motivated because the subjects were not required to perform a task on fractions. We therefore predict the same BOLD signal distance effect in children that have acquired number symbols but have yet to master basic arithmetic.

We would also expect to obtain similar results with nonverbal, nonsymbolic proportion stimuli. Recent data from nonhuman primates suggest that monkeys grasp the concept of proportionality when trained to discern the ratio of line lengths (Vallentin and Nieder, 2008). Subsequent electrophysiological recordings from the prefrontal cortex revealed strong similarities in the code for absolute and relative quantity: neurons discharged maximally to a preferred proportion, and activity dropped off gradually as the distance between the favorite and the presented stimulus increased. Interestingly, the prefrontal cortex was also found to represent fractions independently of notation in the current study (Fig. 4). With fMRA experiments comparable with those used for investigating absolute number in humans (Piazza et al., 2004, 2007; Ansari et al., 2006; Cantlon et al., 2006; Cohen Kadosh et al., 2007), we now link multiple lines of evidence to show that in the same areas processing numerosity, neural populations are tuned to fractions. This indicates that the human prefrontal cortex and particularly the anterior IPS represent both absolute and relative magnitude with the same analog magnitude code.

In contrast to nonsymbolic proportions, fractions are believed to be unintuitive and difficult to comprehend, despite the semantically analogous construct. Children require formal teaching to understand and correctly use fractions, and even adults are reported to treat numerator and denominator in separation, implying the term is processed by separate operations on integers (Bonato et al., 2007). Here, we demonstrate that in the absence of a specific task, we do have access to an automatic representation of relative quantity. Our results advocate a less rigid and formalized view of fractions, discouraging their primary use as mere placeholders for rational, decimal numbers. By adopting a more instinctive, natural approach to fractions, mathematical education could be modified to help us better exploit their formidable neuronal basis.

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