

Distinct Representations of Magnitude and Spatial Position within Parietal Cortex during Number–Space Mapping

Frank J. Kanayet, Andrew Mattarella-Micke, Peter J. Kohler, Anthony M. Norcia, Bruce D. McCandliss, and James L. McClelland

Abstract

■ Mapping numbers onto space is foundational to mathematical cognition. These cognitive operations are often conceptualized in the context of a “mental number line” and involve multiple brain regions in or near the intraparietal sulcus (IPS) that have been implicated both in numeral and spatial cognition. Here we examine possible differentiation of function within these brain areas in relating numbers to spatial positions. By isolating the planning phase of a number line task and introducing spatiotopic mapping tools from fMRI into mental number line task research, we are able to focus our analysis on the neural activity of areas in anterior IPS (aIPS) previously associated with number processing and on spatiotopically organized areas in and around posterior IPS (pIPS), while participants pre-

pare to place a number on a number line. Our results support the view that the nonpositional magnitude of a numerical symbol is coded in aIPS, whereas the position of a number in space is coded in posterior areas of IPS. By focusing on the planning phase, we are able to isolate activation related to the cognitive, rather than the sensory–motor, aspects of the task. Also, to allow the separation of spatial position from magnitude, we tested both a standard positive number line (0 to 100) and a zero-centered mixed number line (–100 to 100). We found evidence of a functional dissociation between aIPS and pIPS: Activity in aIPS was associated with a landmark distance effect not modulated by spatial position, whereas activity in pIPS revealed a contralateral preference effect. ■

INTRODUCTION

Mapping number to space is fundamental to mathematical reasoning. This close relationship is reflected in the Cartesian coordinate plane used to plot functions, in the unit circle engaged for solving trigonometric problems, and in the number line drawn to teach basic math concepts to children. Spatial representations are essential for grasping abstract numerical concepts. Therefore, mathematical reasoning must be understood within the context of the cognitive and neural mechanisms that connect number to space.

One important research tradition raises the possibility that the cognitive relation of number to space is fundamental to the way we represent numbers. Evidence taken in support of this possibility includes the spatial–numerical association of response codes (SNARC) effect (Dehaene, Bossini, & Giraux, 1993), spatial biases influenced by the presence of large or small numbers in a line bisection task (Fischer, 2001), and the impact of number on spatial attention (Fischer, Castel, Dodd, & Pratt, 2003; Zorzi, Priftis, & Umiltà, 2002). These results have led many researchers to be inspired by the concept of the “mental number line.”

However, the mental number line can be understood in at least two different ways: One interpretation (which we will call the “positional view”) states that mental rep-

resentations of numbers are intrinsically organized by position, potentially as a result of the brain “recycling” the neural architecture used to represent space (Chen & Verguts, 2012; Knops, Thirion, Hubbard, Michel, & Dehaene, 2009; Dehaene & Cohen, 2007). An alternative interpretation, which we will call the “magnitude view,” holds that numbers are represented as an approximate magnitude (Mix, Levine, & Newcombe, 2016; Verguts & Fias, 2004; Dehaene & Changeux, 1993), which is not intrinsically positional, but which can be mapped onto position in an experience- and context-dependent fashion by providing a positional reference (either landmarks or an origin, direction, and scale).¹ If so, number–space mapping might be a matter of relating the magnitude representation to an explicitly positional representation. Under this interpretation, the SNARC effect and other evidence of number–space association can be explained as reflecting a learned association between number and space, rather than an intrinsically spatial representation of number, consistent with the view that the use of position to represent number is a relatively recent historical development (Núñez, 2011).

Here we explore this issue in the context of a task that requires participants to explicitly map number into space: number line marking. The act of linking numbers to positions on a number line is closely related to math skill (Geary, Hoard, Nugent, & Byrd-Craven, 2008; Laski

& Siegler, 2007; Booth & Siegler, 2006). Furthermore, interventions that improve line-marking accuracy are associated with improvements in arithmetic performance (Booth & Siegler, 2008; Siegler & Ramani, 2008), and greater understanding of number may affect accuracy in marking the number line (Link, Nuerk, & Moeller, 2014). Line marking remains relevant across a range of different types of numbers encountered at different ages, from whole numbers between 0 and 100 in the early school years (Siegler & Opfer, 2003) to more complex and abstract types of numbers such as negative numbers and fractions (Siegler & Lortie-Forgues, 2014). These connections between number line marking and mathematical skill development have been used to support the concept of a mental number line.

For the purposes of understanding how numbers are explicitly mapped into a spatial frame of reference, number line studies have focused on analyzing the strategies used by participants during number line marking. Using behavioral measures (such as the RT to place a mark on a line or the amount of error in positioning a number on a line; Ashcraft & Moore, 2012; Barth & Paladino, 2011; Siegler & Opfer, 2003), eye tracking (Schneider et al., 2008), and finger trajectories on a tablet (Dotan & Dehaene, 2013), studies have found that end- and mid-points are commonly used as landmarks by accurate participants.

In the brain, the relationship between number and space has been explored via the study of patients with parietal lesions (Walsh, 2003; Zorzi et al., 2002; Cipolotti, Butterworth, & Denes, 1991) and via common activation in the intraparietal sulcus (IPS). In their seminal article, Dehaene, Piazza, Pinel, and Cohen (2003) identified a candidate brain region for the instantiation of the mental number line in a region they identified as the horizontal segment of the intraparietal sulcus (hIPS). This area has been continually found to play a significant role in a wide variety of number processing tasks (Sokolowski, Fias, Mousa, & Ansari, 2016; Arsalidou & Taylor, 2011) and might be considered to be the foundational representation of number in the brain. On the positional view described above, hIPS would be viewed as housing a spatially organized representation of the mental number line. However, under the magnitude view, the foundational representation in hIPS might represent numbers in terms of their magnitudes rather than their positions. Under the latter view, it is important to consider whether other brain areas might be involved in constructing a positional representation of numbers.

Within the IPS, several studies have attempted to subdivide this spatially extended sulcus based on cytoarchitectural features (Choi et al., 2006), anatomical connectivity (Schel & Klingberg, 2016; Bray, Arnold, Iaria, & MacQueen, 2013), or functional characteristics such as topographic maps of visual space (see Silver & Kastner, 2009, for a review). Although the divisions based on these different efforts do not match exactly, there is a consistent and im-

portant distinction between the anterior and posterior areas of IPS. Anterior IPS (aIPS) areas are primarily connected to frontal cortex, overlap with the peak voxels from meta-analytic papers on number processing (Arsalidou & Taylor, 2011; Dehaene et al., 2003), and lack topographic maps of visual space (Schel & Klingberg, 2016; Bray et al., 2013; Silver & Kastner, 2009), consistent with a magnitude-based representation. In contrast, posterior IPS (pIPS) areas have stronger connections to occipital visual regions and contain topographic maps of visual space analogous to those found in neighboring occipital cortex. Thus, pIPS and neighboring regions of the posterior superior parietal lobule (PSPL) appear to be plausible candidates for participation in the representation of numbers in terms of positions in space. Considering first the PSPL, Dehaene et al. (2003) also proposed that the PSPL was responsible for engaging visuospatial attention to specific regions of the mental number line. Recent studies seem to agree with this idea. For example, Knops et al. (2009) found that it was possible to classify addition and subtraction trials from brain activity in PSPL, but not from hIPS, collected during rightward and leftward eye movements. From the perspective of the topographic maps, the area labeled as PSPL by Dehaene et al. overlaps with topographic maps identified in areas called IPS3 and SPL1. In this article, we take advantage of this distinction between pIPS and aIPS to probe for commonalities and differences among these brain regions that may play a role in a number to space mapping task.

Despite significant behavioral research on the ability to map number onto space over development and extensive cognitive neuroscience research exploring brain representations of both number and space, the neural basis for the mapping between number and space has not yet been explored extensively. A recent study by Vogel, Grabner, Schneider, Siegler, and Ansari (2013) is a notable exception to this gap in the literature. In this study, participants viewed a number and placed it on a number line during fMRI scanning. Number line marking was found to engage the same regions in aIPS previously identified across other number processing tasks. In addition, a small area within the broader aIPS was found to increase activation parametrically with the distance between the number to be estimated and the closest landmark (i.e., left endpoint, right endpoint, and midpoint). This study provides important initial evidence that the process of linking numbers to space relies on the same cortical regions that are often identified in the number literature.

Although the study by Vogel and colleagues (2013) is an important first step, several key questions about how these subregions of IPS support the positional representations of numbers remain unanswered. In this article, we focus on these questions as the main goals of our study.

Because the number line-marking task is fundamentally about mapping numbers to space, it is ideal for a more in-depth exploration of the role of pIPS as well

as aIPS during number processing. In particular, number line marking allows us to ask whether areas that are active during the process of estimating the positions of numbers on a line include topographic visual maps identified in pIPS and other areas of visual cortex (Wandell, Dumoulin, & Brewer, 2007). Furthermore, the task allows for the possibility of distinguishing between the positional and magnitude views of the role of aIPS in number–space mapping. For example, because visual topographic maps preferentially represent the contralateral hemifield, one might predict that positional representations of number should exhibit a bias toward the hemisphere contralateral to their position on the number line. Under the interpretation of the aIPS as the locus of a representation of numerical magnitude, we would expect that a preferential representation of the contralateral hemifield would be seen in pIPS, but not in aIPS.

A key finding from the study of Vogel et al. (2013) that might be seen as supporting the view that the aIPS represents position explicitly was the observation that a region in the aIPS showed a landmark distance effect. However, this finding is also consistent with the idea that the aIPS representation is not explicitly spatial. Indeed, Vogel et al. refer frequently to this representation as a magnitude representation and suggest that greater activation of such a representation may be required when the position to be marked is further from the nearest landmark because of the greater effort required under these circumstances. In short, it is possible for a representation of number to reflect landmark distance, whether or not such a representation is explicitly spatial.

In this study, we take a different approach, probing more directly for evidence of spatial positional coding within the number line task and introducing three main innovations. First, to address positional coding of number in different regions of parietal cortex, we leverage recent advances in topographic analysis to identify and draw relevant ROIs. We focus our analysis on several ROIs comparing topographically organized regions extracted from a recently developed atlas (Wang, Mruczek, Arcaro, & Kastner, 2015) with ROIs in aIPS extracted from the literature on number processing (Vogel et al., 2013; Dehaene et al., 2003). Within each area, we consider whether there are preferential representations in the hemisphere contralateral to the number line position (a sign of a positional code) or whether there is instead a landmark distance effect independent of contralateral versus ipsilateral position, a finding that would be consistent with a number-as-magnitude representation.

Second, we employed a design that allows us to target the cognitive aspects of mapping number onto space rather than the overt sensory–motor processes of marking a position on a line. We achieve this by separating the number line estimation task into two phases: (1) the encoding phase, in which participants think about the number and where on the number line they want to place it, and (2) the marking phase, in which they

can move the cursor and their eyes to mark the number line. During analysis, we focus on activity during the encoding phase, allowing us to separate processes of encoding the magnitude of the number and the estimation of its relative position on the number line—processes that would appear to be more closely related to mathematical representation and processing itself—from the purely motor activity of making mouse and eye movements to execute and monitor the placement of the cursor on the number line. Because Vogel et al. measured neural activity for the full duration of the line-marking task, it was not possible to make these distinctions.

Our third innovation allows us to dissociate spatial position from numerical magnitude and to explore the cognitive and neural processes involved in mapping a wider range of numbers onto space. We achieve this by using two versions of the line-marking task, including a new version that uses both positive and negative numbers spanning a range from -100 to 100 , in addition to the more standard version in which the numbers range from 0 to 100 . Given the range 0 to 100 , smaller magnitudes are associated with positions on the left, and larger magnitudes are associated with positions on the right. But with the range -100 to 100 , magnitude (defined as a number's absolute value) increases symmetrically with position in both directions from the center of the line. This allows us to explore hemispheric lateralization of a representation of a number's position, unconfounded from left–right differences in magnitude. In addition, this design allows us to examine the mapping of negative as well as positive numbers onto space. This extension is important, because negative numbers are essential in many branches of mathematics, and knowing how to map negative as well as positive numbers to space is central to understanding the Cartesian plane, which in turn is essential to the understanding of algebra, analytic geometry, and many more advanced topics in mathematics. Furthermore, as we shall see, our design allows us to investigate the generality of strategic landmark use and of spatial biases that may be associated with landmark use (Barth & Paladino, 2011) across a wider range of numbers. To our knowledge, our study is the first to study the neural basis of mapping both positive and negative numbers onto space. We are aware of only two previous behavioral line-marking experiments using both positive and negative numbers (Young & Booth, 2015; Ganor-Stern & Tzelgov, 2008). Because the effects of range on spatial bias and landmarking behavior were not the focus of either article, it is not possible to extract strong conclusions about these topics.

In summary, our study extends the investigation of the neural basis of number representation and the mapping of number onto space, focuses on the specifically cognitive aspects of mapping number onto space, and extends this investigation to negative as well as positive numbers.

METHODS

Participants

Twenty-four adults participated (mean age = 25.9 years, range = 18–44 years; 16 women). All participants were right-handed, had normal or corrected-to-normal vision, and reported no neurological problems. Four participants were excluded because of scanner problems and one for not understanding the task. Written consent was obtained from all participants before the study under a protocol that was approved by the institutional review board of Stanford University.

Design and Procedure

Participants were recruited to play a number game and were guaranteed \$24 for participating plus a variable amount based on performance. On average, each participant received \$32. After giving consent and completing the metal screening, participants answered a 20-question math questionnaire obtained from an SAT practice test. Finally, before entering the scanner, all participants had the opportunity to practice the tasks under the guidance of the experimenter to make sure that they understood the instructions and procedures correctly.

The experiment consisted of three different tasks: two number line estimation tasks and one control word task. The positive number line task included numbers from 0 to 100, the mixed number line task included numbers from –100 to 100, and the word task included two-letter words. For all three tasks, participants were required to place the cursor in the correct position of a horizontal line in the middle of the screen. Correct positions for all stimuli were matched between tasks. The experiment consisted of four runs, each lasting 10 min. Each run included a full pass through all three tasks and all stimuli per task. The order of tasks was selected randomly for each run, and within run, the order of stimuli was also randomized. All tasks included 16 different stimuli, with 16 corresponding positions. For the positive task, the stimuli used were 16 numbers selected from the 20 used by Vogel et al. (2013): 3, 7, 11, 21, 28, 33, 36, 45, 57, 60, 65, 74, 77, 85, 90, and 98. For the mixed task, the stimuli corresponded to the set of numbers that can be placed on the same positions on the mixed number line as the stimuli in the positive task: –94, –86, –78, –58, –44, –34, –28, –10, 14, 20, 30, 48, 54, 70, 80, and 96. Finally, for the word task, the stimuli were a set of 16 two-letter words: of, is, me, we, he, it, so, by, do, am, as, my, or, ox, if, and be. Words were randomly assigned to positions on the number line, which corresponded to the positions used for the other two tasks. The position of particular word varied randomly between blocks and between participants. At the end of each task, we showed feedback to participants indicating their score for the task, and what type and how many errors were committed during that task, as well as how many accumulated errors and scores

they had up to that point in the experiment. We wrote our experiment in MATLAB (2015; The MathWorks, Natick, MA), using the Psychophysics Toolbox (version 3; Kleiner, Brainard, & Pelli, 2007; Brainard, 1997; Pelli, 1997).

Number Line Estimation Tasks

A white horizontal line on a gray background was presented on the middle of the screen extending for 10.5° of visual angle and staying on the screen for the duration of the block. For the positive task, the left end of the number line was marked with a “0” and the right end was marked with a “100.” For the mixed task, the right end of the number line was marked with “–100” and the left end was marked with “100.” Before the beginning of each trial, a fixation box appeared 250 pixels above the center of the line to signal that a number was going to appear and to instruct participants to fixate on the box.

Each trial was divided into two phases: an encoding phase and a marking phase. During the encoding phase, a number appeared briefly (500 msec) in the middle of the fixation box. Once the number disappeared from the screen, a red dot appeared at the location previously occupied by the number and stayed on the screen for a variable period between 2.5 and 6.5 sec.

During this period, participants were instructed to keep their eyes on the red dot and not move the trackball, while thinking about the number and considering what the correct position on the number line might be. They were also instructed to not move their eyes or the trackball. The start of the marking phase was signaled by the red dot changing to green. Participants were instructed to press the button on the trackball as soon as the dot changed to green to activate the cursor and to use the trackball to move the cursor to a position they thought was correct for the specific number and click the button again to mark the location. After the first button-press, the trackball cursor appeared in the middle of the line.² Participants had 3 sec to move the cursor to the desired position and make a mark. This deadline was selected based on piloting to make the task demanding, while still giving participants enough time, considering the relatively slow speed of the trackball. After the 3 sec had passed, the cursor and the box disappeared to signal the end of the trial and a variable inter trial interval between 3 and 7 sec was used before the beginning of the following trial (see Figure 1).

One of the main goals of this study was to understand the processes of encoding the magnitude of a number and estimating its relative position on a number line, without the influence of line-marking behavior. We made several design decisions to ensure that participants were actively engaging in thinking about the number and its corresponding position on the line during the encoding phase. To maximize performance, we awarded participants with 5 cents per correct trial, which over the course of the whole experiment amounted to an average

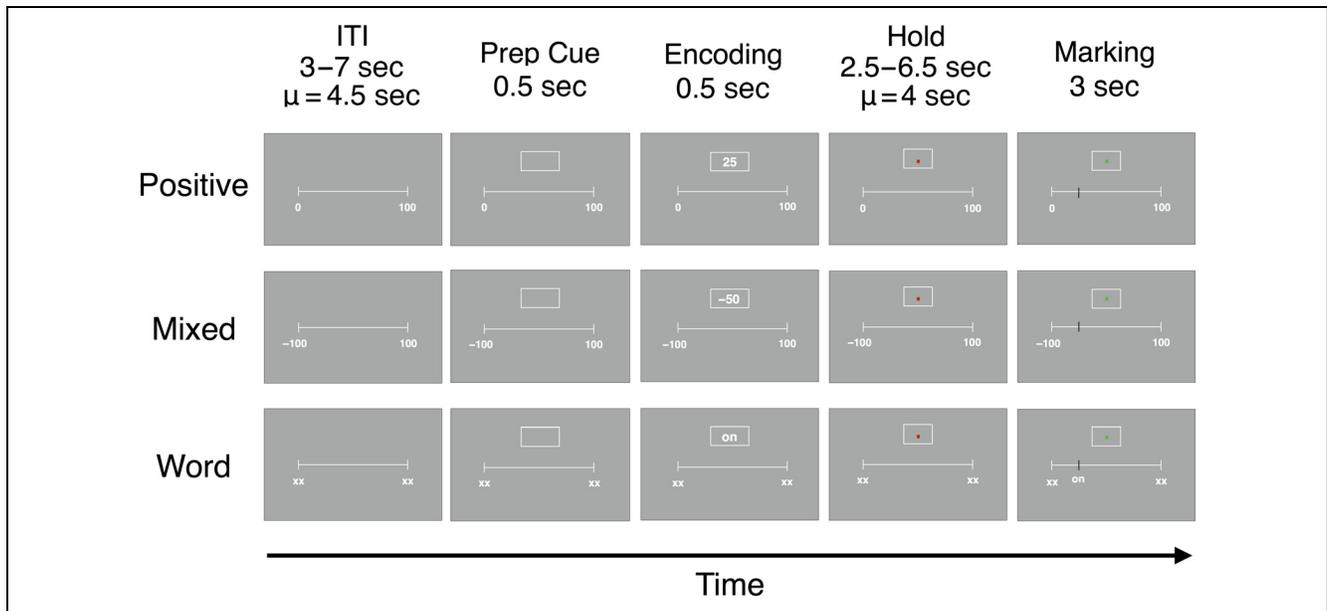


Figure 1. Experimental design. At the beginning of each trial, participants saw a number line in the middle of the screen for a variable period of 3–7 sec. After this, a preparation cue appeared for 0.5 sec to indicate the beginning of the trial. The preparation cue was followed by an encoding phase, where a positive number, negative number, or word was presented for 0.5 sec. This was followed by a hold period indicated by a red dot for 2.5–6.5 sec. During the hold period, participants were instructed to fixate on the dot and think about where they wanted to place the number on the number line. When the red dot turns green, the marking phase starts, and participants have 3 sec to activate the cursor and move and mark the number line where they think is appropriate. For the word task, a word appears below the line to indicate the correct position for the word in that trial.

of \$8 extra compensation. Participants could lose compensation for a given trial by responding later than the 3 sec time limit, by marking the line with an error greater than 5%, by moving the trackball before the red dot turned green, or by responding incorrectly to the catch trials that will be described below. Under this design, participants who were not looking at the dot when it turned green would be unlikely to have enough time to answer the trial correctly, which helped ensure that participants maintained fixation during the encoding phase. The time pressure also meant that participants were compelled to think about the position of the number during the encoding phase to be ready to move the cursor during the short marking phase response window.

Control Word Task and Catch Trials

The procedure for the control task was similar to the number line estimation tasks in most aspects, with a few important exceptions. First, end points on the line were labeled with “xx” on both sides. Second, because the words do not imply a correct position for placement, a second word was placed below the line during the encoding phase, indicating the correct position. To ensure that participants kept the stimulus in mind during the delay (as was the case for the number line tasks), we included four catch trials per run in which the word that appeared below the line at marking was different from the word presented at encoding. For these trials, participants were instructed to move the cursor to the word,

but not press the button a second time to mark the number line. To match the three tasks, we also included four catch trials per run for the two number tasks, using different numbers on each run, so at the end of the experiment, all numbers had been used as catch trials exactly once. In the number task catch trials, a black arrow appeared during the marking phase, below the line in the correct position for the number shown during encoding. Participants were instructed to move the cursor to the arrow location, but not press the button to mark the trial.

fMRI Scanning Parameters

Functional and structural MRI data were collected on a 3-T General Electric Discovery 750 (General Electric Healthcare, Little Chalfon, UK) scanner equipped with a 32-channel head coil (Nova Medical, Wilmington, MA) at the Stanford University Center for Cognitive and Neurobiological Imaging. Whole-brain (2.0 mm³) functional images were acquired using a two-band multiplexed (MUX) imaging protocol (Feinberg et al., 2010). Functional images were acquired with an acceleration factor of 2 and had an acquisition matrix of 110 × 110 with 31 slices per band, an echo time of 30 msec, a flip angle of 77°, and a repetition time (TR) of 2 sec. A total of 10 dummy scans (eight required for MUX calibration) were completed before data acquisition to allow for scanner stabilization. Stimuli were projected onto a screen through a mirror, and responses were collected with an MR-compatible trackball. To perform the tissue segmentation necessary

to generate the surface meshes required to generate atlas-based ROIs for each participant and perform surface-based alignment across participants, we collected 1 high-resolution (0.9 mm^3) T1-weighted fast spoiled GRASS whole-brain structural image with IR preparation (matrix = 256×256 , echo time = 2.78 msec, flip angle = 12° , TR = 7.24 msec).

fMRI Preprocessing

fMRI data were analyzed using FEAT 6.00 (fMRI Expert Analysis Tool) from FSL 5.0.9 toolbox (www.fmrib.ox.ac.uk/fsl). Preprocessing of data consisted of brain extraction (Smith, 2002), motion correction (Jenkinson, Bannister, Brady, & Smith, 2002), grand mean intensity normalization of the entire 4-D data set by a single multiplicative factor, high-pass temporal filtering (Gaussian-weighted least-squares straight line fitting, with $\sigma = 50.0$ sec), and boundary-based registration (Greve & Fischl, 2009; Jenkinson et al., 2002; Jenkinson & Smith, 2001). To detect time points corrupted by excessive participant motion, we used FSL's motion outliers script to test for frame-wise displacement (threshold = 0.9). In addition, there was a computer error that resulted in the screen being frozen during 15 trials divided among seven participants. We generated volume-scrubbing regressors that excluded these error trials, as well as trials identified as having excessive motion, from the analysis. Finally, during the process of analysis, we discovered a time misalignment of 1 TR between the timing on the scanner and the timing on the experimental protocol. To confirm this was the case, we conducted tests with a protocol with the same timing parameters but replacing all stimuli with flashing checkerboards to help us identify a clear signal in visual cortex. Using ICA, to identify a component that tracked activity in visual cortex, and autocorrelation analysis, to detect the highest correlation values between the timing on the design matrix and the time course extracted from the independent component analysis visual component, we were able to confirm a consistent 1 TR displacement. Consequently, we corrected all our analyses by subtracting 2 sec from the time course in our design matrices.

fMRI Data Analysis

Because one of the main goals of this article was to study the brain correlates of number line estimation while controlling for response-related activity, we restricted our analysis to the encoding phase. For all analysis described below, we applied the same general analysis pipeline. After preprocessing, we used a standard first-level linear regression at each voxel, using generalized least squares with a voxel-wise, temporally and spatially regularized autocorrelation model, drift fit with Gaussian-weighted running line smoother (100 sec FWHM) as implemented by FSL 5.0.9 using FEAT 6.00 (www.fmrib.ox.ac.uk/fsl). As part of the model, we included extended motion param-

eters (i.e., motion parameters, their derivatives, and their squares), the volume scrubbing regressors described above, and the temporal derivatives of the regressors of interest as nuisance regressors. We also included regressors of no interest for the four catch trials separately for each task and for the 6 sec of break and feedback time in between tasks.

Importantly, to properly capture the activity evoked during the encoding phase, with minimal contamination from the marking phase, we generated regressors of interest using the following strategy: We modeled the encoding phase by convolving a boxcar function representing the onsets of the trials and their duration with a canonical double-gamma hemodynamic response function. Duration of the encoding phase was coded as 3 sec, which corresponds to the 0.5 sec the stimulus was present on the screen plus the minimum hold time (2.5 sec). The marking phase, on the other hand, was modeled using a finite impulse response model with eight regressors and a time window of 16 sec. The logic of this approach was to use a more flexible model for the marking phase to make sure that no activity from the marking phase spilled over into the previous encoding phase. The success of the approach was evidenced in the presence of relevant null results for the control word task.

Although we were cognizant of the potential for contamination from the marking phase when we began our analysis, it is important to emphasize that we did not arrive at this somewhat unusual strategy a priori—some exploration of the data was necessary. We are confident that this strategy is appropriate, however, and the general number task effects reported in the Results section were not fundamentally changed by this approach when compared with a more standard model in which regressors for both the encoding and marking phase were constructed using convolution with a canonical hemodynamic response function.

The resulting parameter estimates for the encoding phase were averaged across runs with a fixed effects model. The next step in the analysis pipeline was to extract the z-statistic maps for the regressors of interest and register them into each participant's anatomical space where maps were transformed into a surface for ROI extraction.

Tissue Segmentation and Cortical Surface Meshes

The FreeSurfer image analysis suite (surfer.nmr.mgh.harvard.edu) was used with default settings to extract boundaries between gray and white matter, as well as boundaries between gray matter and cerebrospinal fluid and generate cortical surface meshes (Dale, Fischl, & Sereno, 1999; Fischl, Sereno, & Dale, 1999). The output was then converted for use in AFNI/SUMA software suite, using a script that also generated standardized versions of the cortical surface meshes for each participant (Argall, Saad, & Beauchamp, 2006). The cortical surface meshes

were used with AFNI/SUMA functions to generate ROIs and to perform surface-based alignment across participants.

ROIs Based on Probabilistic Atlas

Topographically organized visual ROIs were derived from a probabilistic atlas generated by Wang et al. (2015). They used retinotopic mapping to define 25 ROIs covering 22 visual areas in ~50 individual participants, converting the surface data from each individual to surface-based standardized space (Argall et al., 2006), and then assessing the likelihood, across participants, of any particular vector on the standardized surface belonging to a particular ROI (Wang et al., 2015). The atlas was defined using a maximum probability approach, which considers a given vector as part of the set of ROIs if it is more often found within the set, than outside the set, across participants. If so, the vector is then assigned the value of the most likely ROI, and if not, it is considered to be outside the set of ROIs. The maximum probability approach captures much of the overall structure of ROIs defined for individual participants and generalizes well to novel participants that did not contribute to the atlas generation (Wang et al., 2015). We downloaded the atlas from scholar.princeton.edu/sites/default/files/napl/files/probatlas_v4.zip and converted the ROIs from standardized surface space to native surface space for each of our participants, using nearest-neighbor interpolation. We used surface-based clustering to eliminate vertices more than one edge removed from the main cluster of each ROI to ensure that all ROIs consisted exclusively of contiguous vertices. This step eliminated small speckles while having minimal effect on the overall structure and extent of the ROIs. We then created a version of the structural data set associated with the surface meshes that was registered to the experiment data and used that to convert the ROIs from surface space to volume space and registering them to the experiment data. Finally, the ROIs were resampled to match the resolution and extent of the experiment data.

In the article, we only report 16 out of the 25 areas in the atlas. Selection of the ROIs was as following: (1) We merged the dorsal and ventral parts of V1, V2 and V3; (2) we excluded areas TO1 and TO2 because these areas are known to largely overlap with motion-sensitive visual cortex (Amano, Wandell, & Dumoulin, 2009), and we thus considered these areas unlikely a priori candidates for representing the mental number line; (3) by the same logic, we also excluded PHC1 and PHC2, given their overlap with the scene-selective parahippocampal place area (Arcaro, McMains, Singer, & Kastner, 2009); and (4) we set a criterion of 200 resampled voxels across both hemispheres for including a given ROI in the analysis, corresponding to ~25 voxels at our acquisition resolution. IPS5 did not survive this criterion for any subject. For IPS4, 4 out of 19 participants failed this criterion, so we also did not include IPS4 in the analysis. From the remaining areas, we consider as part of pIPS the subset of IPS0, IPS1, IPS2, IPS3, and SPL1 (see Figure 2).

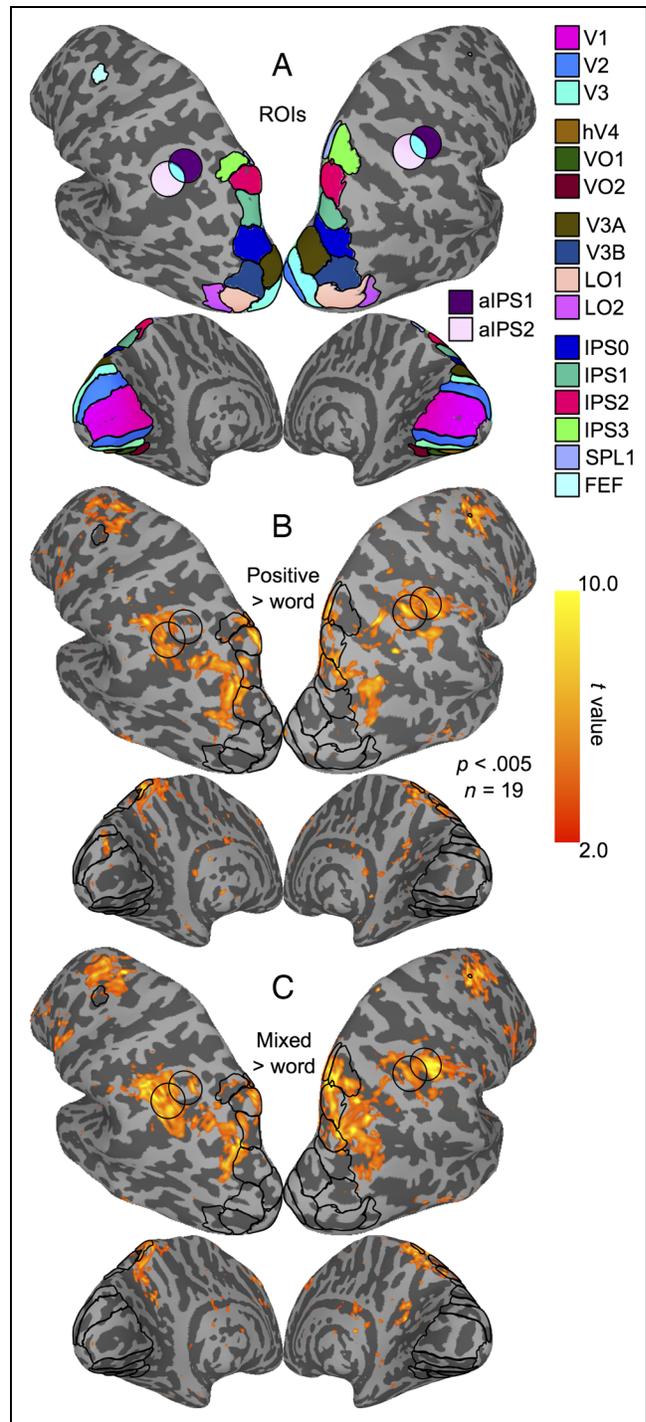


Figure 2. Whole-brain analysis results, shown on the inflated standardized cortical surface mesh of an example participant. (A) ROIs, 16 topographically organized visual areas, defined based on probabilistic atlas, including pIPS (IPS0-SPL1), and two additional areas in aIPS (with their overlap shown separately), based on Talairach coordinates from the literature. (B) t values for the contrast Positive > Word performed for each vector on standardized cortical surfaces, across participants, thresholded by one-sided significance at $p < .005$. (C) t values for the contrast Mixed > Word plotted in the same way.

ROIs Based on Anatomical Locations from the Literature

We generated two additional ROIs in lateral parietal cortex based on Talairach coordinates extracted from the literature. The first was based on the center of activation found by Vogel et al. (2013), whereas the second was based on the center of activation of the hIPS described by Dehaene et al. (2003). We generated a single voxel ROI within each hemisphere, corresponding to the cluster centers for each literature ROI, and then transformed that from Talairach to native volume space for one of our participants. We then projected the single voxel ROI from volume space to standardized surface space. Following the transformation from Talairach to native space, the cluster centers for the first ROI ended up in white matter, so we extended the set of voxels considered to be gray matter to include part of white matter, to be able to project the location onto the surface. The rationale was that this would effectively identify the nearest gray matter location and project that to the standard surface. This step was not necessary for the second ROI. Having thus identified the cluster centers for both ROIs in both hemispheres in a single participant's standardized surface space, we identified the center of the resulting surface cluster and drew a circular ROI around with radius = 10 mm. The resulting ROIs had an area of overlap in both hemispheres (see Figure 2), which was considered separately in our analysis. We now converted the resulting ROIs from standardized surface space to each individual participant's native surface space and from there to native volume space in registration with the experiment data, using the same series of steps used for the atlas ROIs, with the exception of clustering, as these ROIs were by definition contiguous clusters.

Task Contrasts

To identify areas that showed stronger activation for the number task than the control task during the encoding phase, we generated three general linear model contrasts for each participant that compared the activity between the tasks: Positive > Word, Mixed > Word, and Positive > Mixed. For the ROI analysis, we considered only the encoding phase and conducted a two-way repeated-measures ANOVA with Task contrast and ROI as factors. To provide an overview of the effect of task across the whole brain and account for any effects outside our chosen ROIs, we also mapped the contrast data from volume space onto each participant's standardized cortical surface. After this surface-based alignment, we smoothed each participant's data on the surface with a 4-mm FWHM Gaussian filter, averaged the surface data across participants, and tested for significance using a one-sided *t* test.

Landmark Effect

To test for evidence of landmark distance effects, we conducted a parametric model at the first level. Landmark

distance is defined as the closest distance for a particular number from the three hypothesized landmarks (i.e., 0, 50, and 100) used by participants when estimating the positions of numbers on a number line (Vogel et al., 2013). Thus, in the positive task, numbers like 5, 55, and 95 have a landmark distance of 5, whereas 12, 62, and 88 have a landmark distance of 12. Because the cursor always appeared on the middle of the line in our experiment, it will be inherently more effortful to mark stimuli close to the endpoints than the midpoint, so we also included a regressor for distance from middle. Finally, we also tested distance from the left endpoint to test for increases in BOLD activity related to increases in number. For this analysis, we modeled BOLD response as a function of an unmodulated regressor plus three parametric regressors corresponding to the distance from landmark, distance from middle of the line, and distance from left endpoint for each task and phase separately. All regressors were mean-centered.

In the ROI analysis, we first asked whether we could replicate the result of Vogel et al. (2013) by testing if the landmark parametric regressor significantly differed from zero for any of our tasks in our aIPS ROIs based on peak activations from number studies. We then conducted a three-way repeated-measures ANOVA, with Task, ROI, and Hemispheres as factors, to test if this landmark effect extends to the topographic areas from our ROI set.

Contralateral Preference

If numerical information is in fact represented visuospatially in topographically organized areas, then—because these areas preferentially represent the contralateral hemifield—activity for smaller numbers and larger numbers should be preferentially represented in different hemispheres. More specifically, smaller numbers—that will be placed to the left of the midpoint of the number line—should be represented more strongly in the right hemisphere, whereas large numbers—that will be placed to the right of the midpoint of the number line—should be represented more strongly in the left hemisphere. To test this prediction, we used the parametric regressor described in the previous analysis for distance from the left endpoint and submitted into a three-way repeated-measures ANOVA, with Task, ROI, and Hemisphere as factors. To test for the contralateral preference hypothesis, we were interested in particular in identifying regions where this parametric regressor is larger for the left hemisphere than for the right hemisphere.

RESULTS

Behavioral Results

Although the general high accuracy in the performance of the tasks makes the analysis of the degree of linearity of the estimates not very interesting, behavioral results

can provide useful indices of biases and strategy use. Thus, unlike most number line studies that focus on the degree of linearity of the estimates, we focus on the residual errors and estimates of variability as a function of the stimulus and its distance to points of reference. Because the practical and economical constraints of doing fMRI research set a limit on the size of the sample size, we conducted a replication of the behavioral findings from the fMRI experiment (see Appendix). Because this independent sample was found to replicate the first set of results, we report the pooled data from our fMRI and replication experiment below.

During the marking phase, there is an important difference between the number tasks and the word task: During the former, participants have to estimate the position of the number, whereas during the latter, they only need to place the cursor on top of a mark displayed on the line. It follows that the word task should have faster RTs and higher accuracy. As expected, a repeated-measures ANOVA on the median RTs of the three tasks found a significant difference ($F(2, 108) = 15.281, p < .001$; positive = 2.140, $SD = 0.17$; mixed = 2.129, $SD = 0.18$; word = 2.050, $SD = 0.18$). Post hoc analysis revealed that the word task was significantly faster than both the positive ($t(54) = 4.56, p < .001$) and mixed ($t(54) = 4.17, p < .001$) tasks. There was no significant overall difference between the positive and mixed tasks ($t(54) = 0.74, p = .46$).

RTs for all tasks followed a V-shaped pattern where stimuli placed close to the middle of the line showed shorter RTs than stimuli placed closer to the endpoints. This kind of pattern was expected because the cursor always started from the middle of the line. In the word task, participants only need to place the cursor above a mark that indicates the correct position, so we can use the pattern of RTs during the word task as a baseline for the number tasks. Thus, by subtracting the word task from the two number tasks, we can eliminate the effect of the distance from starting point from the RT patterns. This procedure revealed a facilitation effect for both number tasks for numbers near both endpoints (see Figure 3), which might be interpreted as a preparatory

advantage of the number tasks over the word task. This advantage may be based on participant's knowledge about needing to place the cursor very close to the endpoints during the ensuing marking phase. However, for numbers further away from landmarks, this advantage is compensated by the increase on uncertainty about the precise location of the numbers on the number line.

To test for accuracy and precision in the number line marking, we measured the bias and variability of the responses for each task (see Figure 4). To make all tasks comparable, bias (i.e., signed error) for each trial was calculated as the proportion of the signed difference between the correct placement on the number line and the actual placement: $\text{bias} = (d(\text{response}) - d(\text{correct})) / \text{line length}$, where d is the distance in pixels from the left end of the line. A repeated-measures ANOVA on the mean absolute errors revealed a significant effect of Tasks ($F(2, 108) = 302.37, p < .001$; positive = 0.028, $SD = 0.007$; mixed = 0.026, $SD = 0.007$; word = 0.007, $SD = 0.003$). Post hoc analysis showed that the mean absolute error for the word task was significantly smaller than the positive ($t(54) = 25.69, p < .001$) and mixed ($t(54) = 20.62, p < .001$) tasks. On the other hand, the contrast between positive and mixed tasks failed to reach significance ($t(54) = 1.64, p = .107$).

We calculated variability by first calculating the standard deviation for the three placements each participant makes for each stimulus in each of the tasks. Then, we averaged the standard deviations across stimuli to arrive at a variability score for each participant on each task. There were significant differences between tasks in the variability of the placements with a repeated-measures ANOVA ($F(2, 108) = 267.89, p < .001$; positive = 0.018, $SD = 0.004$; mixed = 0.015, $SD = 0.003$; word = 0.006, $SD = 0.003$). Post hoc analysis revealed that the word task was significantly less variable than the positive ($t(54) = 21.47, p < .001$) and mixed ($t(54) = 18.66, p < .001$) tasks. In addition, the mixed task was significantly less variable than the positive task ($t(54) = 5.51, p < .001$).

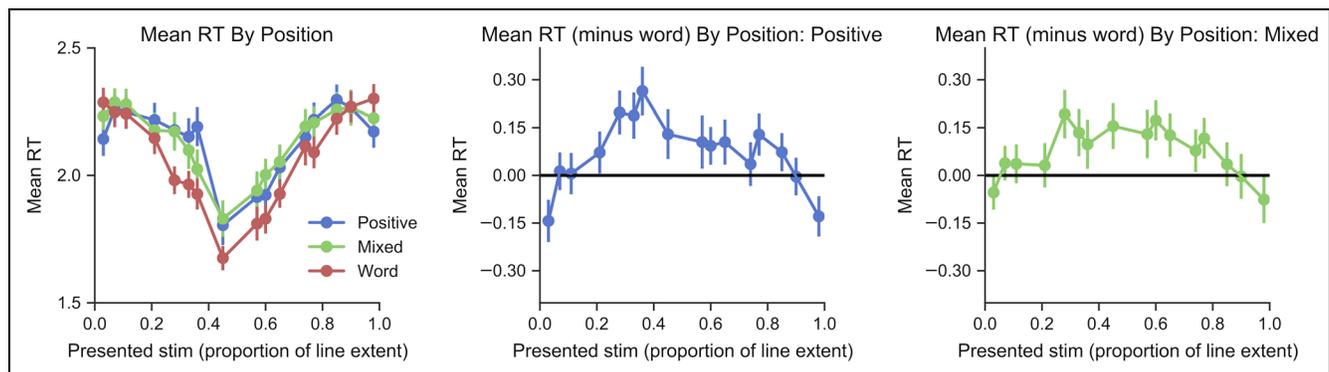


Figure 3. Left: Mean RT patterns as a function of the stimulus presented for the positive (blue), mixed (green), and word (red) tasks. Middle: RT patterns for the positive task after subtracting the RTs from the word task. Right: RT patterns for the mixed task after subtracting the RTs from the word task. Error bars represent ± 2 standard errors.

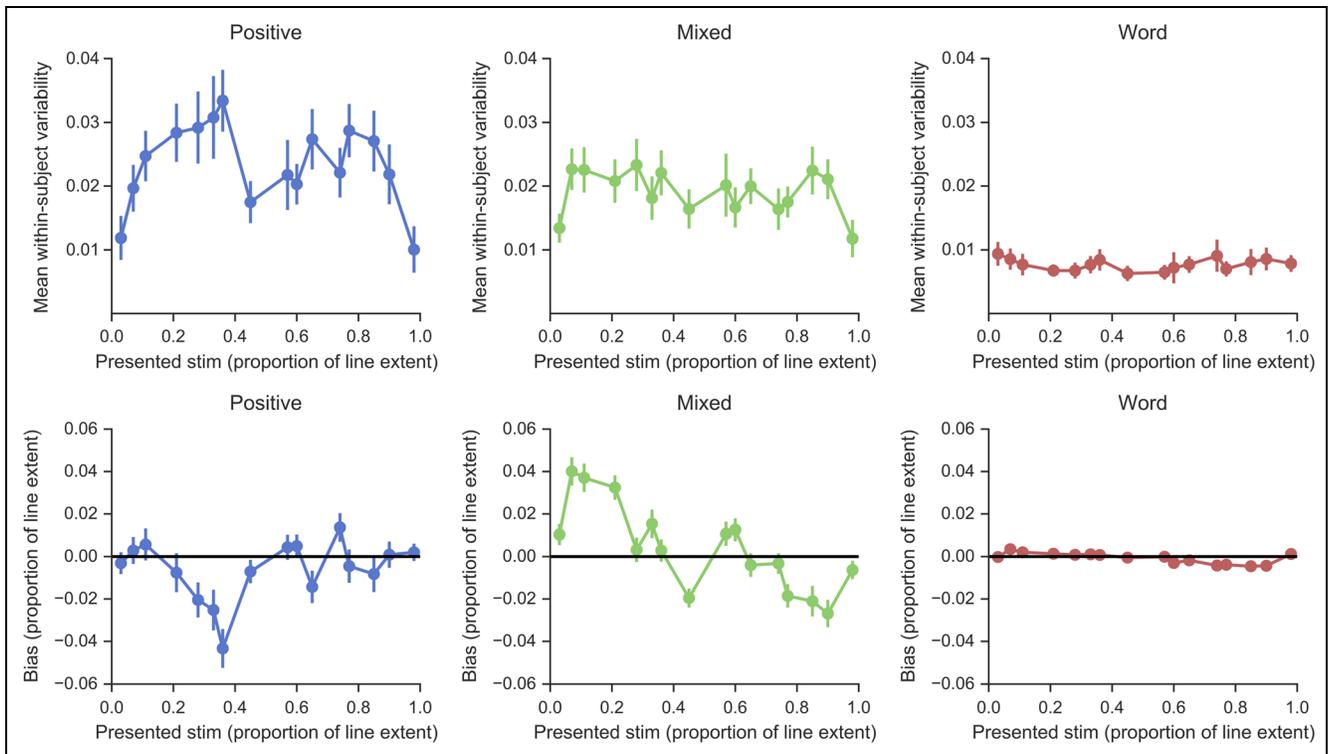


Figure 4. Top: Patterns of mean within-participant variability as a function of stimulus presented for the positive (blue), mixed (green), and word (red) tasks. Bottom: Patterns of bias as a function of stimulus presented. Error bars represent ± 2 standard errors.

The profiles of variability and bias for the different stimuli used provide a more detailed picture of the participants' estimates. For the positive task, there was a landmark distance effect consistent with that reported by Vogel et al. (2013), revealed by the M-shape on the patterns of variability and by a high correlation between each stimulus variability and its landmark distance ($r(14) = 0.76$). There was no such evidence of landmarking behavior for the mixed task ($r(14) = 0.37$).

The bias patterns tell a different story. The mixed task shows a distinctive bias pattern, characterized by an S-shape with an overestimation of small numbers (i.e., closer to -100) and an underestimation of large numbers (i.e., closer to 100). This pattern of moving away from the boundaries is consistent with a compression of the scale similar to that found during development (Barth & Paladino, 2011; Siegler & Opfer, 2003). There is also the same repelling effect around the midpoint, suggesting its use as a landmark for this task. For the positive task, the patterns of bias are not as consistent.

To better understand the effects of rescaling on the bias patterns, we computed a compression index for each participant. To emphasize the boundaries, where the compression is most strongly reflected, we computed the compression index by averaging together the biases in the first and fourth quartiles of our stimuli range. First quartile biases above zero and fourth quartile biases below zero were considered positive indices

of compression, whereas first quartile biases below zero and fourth quartile biases above zero were considered negative indices.

Most participants had a positive compression index on the mixed task, but on the positive task about half of the participants had a negative compression index (i.e., an expansion pattern; see Figure 5). A paired t test revealed that the mixed task ($M = 0.024$, $SD = 0.014$) has a significantly larger compression index than the positive task ($M = 0.001$, $SD = 0.017$; $t(54) = 14.09$, $p < .001$). To test if participants' compression indices were significantly different from zero, we calculated the 95% confidence interval for each participant's compression index and counted the number of participants where the confidence interval does not contain zero. For the positive task, we found that 14 participants (25%) had a compression index below zero and that another group of 13 participants had a compression index above zero (24%). For the mixed task, we found that 46 participants (84%) had a compression index above zero and none below zero. A Fisher's exact test shows that the proportions of participants with significant bias are different between the two tasks (odds ratio = 5.30, $p = .0002$). We considered the possibility that the immediately preceding task might cause scaling errors. However, when we looked at data from the first run (dividing participants between the ones that saw the positive task first and the ones that saw the mixed task first), we found no difference in degree of compression that depended on task order.

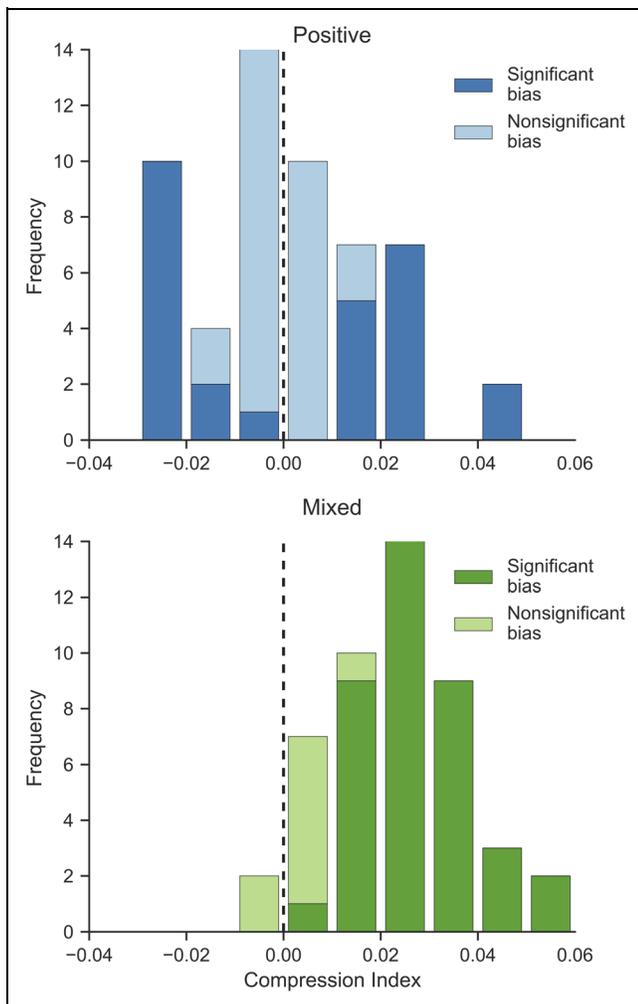
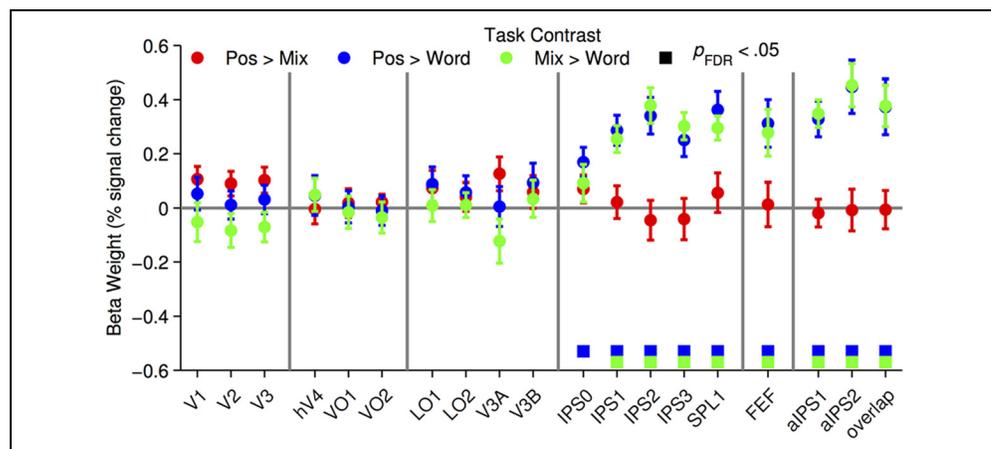


Figure 5. Histograms of the distribution of the compression index for the positive (blue) and mixed (green) tasks. Darker shade represents participants with compression indices significantly different from 0 ($p < .05$).

Finally, we correlated our math measure with several measures of performance in the number line task, but none were significant at a level that would exceed experiment-wide correction.

Figure 6. Average beta-weights associated with each of the three task contrasts, for each of the 19 bilateral ROIs, including the overlap between aIPS1 and aIPS2. Squares in the bottom part of the plot indicate significance as p values $< .05$, false discovery rate-corrected over the 19 ROIs.



fMRI Results

Task Contrasts

The first goal of our study was to establish the existence of number-related activity before the presence of line-marking behavior such as moving the cursor or making saccades to monitor the fine-tuning of the line marking. Thus, the aim of the first analysis was to identify brain regions with stronger activation for the number tasks than for the word task during encoding. A two-way repeated-measures ANOVA with Task and ROIs as factors revealed a main effect of Task ($F(2, 36) = 2.35$; $p = .05$), with the positive and mixed tasks showing more overall activity, and a highly significant effect of ROI ($F(17, 306) = 31.68$; $p < .0001$), with more anterior regions exhibiting greater activity. Most importantly, there was a significant Task \times ROI interaction ($F(34, 612) = 2.25$; $p = .003$). We explored this interaction further with t tests and found no differences between the positive and mixed task for any ROI (false discovery rate-corrected $p > .05$); however, both number tasks showed significantly greater activation than the word task in a network of brain areas that included regions of the frontoparietal network, often associated with number processing (see Figure 6). This network included all three aIPS ROIs that we investigated. It also included four of the five topographically organized ROIs within parietal cortex (IPS1–IPS3, SPL1) with only the positive task reaching significance in IPS0 (see Figure 6). Last, the network included the FEFs. None of the occipital ROIs reached significance. Overall, the two number contrasts produced very similar patterns of activation (see Figure 2).

A second goal of our study was to investigate the functional overlap between pIPS and aIPS areas. We accomplished this by looking at two indices: one of numeric processing and one of spatial coding. To identify activity associated with number processing, we used the neural landmark effect proposed by Vogel and collaborators (2013). We identified spatial coding by looking for areas that had a contralateral preference.

Landmarks

To test for landmark effects, we constructed a parametric regressor that captures the distance of each stimulus to the closest landmark. After extracting parameter estimates for each ROI, we tested whether we could replicate the neural landmark effect found in Vogel et al. (2013) in the left and right hemisphere for the aIPS ROIs generated from peak voxels extracted from previous literature on number processing (Vogel et al., 2013; Dehaene et al., 2003). We tested if the parameter estimates of the landmark regressor were significantly greater than zero, using a t test. This analysis revealed a significant effect for the mixed task in bilateral aIPS1 and in the left, but not right, hemisphere of aIPS2 (uncorrected $p < .05$). There were no significant effects for the positive or word tasks (see Table 1). We then tested if the landmark effect extends to the topographic areas in our ROI set by conducting a three-way repeated-measures ANOVA with Task, ROI, and Hemisphere as factors. There were no significant main effects or interactions (Task \times ROI \times Hemisphere, $F(34, 612) = .95, p = .558$; all other p values $> .1$).

Contralateral Preference

If, during the process of mapping numbers to space, participants use topographic maps to represent numeric information visuospatially, we would expect to find evidence of contralateral preference during the encoding phase. More specifically, we would expect that the parameter estimate of the distance from the left endpoint regressor should be larger in the left hemisphere than in the right hemisphere. We formalized this by computing a contralateral preference index by subtracting right hemisphere parameter estimates from left hemisphere estimates, separately for each ROI and participant. If this index is bigger than zero, it indicates a contralateral preference.

First, we computed a three-way repeated-measures ANOVA on the parameter estimates with Task, ROI, and Hemisphere as factors and found a significant interaction between Hemisphere and Task ($F(2, 36) = 4.90, p = .013$) and a significant interaction between Hemisphere and ROI ($F(17, 306) = 1.84, p = .023$). This result might indicate the expected contralateral preference for the positive and mixed tasks, for some ROIs, but not others. To confirm this, we ran a three-way ANOVA, which only considered the tasks of interest (positive and mixed) and found a significant Hemisphere \times ROI interaction ($F(1, 18) = 2.19, p = .005$), whereas the Hemisphere \times Task interaction did not reach significance ($F(1, 18) = 0.27, p = .998$), indicating that the task interaction in the first ANOVA was driven by the word task.

We further explored the data by running one-tailed t tests on the Contralateral Preference Indices for each ROI (see Figure 7). For the mixed task, we found a significant contralateral preference in V1, LO1, LO2, V3B, IPS0, IPS1, and IPS3. For the positive task, there was a significant contralateral preference in VO1, LO1, LO2, IPS2, and SPL1 (uncorrected $p < .05$). Importantly, we found no contralateral preference on any of the aIPS areas for any tasks. As expected, there was no contralateral preference effect for the word task in any ROI.

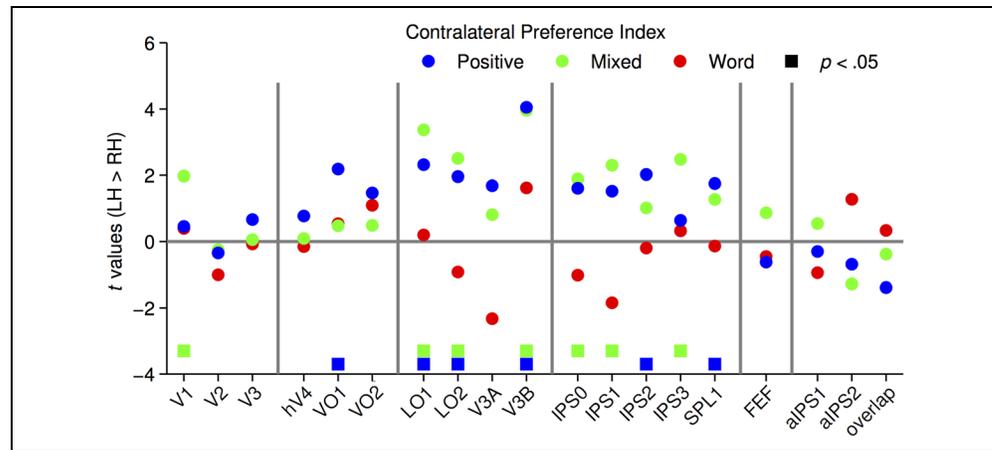
DISCUSSION

In this study, we investigated the relationship between number and space with a number line-marking task that explicitly required participants to map numbers to space using predefined endpoints that establish a particular frame of reference. Our investigation had three primary goals: (1) to study the functional overlap or dissociation between pIPS and aIPS, (2) to focus on the cognitive processes involved in number line estimation separately from the motor processes involved in actually marking the number line, and (3) to extend the range of numbers

Table 1. Statistics for Neural Landmark Effect for aIPS ROIs Segregated by Task and Hemisphere

ROI	Task	Left Hemisphere			Right Hemisphere		
		M (SD)	t	p	M (SD)	t	p
aIPS1	Positive	0.058 (0.249)	1.01	.163	0.029 (0.361)	0.35	.366
	Mixed	0.109 (0.204)	2.32	.016	0.110 (0.252)	1.89	.037
	Word	-0.028 (0.261)	-0.47	.678	-0.025 (0.360)	-0.30	.617
aIPS2	Positive	0.018 (0.360)	0.21	.416	0.063 (0.379)	0.72	.416
	Mixed	0.280 (0.303)	4.02	.001	0.110 (0.366)	1.31	.103
	Word	-0.035 (0.421)	-0.36	.639	-0.064 (0.428)	0.65	.737
Overlap	Positive	0.057 (0.299)	0.82	.210	-0.032 (0.421)	-0.33	.628
	Mixed	0.104 (0.270)	1.68	.055	0.088 (0.456)	0.84	.207
	Word	0.016 (0.450)	0.16	.438	-0.124 (0.465)	-1.16	.869

Figure 7. *t* Values associated with the contralateral preference index, for each of the 19 bilateral ROIs. Squares in the bottom part of the plot indicate one-tailed significance as uncorrected $p < .05$.



used with a mixed range of negative and positive numbers to unconfound magnitude from position. We now discuss the main implications of our findings from pursuing each of these goals. In subsequent sections, we consider in more detail several of our specific findings and their interpretation.

With respect to the first goal, we found evidence of a spatial organization in pIPS but not in aIPS, an area previously reported as important for number processing in multiple studies. Conversely, the neural landmark effect, an index previously treated as reflecting number processing effort (Vogel et al., 2013—see Neural Landmark Effect section below) was only found in the aIPS, but not in the topographic maps in pIPS we studied. Together these findings support a functional characterization in which there are distinct roles for different regions of IPS in the processing of numeric information. Under this characterization, the aIPS represents numerical magnitude, whereas more posterior areas with topographic maps support a representation of a number’s spatial position. This view appears to be largely consistent with the literature on the role of the aIPS in number processing. Although the idea that this area is the locus of a “mental number line” is very prominent, many classic studies implicating aIPS (Arsalidou & Taylor, 2011; Dehaene et al., 2003) have focused on representations of numerical magnitudes rather than numerical positions and indeed Vogel et al. (2013) discussed activation in aIPS as a magnitude representation. Thus, it appears that our results are consistent with a view held by many investigators, in which the representation of number in aIPS is not treated as intrinsically positional in nature, but rather is thought to represent numbers in terms of their magnitude.

It is important to note that a magnitude representation shares important properties with a positional representation, allowing one to be mapped onto the other. Key among the shared properties are order and extent of difference (which, in a positional representation, corresponds to distance between positions). Thus, for three magnitudes, as for three positions on a line, if no two are equal, then one must be between the other two,

and it is usually convenient to assign a sense to the values, using terms like “greater than” for magnitude or “to the right of” for position. Furthermore, the difference between the smallest and the largest of three magnitudes must be greater than the difference between the intermediate and either of the other two, just as the distance between the leftmost and the rightmost of three positions must be greater than the distance between either of these positions and the intermediate position.

Although positions and magnitudes share these properties, a representation need not be positional for these properties to hold. Therefore, we argue it is useful to distinguish between a magnitude representation with order and extent of difference and a positional representation that involves additional properties, such as linear spacing, direction in space, and two or more landmarks or alternatively one landmark and a unit length for scaling purposes. We certainly agree that reasoning about numbers often involves positioning them relative to reference points, either externally in space or internally in a mental analog of external spatial position. Our findings are consistent with the idea that those aspects of a mental state corresponding specifically to the position of a number in external space are associated with pIPS, though a magnitude representation in aIPS may accompany a representation of spatial position.

Our second goal was to focus on the cognitive processes of number line estimation separately from the overt movements associated with line marking. The results reported in this article are all extracted from the encoding phase of our task during which participants maintained fixation above the midpoint of the number line and, therefore, correspond to the time before participants start to move the cursor or make eye movements that could depend on the position to be marked. A contrast of the number tasks against the word control task showed greater activity for the two number tasks than the control task in a network of areas very similar to that reported by Vogel et al. (2013) and many other number processing studies (Arsalidou & Taylor, 2011; Dehaene et al., 2003). All three of our tasks shared the same display layout and fixation

requirements. Because participants could not predict where they would place a word during the control task encoding phase, it appears reasonable to treat the greater activity for number over word tasks in a given region as reflecting the coding of number or of the location where participants expect to place the number or processes related to this placement, such as action planning or spatial attention. This conclusion also applies to our analyses of contralateral preference and landmarking, as they were performed on the same encoding phase data. These analyses revealed similar effects for the two number tasks, but not for the word control task, further confirming that our design isolated number-relevant processes during the encoding phase. The fact that pIPS showed contralateral preferences while aIPS showed a neural landmark effect also provides new insights to interpret the activations found in pIPS in Vogel et al. (2013). In their study, activity in pIPS was shared by their number and brightness tasks, whereas aIPS was significantly more activated by the number task. Our results suggest that the shared activity in pIPS might correspond to the result of translating a magnitude code of either brightness or number into a positional code required to mark an appropriate position on the number line. We return to the question of the relationship of this positional code to number in a later section.

The third goal of the study was to extend the analysis of the neural correlates of number line estimation to ranges beyond the canonical 0 to 100 number line. Here we also included a mixed task in which estimation was performed on a number line ranging from -100 to 100 . One reason why using these ranges is enlightening is because it allows us to separate the spatial locations of numbers from their magnitude. In particular, the numbers between 0 and 100 are located in the right hemifield in the mixed task, whereas half of them are located in the left hemifield in the positive task. Therefore, contrasting the two tasks controls for the magnitude of the numbers and their relation to particular spatial positions. The fact that we found a contralateral preference in pIPS for both tasks shows that the spatial position of these numbers is not intrinsic, and depends on the position, direction, and scale determined by the numeric ranges used in our study, and removes the possibility that the positional effect is an invariant correlate of magnitude per se.

Neural Landmark Effect

We defined our neural landmark effect as the larger BOLD response to stimuli that are located farther from the selected landmarks. In this case, these landmarks correspond to both the visually labeled endpoints and the implied midpoint of the number line. Vogel and collaborators (2013) interpreted a similar landmark effect as a measure of effort based on the increased uncertainty that results from being further away from landmark positions. The fact that we find evidence of a landmark effect in

aIPS but not in pIPS suggests a functional differentiation between these areas and supports our claim that the attributions of functions to IPS in the number literature should keep moving toward more precise descriptions of the distinctions between subregions of IPS. As described above, our experiment design allowed us to test for a landmark effect before the onset of overt motor movements involved in actually positioning the cursor at the appropriate place on the externally visible number line. The presence of a landmark distance effect in our mixed task shows that landmark distance is important for the neural computations needed for deciding where to place the number and not simply for implementing motor responses, a distinction that could not be made in the previous study (Vogel et al., 2013). Thus, following their line of reasoning, the preparation or maintenance of a representation of a number would appear to require more activity in aIPS when it is further from an available landmark.

We did not expect evidence of a landmark effect to be restricted to our mixed (-100 to 100) task, and indeed, Vogel et al. (2013) found such an effect in a purely positive (0 to 100) line-marking task. Although it is important to keep in mind that our analyses are restricted to the encoding phase, further research is necessary before we can fully understand the reasons for our findings and the differences between our findings and those of Vogel et al. (2013). We will return to this issue after considering behavioral differences between the two line-marking tasks (see Landmark Effects in the Mixed and Positive Line-marking Tasks section below).

Contralateral Preference Effect

The contralateral preference effect consists of higher BOLD response for stimuli that will be placed on the contralateral side of the number line during the marking phase compared with the stimuli that will be placed on the ipsilateral side of the number line. This contralateral preference is expected of areas of the brain that are topographically organized. As has been demonstrated extensively (Silver & Kastner, 2009; Swisher, Halko, Merabet, McMains, & Somers, 2007), these topographic maps of visuospatial information on each hemisphere represent preferentially information from the opposite hemifield. In our study, we found evidence of contralateral preference for our number tasks in several topographically organized maps and especially in pIPS. However, we did not find any evidence of contralateral preference in our aIPS ROIs. Our results suggest that numeric information—at least during number line estimation—is represented in different ways by different regions within IPS. As discussed above, these findings are consistent with a magnitude- but not position-based representation of number in aIPS. Furthermore, these results are consistent with a recent study of spatial working memory (Brigadoi et al., 2016). This study reported a lateralized memory load effect in pIPS, but not

in aIPS: that is, the memory load effect for laterally positioned items in pIPS was greater in the contralateral hemisphere, whereas aIPS showed a memory load effect independent of the laterality of the items' positions. Thus, just like in the present article, position dependence appears to be associated with posterior and not anterior regions within IPS.

Recently, Harvey, Klein, Petridou, and Dumoulin (2013) reported topographic maps for numerosities in parietal cortex. This is an important finding with potential implications for the view that there is an intrinsically spatial representation of number. That said, there are important differences between our results and theirs that are worth noting. First, because Harvey et al.'s (2013) results are driven by dot displays rather than numerical symbols, they may reflect a perceptual representation of numerosity, rather than a representation (like the one in aIPS) that can arise either from perceptual or symbolic inputs (i.e., numerals). Second, the topographic map appears to span a limited range (i.e., from 1 to 7 dots), whereas our results span a much larger range. Third, unlike Harvey et al., our results do not imply a fixed topographic organization of the representation of numerical magnitude. Instead, our results suggest a context-dependent mapping of number onto the visuospatial topographic maps previously identified in pIPS. Further research is needed to understand how topographic maps of dots from 1 to 7 connect to the positional and magnitude codes described here, especially because our results suggest that these effects can play out differently depending on the number range.

The fact that we find contralateral effects in both the positive and mixed tasks suggests that the representation of number in pIPS is context dependent, in the sense that it is determined not only by the magnitude but also by the reference points and their spatial locations. In other words, the contralateral effect can only occur after mapping the number into space in the specific context determined by the reference points. This context dependence means that the same number (i.e., 25) would drive higher activation in the visual maps of the right hemisphere when presented in the context of the positive task, but higher activation in the visual maps of the left hemisphere in the context of the mixed task. It is also important to note that we do not find the contralateral effect in every ROI analyzed. On one hand, we do not find contralateral effect in aIPS, which, combined with the landmark effect, suggests that activity in aIPS is better characterized as a magnitude representation. On the other hand, we also do not find contralateral effects in V1–V3 or FEF, thus suggesting this is not a purely visual attention effect, because many studies find that activity in these areas is modulated by visual attention (Gandhi, Heeger, & Boynton, 1999; Martinez et al., 1999; Somers, Dale, Seiffert, & Tootell, 1999).

Dehaene and colleagues (2003) had already noted the importance of posterior parietal cortex for visuospatial processing of numeric information. In particular, they proposed that PSPL played an important role in directing

attention onto the mental number line. In the context of our study, the peak of their reported PSPL activity corresponds to the anterior edge of our IPS3 maps. Our findings therefore highlight the fact that there is a natural reason for the characterization of PSPL as an area involved in visuospatial processing of numeric information: namely, that PSPL is part of the network of areas in posterior parietal cortex with topographic maps of visual space.

An issue our research leaves open is the question of whether the activations we find in topographically mapped areas are in any sense numerical. In our view, it is plausible that similar activations would occur if positions were signaled without numbers—for example, with arbitrary nonnumerical cues that participants learn to associate with different spatial positions or by variations in a nonnumerical magnitude such as brightness, as in Vogel et al. (2013). Once a number has been mapped to a spatial position in the context of a number line with some origin, scale, and orientation, one may question whether there is a meaningful difference between a “purely” spatial representation and a “numeric–spatial” representation. One possibility is that the representation in pIPS is purely positional but constitutes part of a composite representation distributed across aIPS, pIPS, and other areas activated in our number line-marking tasks³ that should be viewed as jointly numerical and spatial.

To address these issues further, it will be useful to study numeric tasks that do not require explicit mappings of numbers to space or that contrast numbers with other stimuli (e.g., brightness) that can also be organized one-dimensionally. Indeed, there are recent papers that suggest that topographically mapped brain representations may play a role in number processing even when mapping to space is not required. For example, activity in pIPS (but not in aIPS) during rightward and leftward saccades predicted activity during mental addition and subtraction, respectively (Knops et al., 2009). Similarly, Schwiedrzik, Bernstein, and Melloni (2016) found that adapting to rightward or leftward eye movements led participants to under- or overestimate numerosities, respectively. These results, along with behavioral findings such as the SNARC effect, suggest that number and space are often associated and spatial processing may often co-occur with and even influence number processing. If this is the case, investigations on the interactions of number and space should probably be focused on pIPS, rather than in aIPS.

Future research should investigate more broadly how magnitude and positional representations contribute to mathematical reasoning and performance even in a wider range of cases where the task does not require mapping of number onto external space as in an explicit line-marking task. In addition to the evidence that shows that performance on number line tasks is related to higher overall math achievement (Booth & Siegler, 2008; Siegler & Ramani, 2008), it has been suggested that individuals who rely on visualizing the positions of different

quantities relative to each other may perform better on certain types of verbal math problems than those who use a more lexically driven arithmetic strategy (Mayer, Lewis, & Hegarty, 1992). If so, visualizers might show evidence of activation of topographic specific regions in parietal cortex when solving these types of problems.

Behavioral Differences between the Positive and Mixed Line-marking Tasks

Using different ranges in our two versions of the line-marking task makes it possible to study how participants respond to a rescaling of the mapping of numbers onto space. We studied rescaling in our behavioral data by looking at the bias patterns in the two number tasks. We treated overestimation in the first quartile and underestimation in the fourth quartile as evidence of scale compression, and we treated the reverse pattern (underestimation in the first quartile and overestimation in the fourth quartile) as evidence of expansion. Interestingly, although most participants had a significant compression index for their mixed task estimates, only a quarter of participants showed significant compression in the positive task, whereas another quarter showed significant expansion. The compression pattern found for the mixed task is similar to patterns typically found in the number development literature and is consistent with the compressive scaling of numbers as captured by a logarithmic or power function (Barth & Paladino, 2011; Siegler & Opfer, 2003). The pattern of results found for the positive task is less typical but is consistent with other findings in the literature that have reported expansion patterns in grouped adult estimates (Brez, Miller, & Ramirez, 2015; Slusser, Santiago, & Barth, 2013; Ashcraft & Moore, 2012). One way to understand the differences between tasks is to propose that some participants have difficulty flexibly rescaling their number–space mappings when the range of the number line varies across different groups of trials. In the positive task, the line to be marked spans 100 units whereas in the mixed task the same line spans 200 units. Thus, a participant using a scale appropriate for the positive task during the mixed task might place a number like -90 at 10% of the total line length from the left endpoint when it is only 5% away. Similarly, a participant using the scale appropriate for the mixed task in the positive task might place 10 only 5% of the total line length from the left endpoint when it in fact is 10% away.

Landmark Effects in the Mixed and Positive Line-marking Tasks

Using tasks with different ranges also opens the opportunity to study the strategic use of landmarks to mark the line more precisely. Our results on landmark use are somewhat inconsistent. For the positive task, we find behavioral evidence of the advantage of being close to both endpoints in the patterns of RT and variability of the

estimates—when we subtracted the average RTs during the control task from the number tasks, we found a facilitation effect for the stimuli that were very close to both endpoints. Similarly, participants tended to show less variability in their estimates for numbers that were close to the endpoints. In addition, participants showed a strong correlation between their variability patterns and distance to landmark for the positive task. For the mixed task, the bias pattern suggests a repellent effect from the endpoints and also from the midpoint. This repellent effect can be interpreted as another indication of use of the midpoint as landmark. Our results are consistent with what previous literature on number line estimation strategies has found. In particular, an eye-tracking study with children from first, second, and third grades found that the best predictor of fixation time is distance to closest landmark (Schneider et al., 2008). Similarly, when adults' finger trajectories are tracked on a tablet during a number line-marking task, the distance to reference points was the second most important predictor of trajectory, only behind the actual value of the presented number (Dotan & Dehaene, 2013). Previous studies have also found an “M-shaped” pattern in mean absolute errors (Vogel et al., 2013; Ashcraft & Moore, 2012). However, mean absolute errors conflate bias and variability. In our results, we find evidence of landmark strategies in the variability patterns of the positive task and in the patterns of bias of the mixed task. To understand these differences further, we hope that future studies will report the patterns of bias and variability separately.

Neurally, the results of our ROI analysis revealed significant neural landmark effects for the mixed task—but not for the positive task—in the aIPS set of ROIs. As noted above, we were surprised by the difference in the neural landmark effect between the findings in the positive condition of our study and those in the corresponding condition of Vogel et al. (2013). One reason for these differences might be the fact that we are focused on the encoding phase, and thus, the effects might be subtler and thus only detectable in the more difficult mixed task. This would be consistent with Vogel et al.'s interpretation of their landmark effect reflecting increased effort. Alternately, it is possible that strategy differences in the positive task among our participants affected our ability to detect a neural landmark distance effect in this condition in our study. In the positive task, bias patterns were more variable than in the mixed task, and several participants showed biases near zero. These participants might have used strategies different from the standard endpoints-plus-midpoint landmark strategy, including possibly using additional landmarks (e.g., at 25 and 75) or different landmarks. Because the landmark effect tested here assumes that participants use only the endpoints and midpoint as landmarks, variability across participants in the landmarks used might explain why we could not detect a neural landmark effect despite a strong correlation between variability in the marked position and landmark

distance. Our best efforts to identify different landmarking strategies at the individual level were not successful, indicating that more research will be necessary to further clarify this issue.

Conclusions

Mapping numbers to space is fundamental to many aspects of mathematics, and multiple sources of evidence have pointed toward the existence of an important relationship between numbers and space. The concept of the mental number line captures this idea, and the aIPS has emerged as the top candidate brain region to support a mental representation of number (Dehaene et al., 2003), and we confirm and replicate the presence of number-relevant activation in aIPS. But what is the best way to characterize the representation of number in this area? Our results are more consistent with the view that there is a functional dissociation between a magnitude code and a spatial code of number during the planning and encoding operations that occur before marking a number line. Specifically, our findings are consistent with the hypothesis that aIPS areas associated with number processing code magnitude; that the visuospatial topographic maps of pIPS provide a substrate for the brain representation of a number's position in a space; and that the number line task draws upon these two regions in a flexible, context dependent fashion.

APPENDIX

Behavioral Replication Methods

Because the practical and economical constraints of doing fMRI research set a limit on the size of the sample, we decided to conduct a replication of the behavioral findings to confirm the above results. For this replication, we tried to maintain the protocol as close as possible to the original. Besides the fact that participants are sitting in a quiet room and not lying on a loud scanner, other differences between the two experiments include the use of a different trackball and the monetary rewards received by participants. For the trackball, we made sure that the speeds of both devices were as similar as possible, and average RTs, rates of missed trials, and accuracy confirm that the trackballs were well matched. In terms of monetary compensation, we maintained the same hourly rate and rate of 5 cents per correct trial, but because the scanner appointment is much longer by nature, participants in the scanner earned on average \$12 more than participants in the behavioral replication.

Sample:

Forty adults participated (mean age = 21.1 years, range = 18–32 years; 24 women). Thirty-seven participants were right-handed, and all participants had normal

or corrected-to-normal vision and reported no neurological problems. Four participants were excluded from the analysis: two of them for missing over 15% of the trials and two more for not understanding the task correctly.

Acknowledgments

This work was supported in part by grant SNI-SG1-16 from the Stanford Neurosciences Institute. We thank Daniel Ansari and Stephan Vogel for providing unpublished behavioral data and methodological details from Vogel et al. (2013). We would also like to thank Anthony Wagner for his help during the design phase of the study and Russell Poldrack for consultations on the analysis of the fMRI data. Finally, we thank Robert Dougherty and the Staff of the Stanford Center for Neurobiological Imaging for detailed consultations on the analysis of our fMRI data.

Reprint requests should be sent to James L. McClelland, Department of Psychology, Stanford University, Room 344, Jordan Hall, Bldg 420, 450 Serra Mall, Stanford, CA 94305, or via e-mail to James L. McClelland or Frank J. Kanayet: mcclelland@stanford.edu, frankanayet@gmail.com.

Notes

1. Many authors use the word “abstract” to characterize the magnitude representation. However, a magnitude might correspond to an extent, which could be spatial in the sense of taking up some amount of space, without being positional. For this reason, we focus on the distinction between magnitude and position, though (with others) we will often use “spatial” as though it was a synonym for “positional.”
2. We chose to start the cursor in the middle of the line because we wanted our methods to replicate as closely as possible the methods presented in Vogel et al. (2013). It is important to note that, after we had already conducted the study, Vogel and collaborators issued a corrigendum stating that the cursor starting position was randomly chosen for each trial.
3. It is important to note here that, because there is significant activation for the contrast between the number tasks and the word task in an area lateral to our pIPS ROIs (see Figure 2), we cannot claim that aIPS is the only area that codes magnitude or shows a landmark effect or that lateralization of activation is restricted to the specific pIPS areas that were the focus of our ROI analysis.

REFERENCES

- Amano, K., Wandell, B. A., & Dumoulin, S. O. (2009). Visual field maps, population receptive field sizes, and visual field coverage in the human MT+ complex. *Journal of Neurophysiology*, *102*, 2704–2718.
- Arcaro, M. J., McMains, S. A., Singer, B. D., & Kastner, S. (2009). Retinotopic organization of human ventral visual cortex. *Journal of Neuroscience*, *29*, 10638–10652.
- Argall, B. D., Saad, Z. S., & Beauchamp, M. S. (2006). Simplified intersubject averaging on the cortical surface using SUMA. *Human Brain Mapping*, *27*, 14–27.
- Arsalidou, M., & Taylor, M. J. (2011). Is $2 + 2 = 4$? Meta-analyses of brain areas needed for numbers and calculations. *Neuroimage*, *54*, 2382–2393.
- Ashcraft, M. H., & Moore, A. M. (2012). Cognitive processes of numerical estimation in children. *Journal of Experimental Child Psychology*, *111*, 246–267.

- Barth, H. C., & Paladino, A. M. (2011). The development of numerical estimation: Evidence against a representational shift. *Developmental Science, 14*, 125–135.
- Booth, J. L., & Siegler, R. S. (2006). Developmental and individual differences in pure numerical estimation. *Developmental Psychology, 42*, 189–201.
- Booth, J. L., & Siegler, R. S. (2008). Numerical magnitude representations influence arithmetic learning. *Child Development, 79*, 1016–1031.
- Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision, 10*, 433–436.
- Bray, S., Arnold, A. E. G. F., Iaria, G., & MacQueen, G. (2013). Structural connectivity of visuotopic intraparietal sulcus. *Neuroimage, 82*, 137–145.
- Brez, C. C., Miller, A. D., & Ramirez, E. M. (2015). Numerical estimation in children for both positive and negative numbers. *Journal of Cognition and Development, 17*, 341–358.
- Brigadoi, S., Cutini, S., Meconi, F., Castellaro, M., Sessa, P., Marangon, M., et al. (2016). On the role of the inferior intraparietal sulcus in visual working memory for lateralized single-feature objects. *Journal of Cognitive Neuroscience, 29*, 337–351.
- Chen, Q., & Verguts, T. (2012). Spatial intuition in elementary arithmetic: A neurocomputational account. *PLoS One, 7*, e31180.
- Choi, H.-J., Zilles, K., Mohlberg, H., Schleicher, A., Fink, G. R., Armstrong, E., et al. (2006). Cytoarchitectonic identification and probabilistic mapping of two distinct areas within the anterior ventral bank of the human intraparietal sulcus. *Journal of Comparative Neurology, 495*, 53–69.
- Cipolotti, L., Butterworth, B., & Denes, G. (1991). A specific deficit for numbers in a case of dense acalculia. *Brain, 114*, 2619–2637.
- Dale, A. M., Fischl, B., & Sereno, M. I. (1999). Cortical surface-based analysis. I. Segmentation and surface reconstruction. *Neuroimage, 9*, 179–194.
- Dehaene, S., Bossini, S., & Giraux, P. (1993). The mental representation of parity and number magnitude. *Journal of Experimental Psychology: General, 122*, 371–396.
- Dehaene, S., & Changeux, J. (1993). Development of elementary numerical abilities: A neuronal model. *Journal of Cognitive Neuroscience, 5*, 390–407.
- Dehaene, S., & Cohen, L. (2007). Cultural recycling of cortical maps. *Neuron, 56*, 384–398.
- Dehaene, S., Piazza, M., Pinel, P., & Cohen, L. (2003). Three parietal circuits for number processing. *Cognitive Neuropsychology, 20*, 487–506.
- Dotan, D., & Dehaene, S. (2013). How do we convert a number into a finger trajectory? *Cognition, 129*, 512–529.
- Feinberg, D. A., Moeller, S., Smith, S. M., Auerbach, E., Ramanna, S., Gunther, M., et al. (2010). Multiplexed echo planar imaging for sub-second whole brain fMRI and fast diffusion imaging. *PLoS One, 5*, e15710.
- Fischer, M. H. (2001). Cognition in the bisection task. *Trends in Cognitive Sciences, 5*, 460–462.
- Fischer, M. H., Castel, A. D., Dodd, M. D., & Pratt, J. (2003). Perceiving numbers causes spatial shifts of attention. *Nature Neuroscience, 6*, 555–556.
- Fischl, B., Sereno, M. I., & Dale, A. M. (1999). Cortical surface-based analysis. II: Inflation, flattening, and a surface-based coordinate system. *Neuroimage, 9*, 195–207.
- Gandhi, S. P., Heeger, D. J., & Boynton, G. M. (1999). Spatial attention affects brain activity in human primary visual cortex. *Proceedings of the National Academy of Sciences, U.S.A., 96*, 3314–3319.
- Ganor-Stern, D., & Tzelgov, J. (2008). Negative numbers are generated in the mind. *Experimental Psychology, 55*, 157–163.
- Geary, D. C., Hoard, M. K., Nugent, L., & Byrd-Craven, J. (2008). Development of number line representations in children with mathematical learning disability. *Developmental Neuropsychology, 33*, 277–299.
- Greve, D. N., & Fischl, B. (2009). Accurate and robust brain image alignment using boundary-based registration. *Neuroimage, 48*, 63–72.
- Harvey, B. M., Klein, B. P., Petridou, N., & Dumoulin, S. O. (2013). Topographic representation of numerosity in the human parietal cortex. *Science, 341*, 1123–1126.
- Jenkinson, M., Bannister, P., Brady, M., & Smith, S. (2002). Improved optimization for the robust and accurate linear registration and motion correction of brain images. *Neuroimage, 17*, 825–841.
- Jenkinson, M., & Smith, S. M. (2001). A global optimization method for robust affine registration of brain images. *Medical Image Analysis, 5*, 143–156.
- Kleiner, M., Brainard, D., & Pelli, D. (2007). What's new in Psychtoolbox-3? *Perception, 36*, 14.
- Knops, A., Thirion, B., Hubbard, E. M., Michel, V., & Dehaene, S. (2009). Recruitment of an area involved in eye movements during mental arithmetic. *Science, 324*, 1583–1585.
- Laski, E. V., & Siegler, R. S. (2007). Is 27 a big number? Correlational and causal connections among numerical categorization, number line estimation, and numerical magnitude comparison. *Child Development, 78*, 1723–1743.
- Link, T., Nuerk, H. C., & Moeller, K. (2014). On the relation between the mental number line and arithmetic competencies. *Quarterly Journal of Experimental Psychology, 67*, 1597–1613.
- Martinez, A., Anllo-Vento, L., Sereno, M. I., Frank, L. R., Buxton, R. B., Dubowitz, D. J., et al. (1999). Involvement of striate and extrastriate visual cortical areas in spatial attention. *Nature Neuroscience, 2*, 364–369.
- Mayer, R. E., Lewis, A. B., & Hegarty, M. (1992). Mathematical misunderstandings: Qualitative reasoning about quantitative problems. *Advances in Psychology, 91*, 137–153.
- Mix, K. S., Levine, S. C., & Newcombe, N. S. (2016). Development of quantitative thinking across correlated dimensions. In A. Henik (Ed.), *Continuous issues in numerical cognition* (pp. 1–33). London: Elsevier.
- Núñez, R. E. (2011). No innate number line in the human brain. *Journal of Cross-Cultural Psychology, 42*, 651–668.
- Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision, 10*, 437–442.
- Schel, M. A., & Klingberg, T. (2016). Specialization of the right intraparietal sulcus for processing mathematics during development. *Cerebral Cortex, 27*, 4436–4446.
- Schneider, M., Heine, A., Thaler, V., Torbeyns, J., De Smedt, B., Verschaffel, L., et al. (2008). A validation of eye movements as a measure of elementary school children's developing number sense. *Cognitive Development, 23*, 409–422.
- Schwiedrzik, C. M., Bernstein, B., & Melloni, L. (2016). Motion along the mental number line reveals shared representations for numerosity and space. *eLife, 5*, 10806.
- Siegler, R. S., & Lortie-Forgues, H. (2014). An integrative theory of numerical development. *Child Development Perspectives, 8*, 1–7.
- Siegler, R. S., & Opfer, J. E. (2003). The development of numerical estimation: Evidence for multiple representations of numerical quantity. *Psychological Science, 14*, 237–243.
- Siegler, R. S., & Ramani, G. B. (2008). Playing linear numerical board games promotes low-income children's numerical development. *Developmental Science, 11*, 655–661.

- Silver, M. A., & Kastner, S. (2009). Topographic maps in human frontal and parietal cortex. *Trends in Cognitive Sciences, 13*, 488–495.
- Slusser, E. B., Santiago, R. T., & Barth, H. C. (2013). Developmental change in numerical estimation. *Journal of Experimental Psychology: General, 142*, 193–208.
- Smith, S. M. (2002). Fast robust automated brain extraction. *Human Brain Mapping, 17*, 143–155.
- Sokolowski, H. M., Fias, W., Mousa, A., & Ansari, D. (2016). Common and distinct brain regions in both parietal and frontal cortex support symbolic and nonsymbolic number processing in humans: A functional neuroimaging meta-analysis. *Neuroimage, 146*, 376–394.
- Somers, D. C., Dale, A. M., Seiffert, A. E., & Tootell, R. B. (1999). Functional MRI reveals spatially specific attentional modulation in human primary visual cortex. *Proceedings of the National Academy of Sciences, U.S.A., 96*, 1663–1668.
- Swisher, J. D., Halko, M. A., Merabet, L. B., McMains, S. A., & Somers, D. C. (2007). Visual topography of human intraparietal sulcus. *Journal of Neuroscience, 27*, 5326–5337.
- Verguts, T., & Fias, W. (2004). Representation of number in animals and humans: A neural model. *Journal of Cognitive Neuroscience, 16*, 1493–1504.
- Vogel, S. E., Grabner, R. H., Schneider, M., Siegler, R. S., & Ansari, D. (2013). Overlapping and distinct brain regions involved in estimating the spatial position of numerical and non-numerical magnitudes: An fMRI study. *Neuropsychologia, 51*, 979–989.
- Walsh, V. (2003). A theory of magnitude: Common cortical metrics of time, space and quantity. *Trends in Cognitive Sciences, 7*, 483–488.
- Wandell, B. A., Dumoulin, S. O., & Brewer, A. A. (2007). Visual field maps in human cortex. *Neuron, 56*, 366–383.
- Wang, L., Mruczek, R. E. B., Arcaro, M. J., & Kastner, S. (2015). Probabilistic maps of visual topography in human cortex. *Cerebral Cortex, 25*, 3911–3931.
- Young, L. K., & Booth, J. L. (2015). Student magnitude knowledge of negative numbers. *Journal of Numerical Cognition, 1*, 38–55.
- Zorzi, M., Priftis, K., & Umiltà, C. (2002). Brain damage: Neglect disrupts the mental number line. *Nature, 417*, 138–139.