Order and Magnitude Share a Common Representation in Parietal Cortex

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Abstract

■ The role of the intraparietal sulcus (IPS) in the representation of numerical magnitude is well established. Recently, there has also been speculation that the IPS is involved in the representation of ordinal information as well. These claims, however, overlook the fact that all neuroimaging paradigms in which participants make judgments about either magnitude and/or order result in a behavioral distance effect (i.e., the comparison is easier when the stimuli span a greater distance). This leaves open two possibilities: It may be that activation of the IPS is due to the mechanism that yields distance effects, or it may be that the IPS is involved in the representation of information about both magnitude and order. The current study used fMRI to compare a magnitude task in which participants show distance effects to an order-judgment task that yields reverse-distance effects. The results reveal activation of the IPS for both the magnitude and order tasks that is based on participants' strategies as opposed to the actual distance between the numbers. This leads to the conclusion that the IPS represents a mental number line, and that accessing this line can lead to distance effects when participants compare magnitudes and to reverse-distance effects when participants check for order. ■

INTRODUCTION

Although numbers are most frequently used to indicate magnitude (e.g., there are *three* apples on the table), there are other ways in which numbers can be used. For example, numbers can also be used to specify ordinal, or position information (e.g., the runner came in *3rd* place). Although these two features of numbers are seemingly different, a recent article about the neural basis of number processing by Jacob and Nieder (2008) makes the claim that magnitude and order information are processed by similar brain regions. However, this claim rests on a thin evidential base in that it relies almost exclusively on tasks that assess numbers in terms of their magnitude. These tasks often involve asking participants to pick out the smaller or larger of two numbers, or to decide whether a given number is smaller or larger than some target number. These magnitude-comparison tasks lead to a prominent behavioral effect, known as the distance effect (DE), which refers to the fact that comparison of two numbers is accomplished more quickly and with greater accuracy when they span a greater distance (Dehaene, Dupoux, & Mehler, 1990; Moyer & Landauer, 1967). This fact has led to the view that numbers are represented on an analog mental number line for which it is more difficult to discriminate numbers that are closer together (Dehaene, 2003; Gallistel & Gelman, 2000; Whalen, Gallistel, & Gelman, 1999; Wynn & Donlan, 1998; Dehaene & Changeux, 1993).

There have also been neuroimaging studies investigating the neural mechanisms of these magnitude-comparison tasks. This work shows that the intraparietal sulcus (IPS) becomes active in a distance-dependent manner, with greater activation for comparisons of numbers that are closer together in magnitude (Piazza, Pinel, Le Bihan, & Dehaene, 2007; Ansari, Dhital, & Siong, 2006; Ansari, Fugelsang, Dhital, & Venkatraman, 2006; Wood, Nuerk, & Wilmes, 2006; Kaufmann et al., 2005; Piazza, Izard, Pinel, Le Bihan, & Dehaene, 2004; Pinel, Piazza, Le Bihan, & Dehaene, 2004; Pinel, Dehaene, Rivišre, & LeBihan, 2001; Pinel et al., 1999). Other evidence for the role of the IPS in magnitude processing comes from patients with lesions that include this region who show deficits specific to magnitude-comparison tasks (Lemer, Dehaene, Spelke, & Cohen, 2003; Dehaene & Cohen, 1997). Also, it has been shown that the use of repetitive transcranial magnetic stimulation to the IPS results in deficits on magnitude-comparison tasks (Sandrini, Rossini, & Miniussi, 2004). Taken together, this body of research has led to the view that the IPS is involved in the representation of a mental number line that is accessed when magnitudes are compared (Ansari, Fugelsang, et al., 2006; Piazza et al., 2004; Pinel et al., 2001, 2004; Dehaene, Dehaene-Lambertz, & Cohen, 1998).

The few studies that have investigated the processing of ordinal information for numbers suggest that the processing of magnitude and order information may differ. Turconi, Campbell, and Seron (2006) assessed order processing by having participants decide whether two

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numbers were in the correct order. Performance on this task was compared to a magnitude-comparison task in which subjects had to choose the larger (or smaller) of the two numbers. When participants were shown two numbers and asked the question, ''Are the numbers in the correct order?'', they showed reverse-distance effects (RDEs) if the small-distance numbers were adjacent and ascending (e.g., 6_7 is faster than 4_7) and DEs for all descending-pair comparisons; however, when they had to choose the larger or smaller of two numbers, they showed DEs regardless of adjacency or whether the numbers were ascending or descending. The RDE suggests a scanning mechanism that accesses each number serially, taking longer when they span a greater distance; it may be a distinct order-related process. Supporting evidence comes from a study by Franklin, Jonides, and Smith (2006) which shows that when participants are deciding whether three 2-digit numbers are in the correct order, RDEs are also seen for both ascending and descending number triplets that are not adjacent.

There appears to be a discrepancy here. On the one hand, behavioral evidence indicates a dissociation between the processes involved in operations having to do with magnitude versus order. On the other hand, Jacob and Nieder (2008) cite evidence for the similarity of these processes based largely on a recent fMRI study by Fias, Lammertyn, Caessens, and Orban (2007). In this study, brain activation during an order task with letters (which of two letters is later in the alphabet) was compared with that of a magnitude task with numbers (which of two numbers is larger). When each task was contrasted with a control condition in which participants had to respond to the letter or number that dimmed, the IPS was similarly active in both tasks. The authors therefore suggest that the IPS is responsible for processing both magnitude and order information. However, there is an alternative interpretation of these data: that the IPS is active for both magnitude and order tasks not because this region reflects magnitude and order processing per se but because it reflects the DEs that are present for both tasks. That is, in both tasks, it was easier to make a decision when either the numbers or letters were farther apart. This is so for all neuroimaging research that has used magnitude and/or order tasks; they all resulted in DEs. Thus, is the IPS commonly responsible for the processing of order and magnitude, or is the IPS commonly responsible for production of DEs? That is the question we address.

The Present Study

In order to address this question, we used fMRI to compare a magnitude task (i.e., ''Is the number larger/smaller than 65?'') that yields DEs with an order task (i.e., ''Are the three numbers in the correct order?'') that yields RDEs in the same group of participants. If the IPS is sensitive to the distance between numbers, regardless of the actual behavioral effects of distance, it should be more active when the numbers are closer together for both magnitude and order tasks (i.e., show DEs). If the IPS is sensitive to participants' strategies, then the activation should be consistent with DEs for the magnitude task (i.e., greater activation for near vs. far trials) and RDEs for the order task (i.e., greater activation for the far vs. near trials). It is also possible that the IPS is only sensitive to tasks that show DEs behaviorally and, therefore, will only be active for the magnitude task. Our experiment is innovative because we use a common set of stimuli (numbers) for both tasks, and because this is the first neuroimaging study to use a number task that shows RDEs. These two features yielded new information regarding the role of the IPS in number representation.

METHODS

Participants

Seventeen University of Michigan students (age range = 18–28 years; mean age = 21.8 years; 7 men) participated in this study. Participants were right-handed and native English speakers with normal or corrected-to-normal vision. Participants were health-screened and informed consent was obtained in accordance with the University of Michigan Institutional Review Board. Participants were paid an average of $40 including a bonus based on performance. Two participants were removed from imaging analyses due to movement exceeding 7 mm. All other participants' movement parameters did not exceed 3 mm.

Stimuli

The stimuli for the order task consisted of trials with three 2-digit numbers ranging from 11 to 99. The three numbers were ordered in the forward (e.g., 13, 14, 16), backward (e.g., 16, 14, 13), or mixed direction (e.g., 16 13 14). The distance between the largest and smallest of the three numbers displayed was either three units (near trials) or six units (far trials), with an equal number of each. For the small-distance trials, the distance between the first two numbers for the forward direction was always one unit and the distance for the second two numbers was always two units (e.g., 22 23 25). For the large-distance trials, the distance between the first two numbers for forward trials was always four units and the distance for the second two numbers was always two units (e.g., 22 26 28). The backward trials were created by simply reversing the direction of the forward trials (e.g., small distance: 25 23 22; large distance: 28 26 22). For the mixed trials, the first two numbers were ascending for half of the trials, and descending for the other half.

In order for there to be an equal number of ''yes'' and ''no'' responses, half of the trials were in the forward direction, one-fourth were backward, and one-fourth were mixed. The analyses focused on the forward trials, which are most indicative of order processing because participants were required to focus on all three numbers to do the task correctly. This was not true for backward trials or mixed trials in which the first two numbers were descending (e.g., 17 13 14), where participants could respond correctly by attending only to the first two numbers. The stimuli for the magnitude task consisted of two-digit numbers ranging from 35 to 96. Half of the trials were close to 65 (near; 61–64_66–69), whereas the other half were far from 65 (far; 33–44_87–96).

Behavioral Procedure

E-Prime experimental software (Psychology Software Tools) was used for stimulus presentation and for recording behavioral data. The stimuli were presented in black with a white background and were projected onto a screen at the head of the scanner. Participants viewed the screen via a pair of goggles with a mirror attached. Responses were collected using two 5-button response units attached to the left and right hands (MRI Devices).

Participants received eight runs of the order task, followed by two runs of the magnitude task. Each run consisted of 20 trials, for a total of 160 order and 40 magnitude trials. The sequence of events on an order trial was as follows: A yellow square appeared for 200 msec to alert participants and this was followed by a blank screen for 1800 msec. Next, the three numbers appeared side by side on the screen for 2000 msec. Finally, a fixation cross appeared for a duration between 6000 and 14000 msec randomly jittered in 2-sec increments. Each trial lasted 14 sec on average. Participants were instructed to respond with the left index finger if the items were in the correct order (forward trials), and with the right index finger if the numbers were in the incorrect order (backward and mixed trials).

The sequence of events on magnitude trials was the same as on order trials except that a single number appeared on the screen for 200 msec and a fixation cross appeared for between 7800 and 15800 msec randomly jittered in 2-sec increments. Participants were instructed to respond with the left index finger if the number was less than 65 and the right index finger if the number was greater than 65. Before scanning, participants went through 20 practice trials for each task.

Imaging Parameters

Images were acquired on a GE Signa 3-T scanner equipped with a standard quadrature head coil. Head movement was minimized using foam padding and a cloth restraint strapped across participants' foreheads. Functional T2*-weighted images were acquired using a spiral sequence with 40 contiguous slices with $3.44 \times 3.44 \times 3$ mm voxels (repetition time [TR] = 2000 msec, echo time [TE] = 30, flip angle = 90°, and field of view [FOV] = 22). A T1-weighted gradient-echo (GRE) anatomical overlay was acquired using the same field of view and slices as the functional scans (TR = 250, TE = 5.7, and flip angle = 90°). Additionally, a 106-slice high-resolution T1-weighted anatomical image was collected using spoiled gradient-recalled acquisition in steady state (SPGR) imaging (TR = 10.5, TE = 3.4, flip angle = 25°, FOV = 24, 1.5 mm slice thickness). Each SPGR was corrected for signal inhomogeneity (G. Glover and K. Kristoff, Tools/vol_homocor.html) and skull-stripped using FSL's Brain Extraction Tool (www.fmrib.ox.ac.uk/fsl). These images were then normalized to the MNI template (avg152t1.img) using SPM2 (Wellcome Department of Cognitive Neurology, London). Functional images were corrected for slice-time differences using 4-point sinc interpolation (Oppenheim & Schafer, 1999) and head movement, using MCFLIRT (Jenkinson, Bannister, Brady, & Smith, 2002). Spatial normalization transformations and 8-mm FWHM isotropic Gaussian smoothing were applied to all functional images prior to analysis using SPM2. All analyses included a temporal high-pass filter (128 sec) and each image was scaled to have a global mean intensity of 100.

Whole-brain analyses were conducted using the General Linear Model implemented in SPM2. For both the magnitude and order tasks, event onset times for the trials were convolved with the canonical hemodynamic response function. Contrast images for each participant were subjected to a random effects group analysis.

Because we were interested in the effects of distance for both tasks, there were four possible contrasts: magnitude near > far, magnitude far > near, order near > far, order far > near. Based on these contrasts, we identified voxels which were active in both tasks (common regions) and those that were specific to one of the two tasks (unique regions).

In order to determine the common regions, both tasks had to show activation that was significant at $p < .01$, uncorrected for multiple comparisons (leading to a conjoint threshold of $p < .0001$), with more than 20 contiguous voxels. The unique regions were determined to be areas that showed activation at $p < .001$ in only one of the tasks, showed no activation in the other task at an even lower threshold of $p < .05$ uncorrected, and consisted of more than 20 contiguous voxels (see Wager et al., 2005; Fan, Flombaum, McCandliss, Thomas, & Posner, 2003 for similar thresholding techniques).

RESULTS

Behavioral Results

The behavioral results reveal that for the magnitude task, participants show DEs, taking longer for near versus far trials; whereas in the order task participants show RDEs, taking longer for the far trials (see Figure 1). This Distance by Task interaction was significant for both reaction times [$F(1, 14) = 22.18$, $p < .0001$] and

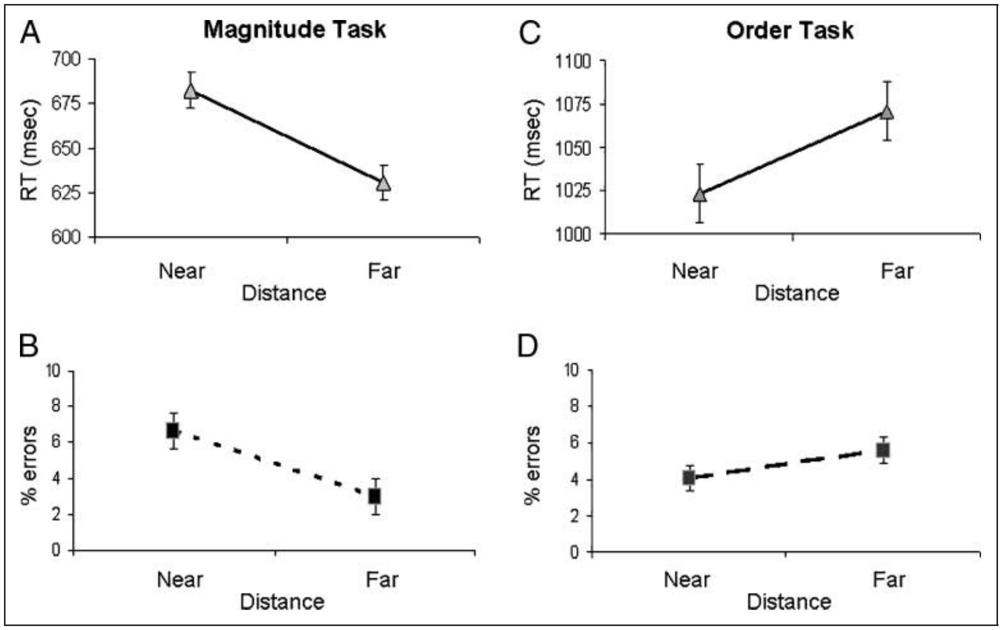

Figure 1. Reaction times and accuracies for the magnitude task (A, B) and order task (C, D). Participants show a DE for the magnitude task and an RDE for the order task. Error bars representing 95% confidence intervals are plotted for this figure using methods taken from Loftus and Masson (1994).

accuracy [$F(1, 14) = 7.27$, $p = .01$]. There was also a main effect of task for reaction time [$F(1, 14) = 288.00$, $p < .0001$] with participants taking longer for the order task (1046.9; $SE = 30.8$) compared to the magnitude task (656.1; $SE = 21.1$). These behavioral results are consistent with the hypothesis that different strategies are engaged for the magnitude and order tasks.

fMRI Results

The fMRI results are displayed in Figure 2. There were no common regions that were modulated by the actual distance between the numbers. The regions that were common to both tasks showed greater activation for the more difficult comparison in each task. Specifically, the IPS was active for both the magnitude near > far and order far > near. The MNI coordinates of this activation (−40, −52, 52) are within a few millimeters of those reported in previous studies of number processing (Piazza et al., 2004; Naccache & Dehaene, 2001; Pinel et al., 1999, 2001; Pesenti, Thioux, Seron, & De Volder, 2000; Dehaene et al., 1999). In addition to the activations shared by the magnitude and order task, we also investigated the activations unique to each of the tasks. Activations unique to the magnitude task (magnitude near > far) consisted of the left IPS and the left superior parietal lobule (SPL). There was also one unique activation for the order task (i.e., order far > near) in the cerebellar vermis (see Table 1 for all common and unique coordinates).

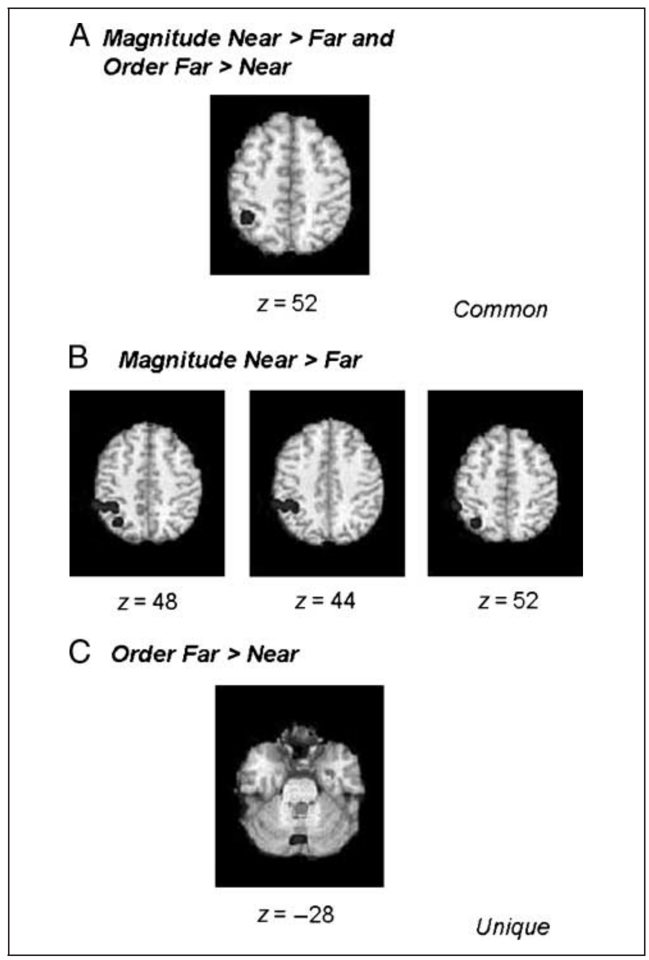

Figure 2. fMRI results showing common and unique regions. (A) The common activation in the IPS for the magnitude near > far and order far > near contrasts. (B) The unique activation for the magnitude near > far contrast in the IPS and the SPL. (C) The unique activation for order far > near in the cerebellar vermis.

DISCUSSION

These results show that activity in the IPS is related to magnitude and order processing and reflects the

Table 1. Common and Unique Regions Active for Both Order and Magnitude Tasks

						Activity (Peak t Score)	
Regions	*BA*	*x*	*y*	*z*	*No. of Voxels*	*Mag Near > Far*	*Order Far > Near*
Common Regions							
Mag Near > Far and Order Far > Near							
Left IPS	40	−40	−52	52	27	3.45	3.11
Unique Regions							
Mag Near > Far							
Left IPS	40	−42	−44	46	53	4.06	
Left IPS	40	−58	−42	48	44	4.88	
Left SPL	7	−34	−64	52	26	4.51	
Order Far > Near							
Cerebellar Vermis		2	−74	−26	35		4.45

IPS = intraparietal sulcus; SPL = superior parietal lobule.

participants' strategies which differed for the magnitude and order tasks. This is the first study to show that activity in the IPS for magnitude comparison tasks is not tied to the behavioral DEs present for these types of tasks. For the magnitude task, we replicated the findings from a number of studies showing greater IPS activation when comparing near to far trials (Piazza et al., 2004, 2007; Ansari, Fugelsang, et al., 2006; Kaufmann et al., 2005; Pinel et al., 1999, 2001, 2004). The order task comparison that produced the most similar activation was consistent with the behavioral RDEs, with greater activation when comparing far to near trials. These findings strengthen the claim that the IPS represents a mental number line that can underlie both magnitude and order information. The novel finding is that different processes are involved in accessing this mental number line: a magnitude comparison process reflected by DEs and a scanning process reflected by RDEs.

In addition to the IPS's involvement for both the magnitude and order tasks, our analyses revealed unique areas as well. The unique activations for the magnitude task were in other parietal regions in the IPS and in the SPL. These unique activations may be involved in processes that lead to DEs. This is consistent with work by Dehaene (2003), which suggests that the posterior superior parietal system plays a role in orienting verbal and visual attention when accessing numerical magnitude information.

Unique activation for the order far > near contrast was seen in the cerebellar vermis. This is consistent with other studies suggesting the involvement of the vermis in the processing of order information. For example, the cerebellum is involved in sequential operations for both word and sentence production (Fabbro, Moretti, & Bava, 2000) and lesions to the cerebellar vermis are associated with reading errors largely due to the transposition of letters (Moretti, Bava, Torre, Antonello, & Cazzato, 2002). Therefore, this area of the cerebellum may be involved in the scanning process that results in RDEs.

Although the current claim is that IPS activation is tied to order and magnitude processing, an alternative interpretation is that this activation is instead related to difficulty within a task. That is, the alternative interpretation would be that more difficult comparisons yield greater activation regardless of task (i.e., near trials for magnitude and far trials for order judgments). Along these lines, Gobel, Johansen-Berg, Behrens, and Rushworth (2004) suggested that IPS activation reported in magnitude tasks is attributable to response selection and not magnitude processing per se. However, subsequent studies have addressed these concerns. For example, Ansari, Fugelsang, et al. (2006) used a numerical Stroop task and showed that activation in the IPS does not correlate with response selection demands; rather, the activation is sensitive to the numerical distance between numbers. Also, there have been studies that show DEs in the IPS for paradigms in which the participants are not required to make a response at all. For example, Piazza et al. (2004, 2007) and Ansari, Dhital, et al. (2006) have shown that IPS activation relates to numerical distance even when participants passively view changes in the numerosity of stimulus arrays. In addition, if the IPS is active simply based on the difficulty of the trial type, then it should show up in other tasks that compare "hard" to "easy" trials, which is not always the case. For example, a meta-analysis of the flanker task (comparing incongruent to congruent trials or identical trials) shows no IPS activation even though incongruent trials are more difficult (Nee, Wager, & Jonides, 2007). Taken together, these studies suggest that the common IPS activation in the present study is related to the underlying magnitude and order representations rather than just the difficulty within each of the tasks.

Our data, therefore, support the claim that magnitude and order information are essentially ''two sides of the same coin'' (Jacob & Nieder, 2008). Both types of information are likely represented along a spatial continuum in the IPS and, as such, this can be thought of in terms of a mental number line. The term ''magnitude'' is used when the ends of that representation can be referred to as ''big'' or ''small,'' whereas ''order'' is used when those extreme values can be referred to as belonging to the ''beginning'' or ''end'' of the representation. This is consistent with work showing the involvement of similar parietal regions when accessing information about both spatial relations and temporal relations (which can be mapped spatially) from memory (Hayes, Ryan, Schnyer, & Nadel, 2004). In addition to the similarity in how magnitude and order information are represented as a mental number line, the present results suggest that different processes are used when accessing this information. A comparison process is used for the magnitude task which results in DEs because numbers that are closer together are more difficult to discriminate. A scanning process is used for the order task, which accesses each number in serial order and facilitates the processing of numbers that are closer together leading to RDEs. Taken together, these results provide new insights into the neural mechanisms underlying the representation and processing of magnitude and order information for numbers.

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