

The Involvement of the Inferior Parietal Cortex in the Numerical Stroop Effect and the Distance Effect in a Two-digit Number Comparison Task

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Abstract

■ The neural mechanism of number representation and processing is currently under extensive investigation. In this functional magnetic resonance imaging study, we designed a number comparison task to examine how people represent and compare two-digit numbers in the brain, and whether they process the decade and unit digits in parallel. We manipulated the decade–unit–digit congruency and numerical distance between the pairs of numbers. We observed both Stroop-like interference and

the distance effect in the participants' performance. People responded more slowly to incongruent pairs of numbers and pairs of a smaller distance. The inferior parietal cortex showed common and distinct patterns of activation for both attentional selection and number comparison processes, and its activity was modulated by the Stroop-like interference effect and the distance effect. Taken together, these results support both parallel and holistic comparison of two-digit numbers in the brain. ■

INTRODUCTION

How do humans represent and process numbers? Are there any dedicated neural networks underlying human mathematical thinking? Recently, these questions have been extensively studied in the field of cognitive neuroscience (Feigenson, Dehaene, & Spelke, 2004; Walsh, 2003; Simon, 1999; Dehaene, Dehaene-Lambertz, & Cohen, 1998) using a variety of techniques, including psychophysical analysis of behavioral performance (Dehaene, 1992), neuropsychological examination of patients with deficits in number processing (see Dehaene, Piazza, Pinel, & Cohen, 2003 for a review), functional imaging of the human brain (Dehaene, Molko, Cohen, & Wilson, 2004), as well as recording of neuronal firing in animals (Nieder, 2005).

Results from these studies suggest that there may exist a specialized neural module in the brain—the inferior parietal cortex, and more specifically, areas along the bilateral intraparietal sulcus (IPS)—for numerical information processing (but see Shuman & Kanwisher, 2004). This region has been found to be active in many cognitive tasks that involve processing numbers, such as counting, magnitude comparison, and arithmetic operations (Cohen Kadosh et al., 2005; Göbel, Johansen-Berg, Behrens, & Rushworth, 2004; Pinel, Piazza, Le Bihan, & Dehaene, 2004; Shuman & Kanwisher, 2004;

Eger, Sterzer, Russ, Giraud, & Kleinschmidt, 2003; Fias, Lammertyn, Reynvoet, Dupont, & Orban, 2003; Fulbright, Manson, Skudlarski, Lacadie, & Gore, 2003; Piazza, Mechelli, Butterworth, & Price, 2002; Simon, Mangin, Cohen, Le Bihan, & Dehaene, 2002; Pinel, Dehaene, Riviere, & LeBihan, 2001; Zago et al., 2001; Cowell, Egan, Code, Harasty, & Watson, 2000; Menon, Rivera, White, Glover, & Reiss, 2000; Pesenti, Thioux, Seron, & De Volder, 2000; Rickard et al., 2000; Stanescu-Cosson et al., 2000; Burbaud et al., 1999; Chochon, Cohen, van de Moortele, & Dehaene, 1999; Dehaene, Spelke, Pinel, Stanescu, & Tsivkin, 1999; Pinel et al., 1999; Dehaene et al., 1996). Damage or lesion in this region may result in a selective deficit in numerical processing, such as acalculia (Lemer, Dehaene, Spelke, & Cohen, 2003; Martory et al., 2003; Crutch & Warrington, 2001; Basso, Burgio, & Caporali, 2000; Dehaene & Cohen, 1991, 1997; Cipolotti, Warrington, & Butterworth, 1995; Ardila & Rosselli, 1994; Takayama, Sugishita, Akiguchi, & Kimura, 1994; Cipolotti, Butterworth, & Denes, 1991). Animal research has also implicated that neuronal firing in the IPS of monkeys is increased during numerical judgment (Nieder & Miller, 2004; Sawamura, Shima, & Tanji, 2002).

One recent view links the role of the inferior parietal cortex in human numerical processing with this region's heavy involvement in human spatial representation and attentional control (Hubbard, Piazza, Pinel, & Dehaene, 2005). This view is intuitively appealing in the sense that numbers, as a type of abstract representation for quantity, are often associated with concepts that possess clear

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spatial semantics, such as size and distance. The view is also consistent with the well-documented claim that numbers are represented in the mind through a logarithmically compressed “mental number line” (Piazza, Izard, Pinel, Le Bihan, & Dehaene, 2004), which is spatially defined and oriented from left (small) to right (large) (Fias & Fischer, 2005; Dehaene, 1997).

Although this abstract “mental number line” entails a format (e.g., symbolic or nonsymbolic) and modality (e.g., visual or verbal) independent number representation, whether such a representation implies the existence of a dedicated neural substrate such as the inferior parietal cortex for number processing remains debated (Shuman & Kanwisher, 2004; Eger et al., 2003). For example, Shuman and Kanwisher (2004) argued that the IPS activation for numerical processing tasks was most likely due to the use of symbolic numbers and could not necessarily be generalized to nonsymbolic numerical processing. They found no consistent IPS activation across a series of experiments using tasks involving numerical comparison of dots, numerosity repetition of different shapes, and numerical judgment of dot arrays or flash sequences with varying distances.

In contrast, many recent functional magnetic resonance imaging (fMRI) studies found common activations of the inferior parietal cortex by various types of numerical judgment tasks that involved both symbolic and nonsymbolic stimuli (Cohen Kadosh et al., 2005; Pinel et al., 2004; Fias et al., 2003). Fias et al. (2003) instructed participants to make a comparative judgment about the magnitude of pairs of symbolic or nonsymbolic stimuli, including angles, lines, and numbers. They compared this magnitude comparison task with a perceptual task in which participants had to detect which of those same pairs was dimming. They found common activation of the left posterior IPS for the magnitude comparison task, regardless of the stimulus format. Pinel et al. (2004) presented a pair of single digits on the screen, differing in numerical magnitude, luminance, and physical size, and instructed the participants to make a comparative judgment on the basis of one of these attributes. They also manipulated the distance between the stimuli such that the pair with a relatively smaller distance was made of stimuli close in any of these three dimensions (e.g., 1 and 3 for magnitude comparison). They found that all three comparison tasks significantly activated large overlapping areas in the inferior parietal cortex, more specifically along the bilateral IPS. In addition, they found that this activation was modulated by the distance effect—the smaller the distance between the two stimuli in any dimension, the harder the task (indicated by increased reaction time [RT]), and the stronger the activation of these regions. Cohen Kadosh et al. (2005) reported a similar study in which the same three numerical comparison tasks used by Pinel et al. were compared. Instead of manipulating the three dimensions orthogonally, they kept the task-

irrelevant features constant (e.g., during number comparison, the size and luminance of the two numbers were the same) so that the task-irrelevant attributes would not interfere with the judgment on the task-relevant dimension. Similar to Pinel et al., they also found a great deal of overlapping activation in the bilateral IPS for all three comparison tasks. However, they found that only the left anterior IPS showed the distance effect specific to number comparison, whereas the left posterior IPS was commonly modulated by the distance effect of all types of stimuli.

Giving these seemingly conflicting findings, Göbel et al. (2004) suggested that IPS activation during comparative tasks of numerical magnitude might not necessarily reflect number processing per se, and could be explained by different selection mechanisms inherently embedded in these tasks. When they compared a number comparison task and a perceptual task that also involved response selection, they found no significant difference in IPS activation. Moreover, they did not find activation consistently modulated by the distance effect, although the region of interest (ROI) analysis revealed modulation of the right posterior IPS by the distance effect.

The main goal of this study is to further investigate whether the IPS is specifically involved in the numerical judgment task, or part of the attentional network in charge of selection-related process. A classic paradigm to examine attentional control is a Stroop-like task, which typically involves selecting among conflicting task-relevant and task-irrelevant information. In order to examine the relative contribution from numerical processing and attentional control, we conducted an fMRI study using a two-digit number comparison task, in which the decade and unit digits of the number pairs could be either congruent or incongruent. For example, for the congruent pairs (e.g., 69 and 51), both the decade and unit digits of the larger number were greater than those of the smaller number (e.g., $6 > 5$ and $9 > 1$), whereas for the incongruent pairs (e.g., 67 and 49), the relative size of the decade and unit digits was incongruent such that the decade digit was larger but the unit digit was smaller in the larger number than in the smaller number, respectively (e.g., $6 > 4$ but $7 < 9$). Behavioral studies using this task have found a Stroop-like interference effect (Zhang & Wang, 2005; Nuerk, Weger, & Willmes, 2001). That is, it took people longer to decide which number was bigger/smaller for the incongruent pairs, although the distances between both the congruent and incongruent pairs were kept the same. Sometimes this Stroop-like effect was even strong enough to reverse the distance effect (Zhang & Wang, 2005).

In the current study, we examined the neural substrates underlying the interplay of these factors by using pairs of numbers of two distance levels (18 and 27). These two distance levels entailed that the difference

between the decade digits of the incongruent pair was the same as the difference between the unit digits, but in opposite sign (e.g., the distance of the pair was $67 - 49 = 18$, the decade–digit difference was $6 - 4 = 2$, and the unit–digit difference was $7 - 9 = -2$). This ensured that the comparison of the two numbers was not biased toward the processing of either the decade digits or the unit digits. We expected that in addition to observing a distance effect in the comparison, we would also obtain a Stroop-like interference effect. Additional attentional control needs to be exerted to counter the interference caused by the incongruent unit digits and enable the observer to correctly compare the two numbers. By comparing brain activation induced by processes involved in the distance effect and the Stroop-like effect, we can then examine common and distinct contribution of the IPS in numerical processing and attentional selection.

Another purpose of this study is to further clarify the nature of the “mental number line” representation in the brain for the abstract semantic magnitude. According to Dehaene, Dupoux, and Mehler (1990), people encode a two-digit number as a holistic entity and represent it at a relative position along a logarithmically compressed “mental number line.” They found that RTs of number comparison could be accounted for by the overall distance between the two numbers. For example, when participants were asked to compare a number to a standard reference number (e.g., 65), it took them longer for 59 than for 51, even though in both cases the same decade digit (5) alone was sufficient for them to make the decision. However, as Nuerk et al. (2001) pointed out, the overall distance and the individual differences in the decade and unit digits were confounded. When these factors were carefully controlled, the individual digits in the two-digit numbers also affected number comparison performance, indicating that the decade and unit digits might be encoded individually and compared in a parallel fashion. In fact, Zhang and Wang (2005) fitted the RT data with three comparison models—sequential, parallel, and holistic—and found that the parallel comparison model provided better fitting than the other two alternative models in most cases. Examining the neural activation patterns underlying the Stroop-like effect and the distance effect would provide additional insights for distinguishing among different number comparison processes in the brain. For example, if people process the numbers holistically, the relative sizes between the decade and unit digits in the number pair would be irrelevant. Consequently, there would be no need to recruit attentional control in number comparison. On the other hand, if a parallel comparison of the decade and unit digits indeed plays a role in the task, the Stroop-like effect, given the nature of decade–unit–digit incongruency, would activate the attentional network usually identified in the classic color–word Stroop task. We therefore expect to ob-

serve activation of the fronto-parietal network for the incongruent pairs, as compared to the congruent pairs. Although we anticipate that both number comparison and attentional control would activate overlapping parts of the inferior parietal cortex, it is possible that the two processes might exhibit distinct neural profiles in the inferior parietal areas as well.

METHODS

Participants

Twelve right-handed, native English speakers (age range 18–45 years; 7 women) were recruited from the local community. All participants had normal or corrected-to-normal vision. A signed informed consent form approved by the University of Kentucky Institutional Review Board was obtained from each participant prior to the experiment.

Design and Stimuli

Stimuli were pairs of two-digit numbers presented in the center of the screen above and below the fixation. The task was to compare these two numbers and decide which number was larger or smaller. Half of the participants were randomly assigned to judge which number was larger and the other half judged which number was smaller. There were four different types of stimuli determined by the two independent factors. One factor was the distance between the two numbers, with two levels—18 and 27. The other factor was the congruency between the relative sizes of the decade and unit digits, with two levels—congruent and incongruent. For example, a congruent pair of numbers with the distance of 18 (thereafter shortened as C18) are 21 and 39, in which the decade digit and the unit digit in the larger number are both greater than those in the smaller number, respectively (i.e., $3 > 2$ and $9 > 1$). On the contrary, an incongruent pair of numbers with the distance of 18 (I18), for example, are 33 and 51, in which the decade digit is greater (by 2), but the unit digit is smaller (also by 2), in the larger number than those in the smaller number, respectively (i.e., $5 > 3$ but $1 < 3$). The same manipulation was applied to the pairs of numbers with the distance of 27. An example of the congruent pair of numbers (C27) are 42 and 69 (i.e., $6 > 4$ and $9 > 2$), and of the incongruent pair of numbers (I27) are 26 and 53 (i.e., $5 > 2$ but $3 < 6$). The reason we chose the distances of 18 and 27 was that in the *incongruent* pairs, the differences of the decade digits and the unit digits between the two numbers were equal but in opposite direction (2 and -2 for the distance of 18, 3 and -3 for the distance of 27). This ensured the comparison of the two numbers was not biased toward the processing of either the decade digits or the unit digits.

Procedures

A boxcar design was implemented with each of the two sessions consisting of 12 active blocks (three for each of the four conditions), with a fixation block interleaved between the active blocks, starting and ending with a fixation block. The fixation block consisted of eight trials of two double-zero, one above the other. Participants passively viewed the fixation condition without making a response. Twelve pairs of two-digit numbers from each of the four conditions were randomly sampled within an active block of eight trials. Each trial lasted 2000 msec, starting with a fixation for 300 msec, followed by the pair of numbers one above the other for 1500 msec, and a blank screen for another 200 msec. Participants were instructed to compare these two numbers and respond as quickly and accurately as possible by pressing the button in one of the two hands. The vertical position of the two numbers was randomly assigned, resulting in half of the trials with the smaller number above the larger number. Half of the participants were instructed to press the button in their left hand for the smaller number and the other half were to press the button in their right hand. The order of the active conditions was counterbalanced across two sessions within each participant as well as across participants. Postexperiment debriefing suggests that participants were not aware of the nature of the blocks.

Data Acquisition

A 3-T Siemens Trio MRI system located at the University of Kentucky Magnetic Resonance Imaging and Spectroscopy Center equipped for echo-planar imaging (EPI) was used for data acquisition. The EPI images were acquired using the BOLD technique (TR = 2000 msec, TE = 29 msec, flip angle = 76°), each consisting of 34 contiguous axial slices (matrix = 64 × 64, in-plane resolution = 3.5 × 3.5 mm², thickness = 3.5 mm, no gap). A high-resolution T1-weighted MP-RAGE anatomical set (192 sagittal slices of full head, matrix = 224 × 256, field-of-view = 224 × 256 mm², slice thickness = 1 mm, no gap) was collected for each participant.

Stimuli were presented using a high-resolution rear projection system with responses recorded via two fiber-optic response pads, each with one button. A computer running E-Prime controlled stimulus presentation and the recording of responses. In addition, the timing of the stimulus presentation was synchronized with trigger pulses from the magnet.

Image Preprocessing

Prior to statistical analysis, the first four volumes of each session were discarded to allow the MR signal to reach steady state. The remaining images in each par-

ticipant's time series were motion-corrected using the MCFLIRT module of the FSL (FMRIB's Software Library, v3.1) package (www.fmrib.ox.ac.uk/fsl). Images in the data series were then spatially smoothed with a 3-D Gaussian kernel (FWHM = 7 × 7 × 7 mm³), and temporally smoothed using a high-pass filter (cutoff point of 96 sec). The FEAT (FMRIB's Expert Analysis Tool) module of the FSL package was used for these steps and later statistical analysis.

Voxel-based Whole Brain Analysis

First, customized square waveforms for each participant were generated for the individual's specific counterbalanced order of experimental conditions. These waveforms were convolved with a double gamma hemodynamic response function. For each participant, we used FMRIB's Improved Linear Model (FILM), with local autocorrelation correction, to estimate the hemodynamic parameters for the different explanatory variables (EVs) (e.g., one for each of the four conditions—C18, I18, C27, and I27) and generate statistical contrast maps of interest (e.g., a contrast between EVs for incongruent and congruent conditions).

Each of the two sessions for each participant was analyzed separately and the average of these two sessions for each individual was obtained through higher level analysis using the FMRIB's Local Analysis of Mixed Effects (FLAME) module (Stage 1 only). The contrast maps were warped into common stereotaxic space before mixed-effects group analyses were performed. This involved registering the average EPI image to the MP-RAGE image from the same participant, and then to the ICBM152 T1 template, using the FMRIB's Linear Image Registration Tool (FLIRT) module.

Contrast maps of parameter estimates (PE) were transformed into a common stereotaxic space using the above-mentioned three-step registration prior to the group analyses with FLAME to obtain the group mean of brain activation.

To generate a conjunction map to reveal common activation across conditions, we first thresholded the activation map of each task condition versus baseline and created a mask by intersecting these thresholded maps. We then applied this mask to the activation map of all task conditions versus baseline to identify the regions commonly activated by these four conditions.

Region-of-interest Analysis

To identify the regions of brain activation, we defined the ROIs first by clusters of 10 or more contiguous voxels (Xiong, Gao, Lancaster, & Fox, 1995) in which PE values differ significantly from zero ($Z > 2.81$, $p < .005$, two-tailed). Using the Mintun peak algorithm (Mintun, Fox, & Raichle, 1989), we further located the local peaks

(maximal activation) within each ROI. Additional ROI analyses were performed using the average PE values extracted from a $3 \times 3 \times 3$ cube centered on the peak voxel of each ROI.

To assess the relationship between brain activation patterns and behavioral performance, we correlated brain activation values extracted from ROIs mentioned above with participants' RTs. We treated individual conditions (e.g., C18, C27, I18, and I27) within subject as distinct data points ($n = 48$). This helps rule out the task difficulty confound inherently imposed by the experimental manipulations (e.g., the distance effect and the interference effect).

RESULTS

Behavioral Data

The effects of the decade–unit–digit congruency and distance between the pairs of numbers on the RT and accuracy were tested using repeated-measures ANOVA analyses.

The average RTs of the four conditions are shown in Figure 1A. The main effects of both factors were significant. Participants responded more slowly to the incongruent pairs than they did to the congruent pairs [$F(1,11) = 9.92, p < .01$]. They also responded more slowly to the pairs of the smaller distance (i.e., 18) than they did to those of the larger distance (i.e., 27) [$F(1,11) = 9.25, p < .05$]. The interaction between the two factors was not significant [$F(1,11) = 0.02$]. Each effect had the size of about 20 msec, though small, was nonetheless reliable. Participants' responses were slower to the C18 pairs (mean = 684 msec) than to the C27 pairs (mean = 666 msec). It also took them longer to compare the I18 pairs (mean = 710 msec) than the I27 pairs (mean = 690 msec).

The overall accuracy was 96.7% and all participants' average accuracy was above 85%. No significant difference across conditions was observed for accuracy (see Figure 1B). The interaction between the congruency and distance factors was marginally significant [$F(1,11) = 4.574, p = .056$]. Post hoc pairwise t tests were per-

formed to test whether there was significant difference in response accuracy between any pairs. None of these t tests revealed any statistical significance (all uncorrected p values $>.1$). Therefore, there was no speed–accuracy tradeoff.

We performed additional analyses separating behavioral measures of two sessions within participants. ANOVA tests revealed no session-related effect, either for the main effect of session or for any interaction between session and other independent variables (e.g., distance or congruency). This suggested that practice/priming related performance improvement was minimal.

Imaging Data

Brain Areas Commonly Activated by All Task Conditions versus Fixation Baseline

A conjunction analysis was performed (see Experimental Procedures) such that regions commonly activated by all task conditions were identified (see Table 1). These included the bilateral inferior parietal sulcus, possibly for numerical processing and/or attentional selection. Because participants were not required to make any overt response to the baseline condition, some regions not specifically related to numerical processing per se were activated as well, such as the primary motor cortex, supplementary motor areas (SMA) and pre-SMA, the basal ganglia (caudate nucleus and putamen), and the cerebellum for the motor-related response. Areas related to visual processing of the number form were also activated, including the inferior occipital gyrus and fusiform gyrus.

Areas Sensitive to the Congruency Effect between the Decade and Unit Digits (Incongruent vs. Congruent Pairs)

Brain areas activated for the incongruent versus congruent pairs of numbers are listed in Table 2. The typical fronto-parietal attentional network in charge of resolving interference was activated (see Figure 2A). These included the bilateral middle frontal gyrus, the bilateral inferior

Figure 1. The reaction time (A) and accuracy (B) of the number comparison task as a function of the decade–unit–digit congruency and distance between the pairs of numbers. The vertical lines represent 95% confidence intervals. The confidence intervals for accuracy are too small (0.014) to show up.

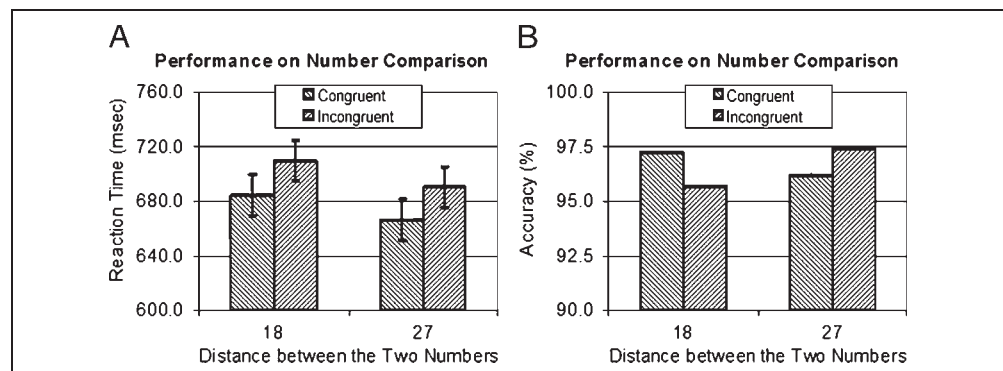


Table 1. Brain Areas Activated by All Number Comparison Tasks with Regards to the Baseline (Two 00s without Overt Response)

<i>Label</i>	<i>BA</i>	<i>Cluster Size</i>	<i>x</i>	<i>y</i>	<i>z</i>	<i>Max Z</i>	<i>Incong vs. Cong*</i>	<i>18 vs. 27*</i>
<i>Numerical Processing/Attention</i>								
Inferior parietal sulcus	7/40	825	-34	-48	44	5.21	.005	.162
	40	216	26	-56	42	3.94	.001	.065
<i>Visual Processing</i>								
Fusiform gyrus	19	2330	-44	-66	-16	5.78	.053	.633
Inferior occipital gyrus	19	807	44	-82	-10	5.38	.039	.835
<i>Motor Processing</i>								
Precentral sulcus	6	140	24	-12	54	5.03	.010	.035
	6	92	-48	4	38	4.30	.016	.081
SMA/pre-SMA	6	970	-24	-8	58	4.79	.003	.173
Cerebellum		801	28	-58	-30	5.53	.309	.029
Vermis		214	2	-48	-34	5.07	.790	.832
Putamen		149	-20	6	10	4.53	.057	.030
Thalamus		61	-16	-10	2	4.75	.036	.311
Caudate nucleus		31	22	-12	18	4.17	.004	.213
Midbrain		280	8	-20	-14	4.93	.696	.015

*Numbers refer to the *p* values for the ANOVA tests. **Bold** font highlights the *p* values less than .05.

Table 2. Brain Areas Activated for the Contrast between the Incongruent versus Congruent Pairs

<i>Label</i>	<i>BA</i>	<i>Cluster Size</i>	<i>x</i>	<i>y</i>	<i>z</i>	<i>Max Z</i>
Middle frontal gyrus	45	901	44	34	22	3.68
	46	67	-32	40	12	3.11
	47	45	36	48	4	3.33
Inferior frontal gyrus	44	283	-40	-4	32	3.26
	45	164	-44	30	20	3.59
	48	40	48	12	8	3.25
Anterior cingulate gyrus	32	27	12	20	30	3.26
Pre-SMA	6	220	12	6	54	3.52
Precentral gyrus	6	1053	40	-4	48	3.59
	6	86	-22	-6	54	3.22
Insula	47	71	34	22	4	3.09
Inferior parietal sulcus	40	367	-24	-56	38	3.75
	7/40	1020	30	-58	44	3.51
Middle occipital gyrus	18	370	-26	-86	2	3.32
	18	115	34	-82	10	3.28
	19	68	-28	-76	28	3.13

frontal gyrus, the right insula, and the bilateral inferior parietal sulcus. Connected to the right middle frontal gyrus cluster, we also observed activation at the anterior cingulate cortex (ACC), extended to the pre-SMA.

Other activated areas, not usually associated with attentional control, were the bilateral precentral gyrus and bilateral middle occipital cortex.

Areas Sensitive to the Distance Effect between the Pairs of Numbers (Distance of 18 vs. Distance of 27)

Besides activation in the right inferior parietal sulcus, several frontal regions showed activation modulated by the distance effect (see Figure 2B and Table 3). They were the middle frontal gyrus, the inferior frontal gyrus, the ACC, and the insula. The thalamus showed increased activity as well when the distance between the numbers was smaller (18 vs. 27).

Common and Distinct Activation of the Inferior Parietal Cortex by Overall Tasks, the Stroop Effect, and the Distance Effect

As can be seen in Figure 3, there was a great deal of overlap (in green) in the inferior parietal cortex for both overall tasks (in blue) and the Stroop effect (in yellow). In general, number comparison tasks activated the

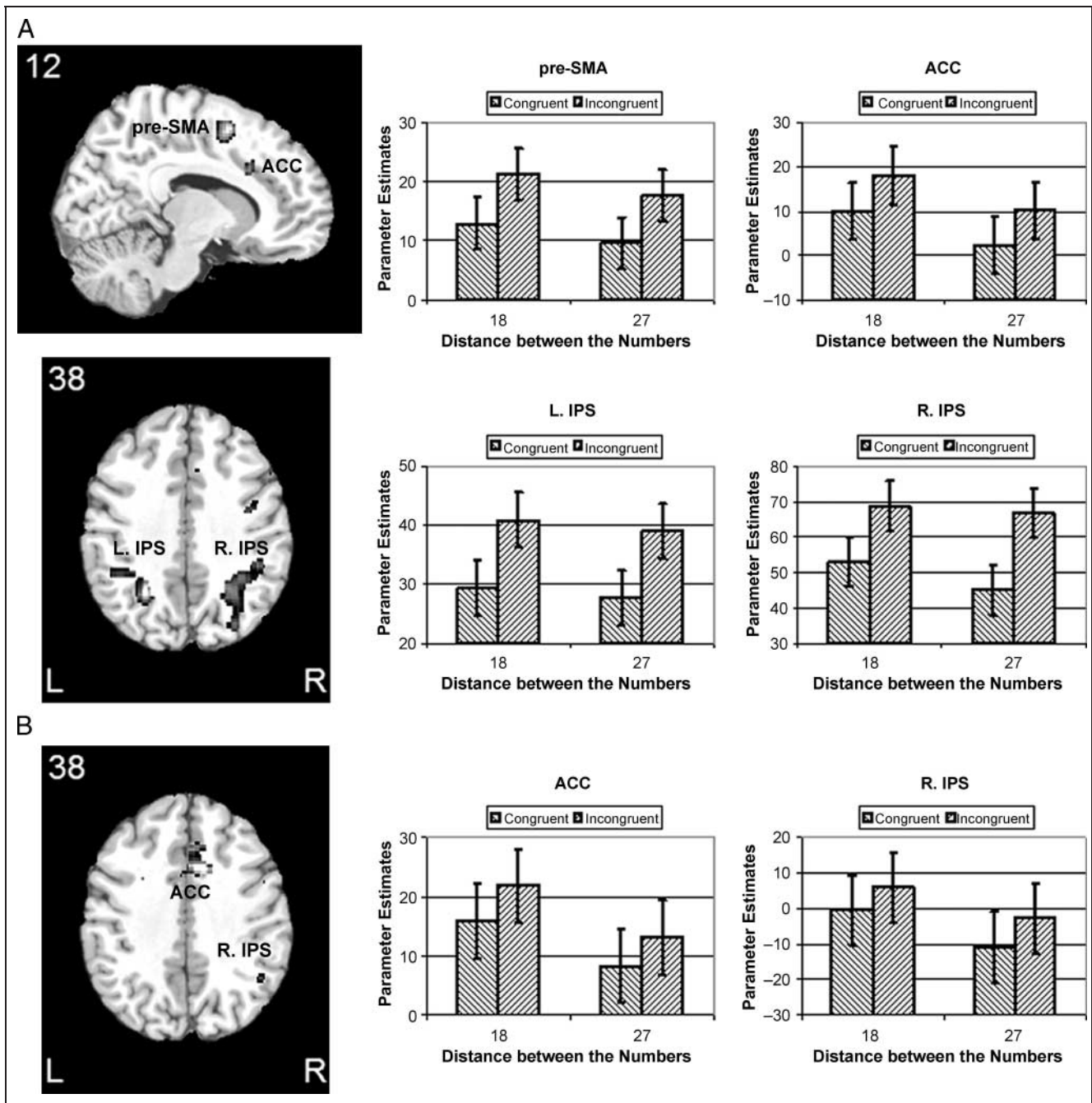


Figure 2. Brain areas modulated by the main effects of the decade–unit–digit congruency (A: incongruent vs. congruent) and distance (B: distance of 18 vs. 27).

bilateral inferior parietal cortex, extending horizontally and laterally along the IPS from the angular gyrus into the supramarginal gyrus. The IPS activation was greater in the left than the in right IPS. In contrast, IPS activation by attentional control (i.e., incongruent vs. congruent pairs) was more pronounced in the right hemisphere. Given these patterns, we performed an ANOVA test between the two regions (left vs. right IPS) and Stroop interference manipulation (incongruent vs. congruent pairs) and found that there was a significant Region \times Congruency interaction. The right IPS was modulated by

the Stroop effect to a higher degree than the left IPS [$F(1,11) = 7.27, p < .05$].

The area activated by the distance effect (in red) was in the right IPS, more lateral than the overlapping right IPS identified above in the tasks versus baseline contrast and the Stroop effect.

Additional Findings from ROI Analysis

There was no significant interaction between the two experimental manipulations on brain activity, with the

Table 3. Brain Areas Activated for the Contrast between the Distance of 18 and the Distance of 27

Label	BA	Cluster			Max Z	
		Size	x	y		z
Middle frontal gyrus	46	113	30	54	20	3.34
Inferior frontal gyrus	45	46	56	18	-4	3.47
Anterior cingulate gyrus	24/32	1065	12	14	38	3.69
Insula	48	128	-48	12	0	3.21
Inferior parietal sulcus	40	15	48	-54	38	3.01
Thalamus		33	8	-12	4	3.17

voxel-based whole brain analysis. Given the nonoverlapping nature of IPS activation modulated by the Stroop effect and the distance effect, we ran ROI-based analyses, in hopes of increasing statistical power, to confirm that we did not miss any interaction between these two

effects. ANOVA tests on the ROIs identified in tasks versus baseline (see Table 1) revealed that two IPS peaks, the left IPS (-34, -48, 44) and the right IPS (26, -56, 42), also showed modulation by the Stroop effect. The right IPS activation showed marginal modulation by the distance effect ($p = .065$). It overlapped with the right IPS (30, -58, 44) found in the Stroop effect, but was more medial than the smaller one (48, -54, 38) identified in the distance effect. Still there was no significant interaction between two effects observed on these IPS ROIs identified in the task versus baseline contrast.

To examine the relationship between task difficulty and activation in the inferior parietal and medial frontal areas, we correlated the peak intensity of these ROIs with participants' RTs of different conditions. The results are shown in Table 4. Only activity in the right IPS peak identified in the Stroop effect was positively correlated with RTs, whereas pre-SMA activation was negatively correlated with RTs. There were significant

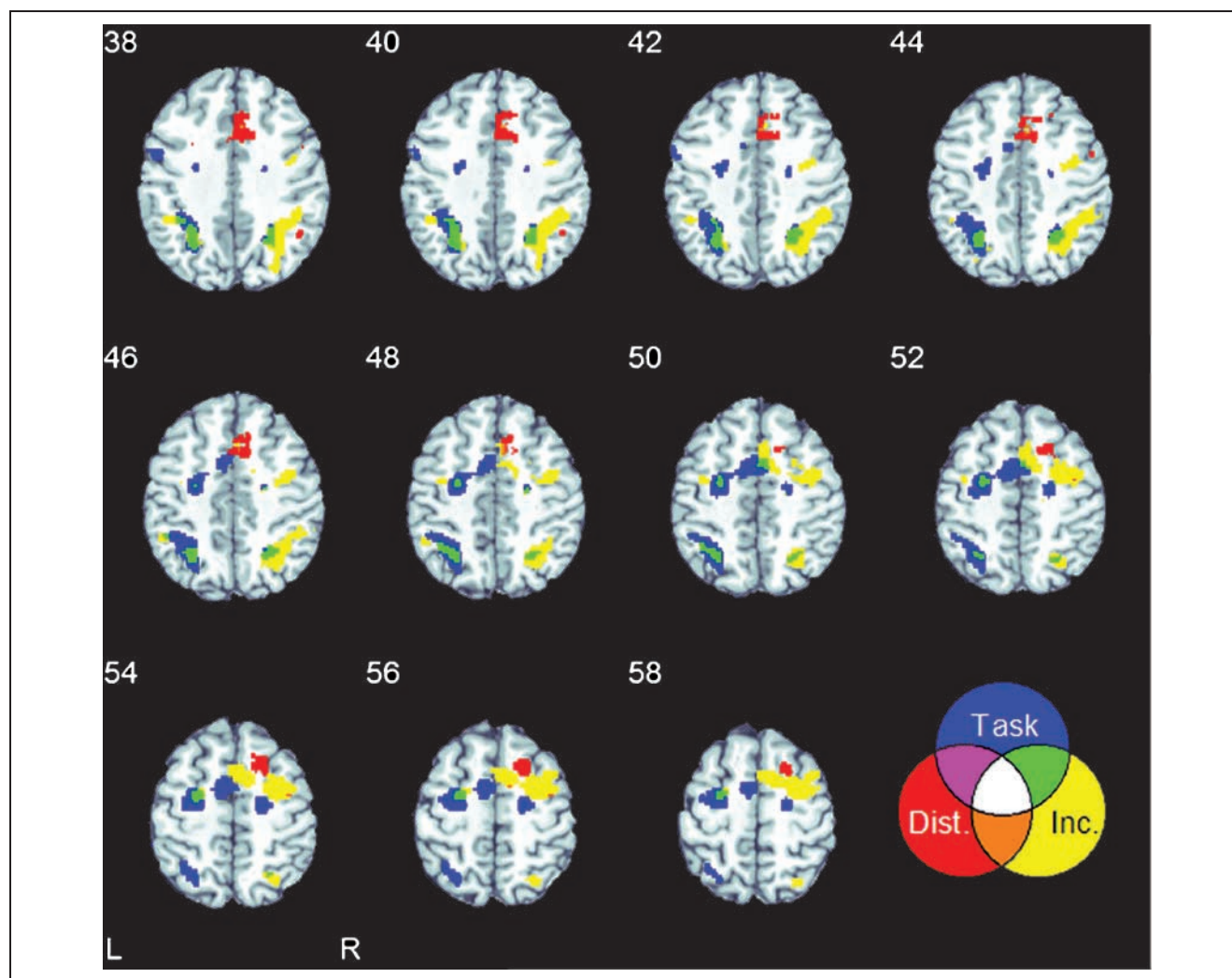


Figure 3. The common and distinct activation of the IPS by the task versus baseline (in blue), the Stroop effect (in yellow), and the distance effect (in red) are shown in the overlay. Task = tasks versus baseline; Dist. = the distance effect; Inc. = Stroop incongruity effect.

Table 4. Correlation between Reaction Times and Brain Activities in the IPS, ACC, and Pre-SMA

<i>Pearson Coefficients</i> (<i>n</i> = 48)	<i>Reaction Time</i>	<i>ACC</i> (<i>Stroop</i>)	<i>Pre-SMA</i> (<i>Stroop</i>)	<i>L. IPS</i> (<i>Stroop</i>)	<i>R. IPS</i> (<i>Stroop</i>)	<i>ACC</i> (<i>Distance</i>)
ACC (Stroop)	-.148					
Pre-SMA (Stroop)	-.354*	.744**				
L. IPS (Stroop)	-.196	.090	-.072			
R. IPS (Stroop)	.629**	.084	-.162	-.059		
ACC (Distance)	-.273	.539**	.529**	.273	-.030	
R. IPS (Distance)	.084	.161	.221	-.506**	.206	.046

* $p < .05$ (two-tailed).

** $p < .01$ (two-tailed).

correlations among the activities of different brain areas as well. A positive correlation was found in the two peaks of the Stroop effect at the ACC and pre-SMA. Activity of the ACC identified in the distance effect correlated positively with both the ACC and pre-SMA from the Stroop effect.

DISCUSSION

The Common and Distinct Roles of the IPS in Numerical Comparison and Attentional Selection

The inferior parietal cortex is actively involved in attentional tasks, such as spatial attention (Rushworth, Johansen-Berg, Göbel, & Devlin, 2003). Its role in spatial attention is consistent with the traditional distinction between the ventral “what” pathway and the dorsal “where” pathway (Mishkin, Ungerleider, & Macko, 1983). Damage in this area usually results in the disruption of perceptual processes involving spatial attention, as often observed in neglect patients (Pouget & Driver, 2000; Driver & Mattingley, 1998). Given the nature of spatial representation of numerical information as suggested by Fias and Fischer (2005) and Dehaene (1997), it is not surprising to associate this region with numerical judgment as well.

Likewise, the inferior parietal cortex, typically in the left hemisphere, is often activated in nonspatial attentional tasks, such as a color–word Stroop task (Banich et al., 2000). Its activation is usually observed in tandem with activation of other frontal regions such as the dorsolateral prefrontal cortex. One recent view of attentional control suggests that the inferior parietal cortex is part of the attentional network involved in exerting top-down goal-directed selection for stimuli and responses (Corbetta & Shulman, 2002).

Consistent with these views, we observed activation of the inferior parietal cortex by both number comparison and attentional selection in our task. There is a great

deal of overlap in the IPS bilaterally (see Figure 3). Nonetheless, these two processes show distinct activation patterns in the IPS. Similar to previous findings (Cohen Kadosh et al., 2005; Eger et al., 2003; Fias et al., 2003; Chochon et al., 1999), number processing is more pronounced in the left IPS than in the right IPS. On the other hand, the Stroop interference effect is associated more with the right IPS than the left IPS. This seems to be at odds with the literature on the attentional network, typically identified with the Stroop task, which usually finds left inferior parietal activation (Laird et al., 2005). However, we speculate that this more right-lateralized activation of the IPS may reflect attentional modulation on number processing as discussed in the next section.

Stroop-like Interference in Two-digit Number Comparison

The Stroop-like interference effect observed in the behavioral performance and its associated brain activation pattern bring forth another important implication in terms of the nature of number representation and processing in the brain. A prominent theory in this field suggests that regardless of the external representation of numbers, we form an abstract mental representation of quantity along a “mental number line” in the brain (Dehaene, 1997). This theory can explain many of the behavioral phenomena regarding numerical processing, such as the distance effect and spatial–numerical association of response codes (SNARC) effect (Fias & Fischer, 2005; Dehaene, Bossini, & Giraux, 1993). The smaller the distance between the two numbers, the closer they are “marked” along the “mental number line,” and therefore, the harder it is to discriminate them. This view implies the holistic representation and processing of multidigit numbers, as the individual digits lose their identities after the whole numbers are encoded into abstract semantic quantities.

However, recent behavioral findings by Zhang and Wang (2005) and Nuerk et al. (2001) pose a challenge to the above view. They observed that the individual digits maintained their distinct characteristics and influenced the number comparison process, as well as the whole numbers did. Nuerk et al. found that during a number comparison task with two-digit numbers, people responded more slowly when the unit digits were incongruent with the decade digits in terms of their relative magnitudes, although the distance between the numbers was controlled. This Stroop-like effect indicates that people process the individual digits in parallel, instead of holistically. Zhang and Wang further examined this Stroop-like effect with computational simulation of three models of number representation—sequential, parallel, and holistic, and provided additional support for the parallel comparison model.

The current study presented additional neuroimaging evidence for such a parallel processing model. We not only observed the reliable Stroop-like effect in the behavioral results but also identified activation of the attentional network typically associated with such an interference effect. To overcome the interference imposed by the incongruent relative sizes of the unit digits (e.g., the larger unit digit in the smaller number), people need to shift attention to the decade digits and rely more on the decade digits to make the correct comparison. In addition to observing activation of the fronto-parietal network for such attentional selection, we also found that the IPS activity was modulated by attentional selection. We speculate that the greater *right* IPS activation for the incongruent pairs indicates the enhanced processing of the decade digits displayed in the *left* visual field. Although we did not explicitly control for the hemifield presentation of the decade and unit digits, it was likely that the decade digits of both numbers—on the *left* visual field—were projected to the *right* hemisphere and the unit digits—on the *right* visual field—were projected to the *left* hemisphere. Due to the interference caused by the unit digits in the incongruent pairs, we would expect that people shift their attention to the *left* and enhance processing of the decade digits in order to overcome the interference and make correct responses. Therefore, the greater activation in the *right* IPS may indicate up-regulation of number comparison on the decade digits in the *left* visual field. This interpretation accords well with hemispatial neglect studies, in which damage in the right parietal cortex usually results in neglect to the left visual field (Halligan, Fink, Marshall, & Vallar, 2003). Future study with explicit control of hemifield visual presentation is needed to provide better support for this conjecture.

The Stroop-like effect is not specific to the vertical presentation of the numbers, which may promote column-wise comparison in parallel. Other studies have found the robust Stroop-like effect even when two numbers are

presented diagonally (Nuerk, Weger, & Willmes, 2004) or horizontally (Zhang & Wang, 2005).

The Stroop effect in the behavioral performance and on IPS activation suggests that the IPS is recruited by number comparison and its activity can be modulated by attentional control. These results also lend support to the parallel processing model of the decade and unit digits. However, it does not rule out the holistic processing of two-digit numbers, which is discussed next.

The Distance Effect and its Modulation on IPS Activation

The typical distance effect was also obtained. The closer the distance between the two numbers, the harder the task. The brain areas associated with this effect consist mainly of the ACC and the right prefrontal cortex. However, activation in these regions was not necessarily related to task difficulty and the ROI analysis did not yield significant correlation between RTs and activation of the ACC. It is also not likely that ACC activation in this effect and the Stroop effect mentioned above resulted from response errors. First, participants made very few errors overall. The distance and congruency between numbers did not result in significant difference in error rates across conditions. Second, error-related ACC activation documented in the existing literature is more rostral than what was observed in the current study. Previous studies suggest that the ACC and the right prefrontal cortex are more heavily involved in selection at the response stage—they are particularly active when there is greater ambiguity or competition between alternative responses, such as in the color–word Stroop task (Liu, Banich, Jacobson, & Tanabe, 2006; Milham et al., 2002).

Unlike the strong distance effect on bilateral IPS activation reported previously (Cohen Kadosh et al., 2005; Pinel et al., 2001, 2004), we only observed a small cluster in the right IPS (close to the angular gyrus) modulated by the distance effect. This area was more active when the distance between the numbers was close. This right inferior parietal activation was more lateral than those identified in the task versus baseline and Stroop effect discussed above. A possible reason for such a weak modulation of the IPS by the distance effect may be due to the choice of the two distance levels—18 and 27. According to the logarithmically compressed number line suggested by the evidence found in Piazza et al. (2004), these two distance levels are relatively large (compared to the single digit numbers) and close to each other on a logarithm scale. This may account for the small distance effect shown in the IPS. The relatively large distances used in the current study may also account for the lack of significant modulation of the left IPS by the distance effect because the task may rely more on approximate than exact comparison. Andres, Seron, and Olivier (2005) found that single-pulse transcranial

magnetic stimulation (TMS) in the left posterior parietal cortex (PPC) alone was enough to disrupt number comparison of close distance (i.e., close to 5), whereas bilateral TMS was necessary to alter discrimination of digits far from 5. They suggested that the left PPC is involved in exact comparison, whereas approximation relies more on the right PPC.

The distance effect implies that holistic representation may also play a role in the number comparison task. Consider a scenario that participants base their responses on the decade digits during comparison (e.g., serial processing). Because the difference between the decade digits is relatively small (between 1 and 3), this small difference alone cannot produce a reliable distance effect. Also consider the examples from I18 (e.g., 37 and 19) and C27 (e.g., 59 and 32), the distances of the decade digits in both pairs are the same (i.e., 2). Yet the I18 pairs are the hardest and the C27 pairs are the easiest. This rules out the serial processing account.

Likewise, the sum of the distances between the decade digits and unit digits cannot account for the distance effect. Now imagine that participants just compare both the decade and unit digits in parallel and make a decision on the basis of the pooled results (e.g., parallel processing). Consider the examples from C18 (e.g., 49 and 31) and C27 (e.g., 68 and 41), the sum of the distances between the decade digits and unit digits in both pairs is the same [i.e., $(4 - 3) + (9 - 1) = 9$ or $(6 - 4) + (8 - 1) = 9$]. Yet the C18 pairs are harder than the C27 pairs. Therefore, holistic representation of numbers might be necessary to account for the distance effect. However, this interpretation is based on the assumption of equal weighing of the decade and unit digits in a parallel processing model. As a matter of fact, the line between parallel and holistic processing becomes fuzzy when different weights are assigned to the decade and unit digits. On one extreme, the decade and unit digits are weighed equally, which leads to the case of parallel processing. On the other extreme, if the decade digits are weighed 10 times as much as the unit digits, a holistic comparison automatically follows. Any other weighting schemes would result in some combination of holistic and parallel processing. In this sense, the observed distance effect and its modulation on the IPS activity in the current study lend support to the holistic processing model as well.

Task Difficulty and Brain Activation

A possible contribution to activation in the IPS, other than the suggested attentional selection and numerical comparison processes, may be related to task difficulty. Because both the Stroop effect and the distance effect affected task difficulty as indexed by behavioral performance, we verified whether IPS activation was an artifact of task difficulty by correlating RTs with activation in the IPS and two other medial frontal areas (ACC and pre-

SMA) typically associated with task performance. The results indicated that task difficulty could only account for activation in the right IPS, but not in the left IPS. The negative correlation between the pre-SMA activation and RTs supports the role of pre-SMA in response selection (Rushworth, Walton, Kennerley, & Bannerman, 2004). The higher the pre-SMA is activated, the more efficient it is working, and the shorter the RTs. Although activity in the ACC did not directly correlate with RTs, it did positively correlate with activity in the pre-SMA, suggesting complementary functions of these two adjacent brain structures.

In summary, by manipulating congruency and distance between the decade and unit digits in two-digit numbers, we found that the bilateral IPS is actively engaged in numerical comparison. The IPS activity is strongly modulated by attentional selection, especially in the right hemisphere. The distance effect also modulates activation in the IPS, but not as strong as the Stroop effect. The modulation is limited in the right IPS, located more lateral than the one by the Stroop effect. These suggest that the IPS may be involved in both attentional selection and numerical comparison while each process recruits distinct subregions of the IPS. Taken together, the Stroop effect and the distance effect manifested in the behavioral performance and associated neural profiles also lend support to both parallel and holistic representation of numerical information in the brain.

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