

Dissociating response conflict from numerical magnitude processing in the brain: An event-related fMRI study

Daniel Ansari,^{a,*} Jonathan A. Fugelsang,^b Bibek Dhital,^a and Vinod Venkatraman^c

^aNumerical Cognition Laboratory, Department of Education, Dartmouth College, 3 Maynard Street, Raven House, Hanover, NH 03755, USA

^bDepartment of Psychology, University of Waterloo, Ontario, Canada

^cCognitive Neuroscience Laboratory, SingHealth, 169611, Singapore

Received 22 December 2005; revised 7 April 2006; accepted 8 April 2006
Available online 30 May 2006

Functional neuroimaging studies of numerical cognition have repeatedly associated activation of the intraparietal sulcus (IPS) with number processing. During number comparison, the IPS has been found to be modulated by the numerical distance. This has led to the contention that the IPS houses the internal representation of numerical magnitude. However, this theory has been challenged by the argument that IPS activation may reflect domain-general response selection. In the present study, we used the numerical size congruity paradigm to further elucidate the role played by the IPS in number comparison. In an event-related, functional magnetic resonance imaging (fMRI) study, participants judged which of two number words was numerically larger. In addition to the numerical distance, physical stimulus size was varied such that physical size and numerical magnitude were either (a) congruent (e.g., numerically smaller number printed in smaller font) or (b) incongruent (e.g., numerically larger number printed in smaller font). This allowed for the study of both the main effects and the interaction of numerical distance and stimulus congruency. A main effect of numerical distance was found in bilateral regions of the IPS. However, these parietal areas were not significantly modulated by congruency or the interaction of distance and congruency. Instead, the main effect of congruency and an interaction of distance and congruency were observed in anterior cingulate and prefrontal cortices. These findings suggest some degree of independence between the processing of numerical distance and size congruity, lending support for the hypothesis that distance effects in IPS reflect the underlying representation of numerical magnitude.

© 2006 Elsevier Inc. All rights reserved.

Keywords: Size congruity; Distance effect; Intraparietal sulcus; Conflict; Numerical cognition

Introduction

A plethora of recent neuroimaging studies have implicated the parietal lobes in number processing (for a review, see Dehaene et al., 2003). Associations between parietal lobe activation and numerical cognition range from calculation (Gruber et al., 2001; Venkatraman et al., 2005) to activation during passive viewing of changes in non-symbolic numerosity (Ansari et al., 2006; Piazza et al., 2004). In particular, bilateral regions of the intraparietal sulcus (IPS) have consistently been found to be activated during numerical magnitude processing. In a growing number of studies, the activation of the IPS bilaterally has been associated with the numerical distance effect. Behaviorally, it has been well replicated that when adults and children compare the numerical magnitude of two numbers (number words, Arabic numerals or non-symbolic numerosities), an inverse relationship between reaction time and numerical distance is found. In other words, the larger the numerical distance between two numbers, the faster participants judge their relative numerical magnitude (Dehaene et al., 1990; Moyer and Landauer, 1967; Sekuler and Mierkiewicz, 1977).

Several neuroimaging studies in adults have revealed that bilateral regions of the IPS are significantly modulated by numerical distance (Fulbright et al., 2003; Kaufmann et al., 2005; Pinel et al., 1999, 2001, 2004). Consistent with behavioral findings, these neuroimaging data reveal greater activation of the IPS during processing of small compared to large distances. Against the background of these studies, it has been postulated that the IPS houses the internal representation of approximate numerical magnitude (Dehaene et al., 2003, 2004).

Recently, however, the specificity of parietal activation during number processing, and in particular during number comparison, has been called into question. For example, it is well established that the IPS is modulated by response selection in tasks that do not involve any number processing (Culham and Kanwisher, 2001; Jiang and Kanwisher, 2003; Rushworth et al., 2003). Because number comparison involves response selection, it has been argued that distance-related activation of the IPS may be difficult to

* Corresponding author. Fax: +1 603 646 3968.

E-mail address: Daniel.Ansari@Dartmouth.Edu (D. Ansari).

URL: <http://www.dartmouth.edu/~numcog> (D. Ansari).

Available online on ScienceDirect (www.sciencedirect.com).

disentangle from activation caused by response selection. Indeed, Gobel et al. (2004) showed that when activation underlying non-numerical comparison with similar task difficulty is subtracted from the number comparison-related activation, no significant numerical distance effects in the IPS remain. Such findings call into question the extent to which numerical distance effects in the IPS are reflective of a numerical magnitude system over and above response selection and stimulus-related activations (Gobel and Rushworth, 2004). However, recent findings suggest that distance effects in the IPS are obtained even when the tasks involve no response selection component (Ansari et al., 2006; Piazza et al., 2004), significantly questioning the argument that numerical distance effects on the IPS can be explained by recourse to domain-general response selection. Furthermore, task versus control contrasts leave open the possibility that differences between control and experimental tasks other than those explicitly manipulated can cause the absence or presence of significant differences in activation.

The presently available data cannot fully resolve the debate over what representational mechanisms are reflected by parietal engagement during number processing. Perhaps the best way to dissociate activation related to response selection from activation correlated with numerical magnitude processing is to use a paradigm that varies both numerical distance and the response selection demands within a single task.

The ‘size congruity’ or ‘number stroop’ paradigm does exactly this. The size congruity effect refers to the conflict that occurs between physical (size of Arabic numerals or number words) and semantic (numerical magnitude) stimulus attributes when they are presented simultaneously. In numerous behavioral experiments, with both adults and children, it has been shown that the size of an Arabic numeral or number word interferes with the processing of magnitude information (Besner and Coltheart, 1979; Girelli et al., 2000; Henik and Tzelgov, 1982; Rubinsten et al., 2002; Schwarz and Ischebeck, 2003). In other words, when subjects are asked to compare which of two numbers is numerically larger, they are faster when the semantically larger numeral is also printed in a larger font (congruent trial) than if the numeral printed in the larger font is numerically smaller (incongruent trial). By varying both the numerical distance and the physical size in these paradigms, it is possible to detect both main effects and interactions of response conflict (by manipulating congruency) and numerical magnitude processing (by manipulating numerical distance).

In view of the above, the ‘size congruity paradigm’ can serve to disentangle neural correlates of semantic magnitude processing from those regions modulated by response selection and response conflict components of task-related processing. Against this background, a number of hypotheses can be put forward. Firstly, if the IPS is involved in numerical magnitude processing independently of response conflict processing, one should expect to find a main effect of numerical distance on these cortical regions. Furthermore, one should not expect these regions to be modulated by main effects of congruency (incongruent > congruent) or the interaction of numerical distance and congruency. Secondly, consistent with a large body of neuroimaging studies of conflict-related activation, it can be predicted that main effects of congruency and interactions between congruency and distance are correlated with activation in regions in and around the anterior cingulate cortex (ACC) as well as the dorsolateral prefrontal cortex (DLPFC) (Botvinick et al., 1999, 2004; Bush et al., 1998; MacDonald et al., 2000; Pardo et al., 1990; Ridderinkhof et al.,

2004). However, if the IPS is involved in both response conflict and magnitude processing and in their interaction, then the IPS should also reveal a main effect of congruency and/or an interactive effect of Congruency \times Distance.

In a recent functional magnetic resonance imaging (fMRI) study of the size congruity effect, Kaufmann et al. (2005) found main effects of congruency on regions in ACC and DLPFC. Furthermore, an analysis of the distance effect using stimuli of the neutral condition (no manipulation of size congruency) revealed a main effect of distance on bilateral parietal regions. These findings suggest that whereas frontal regions are engaged by response conflict processing, parietal regions are modulated by numerical distance. However, because Kaufmann et al. (2005) only investigated the main effects of congruency and distance, it cannot be established whether parietal areas also exhibit Distance \times Congruency interaction effects, which would additionally implicate these regions in response-related processing rather than solely in numerical magnitude representation. Furthermore, Kaufmann et al. (2005) investigated main effects of distance on functional neuroanatomy using only their neutral stimuli. This leaves open the possibility that such main effects of distance are absent when the congruency of numerical stimuli is varied at the same time as numerical distance. In a recent study, Pinel et al. (2004) revealed that a distance effect on parietal regions exists even when distance and congruity vary simultaneously. However, these authors only tested for the main effect of distance and congruity and not their interaction, which, as noted above, leaves open the possibility of a Congruency \times Distance interaction in parietal regions. In the present study, we address these open questions in an effort to further investigate the role played by the IPS in magnitude versus response-related conflict processing by examining both main and interactive effects of distance and congruency on functional neuroanatomy.

Method

Participants

Fourteen, right-handed volunteers (8 females), mean age 21 years, 3 months (range: 18 years, 9 months–24 years, 9 months) participated in this study. All participants provided written informed consent in compliance with Dartmouth College’s Committee for the Protection of Human Subjects.

Task design and stimuli

Participants were presented with pairs of number words ranging from one to nine. Visual stimuli were presented using a Dell 800 latitude computer running e-prime presentation software (Psychological Software Tools, Pittsburgh, PA). Stimuli were projected to participants with an Epson (model ELP-7000) LCD projector onto a screen positioned at the head end of the scanner bore. Participants viewed the screen through a mirror. Number words were presented equidistant from a central fixation dot. Participants were provided with a fiber-optic button box and were asked to press, as quickly and as accurately as they could, the button corresponding to the side on which the numerically larger word was presented.

Data were acquired in three event-related functional runs. Each run consisted of 72 trials divided into three conditions (incongruent, congruent or neutral) consisting of 24 stimuli for each condition. In all three conditions, large stimuli were printed in

Arial font size 58 whereas small stimuli were presented in Arial font size 30. The specific parameters for the stimuli in the three conditions were as follows:

1. Incongruent—these trials consisted of pairs of number words where the font size of the numerically smaller number was printed in the larger font (e.g., **ONE** nine).
2. Congruent—for these trials, numerically larger number words were printed in the larger font (e.g., one **nine**).
3. Neutral—for these trials, number words were presented in the same font size regardless of numerical size. To equate the amount of visual stimulation with the incongruent and congruent trials, we presented half of the neutral trials in the large font size and the other half in the small font size (e.g., one nine or one nine).

Within each run, the numerical distance between pairs of number words was varied systematically. Specifically, the numerical distance between number pairs varied from 1 to 7. To allow for the assessment of the effect of distance on reaction times and associated brain activations, we divided trials into those with small (1, 2 and 3) and large (5, 6 and 7) numerical distances. Within each stimulus run, half of the trials (36) were small distance trials and the other half (36) were large distance trials.

Each trial started with the presentation of the number pair for a duration of 650 ms. The presentation of number pairs was followed by the appearance of the central white fixation square against a black background. Fixations following the number pairs were presented for either 1850, 4350 or 6850 ms. These three fixation durations each followed a third (24) of the stimulus trials. Variable intervals between stimulus trials ('jitter' trials) are necessary in event-related fMRI studies to allow better deconvolution of the hemodynamic signal unique to each trial. The order of presentation of condition (incongruent, congruent and neutral), distance (large and small) and fixation duration (4350, 6850 or 9350 ms) was completely counterbalanced.

Data acquisition

Functional images were acquired in a 1.5-T General Electric whole body MRI scanner. A standard birdcage head coil was used and head movements were restricted through the use of a foam pillow. Using a fast spin echo sequence, 25 T1-weighted structural slices were acquired in the axial plane. Coplanar to the T1-weighted structural images, functional images were acquired using a gradient echo planar T2*-sequence sensitive to blood oxygenation level-dependent (BOLD) contrast. Image volumes consisted of 25 non-contiguous slices (4.5 mm thickness, 1 mm gap, 64 × 64 matrix, repetition time = 2.5 s, TE = 40 ms, flip angle = 90°, field of view = 24 × 24 cm) covering the whole brain. Each functional run consisted of 164 acquisitions. Three-dimensional whole-brain,

high-resolution (0.94 × 0.94 1.2), T1-weighted images were acquired in the sagittal plane using a standard GE SPGR 3-D sequence.

Data analysis

Structural and functional images were analyzed using Brain Voyager QX 1.2.6 (Brain Innovation, Maastricht, Holland). Functional images were corrected for slice time acquisition differences, head motion and linear trend. Functional images were aligned to the T1-weighted coplanar images and subsequently to the three-dimensional high-resolution scans. The realigned data set was then transformed into Talairach space (Talairach and Tournoux, 1988).

Following Boynton et al. (1996), the expected BOLD signal change was modeled using a gamma function (tau of 2.5 s and a delta of 1.5). Random-effects analyses were performed to examine the effects of all three predictors. Voxels were considered to be significantly activated when they passed a threshold of $P < 0.0001$, uncorrected.

Results

Behavioral results

Reaction time data

Reaction times were subjected to a 2 (distance) × 2 (congruency) repeated analysis of variance (ANOVA). This analysis revealed a main effect of distance [$F(1,13) = 19.1$, $P < 0.001$] and a main effect of congruency [$F(1,13) = 3.8$, $P < 0.001$]. There was no interaction between distance and congruency [$F(1,13) < 1$, n.s.].

Accuracy data

Given the low number of errors (see Table 1) between subjects and conditions, no statistical analysis of the accuracy data was conducted.

fMRI results

In the same way as for the reaction time data, a voxel-wise 2 (distance) × 2 (congruency) ANOVA was calculated. Table 2 shows all areas that revealed significant main effects of distance, congruency and those areas revealing a significant Distance × Congruency interaction (all activation at $P < 0.0001$, uncorrected). In order to better understand the Congruency × Distance interactions in the cingulate gyrus, dorsolateral prefrontal cortex and ventrolateral prefrontal cortex (see Figs. 3 and 4), we calculated post hoc simple effects contrasts for each of the four possible comparisons. Significant effects ($P < 0.0001$, uncorrected) were revealed for

Table 1
Mean accuracy and response times for small and large distance comparison for both congruent and incongruent trials

	Congruent		Incongruent	
	Accuracy (% correct)	Reaction time (ms)	Accuracy (% correct)	Reaction time (ms)
Small distance	98.6 (0.46)	897.6 (173.3)	98.6 (0.52)	934.0 (157.4)
Large distance	97.2 (0.80)	811.2 (178.0)	98.1 (0.66)	851.6 (162.9)

Numbers in parentheses denote standard deviations.

Table 2

Talairach coordinates of activation peaks for main effects of congruency and distance and their interactions

Brain region	Hemisphere	x	y	z	F(1,13)	k
Main effect of congruity (incongruent > congruent)						
Precuneus	R	9	-36	46	18.6	266
Paracentral lobule	L	-21	-36	43	16.7	51
Inferior parietal lobe	R	50	-39	38	21.0	575
Posterior cingulate gyrus	R	5	-24	40	16.2	87
Cingulate gyrus	R	9	18	36	16.7	79
Anterior cingulate gyrus	R	4	40	30	21.7	665
Superior frontal gyrus	L	-23	41	27	20.2	370
Superior frontal gyrus	R	24	45	25	17.0	101
Middle frontal gyrus	R	39	30	20	17.8	345
Middle frontal gyrus	L	-27	32	24	16.2	109
Cingulate gyrus	L	-13	-38	27	17.0	196
Insula	R	27	-24	24	15.3	23
Caudate	R	20	-19	18	20.0	521
Thalamus	R	5	-8	13	16.0	103
Thalamus	L	-6	-10	5	18.3	233
Clastrum	R	31	11	4	18.7	179
Clastrum	L	-31	0	4	19.1	448
Middle frontal gyrus	R	31	42	-5	18.3	41
Putamen	L	-22	14	-10	16.6	79
Parahippocampal gyrus	L	-24	-7	-13	16.2	72
Middle frontal gyrus	L	-26	23	-17	16.0	70
Main effect of distance (small > large)						
Precentral gyrus	R	28	-18	56	20.6	348
Precuneus	L	-12	-49	54	16.3	27
Postcentral gyrus	R	35	-30	48	18.7	335
Medial frontal gyrus	L	1	10	46	15.4	111
Inferior parietal lobule	L	-31	-36	36	20.0	334
Cingulate gyrus	R	11	23	38	15.8	29
Middle frontal gyrus	R	28	-4	39	16.7	60
Medial frontal gyrus	R	19	41	15	18.7	196
Anterior cingulate gyrus	L	-16	36	15	18.2	318
Clastrum	L	-31	13	6	17.4	419
Interaction of congruity and distance effects						
Cingulate gyrus	R	11	3	46	20.3	554
Precentral gyrus	R	52	-2	15	18.3	119
Medial frontal gyrus	L	-23	41	7	19.4	321

Peaks obtained from random effects analysis at $P < 0.0001$, uncorrected threshold (k denotes the cluster size).

the large incongruent > large congruent and congruent small > congruent large, but not the incongruent small > incongruent large or the incongruent small > congruent small contrasts. This was true for all three regions showing a significant Distance \times Congruency interaction.

To compare our data with those reported in previous studies, an analysis of the main effect of distance (small > large) was also computed for the neutral trials. Results of this analysis can be found in Table 3.

Discussion

Although a growing body of neuroimaging studies clearly suggests an association between number processing tasks and bilateral activation of the parietal lobes, there exists controversy over exactly what neurocognitive processes are engaged by parietal regions during number comparison.

In the present study, we used the size congruity or 'number troop' paradigm in an attempt to dissociate the neural correlates of

response selection versus numerical magnitude processing-related components of number comparison. Consistent with the previous findings (Fulbright et al., 2003; Kaufmann et al., 2005; Pinel et al., 1999, 2001), we found significant effects of distance on areas in the left and right inferior parietal lobes. In addition, distance effects were found in several frontal regions (see Tables 2 and 3). Importantly, we did not find any significant main effect of congruency or interactive effect of Congruency \times Distance on those parietal regions exhibiting main effects of numerical distance. Although previous findings had illustrated main effects of distance on parietal regions even when the congruity of number pairs varied simultaneously (Pinel et al., 2004), our findings are the first to demonstrate the absence of an interaction between numerical distance and size congruity on a region in the left inferior parietal lobe. As can be seen from Fig. 2, effects of distance on the activation in the inferior parietal lobule were observed for both incongruent and congruent trials. These findings are inconsistent with an account that attributes parietal activation during number comparison to a response selection mechanism. If indeed the parietal activation during number comparison was solely attributable to response selection, then these areas should have also been modulated by conflict, as conflict places greater demands on response selection mechanisms. Hence, the present findings are consistent with an interpretation that suggests that bilateral parietal regions are engaged by numerical magnitude processing somewhat independently of response selection. In other words, response selection and conflict processing appears to be supported by areas other than the parietal regions modulated by distance.

As can be seen in Figs. 1, 3 and 4), both main effects of congruency (incongruent > congruent) and interactions of congruency and numerical distance were found in the dorsolateral and ventrolateral prefrontal cortex as well as in the ACC. The bar charts indicate that these regions were significantly more activated during incongruent relative to congruent trials. Moreover, distance had a significant effect on these regions only for the congruent condition but not the incongruent condition. In all cases, the activation for small and large distances in the incongruent trials was almost equivalent, suggesting that these regions code for the response selection demands of the tasks independently of number semantics. These findings lend further support to the notion that the ACC and DLPFC are involved in domain-general conflict processing (Botvinick et al., 2004).

The present data suggest that these frontal regions may have little to do with the semantic representation of numerical

Table 3

Talairach coordinates of activation peaks for main effect of distance in the neutral condition

Brain region	Hemisphere	x	y	z	t(13)	k
Main effect of distance for neutral trials (small > large)						
Inferior parietal lobule	L	-35	-48	47	6.2	336
Cuneus	L	-12	-79	34	5.6	94
Inferior parietal lobule	R	35	-44	34	5.3	366
Cingulate gyrus	R	4	9	43	5.6	474
Precuneus	R	26	-76	26	5.4	33
Insula	L	-46	-18	20	5.5	20
Lingual gyrus	L	-17	-62	5	5.7	252

Peaks obtained from random effects analysis at $P < 0.0001$, uncorrected threshold (k denotes the cluster size).

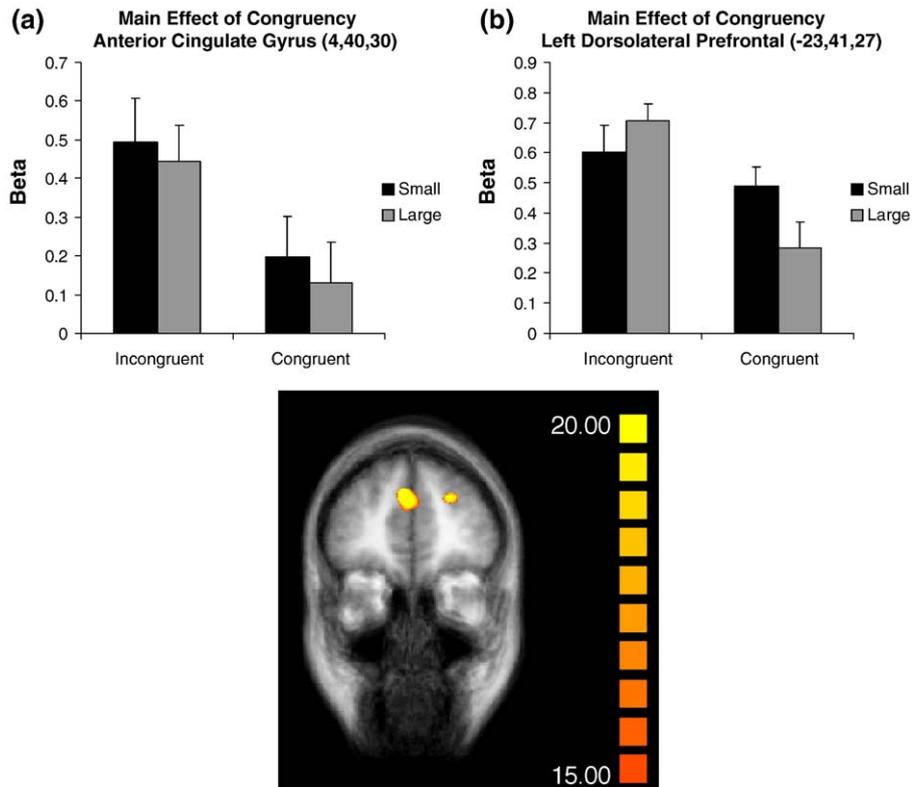


Fig. 1. Coronal slice showing main effect of congruency (incongruent > congruent) on regions in anterior cingulate and left dorsolateral prefrontal cortex. Bar charts depict the beta values (parameter estimates) for small and large distances for both congruent and incongruent conditions. Beta values were obtained from the peak voxel in the regions of interest. Error bars denote the standard error of the mean.

magnitude and more to do with mechanisms of cognitive control necessary to deal with the response selection and conflict processing inherent in the size congruity task. Both the presence of a distance effect in the congruent condition and the absence thereof in the incongruent condition in the frontal regions can be explained by invoking domain-general mechanisms of response selection and cognitive control. In the case of the congruent condition, greater activation during small relative to large distances can be explained by the greater demands the more difficult small number trials place on response selection. In a similar vein, both small and large incongruent trials exert significant demands on response selection and conflict processing mechanisms, explaining why no significant differences in activation were obtained between

these two conditions. The absence of a distance effect for incongruent stimuli in the frontal regions modulated both by the main effect of congruency and the Congruency × Distance interaction strengthens the argument that these areas are more involved in conflict and response selection related processes than they are in the semantic representation of numerical magnitude. Conversely, the presence of a significant distance effect for both congruent and incongruent trials in the left inferior parietal lobule (see Fig. 2) supports the argument that these regions are engaged in numerical magnitude processing to a greater extent than in response selection and conflict processing.

Thus, the present findings reveal that parietal activation during number comparison – and specifically the modulation of these

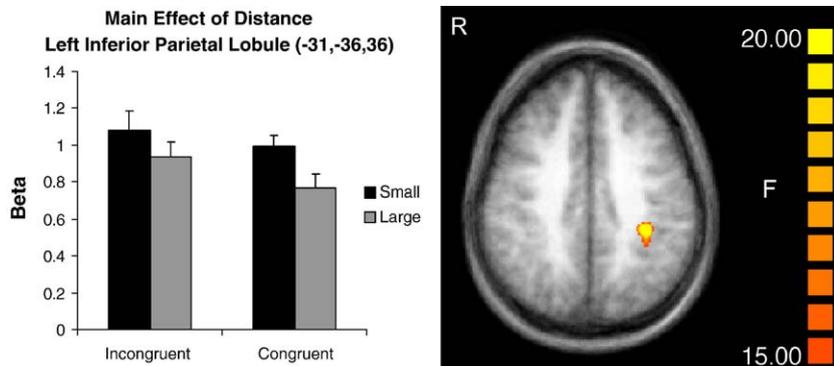


Fig. 2. Axial slice showing main effect of distance (small distance > large distance) on left inferior parietal lobule. Bar charts depict the z scores (parameter estimates) for small and large distances for both congruent and incongruent conditions. Beta values were obtained from the peak voxel in the regions of interest. Error bars denote the standard error of the mean.

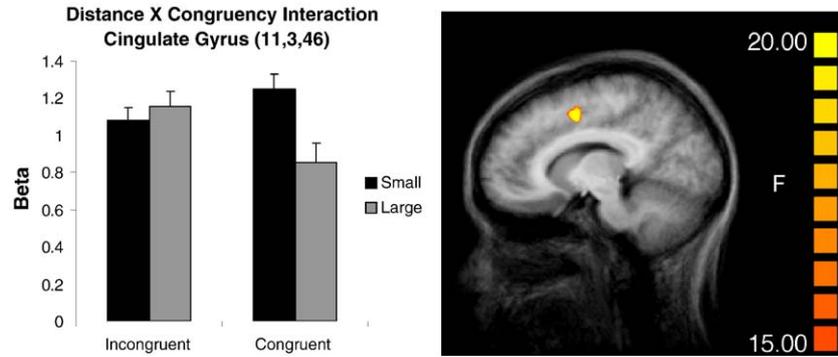


Fig. 3. Sagittal slice showing Distance \times Congruency interaction effect on an area within the cingulate gyrus. Bar charts depict the z scores (parameter estimates) for small and large distances for both congruent and incongruent conditions. Beta values were obtained from the peak voxel in the regions of interest. Error bars denote the standard error of the mean.

cortical regions by numerical distance – cannot solely be explained by recourse to domain-general response selection that has previously been associated with the parietal regions (Culham and Kanwisher, 2001; Gobet and Rushworth, 2004; Rushworth et al., 2003). Unlike previous studies that have used a task versus control comparisons to probe the specific role of parietal regions in number comparison (Fias et al., 2003; Gobet et al., 2004), the present study allowed the evaluation of magnitude-related and response-related activation within a single task using a voxel-by-voxel ANOVA to probe both main effects and interactions of congruity and numerical distance. Our findings lend strength to the hypothesis that modulation of parietal regions by numerical distance reflects an underlying, approximate sense of numerical quantity (Dehaene et al., 2003; Pinel et al., 2001).

In the discussion of the present results, it is important to note that the stimuli that were used to measure distance and congruity effects and their interaction were number words. Most previous behavioral and functional neuroimaging studies that have employed the size congruity paradigm used Arabic numerals as their stimuli. Although the findings do allow for the generalization of previous findings with Arabic numerals to number words, it is important to note the possibility that some of the effects reported here may be notation specific. For example, it is possible that the strength of both main effects and their interaction could be differentially modulated as a function of the notation used to present the stimuli in the size congruity paradigm. Furthermore, the use of number words instead

of Arabic numerals may also explain why a smaller effect of congruity relative to distance was observed in the present findings. It is therefore important for future studies to measure the behavioral effects and neuroanatomical correlates of distance and congruity effects using both Arabic numerals and number words to investigate possible overlap and divergence in the patterns of data.

In the present context, it is important to note that other arguments against domain specificity for number in parietal cortex have been advanced. Recently, two studies have evaluated the hypothesis that parietal regions are involved in domain-general rather than number-specific comparisons by contrasting regions involved in number, luminance and size comparisons (Cohen-Kadosh et al., 2005; Pinel et al., 2004). Results from both studies indicate that parietal activation during number comparison overlaps with other non-numerical comparative judgments, challenging the notion that areas within the parietal lobe are uniquely associated with number comparison. However, Cohen-Kadosh et al. (2005) report some activation in regions of the left IPS that are uniquely associated with number comparison. Interestingly, this region closely overlaps with the left parietal regions found to be modulated by numerical distance in the present study (see Fig. 2). In addition to the results suggesting strong overlap between numerical and non-numerical comparisons in parietal regions, a recent set of studies using non-symbolic stimuli has also challenged the hypotheses that parietal regions house the internal representation of numerical magnitude (Shuman and Kanwisher, 2004).

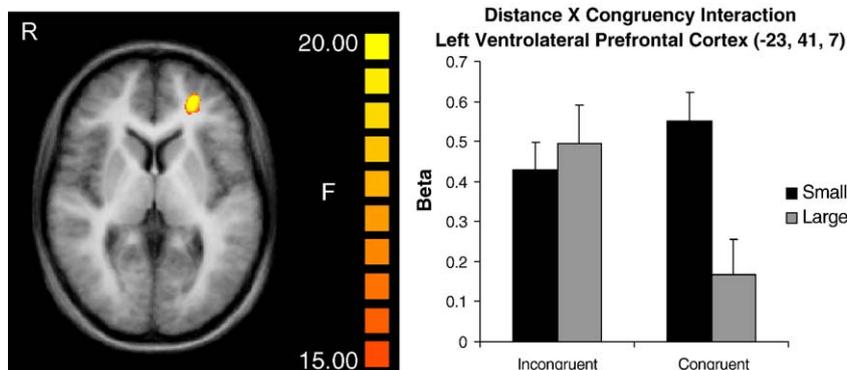


Fig. 4. Axial slice showing Distance \times Congruency interaction effect on left ventrolateral prefrontal cortex. Bar charts depict the z scores (parameter estimates) for small and large distances for both congruent and incongruent conditions. Beta values were obtained from the peak voxel in the regions of interest. Error bars denote the standard error of the mean.

Thus, although the present findings help to disentangle response selection and conflict processing from activation associated with numerical magnitude representation during number comparison, the specificity with which parietal regions encode numerical magnitude remains a hotly contested subject.

Acknowledgments

This work was supported by grants from the Dartmouth College, the Dickey Center for International Understanding, and the Rockefeller Center for the Social Sciences at Dartmouth College. We would like to thank Ian Holloway, Roi Cohen Kadosh, Arishai Henik, Wolf Schwarz, and numerous colleagues for helpful discussion of the results. We would also like to thank Nicolas Garcia for assistance with data analysis and the Dartmouth Brain Imaging Center (DBIC) for technical assistance.

References

- Ansari, D., Dhital, B., Soon, C.S., 2006. Parametric effects of numerical distance on the intraparietal sulcus during passive viewing of rapid numerosity changes. *Brain Res.* 1067, 181–188.
- Besner, D., Coltheart, M., 1979. Ideographic and alphabetic processing in skilled reading of English. *Neuropsychologia* 17 (5), 467–472.
- Botvinick, M., Nystrom, L.E., Fissell, K., Carter, C.S., Cohen, J.D., 1999. Conflict monitoring versus selection-for-action in anterior cingulate cortex. *Nature* 402 (6758), 179–181.
- Botvinick, M.M., Cohen, J.D., Carter, C.S., 2004. Conflict monitoring and anterior cingulate cortex: an update. *Trends Cogn. Sci.* 8 (12), 539–546.
- Boynton, G.M., Engel, S.A., Glover, G.H., Heeger, D.J., 1996. Linear systems analysis of functional magnetic resonance imaging in human V1. *J. Neurosci.* 16 (13), 4207–4221.
- Bush, G., Whalen, P.J., Rosen, B.R., Jenike, M.A., McInerney, S.C., Rauch, S.L., 1998. The counting Stroop: an interference task specialized for functional neuroimaging-validation study with functional MRI. *Hum. Brain Mapp.* 6 (4), 270–282.
- Cohen Kadosh, R., Henik, A., Rubinsten, O., Mohr, H., Dori, H., van de Ven, V., Zorzi, M., Hendlar, T., Goebel, R., Linden, D.E., 2005. Are numbers special? The comparison systems of the human brain investigated by fMRI. *Neuropsychologia* 43 (9), 1238–1248.
- Culham, J.C., Kanwisher, N.G., 2001. Neuroimaging of cognitive functions in human parietal cortex. *Curr. Opin. Neurobiol.* 11 (2), 157–163.
- Dehaene, S., Dupoux, E., Mehler, J., 1990. Is numerical comparison digital? Analogical and symbolic effects in two-digit number comparison. *J. Exp. Psychol. Hum. Percept. Perform* 16 (3), 626–641.
- Dehaene, S., Piazza, M., Pinel, P., Cohen, L., 2003. Three parietal circuits for number processing. *Cogn. Neuropsychol.* 20, 487–506.
- Dehaene, S., Molko, N., Cohen, L., Wilson, A.J., 2004. Arithmetic and the brain. *Curr. Opin. Neurobiol.* 14 (2), 218–224.
- Fias, W., Lammertyn, J., Reynvoet, B., Dupont, P., Orban, G.A., 2003. Parietal representation of symbolic and nonsymbolic magnitude. *J. Cogn. Neurosci.* 15 (1), 47–56.
- Fulbright, R.K., Manson, S.C., Skudlarski, P., Lacadie, C.M., Gore, J.C., 2003. Quantity determination and the distance effect with letters, numbers, and shapes: a functional MR imaging study of number processing. *Am. J. Neuroradiol.* 24 (2), 193–200.
- Girelli, L., Lucangeli, D., Butterworth, B., 2000. The development of automaticity in accessing number magnitude. *J. Exp. Child Psychol.* 76 (2), 104–122.
- Gobel, S.M., Rushworth, M.F., 2004. Cognitive neuroscience: acting on numbers. *Curr. Biol.* 14 (13), 517–519.
- Gobel, S.M., Johansen-Berg, H., Behrens, T., Rushworth, M.F., 2004. Response-selection-related parietal activation during number comparison. *J. Cogn. Neurosci.* 16 (9), 1536–1551.
- Gruber, O., Indefrey, P., Steinmetz, H., Kleinschmidt, A., 2001. Dissociating neural correlates of cognitive components in mental calculation. *Cereb. Cortex* 11 (4), 350–359.
- Henik, A., Tzelgov, J., 1982. Is three greater than 5: the relation between physical and semantic size in comparison tasks. *Mem. Cogn.* 10, 389–395.
- Jiang, Y., Kanwisher, N., 2003. Common neural mechanisms for response selection and perceptual processing. *J. Cogn. Neurosci.* 15 (8), 1095–1110.
- Kaufmann, L., Koppelstaetter, F., Delazer, M., Siedentopf, C., Rhomberg, P., Golaszewski, S., Felber, S., Ischebeck, A., 2005. Neural correlates of distance and congruity effects in a numerical Stroop task: an event-related fMRI study. *NeuroImage* 25 (3), 888–898.
- MacDonald, A.W., Cohen, J.D., Stenger, V.A., Carter, C., 2000. Dissociating the role of the dorsolateral prefrontal and anterior cingulate cortex in cognitive control. *Science* 288 (5472), 1835–1838.
- Moyer, R.S., Landauer, T.K., 1967. Time required for judgements of numerical inequality. *Nature* 215 (109), 1519–1520.
- Pardo, J.V., Pardo, P.J., Janer, K.W., Raichle, M.E., 1990. The anterior cingulate cortex mediates processing selection in the Stroop attentional conflict paradigm. *Proc. Natl. Acad. Sci. U.S.A.* 87 (1), 256–259.
- Piazza, M., Izard, V., Pinel, P., Le Bihan, D., Dehaene, S., 2004. Tuning curves for approximate numerosity in the human intraparietal sulcus. *Neuron* 44 (3), 547–555.
- Pinel, P., Le Clec, H.G., van de Moortele, P.F., Naccache, L., Le Bihan, D., Dehaene, S., 1999. Event-related fMRI analysis of the cerebral circuit for number comparison. *NeuroReport* 10 (7), 1473–1479.
- Pinel, P., Dehaene, S., Riviere, D., LeBihan, D., 2001. Modulation of parietal activation by semantic distance in a number comparison task. *NeuroImage* 14 (5), 1013–1026.
- Pinel, P., Piazza, M., Le Bihan, D., Dehaene, S., 2004. Distributed and overlapping cerebral representations of number, size, and luminance during comparative judgments. *Neuron* 41 (6), 983–993.
- Ridderinkhof, K.R., Ullsperger, M., Crone, E.A., Nieuwenhuis, S., 2004. The role of the medial frontal cortex in cognitive control. *Science* 306 (5695), 443–447.
- Rubinsten, O., Henik, A., Berger, A., Shahar-Shalev, S., 2002. The development of internal representations of magnitude and their association with Arabic numerals. *J. Exp. Child Psychol.* 81 (1), 74–92.
- Rushworth, M.F., Johansen-Berg, H., Gobel, S.M., Devlin, J.T., 2003. The left parietal and premotor cortices: motor attention and selection. *NeuroImage* 20 (Suppl. 1), S89–S100.
- Schwarz, W., Ischebeck, A., 2003. On the relative speed account of number-size interference in comparative judgments of numerals. *J. Exp. Psychol. Hum. Percept. Perform* 29 (3), 507–522.
- Sekuler, R., Mierkiewicz, D., 1977. Children's judgments of numerical inequality. *Child Dev.* 48, 630–633.
- Shuman, M., Kanwisher, N., 2004. Numerical magnitude in the human parietal lobe; tests of representational generality and domain specificity. *Neuron* 44 (3), 557–569.
- Talairach, J., Tournoux, P., 1988. *Co-planar Stereotaxic Atlas of the Human Brain*. Thieme, New York.
- Venkatraman, V., Ansari, D., Chee, M.W., 2005. Neural correlates of symbolic and non-symbolic arithmetic. *Neuropsychologia* 43 (5), 744–753.