Linking visual attention and number processing in the brain: the role of the right temporo-parietal junction in small and large non-symbolic number comparison

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Abstract

There exists a long standing debate regarding whether small and large numerosities engage different networks of processing. The ability to rapidly enumerate small (1-4) numerosities is referred to as 'subitizing' and is thought to be qualitatively different from large numerosity processing. Functional neuroimaging studies have attempted to dissociate neural correlates of small and large number processing by contrasting subitizing with counting of numerosities just outside the subitizing range. In the present study we used functional Magnetic Resonance Imaging (fMRI) to contrast the processing of numerosities in the 'subitizing range' with numerosities requiring estimation. Participants compared sequentially presented slides of either dots or Arabic numerals for their relative magnitude. We show that comparison of non-symbolic numerosities in the subitizing range led to activation of the right temporo-parietal junction, while at the same time this region was found to be suppressed during large numerosity processing. Furthermore, relative suppression of this region was strongly associated with faster response times. In previous studies this region has been implicated in stimulus-driven attention. We therefore contend that activation of the temporo-parietal junction during small number processing and the suppression thereof during large numerosity comparisons reflects differential reliance on stimulus-driven versus goal-directed attentional networks in the brain.

Introduction

There are significant behavioral differences between conditions in which adults and children enumerate small (1-4) versus large numbers of visual items. The ability to rapidly enumerate 1-4 objects has been referred to as 'subitizing' (Kaufman, Lord, Reese, & Volkmann, 1949). An influential theory proposes that subitizing reflects a pre-attentive limited capacity mechanism for the parallel individuation of visual objects (Trick & Pylyshyn, 1994). Therefore this process is thought to be specific to the representation and processing of non-symbolic numerosity. In contrast, the exact enumeration of more than 4 items is supported by counting, which is thought to be a serial process in which attention is shifted from object to object. A third process is represented by estimation, which is the ability to determine the approximate numerosity of arrays of objects that are neither subitizable nor efficiently countable (Dehaene, 1992).

In light of recent evidence that suggests partially dissociated circuits underlie stimulus-driven versus goal-directed visual attention (Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000; Corbetta & Shulman, 2002), we contend that functional neuroimaging presents an opportunity to shed further light on how small and large numerosities may be differentially processed in the human brain; specifically, it is possible that subitizing and large-number estimation differentially engage these attentional networks. Using positron emission tomography (PET) Sathian et al. (1999) found significant differences in activation while participants enumerated different quantities of vertical bars within a display of horizontal bars. While the enumeration of 1-4 vertical bars leads to activation in occipital areas, the enumeration of 5-8 targets lead to the activation of a more extensive network of regions. These findings support the

contention that subitizing and counting are underlain by different neural circuits. While Sathian et al. (1999) found significantly greater activation in different areas for both the subitizing > counting and counting > subitizing contrast, Piazza, Mechelli, Butterworth, & Price (2002), also using PET, failed to find areas exhibiting significantly greater activation for subitizing relative to counting. Similar results were obtained by Piazza et al. (2003) in an event-related fMRI study. Again no areas showed significantly greater activation for the enumeration of 1-3 compared with that of 4-7 dots. Instead, activation in the bilateral posterior parietal cortex and the supplementary/frontal eye fields exhibited significantly greater activation increases for the reverse contrast (counting > subitizing).

Previous studies have sought to isolate regions specifically involved in subitizing by contrasting it with counting. In the present study we take a different approach by contrasting numerical processing of numerosities in the subitizing range with those requiring estimation. Furthermore, we compare small and large number processing of both arrays of dots and Arabic numerals, thereby investigating the degree to which differences between small and large number processing may be stimulus-dependent.

Material and Methods

Participants

13 right-handed participants (mean age: 21 years, 6 months; range 19 years, 10 months - 27 years, 2 months) gave their written consent to participate in the experiment. The experimental procedure and consent form were approved by the Committee for the Protection of Human Subjects at Dartmouth College and all participants signed informed consent

Experimental Tasks

Participants judged which of two sequentially presented arrays of either dots or Arabic numerals was numerically larger. Stimuli were presented sequentially, to ensure that the total number of stimuli per slide presented in the small number condition were within the 'subitizing range' for each slide. Sequential presentation also eliminated the need for participants to saccade back and forth between stimuli when making comparison judgments. Participants were instructed to focus on the fixation cross located at the center of the screen, and press a button in their left hand if the first array was numerically larger, a button in their right hand if the second array was numerically larger, or both buttons simultaneously if the first and the second display were numerically equivalent. Participants were instructed to perform the task as quickly and accurately as they could. Using a standard instruction sheet before the start of the experiment, participants were familiarized with the task. During the acquisition of structural scans and before the acquisition of the functional data, participants practiced all experimental tasks and were given the opportunity to ask clarification questions.

The experimental paradigm consisted of 4 conditions (See Figure 1): (1) Non-symbolic small number comparisons (2) Non-symbolic large-number comparison, (3) Symbolic small-number comparison, (4) Symbolic large-number comparison. To match the numerical ratios of large and small-number comparisons, participants performed relative magnitude judgments with Arabic numerals 1, 2, 3, and 4 (or the equivalent number of dots) in the small conditions and 10, 20, 30, and 40 in the large conditions. Stimuli in all four conditions were presented in 25 second blocks consisting of 8 comparisons each. A block included 6 comparisons in which the numerosity of the first

and second display differed and 2 in which the same numerosity was presented in both displays. Trials in which the numerosity was not varied between the first and second display were included to ensure participants could not infer from the first display whether the second display was necessarily larger or smaller (as would otherwise be the case for 1, 4, 10 and 40). The order of stimulus presentation within a block was randomized for each subject. 4 blocks of each condition were presented (8 trials per block); thus, participants completed 32 trials for each condition. After each block, a 25 second period of rest fixation was included to allow the BOLD signal to return to baseline. Participants were instructed to rest and maintain focus on the central fixation cross during this period.

To control for variables continuous with number in the dot conditions we ensured that for a given trial the two comparison stimuli were equated alone one of three dimensions: individual dot area, overall area and overall perimeter. Therefore in a given block, 2 stimuli were equated for each of the dimensions. Because of the larger number of dots in the large condition the overall area was 10 times larger in the large versus the small condition; however, participants never compared large and small numerosities with one another; therefore, within any given condition, neither individual nor aggregate dot area predicted which of two stimuli in a trial pair represented the larger numerosity. To control for numerical density, average inter-item spacing and overall screen size were held constant across comparisons. The spatial location of dots varied pseudo-randomly between slides. The average spatial distance between items in the first and second display for both small and large dot arrays was equated across conditions to ensure similar demands on eye movements regardless of numerosity. The same was done for symbolic stimuli as well. Distances between first and second stimuli were equated in terms of the

center of gravity of all target items in a display (average location in x-y-coordinates of all dots or the symbolic stimuli in a stimulus array). In this way, central points of stimuli 1 and 2 in a given trial were equated across all conditions and numerosities.

Each run consisted of 2 blocks per condition. Dot and Arabic numeral conditions were presented in separate runs, with 2 runs for each stimulus type resulting in a total of 4 functional runs. In an effort to prevent participants from mapping the non-symbolic stimuli onto Arabic numerals, the non-symbolic runs were always presented first. Because of this fixed order of presentation and the substantial difference in visual characteristics, no analyses directly comparing symbolic and non-symbolic conditions at the whole brain level are presented below.

- FIGURE 1 ABOUT HERE -

Data Acquisition

Functional and structural images were acquired in a 3T Phillips Intera Allegra whole-body MRI scanner (Phillips Medial Systems, The Netherlands) using an 8-Channel Phillips Sense head-coil. A gradient echo-planar imaging $T2^{*}$-sequence sensitive to blood-oxygenation level-dependent (BOLD) contrast was used to acquire functional images. Functional images consisting of 30 noncontiguous slices were acquired in an interleaved order (4mm thickness, 0.5mm gap, 80 X 80 matrix, repetition time (TR): 2500ms, echo time: 35ms, flip angle: 90°, field of view 240 X 240mm) covering the whole brain. For each functional run, 169 volumes were acquired using three-dimensional whole-brain high-resolution T1-weighted images (160) in the sagittal plane (1 x 0.94 x 0.94) with a standard Phillips MPRage 3-D sequence.

Data analysis

Structural and functional images were analyzed using BrainVoyager QX 1.7 (Brain Innovation, Maastricht, Holland). Functional images were corrected for slice-time acquisition differences, head motion, temporal high-pass filtering was applied to remove low-frequency nonlinear drifts of three or fewer cycles per time-course, and linear trend removal. In the spatial domain, data were smoothed with a Gaussian smoothing kernel of 6mm FWHM. Following initial automatic alignment, the alignment of functional images to the high-resolution T1 structural images was manually fine-tuned. The realigned functional data set was then transformed into Talairach space (Tailarach & Tournoux, 1988). The expected BOLD signal was modeled using a two gamma hemodynamic response function (Friston et al., 1998). Baseline levels of activation were estimated by means of 25 second rest/fixation periods between each block of experimental trials. This baseline period was not included as a predictor in the design matrix. Random-effects analysis at the group level was performed using a general linear model (GLM). In all analyses reported, voxels were considered to be significantly activated when they passed false discovery rate correction for multiple comparisons q(FDR) <0.05 (Genovese, Lazar, & Nichols, 2002)

Results

Behavioral Results

Reaction times and accuracy data, separated by condition, can be found in Table 1. The data were analyzed using a 2 (Symbolic/Non-symbolic) X 2 (Small/Large) Analysis of Variance for reaction time and accuracy data separately. In the analyses of the reaction time, data significant main effects of Condition (Symbolic/Non-symbolic) $[F(1,12) = 38.4. p < .0001]$ and Size (small/large) $[F(1,12) = 9.8, p < .009]$ were found. The interaction between Condition and Size was not significant $[F(1,12) = 1.0, p = ns]$. As can be seen from Table 1, participants were significantly faster for symbolic compared with non-symbolic stimuli and in both conditions were faster for small compared with large comparisons. Similarly, for the accuracy data both main effects of Condition $[F(1,12) = 69.9, p < .0001]$ and Size $[F(1,12 = 19.6, p < .001]$ were significant. However, in contrast to the reaction time data, the significant Condition X Size interaction was also revealed to be significant $[F(1, 12) = 8.7, p < .012]$. As inspection of Table 1 suggests, participants were more accurate for symbolic compared with non-symbolic condition as well as more accurate for small compared to large conditions. However, the difference in accuracy between small and large comparisons was significantly greater in the non-symbolic compared with the symbolic number comparison condition.

- TABLE 1 ABOUT HERE -

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fMRI Results

Non-symbolic comparisons

The contrast between small and large non-symbolic number processing revealed greater activation for small compared with large number comparisons in the right temporo-parietal junction (41, -56, 23).Greater activation for the reverse contrast (large > small) was found in the calcarine sulcus (9,-78, 8) and the parieto-occiptal sulcus -(15, -58, 14). A correlation between percent signal change in the right TPJ and reaction time was found for the large dot condition [r(11) = .74, p = .004]. No significant correlation was found between percent signal change in the TPJ and reaction times in the small dot condition [r(11) = .47, p = .106]. No other areas revealed significant differences in this contrast.

In order to isolate networks involved in both small and large non-symbolic number processing, a conjunction analysis of these two conditions was run. This analysis revealed activation in both the left (-40, -37, 46) and right (30, -45, 46) inferior parietal lobule and the left precuneus (-17, -61, 48).

- FIGURE 2 ABOUT HERE –

Symbolic comparisons

The contrasts between the two symbolic conditions did not reveal any significant differences at the selected threshold (q < 0.05, FDR). The conjunction analysis of small and large symbolic number conditions revealed activation in left (-24, -51, 43) and right (25, -51, 46) intraparietal cortex. In addition significant activations for the conjunction analyses of small and large symbolic conditions were found in the right superior frontal gyrus (5, 11, 49), the left (-32, -1, 46) and right (27, 2, 48) middle frontal gyrus, the left

precentral gyrus (-40, 6, 31), the inferior frontal gyrus on the right (44, 10, 28) as well as the claustrum on the right (28, 23, 3).

- FIGURE 3 ABOUT HERE –

Comparison of small and large, symbolic and non-symbolic conditions

The perceptual differences between symbolic and non-symbolic conditions are too large to allow for meaningful whole-brain contrasts to be conducted and these were not the focus of the present investigation. However, to assess the extent to which the difference between small and large non-symbolic conditions in the right TPJ were specific to non-symbolic stimuli, a within ROI ANOVA on the betas extracted from the TPJ was conducted to assess of the main effects and interaction of Format (Symbolic/Non-symbolic) and Size (Small/Large). This analysis revealed a significant effect of size $[F(1,12) = 110.4, p < .0001]$, while the main effect of format was not significant $[F(1,12) = 3.7, p = ns]$. Importantly, a significant interaction between format and size $[F1,12) = 8.2, p < 0.01]$ was found. As can be seen in Figure 2B, this interaction can be explained by the significantly greater difference between large and small non-symbolic conditions (Mean difference in percent signal change: -.38) relative to the difference between large and small symbolic conditions (Mean difference in percent signal change: -.15) in the right TPJ. Since no regions showed a significant difference between small and large symbolic conditions on the whole brain level, no ROI analyses were conducted for this contrast.

Discussion

When participants performed numerosity comparison judgments on sequentially presented displays of non-symbolic numerosities, greater activation for the processing of small compared with large numbers was found in the right posterior temporo-parietal junction (TPJ). The absence of similar effects for the symbolic small and large conditions suggests that this difference is specific to small and large non-symbolic numerosity comparisons. Moreover, activation in the TPJ was suppressed relative to baseline in the large numerosity condition. Furthermore, increased suppression of TPJ activation correlated with faster response times in the large but not small non-symbolic condition.

Numerous behavioral studies suggest differences in the processing of small versus large numerosities in infants, adults and children (Feigenson, Dehaene, & Spelke, 2004; Mandler & Shebo, 1982; Trick & Pylyshyn, 1994; F Xu, 2003; F Xu & Spelke, 2000; F. Xu, Spelke, & Goddard, 2005), though there exists some controversy over whether or not this difference reflects a qualitative difference in processing (Balakrishnan & Ashby, 1991; Gallistel & Gelman, 2000) .

The present study reveals differences in the functional neuroanatomy underlying small and large non-symbolic numerical processing. According to an influential model of the neural basis of visual attention, the right TPJ is involved in an attentional network responsible for stimulus-driven or 'bottom-up' control of attention (Corbetta & Shulman, 2002). Our findings are the first to reveal differential engagement of the TPJ in small and large non-symbolic number processing, thereby linking the literature on the neural basis of small and number processing with models of the neurobiology of visual attention. According to Corbetta and Shulman (2002) a stimulus-driven network involving the TPJ

is contrasted with a more dorsally located goal-driven or 'top-down' network of attention comprised of intraparietal and superior frontal cortex. Consistent with this model, the right TPJ has been found to play a significant role in orienting visual attention to salient, novel or unexpected events, particularly when these events are behaviorally relevant (Fan, McCandliss, Fossella, Flombaum, & Posner, 2005; Kincade, Abrams, Astafiev, Shulman, & Corbetta, 2005). Greater activation in the TPJ has been found during the presentation of targets relative to the presentation of cues. Furthermore, activation in the TPJ responds most when targets occur at unexpected (invalid) locations (Corbetta et al., 2000; Kincade et al., 2005) and is independent of response selection (Astafiev, Shulman, & Corbetta, 2006). Given the sequential presentation of stimuli in the present design and the strong involvement of the TPJ in target detection (Shulman et al., 2003), it is possible that the observed TPJ activity is driven by the appearance of the second array. For small numerosities, it is plausible that objects in the first array are tagged in parallel while the second display acts like a target which is going to guide the relative magnitude judgment.

The TPJ has also been found to respond to changes in the sensory environment, regardless of whether stimulus changes occur in the visual, auditory or somatosensory modalities, suggesting that this region serves to reorient attention to stimuli made salient by their inherent perceptual features (Downar, Crawley, Mikulis, & Davis, 2000, 2002). In light of this body of evidence, it has been proposed the TPJ serves as a "circuit-breaker" for ongoing top-down modulated processing that enables reorientation of visual attention to perceptually novel and/or salient stimuli (Corbetta & Shulman, 2002). Consistent with this, (Marois, Leung, & Gore, 2000) found that the TPJ responds to infrequent ('oddball') changes in object identity, location as well as changes in identity

and location, even when the specific nature of those changes is not given the attentional focus.

Against this background, the present findings of greater TPJ involvement in small relative to large non-symbolic numerosity processing suggest a strong link between stimulus-driven attention and small number processing. Conversely, our findings show relative suppression of this region during large number processing in the non-symbolic task, suggesting that stimulus-driven attentional mechanisms are modulated differentially depending on set size. Moreover the amount of suppression was found to be related to the efficiency of processing large stimuli, as shorter reaction times were associated with suppression or relatively low activation of this area. Consistent with this, visual short term memory (VSTM) has been shown to exhibit a strong capacity limit corresponding to the subitizing range (Marois & Ivanoff, 2005; Todd & Marois, 2004; Y. Xu & Chun, 2006).Furthermore, Todd, Fougnie, & Marois (2005) found that the activation of the TPJ is proportional to set size, even within the range of 1-4 objects. Taken together these findings suggest a key role of the TPJ in supporting the processing of small numbers of objects.

The strong involvement of the right TPJ in small number processing and the suppression thereof in the non-symbolic large-number comparison is consistent with the proposal that subitizing engages different attentional processes relative to large-number processing (Trick & Pylyshyn, 1994). Our findings suggest that during small-number processing, attention is focused on information directly extracted from the stimuli themselves and may therefore be modulated by top-down attention to a lesser degree than is the case for large number processing.

It appears that the TPJ is maximally active during the processing of a very limited number of objects. Thus this region is ideally suited for the processing of small numerosities. However, in the case of large numerosities, attention to individual stimuli is no longer an optimal strategy for making relative numerical judgments, and a different attentional focus needs to be adopted; therefore, strictly stimulus-driven change in the display needs to be ignored in order to map the visual stimulus onto a numerical quantity representation. Hence relative suppression of the TPJ in large numerosity processing may reflect an attentional strategy whereby attention is directed away from individual stimuli and toward the entire array. The finding that individual differences in suppression of the TPJ are related to reaction time supports this hypothesis. In other words the positive correlation between TPJ activation and reaction times in the present study may suggest that suppression of stimulus-driven visuo-attentional networks reflects a more appropriate strategy for the processing of large numerosities. In this context it is important to point out that the present findings do not suggest that the TPJ plays a role in representing small numerosities, or that its involvement in the comparison of small non-symbolic numerosities reflects a number-specific process. Instead, the results suggest that small and large numerosity processing differentially engage a brain region strongly associated with stimulus-driven attention (Corbetta & Shulman, 2002), thereby providing neuroscientific support for the notion that behavioral differences in small and large number processing are strongly related to different mechanisms of visual attention (Trick & Pylyshyn, 1993).

The notion that differential engagement of the TPJ during small and large non-symbolic numerosity comparison reflects differential engagement of stimulus driven

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attentional processes is further supported by the lack of significant differential engagement of small versus large symbolic (Arabic numerals) comparisons within the TPJ. If this region were engaged in the differential representation of small and large number, then a similar pattern should have been found for the non-symbolic and symbolic numerical stimuli. The ROI analyses revealed a significant interaction between Format (Symbolic/Non-symbolic) and Size (Small/Large), showing that a significantly greater difference between small and large conditions for the non-symbolic compared with the symbolic format. Coupled with the absence of significant whole-brain effects of size on this region for the symbolic condition, these results from the whole-brain and less stringent ROI analyses converge to indicate that the effect of size (small vs. large) is significantly greater for the non-symbolic relative to symbolic representations of numerical magnitude.

Furthermore, it does not seem possible that relative suppression of activation in the TPJ during large number processing can be explained by a speed-accuracy trade off. Participants made more errors in the large non-symbolic condition and a significant correlation between reaction time and percent signal change was found in this region, it could be argued that the TPJ is associated with a speed-accuracy trade off whereby fast, erroneous responses lead to greater suppression of this regions, rather than reflecting something special about the way in which small numerosities are processed. However, no significant correlation between speed and accuracy in the large non-symbolic condition was found, indicating that there was no systematic relationship between speed and accuracy and thereby excluding the possibility of this potential confound.

From the behavioral data, it is clear that the large non-symbolic condition was significantly more difficult than the small condition. It could therefore be argued that the activation differences observed between these two conditions in the TPJ reflect difficulty rather than differences related to numerical processing per se. This is unlikely for a number of reasons. A brain region that is significantly modulated by task difficulty across conditions should be significantly correlated with response latencies in all conditions. In other words, if this region exhibited a task-independent difficulty gradient, then we should have found a significant correlation between reaction time and percent signal change in the TPJ for both small and large conditions. However, in the present study, BOLD signal change in the TPJ was found to be related to response latencies only in the large but not the small non-symbolic numerosity comparison condition. Furthermore, in a recent study it was demonstrated that activation of the TPJ in visuo-spatial reorienting is independent of response selection (Astafiev et al., 2006).

The present data are the first to reveal a strong relationship between the TPJ and small number processing. Previous studies comparing subitizing with counting of numerosities just outside the subitizing range either found greater activation for small numerosities in more posterior occipital regions (Sathian et al., 1999), or revealed greater activation in the counting range relative to subitizing in the posterior parietal and frontal regions and were unable to find areas exhibiting greater activation in subitizing relative to counting (Piazza, Giacomini, Le Bihan, & Dehaene, 2003; Piazza et al., 2002). Unlike these studies, the present study compared small number processing with processing of large numbers that are far in excess of any reasonable upper boundary for subitizing that were presented for durations to short to allow for counting. Hence, previous studies may

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have failed to find differences in the TPJ between counting and subitizing because the stimulus-driven processing of numerosities in the subitizing range with those just outside it may not have been sufficiently different in terms of their activation of stimulus-driven versus top-down attentional mechanisms.

We found greater activation in the reverse contrast (large >small) in occipital regions of the calcarine sulcus and its extension into the parieto-occipital sulcus. Against the background of a large body of neuroimaging studies showing that variables related to stimulus size (such as eccentricity and visual angle) parametrically modulate these visual areas (Smith, Singh, Williams, & Greenlee, 2001; Wandell, Brewer, & Dougherty, 2005), this activation can be explained by the greater average stimulus area (see methods) occupied by stimuli in the large condition. Furthermore, in a recent study Ansari, Dhital, & Siong (2006) found that increasing areas of non-symbolic numerosities parametrically modulated a region in the calcarine sulcus close to that found to exhibit greater modulation in the large compared to the small non-symbolic number condition here. The absence of activations in the TPJ for this contrast, suggests that differences between small and large-number processing in the TPJ are independent of differences in stimulus area, and are instead related to the difference in numerical set size between conditions. Hence the present results cannot be attributed to stimulus variables continuous with numerical magnitude.

The results from the conjunction analyses for small and large number processing (See Figure 3) in both the symbolic and non-symbolic conditions strongly implicate bilateral regions of the intraparietal sulcus.

As can be seen from the bar charts in Figure 3, Panels A and B, the amount of activation in these regions did not differ significantly for small and large number processing in both the symbolic and non-symbolic conditions. Moreover the overlap between regions involved in symbolic and non-symbolic processing are consistent with the notion that the IPS represents numerical quantity in a stimulus-independent format (Dehaene, Molko, Cohen, & Wilson, 2004; Fias, Lammertyn, Reynvoet, Dupont, & Orban, 2003; Venkatraman, Ansari, & Chee, 2005). Interestingly, more voxels passed the false discovery rate (FDR) correction in the conjunction analyses of the small and large symbolic conditions compared with the non-symbolic conditions. However, it should be pointed out that the t threshold for the non-symbolic condition at which voxels passed the FDR correction was much higher than for the symbolic conditions, thus making it difficult to discuss differences in extent of activation between the conditions. Furthermore, as can been seen from Panel C in Figure 3, the activations corresponding to the conjunction of small and large non-symbolic conditions were found to be located in the peak region of the IPS activation for the conjunction of small and large symbolic stimuli.

These data strengthen the contention that the observed activation differences in the TPJ between non-symbolic small and large-number processing are likely to be the result of attentional mechanisms rather than processes specific to number. However, the present paradigm only allows for a contrast between large and small numerosity comparison tasks rather than small and large enumeration processes. It is possible that in a paradigm that is focused on pure enumeration rather than comparison, greater differences related to representation may emerge. Recent evidence suggests that even in the absence of an

explicit task, intraparietal regions habituate to large, non-symbolic numerosities (Cantlon, Brannon, Carter, & Pelphrey, 2006; Piazza, Izard, Pinel, Le Bihan, & Dehaene, 2004). The habituation method may be ideally suited to explore differences between small and large numerosities representations in the parietal lobe. Notwithstanding, comparison was common to both small and large conditions in the present study and thus the differences observed were likely driven by differences in the set sizes of to-be-compared non-symbolic numerosities.

In conclusion, the present data reveal a strong difference between non-symbolic small and large number processing in the right temporo-parietal junction, which likely reflects greater reliance for small than large number comparison on stimulus-driven attentional mechanisms in the brain. In light of these data, future research in number processing should be more strongly related to neurobiological models of visual attention.

References

Ansari, D., Dhital, B., & Siong, S. C. (2006). Parametric effects of numerical distance on the intraparietal sulcus during passive viewing of rapid numerosity changes. *Brain Res, 1067*(1), 181-188.

Astafiev, S. V., Shulman, G. L., & Corbetta, M. (2006). Visuospatial reorienting signals in the human temporo-parietal junction are independent of response selection. *Eur J Neurosci, 23*(2), 591-596.

Balakrishnan, J. D., & Ashby, F. G. (1991). Is subitizing a unique numerical ability? *Percept Psychophys, 50*(6), 555-564.

Cantlon, J. F., Brannon, E. M., Carter, E. J., & Pelphrey, K. A. (2006). Functional imaging of numerical processing in adults and 4-y-old children. *PLoS Biol, 4*(5), e125.

Corbetta, M., Kincade, J. M., Ollinger, J. M., McAvoy, M. P., & Shulman, G. L. (2000). Voluntary orienting is dissociated from target detection in human posterior parietal cortex. *Nat Neurosci, 3*(3), 292-297.

Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nat Rev Neurosci, 3*(3), 201-215.

Dehaene, S. (1992). Varieties of numerical abilities. *Cognition, 44*(1-2), 1-42.

Dehaene, S., Molko, N., Cohen, L., & Wilson, A. J. (2004). Arithmetic and the brain. *Curr Opin Neurobiol, 14*(2), 218-224.

Downar, J., Crawley, A. P., Mikulis, D. J., & Davis, K. D. (2000). A multimodal cortical network for the detection of changes in the sensory environment. *Nat Neurosci, 3*(3), 277-283.

Downar, J., Crawley, A. P., Mikulis, D. J., & Davis, K. D. (2002). A cortical network sensitive to stimulus salience in a neutral behavioral context across multiple sensory modalities. *J Neurophysiol, 87*(1), 615-620.

Fan, J., McCandliss, B. D., Fossella, J., Flombaum, J. I., & Posner, M. I. (2005). The activation of attentional networks. *Neuroimage, 26*(2), 471-479.

Feigenson, L., Dehaene, S., & Spelke, E. (2004). Core systems of number. *Trends Cogn Sci, 8*(7), 307-314.

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.

Friston, K. J., Fletcher, P., Josephs, O., Holmes, A., Rugg, M. D., & Turner, R. (1998). Event-related fMRI: characterizing differential responses. *Neuroimage, 7*(1), 30-40.

Gallistel, C. R., & Gelman, I. I. (2000). Non-verbal numerical cognition: from reals to integers. *Trends Cogn Sci, 4*(2), 59-65.

Genovese, C. R., Lazar, N. A., & Nichols, T. (2002). Thresholding of statistical maps in functional neuroimaging using the false discovery rate. *Neuroimage, 15*(4), 870-878.

Kaufman, E. L., Lord, M. W., Reese, T. W., & Volkmann, J. (1949). The discrimination of visual number. *American Jounrnal of Psychology, 62*, 498-535.

Kincade, J. M., Abrams, R. A., Astafiev, S. V., Shulman, G. L., & Corbetta, M. (2005). An event-related functional magnetic resonance imaging study of voluntary and stimulus-driven orienting of attention. *J Neurosci, 25*(18), 4593-4604.

Mandler, G., & Shebo, B. J. (1982). Subitizing: an analysis of its component processes. *J Exp Psychol Gen, 111*(1), 1-22.

Marois, R., & Ivanoff, J. (2005). Capacity limits of information processing in the brain. *Trends Cogn Sci, 9*(6), 296-305.

Marois, R., Leung, H. C., & Gore, J. C. (2000). A stimulus-driven approach to object identity and location processing in the human brain. *Neuron, 25*(3), 717-728.

Piazza, M., Giacomini, E., Le Bihan, D., & Dehaene, S. (2003). Single-trial classification of parallel pre-attentive and serial attentive processes using functional magnetic resonance imaging. *Proc Biol Sci, 270*(1521), 1237-1245.

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.

Piazza, M., Mechelli, A., Butterworth, B., & Price, C. J. (2002). Are subitizing and counting implemented as separate or functionally overlapping processes? *Neuroimage, 15*(2), 435-446.

Sathian, K., Simon, T. J., Peterson, S., Patel, G. A., Hoffman, J. M., & Grafton, S. T. (1999). Neural evidence linking visual object enumeration and attention. *J Cogn Neurosci, 11*(1), 36-51.

Shulman, G. L., McAvoy, M. P., Cowan, M. C., Astafiev, S. V., Tansy, A. P., d'Avossa, G., et al. (2003). Quantitative analysis of attention and detection signals during visual search. *J Neurophysiol, 90*(5), 3384-3397.

Smith, A. T., Singh, K. D., Williams, A. L., & Greenlee, M. W. (2001). Estimating receptive field size from fMRI data in human striate and extrastriate visual cortex. *Cereb Cortex, 11*(12), 1182-1190.

Tailarach, J., & Tournoux, P. (1988). *Co-Planar Stereotaxic Atlas of the Human Brain* New York Thieme Medical Publishers, Inc. .

Todd, J. J., Fougnie, D., & Marois, R. (2005). Visual short-term memory load suppresses temporo-parietal junction activity and induces inattentional blindness. *Psychol Sci, 16*(12), 965-972.

Todd, J. J., & Marois, R. (2004). Capacity limit of visual short-term memory in human posterior parietal cortex. *Nature, 428*(6984), 751-754.

Trick, L. M., & Pylyshyn, Z. W. (1993). What enumeration studies can show us about spatial attention: evidence for limited capacity preattentive processing. *J Exp Psychol Hum Percept Perform, 19*(2), 331-351.

Trick, L. M., & Pylyshyn, Z. W. (1994). Why are small and large numbers enumerated differently? A limited-capacity preattentive stage in vision. *Psychol Rev, 101*(1), 80-102.

Venkatraman, V., Ansari, D., & Chee, M. W. (2005). Neural correlates of symbolic and non-symbolic arithmetic. *Neuropsychologia, 43*(5), 744-753.

Wandell, B. A., Brewer, A. A., & Dougherty, R. F. (2005). Visual field map clusters in human cortex. *Philos Trans R Soc Lond B Biol Sci, 360*(1456), 693-707.

Xu, F. (2003). Numerosity discrimination in infants: evidence for two systems of representations. *Cognition, 89*(1), B15-25.

Xu, F., & Spelke, E. S. (2000). Large number discrimination in 6-month-old infants. *Cognition, 74*(1), B1-B11.

Xu, F., Spelke, E. S., & Goddard, S. (2005). Number sense in human infants. *Dev Sci, 8*(1), 88-101.

Xu, Y., & Chun, M. M. (2006). Dissociable neural mechanisms supporting visual short-term memory for objects. *Nature, 440*(7080), 91-95.

Figure Captions

Figure 1

Example of experimental stimuli and stimulus presentation times for small (A) and large (B) non-symbolic conditions, respectively. The location of stimuli varied from slide to slide. Small and large symbolic conditions have the same stimulus timing, and Arabic numerals were shown in the same locations as the dot stimuli.

Figure 2

(A) Activation map of the small > large contrast for the non-symbolic conditions. (B) Percent signal change for small and large non-symbolic and symbolic conditions in the right TPJ (41, -56, 23). (c) Scatterplot of correlation between percent signal change the activation of the right TPJ for the small > large contrast and reaction times in the large condition.

Figure 3

(A) Axial slice showing results of the conjunction of small and large symbolic conditions. Bar charts depict percent signal change in the left and right intraparietal sulcus (IPS)_for the small and large conditions. (B) Map showing activation of the left (-40, 37,46) and right IPS conjunction of small and large non-symbolic conditions. Bar chars show percent signal change in right and left intraparietal regions for both conditions. (C) Axial slice showing overlay of activation of both conjunction analyses with light colors

showing conjunction of small and large symbolic conditions and dark colors representing the conjunction of small and large non-symbolic conditions.

Table Captions

Table 1

Mean reaction times in milliseconds (ms) and accuracy (% correct) for all four conditions (numbers in parentheses denote standard deviations).
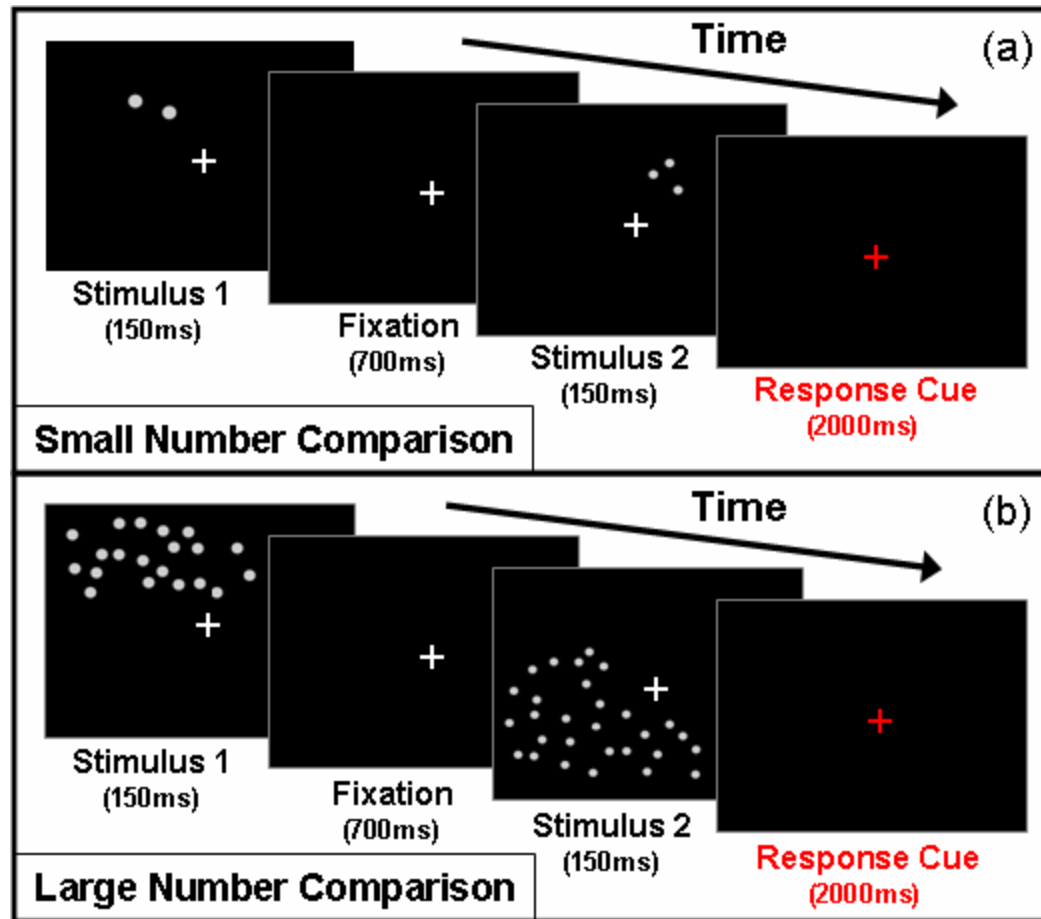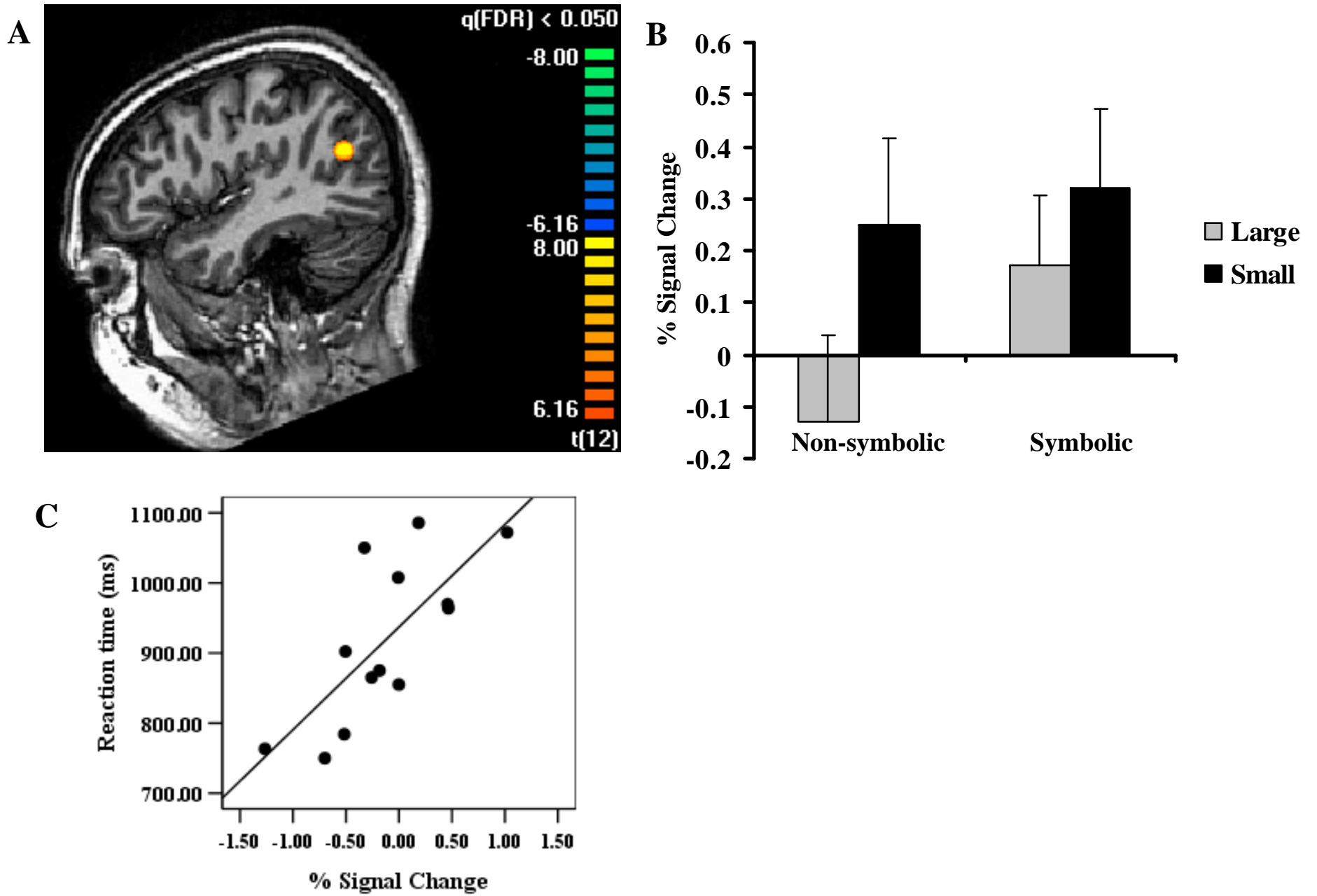
(a) Time

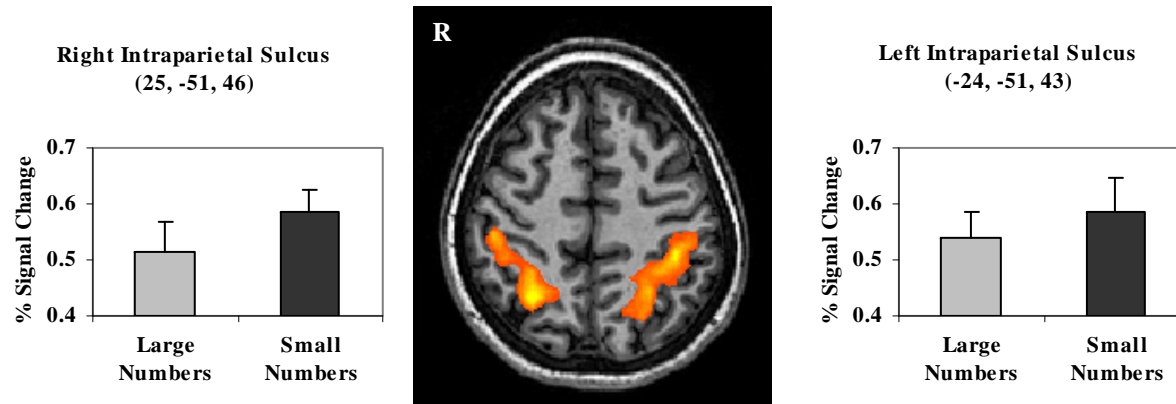Stimulus 1
(150ms)

Fixation
(700ms)

Stimulus 2
(150ms)

Response Cue
(2000ms)

Small Number Comparison

(b) Time

Stimulus 1
(150ms)

Fixation
(700ms)

Stimulus 2
(150ms)

Response Cue
(2000ms)

Large Number Comparison

Figure 1

Figure 2

A

Conjunction of symbolic small and large conditions

Right Intraparietal Sulcus
(25, -51, 46)

Left Intraparietal Sulcus
(-24, -51, 43)

B

Conjunction of non-symbolic small and large conditions

Right Intraparietal Sulcus
(30, -45, 46)

Left Intraparietal Sulcus
(-40, -37, 46)
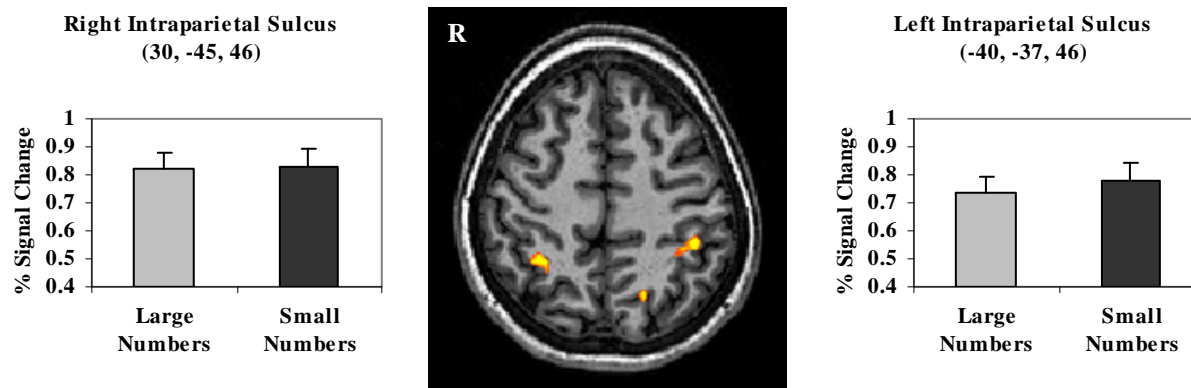
C

Overlay of symbolic and non-symbolic conjunction analyses
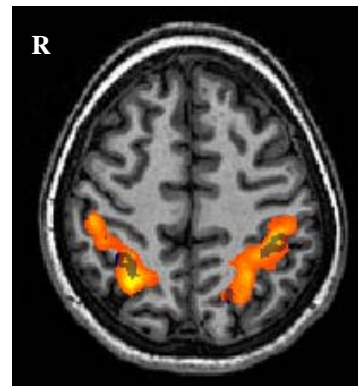
Figure 3

Table 1 Summary of Means for Behavioral Data

Condition	RT (ms) Mean (STD)	Accuracy (% correct) Mean (STD)
Small Number Dots	867.1 (108.2)	92.8 (5.6)
Large Number Dots	918.8 (115.9)	82.9 (6.2)
Small Number Symbols	774.3 (123.6)	97.4 (3.8)
Large Number Symbols	808.8 (118.1)	96.4 (4.9)

Table 1