The Neuroanatomy of Visual Enumeration: Differentiating Necessary Neural Correlates for Subitizing versus Counting in a Neuropsychological Voxel-based Morphometry Study

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Abstract

■ This study is the first to assess lesion–symptom relations for subitizing and counting impairments in a large sample of neuropsychological patients (41 patients) using an observer-independent voxel-based approach. We tested for differential effects of enumerating small versus large numbers of items while controlling for hemianopia and visual attention deficits. Overall impairments in the enumeration of any numbers (small or large) were associated with an extended network, including bilateral occipital and fronto-parietal regions. Within this network, severe impairments in accuracy when enumerating small sets of items (in the subitizing range) were associated with damage to the left posterior occipital cortex, bilateral lateral occipital and right superior frontal cortices. Lesions to the right calcarine extending to the precuneus led to patients serially counting even small numbers of items (indicated by a steep response slope), again demonstrating an impaired subitizing ability. In contrast, impairments in counting large numerosities were associated with damage to the left intraparietal sulcus. The data support the argument for some distinctive processes and neural areas necessary to support subitization and counting with subitizing relying on processes of posterior occipital cortex and with counting associated with processing in the parietal cortex. ■

INTRODUCTION

It has long been established that our ability to enumerate visually presented stimuli varies with the number of items present. Subitizing (a term first coined by Kaufman, Lord, Reese, & Volkmann, 1949) relates to the rapid and efficient enumeration of small numbers of elements (1–4). There are only small increases in RT across the number range (50–80 msec; e.g., Mandler & Shebo, 1982). This ability to enumerate a small collection of items at a glance is found in all known human cultures (Butterworth, 1999), across wide age ranges (including infants; e.g., Antell & Keating, 1983) and even in nonhuman animals (e.g., Hauser, MacNeilage, & Ware, 1996). In contrast, when counting the number of items beyond four, there are substantial increases in RTs (about 200 msec per extra item to be counted) when participants are given unlimited viewing times. When all stimuli are presented for a short duration, errors for more than four items increase linearly as a function of the number of stimuli present (Trick & Pylyshyn, 1993; Mandler & Shebo, 1982). Thus, differences between enumerating small versus large numbers are observed both in estimation (when stimuli are presented briefly) and counting (when presentation durations allow serial counting to take place). Counting larger numbers can be considered a more complex process than subitizing and will call on additional component operations such as individuating and localizing the items, switching attention from item to item, summing the number of items, maintaining a running total, and inhibiting the "recounting" of already counted items (inhibition of return; e.g., Klein, 2000) and is culture-bound (Butterworth, 1999).

However, there remains considerable debate about whether this contrast between efficient enumeration of small numbers and relatively inefficient enumeration of larger numbers is subserved by separable processes. The single-process hypothesis argues that there is no qualitative difference between the enumeration of small and larger numbers and that subitizing is, thus, just fast serial counting (Gallistel & Gelman, 1992), unencumbered by the working memory load (Balakrishnan & Ashby, 1991; Vanoeffelen & Vos, 1982). Consistent with this single-process model of visual enumeration, Ross (2003) suggested that subitizing is merely a consequence of the resolution of estimation mechanisms. He states that the resolution of the visual system needs a just noticeable difference of 25%—because differences in the subitizing range are greater than this performance is efficient for numbers in the subitizing range.

In contrast, other authors have supported dual-process accounts of subitizing and counting—albeit of different varieties. The pattern-matching account suggests that small

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numbers are rapidly enumerated, because they are recognized as distinct patterns (a triangle, a square, and so forth), whereas larger numbers must be counted serially. Consistent with the contribution of pattern recognition, Mandler and Shebo (1982) showed that rapid enumeration could be extended up to seven or eight items if the patterns were familiar (Palmeri, 1997; Lassaline & Logan, 1993; Wolters, Vankempen, & Wijlhuizen, 1987). In addition, Logan and Zbrodoff (2003) demonstrated that participants rate different patterns of the same numerosity as more similar within the subitizing range (<4 items) than outside it (>5 items). This increase in similarity supports the pattern recognition hypothesis for small number enumeration. A second dual-process account is that subitizing is a process distinct from both pattern recognition and serial visual counting and is instead reliant on the parallel, independent processing of up to four items. The FINST (Fingers of Instantiation) model (Trick & Pylyshyn, 1993, 1994; Julesz, 1984) suggests that there can be parallel indexing of a limited set of locations, which enable us to keep track of a limited number of objects in the world (up to 4). This parallel indexing of a small number of items leads to fast subitizing. The limitation on the number of FINSTs available (about 4) means that larger numbers require a separate counting process. The serial counting slope, found when larger numbers of items have to be enumerated, may reflect the serial reassignment of FINSTs to the locations of the additional items and/or contributions from serial counting of extra individual items (Trick & Pylyshyn, 1993, 1994; Julesz, 1984). A similar limitation of four items is proposed for the number of stimuli that can be held in parallel in working memory (Zhang & Luck, 2008). Some neuropsychological support for this parallel processing comes from patients with neglect who are able to subitize elements, yet cannot explicitly localize or serially select them (Vuilleumier & Rafal, 1999).

One way to assess whether subitizing and counting depend on functionally distinct processes is to evaluate if enumeration performance with small and large number displays links to distinct neural regions. However, the findings on this are inconclusive. To date, few imaging studies have directly compared subitizing and counting in a visual enumeration task. Sathian and colleagues (1999) conducted a PET study in which observers had to enumerate the number of vertical bars in a grid containing horizontal distractor bars. A comparison was made between the counting of multiple targets, the subitizing of up to four targets, and RTs to single pop-out targets. They found that there was activation of bilateral occipital extrastriate cortex under subitization conditions (most notably the right middle occipital gyrus) relative to when a single target was detected. Counting larger numbers (5–8 items) led to activation of the same areas (bilateral occipital extrastriate cortex) as well as additional parietal and frontal regions (bilateral superior parietal lobe/intraparietal sulcus [IPS], right inferior frontal regions, and anterior cingulate). Piazza, Mechelli, Butterworth, and Price (2002) used PET to measure brain activity when counting dot patterns. Similar to Sathian et al. (1999), they did not observe any areas where activation for enumerating small numbers was greater than for counting larger numbers. For the opposite contrast (counting > subitizing), they found enhanced activation in bilateral middle/inferior occipital extrastriate cortex as well as in the left posterior IPS and right cerebellum. Because all the areas active in subitizing were also activated in counting, the authors suggest that subitizing and counting are not functionally separate processes. In a similar experiment, this time with fMRI, Piazza, Giacomini, Le Bihan, and Dehaene (2003) again found no greater activation for subitizing than counting, along with a network of occipital (calcarine, middle occipital), parietal (anterior and posterior IPS), insular, prefrontal, and subcortical areas more active in counting than subitizing. However, they also demonstrated that, although many of their critical regions showed linear increases in activity as the number of items increased from four to six items, no region showed increased activation from one to three elements. This is consistent with subitizing depending on the parallel apprehension of items while counting requires serial assimilation.

Contrasting results were reported by Ansari, Lyons, van Eitneren, and Xu (2007) in a task requiring comparison/estimation rather than exact enumeration. They found that the comparison of small numerosities (in the subitizing range) led to activation of the right TPJ, and this contrasted with the data for the estimation of larger numbers where activation in this region was suppressed. Ansari et al. also found greater activation for large than small numerosities in the calcarine and the parieto-occipital sulcus. Similarly, Spolaore, Vetter, Butterworth, Bahrami, and Rees (2008), in a dual task paradigm, found an attentionally modulated response in the right TPJ, specific to small set sizes (in the subitizing range), which did not occur at larger set sizes (see also Vetter, Butterworth, & Bahrami, 2011).

To evaluate the necessity of different brain regions in enumeration, data on the impact of changing brain activity are required—for example, by assessing subitization and counting performance when the regions are lesioned. Here, we asked whether dissociations between subitization and counting are linked to damage to distinct brain areas.

There is a long history of case reports of enumeration difficulties in brain-lesioned patients (e.g., Cipolotti, Butterworth, & Denes, 1991; Seron et al., 1991; Warrington & James, 1967; Mcfie, Piercy, & Zangwill, 1950; Holmes, 1918); however, there has been surprisingly little neuropsychological research published on explicit distinctions between subitizing and counting, and the majority of cases present single dissociations (i.e., patients who can subitize but not count). Dehaene and Cohen (1994) required five simultanagnosic patients to enumerate displays of one to six items. All five demonstrated accurate performance on smaller numerosities (up to 3), whereas their counting of larger numbers (4–6) was severely impaired. Dehaene and Cohen proposed that the patients had a problem in keeping track of previously visited spatial locations. However, good subitizing accuracy can be achieved by using a serial counting strategy (even when parallel subitization processes are impaired), thus examining RTs as well as accuracy is crucial. Indeed, other authors have described neuropsychological cases where, despite good accuracy rates, RTs are disrupted in the subitization range (Ashkenazi, Henik, Ifergane, & Shelef, 2008; Halpern, Clark, Moore, Cross, & Grossman, 2007; Lemer, Dehaene, Spelke, & Cohen, 2003). Such data suggest that the patients adopted a "counting" strategy in the subitizing range, and succeeded in accuracy because of the low memory load. However, it should be noted that counting RTs for larger numbers were also impaired for these patients. We have also previously reported studies in a patient with bilateral parietal lesions and Balint's syndrome who demonstrated a severe impairment in both subitizing and counting (significant numbers of errors on displays of even one or two elements), despite an intact ability to provide coarse estimations of the number of items in displays (Demeyere & Humphreys, 2007). None of the above evidence provides a strong case to argue that subitizing and counting are functionally distinct.

However, we have recently reported a single case, MH, who presented with apparently normal subitizing along with impaired counting (Demeyere, Lestou, & Humphreys, 2010). MH was able to subitize accurately and showed a normal RT slope on his subitization function, but he demonstrated a marked inability to count larger numbers. This suggests that at least some processes are specific to counting and are not required for subitization.

To date, all the neuropsychological evidence for distinct subitization and counting processes has emphasized behavioral differences between small groups of patients, often single cases of preselected individuals. There is a paucity of data on the underlying neural correlates of any impairment in enumeration. The present article provides a first lesion-based analysis of the relations between the different aspects of enumeration in a larger group of patients where the range of performance on visual enumeration is related to a continuous measure of neural integrity. We examined subitization and counting across brain lesioned patients with chronic deficits, correlating behavioral deficits with data from whole-brain analyses of high-resolution MRI scans (similar to the method used in Chechlacz et al., 2010; Acres, Taylor, Moss, Stamatakis, & Tyler, 2009; Tyler & Stamatakis, 2005). We assessed both accuracy measures and RT slopes, enabling us to include both patients with severe difficulties in terms of response accuracy (cf. Dehaene & Cohen, 1994) and those with deficits reflected in slowed RTs rather than accuracy (cf. Ashkenazi et al., 2008; Halpern et al., 2007; Lemer et al., 2003).

By assessing behavior within both the subitizing and counting range in our patients, we aimed to identify the underlying brain regions necessary for these two aspects of enumeration. We deliberately focused on exact enumeration ability, which can be achieved either by counting the items one by one or by subitizing them. For that purpose, the stimuli were presented for an unlimited duration until a response was made. By requiring exact enumeration, as opposed to estimation, we ensured that our task instructions were not confounded with the number of items in the display. We hypothesize that, because subitizing and counting may involve some common processes (e.g., access to number representations and perhaps sometimes when subitization processes are recruited during counting), we will find some overlap in brain areas involved in both behaviors (when associating continuous performance scores to changes in gray and white matter). In line with fMRI findings, we would expect common regions with a network of areas including occipital, parietal, and frontal cortices. However, we also believe that subitization and counting can be dissociated. If subitizing reflects an early parallel visual process, we would expect to find damage to early occipital regions to be selectively linked to poor subitizing performance (even when controlling for visual field deficits), especially if these regions are required more when enumerating exact small numbers than when counting exact large numbers of items. In contrast, we expect a series of higher order regions to be associated with impairments specific to counting larger numbers of items. Because of the complex nature of counting (with aspects of working memory, keeping track of items and locations, etc.), specific regions are harder to predict but could involve parietal areas, including the IPS (the traditional "number area"), but also regions such as the angular gyrus (linked with acquired dyscalculia), the pFC (working memory), and the FEFs (shifting attention). If some distinct areas are found to be involved in subitizing relative to counting, this would be strong evidence that subitizing is a special process that is qualitatively different from serial counting.

METHODS

Participants

All the patients were recruited from the long-term panel of neuropsychological volunteers established by the Behavioral Brain Sciences Group and the Birmingham University Cognitive Screen (www.bucs.bham.ac.uk) at the School of Psychology, University of Birmingham. The only inclusion criteria when recruiting participants were that (a) the patients had acquired brain damage (predominantly stroke) and were not at an acute stage (>12 months post injury) and (b) each patient had a T1-weighted 3T MRI scan. Forty-one brain injury patients agreed to participate (31 men and 10 women). The ages of the patients ranged from 36 to 86 years (mean age = 64 years, *SD* = 11.5 years). In addition, for comparison, to establish the range of performance in a healthy population, eight (one woman, average age = 65 years, *SD* = 6.2 years) age-matched control participants were also included in the study. We included only a relatively small number of healthy controls as the brain lesion analyses were based on comparisons within the patient group. Thirty-four of the patients suffered from stroke, two from anoxia, two from encephalitis, one from cortical degeneration, one from cerebral vascular problem, and one from corticobasal degeneration. All patients' lesions were clearly visible on the T1 MRI scan.

The behavioral data for controls are included for descriptive purposes to categorize whether our patients had impairments for different parts of the counting function and to provide a frame of reference to previous studies.

Each participant provided informed consent according to the procedures in agreement with ethics protocols at the School of Psychology and Birmingham University Imaging Center.

Behavioral Assessment: Visual Enumeration

The experiment was programmed and run using E-Prime 1.1 software (Psychology Software Tools, Sharpsburg, PA). The displays were presented on a black background on a 17-in. monitor with 1024 × 768 pixel screen resolution. Each participant was positioned approximately 65 cm from the screen. The stimuli consisted of one to nine gray dots (red, green, blue: 190, 190, 190), which were drawn randomly within the center 500 × 500 pixels of the screen (visual angle = 14.4°). The dots had a diameter of 25 pixels (visual angle = 1.4°), and any two dots were separated from each other by a minimum distance of one dot diameter.

One trial started with the presentation of a fixation cross in the center of the screen for 1000 msec. Next, the enumeration display appeared and remained on the screen until a response was made. Participants were instructed to enumerate the dots in this display as accurately and quickly as possible. As soon as they felt they knew the correct response, they had to press the space bar and simultaneously articulate their response. When the spacebar was hit, the dot display disappeared and was followed by a blank screen, where the experimenter entered the reported number using the numeric keypad (for a similar method and for a validation of the procedure, see, e.g., Watson & Humphreys, 1999; Atkinson, Campbell, & Francis, 1976). Accuracy and RTs were recorded.

All participants completed six blocks, with each block containing 45 randomly ordered trials (5 per numerosity). This resulted in 30 trials per numerosity (1–9).

Behavioral Data Analysis

There is currently no consensus whether displays with four items should be included in the subitizing range or not and for older people a limit of three has been reported (Watson, Maylor, & Bruce, 2005). In addition, in a previous single-case study, patient MH (Demeyere et al., 2010), who could not accurately count over four items, was found to have intact subitizing accuracy up to four, but RT slopes showed only intact subitizing up to three items. Thus, to ensure that we measure subitizing in all participants (across the age range), we set the limit to three items. Measures of counting performance were based on the enumeration of six,seven, and eight dots, leaving out the nine-dot display as this was the maximum value presented and can show end-effects (see also Trick & Pylyshyn, 1993).[1]

For each patient, we computed an overall accuracy score (1–8) and separate scores for the subitizing range (1–3) and for the counting range (6–8). However, given that subitizing is defined as the ability to rapidly and efficiently enumerate small numbers, typically associated with near-flat RT slopes, we next computed for each patient the RT slope (average step size) separately for the counting (i.e., 6–7–8) and the subitizing (i.e., 1–2–3) range. RT slopes were computed only on correct responses. To ensure the reliability of this measure for the subitizing range, we excluded patients who had low subitizing accuracy (<85%). In addition, we assumed that reliable RT slopes are positive, that is, there should be longer response durations for any additional items. Therefore, RT slopes were computed only based on intervals where patients showed a positive slope. A small number of cases showed selectively slow RTs to one-item displays, hence a negative slope in the subitizing range ($n = 6$). This typically co-occurred with a large slope once data for Display Size 1 were omitted. We suggest that the Display 1 data for such cases were anomalous and reflected an aberrant strategy where patients continued searching for items. In this minority of cases, we discounted data for the item Display Size 1 and computed the RT slope based on numerosities of 2 and 3.

Additional Behavioral Measures

We obtained measures of attentional deficits using data taken from the Birmingham cognitive screen (BCoS; www.bcos.bham.ac.uk). For neglect, this entailed the Apple Cancellation Task (Bickerton, Samson, Williamson, & Humphreys, 2011; Chechlacz et al., 2010), which is similar to the gap detection task of Ota, Fujii, Suzuki, Fukatsu, and Yamadori (2001) and is designed to simultaneously measure egocentric and allocentric neglect. Patients were then classed as either impaired or nonimpaired based on age-category-specific cutoffs. Extinction was measured by assessing whether the patient could detect bilateral finger movements of the experimenter sat opposite the patient as well as unilateral finger movements (www.bcos.bham.ac.uk; Chechlacz et al., 2010). Again, patients were classed as impaired or nonimpaired based on control cutoff scores. Any impairment detected in either extinction or neglect led to the patient being coded as having an attentional deficit. Finally, a measure of the presence of any visual field deficits (e.g., hemianopia) was taken from the patients' clinical records.

Voxel-based Correlation Analyses

Patients were scanned at Birmingham University Imaging Center on a 3T Philips Achieva MRI system with eight-channel phased array SENSE head coil. A standard anatomical scan was acquired using a sagittal T1-weighted sequence (sagittal orientation, echo time/repetition time = 3.8/8.4 msec, voxel size = 1 × 1 × 1 mm, scanning time = ~5 min).

Image Preprocessing

T1 scans from patients were converted using MRICron (Chris Rorden, Georgia Tech, Atlanta, GA). Preprocessing was done in SPM5 (Statistical Parametric Mapping, Welcome Department of Cognitive Neurology, London, United Kingdom). The brain scans were transformed into the standard Montreal Neurological Institute (MNI) space using a modification (Seghier, Ramlackhansingh, Crinion, Leff, & Price, 2008) of the unified-segmentation procedure (Ashburner & Friston, 2005). The unified-segmentation procedure involves tissue classification based on the signal intensity in each voxel and on a priori knowledge of the expected localization of gray matter, white matter, CSF in the brain. To further improve tissue classification and spatial normalization of lesioned brains, we used a modified segmentation procedure (Seghier et al., 2008). This protocol was developed to resolve problems with misclassification of damaged tissue by including an additional prior for an atypical tissue class (an added "extra" class) to account for the "abnormal" voxels within lesions and thus allowing classification of the outlier voxels (Seghier et al., 2008). Whereas earlier versions of SPM struggled with normalizing and segmenting brains containing large lesions (e.g., Tyler & Stamatakis, 2005), the unified-segment procedure as implemented in SPM5 has been shown to be optimal for spatial normalization of lesioned brains (Crinion et al., 2007). Following segmentation, we visually inspected each of the segmented scans to assess whether segmentation and normalization was successful. Finally, the segmented images were smoothed with a 12-mm FWHM Gaussian filter to accommodate the assumption of random field theory used in the statistical analysis (Worsley, 2004).

The preprocessed gray and white matter maps were then used in the analyses to determine voxel by voxel the relationship between brain damage and our measures of visual enumeration (see below).

Voxel-based Morphometry

Scans from 41 patients, segmented into individual white matter and gray matter maps (see above for the preprocessing protocol), were used in the statistical analysis with SPM8. The voxel-by-voxel correlational relationship between the behavioral measures of visual enumeration and the damaged tissue was assessed separately for gray and white matter integrity. We used parametric statistics within the framework of the general linear model (Kiebel & Holmes, 2003). In each statistical model, we included scores for subitizing and counting performance to account for potential covariation effects and to ensure we could test for dissociated neuronal substrates. Additionally, in the statistical model, we added a binary covariate for the presence of a visual field deficit so that any results cannot be explained by patients simply not seeing (part of) the display. We also added a binary covariate detailing whether the patient had any attentional deficit (neglect or extinction) to rule out that errors in subitizing or counting were simply because of impairments in attention to one side of the display. Finally, we also included, as covariates of no interest, etiology of brain damage, age, handedness, and gender.

We tested for regions that showed an association of a decrease in gray matter/white matter with decreases in overall enumeration using conjunction analyses (Friston, Penny, & Glaser, 2005) across subitization and counting performance. The results are reported based on a combination of peak effect size and cluster size and were corrected for multiple comparisons based on either or both. For completion, we report all clusters with at least 100 voxels showing an effect at $p < .001$, uncorrected. To further validate the lesion dissociations for subitizing and counting, we statistically tested the difference between these two measures in the observed foci, that is, that the correlation effects were larger for subitizing than for counting or vice versa. The results of these F tests are reported in the tables. The anatomical localization of the lesion sites was based on the Duvernoy Human Brain Atlas (Duvernoy, Cabanis, & Vannson, 1991) and the Anatomy toolbox (Tzourio-Mazoyer et al., 2002). Brain coordinates throughout are presented in the standardized MNI space.

RESULTS

Behavioral Results

Accuracy

Overall, the patients' accuracy scores ranged from 14.7% to 100% correct across the full range of numerosities (1–8), with an average of 85.5% correct (*SD* = 21.3). The control performance ranged from 97.9% to 100% correct (mean = 99.1, *SD* = 0.6). Twenty-seven (66%) of the patients fell more than 3 *SD*s from the control mean.

Considering each range separately, for the subitizing range (1–3 items), the patients' accuracy scores ranged from 46.7% to 100% correct, with an average of 95.6% (*SD* = 10.2%). Average subitizing accuracy for the controls was 99.9% (*SD* = 0.4), with a range from 98.9% to 100% correct. Using the control group scores (±3 *SD*s), 12 patients are considered impaired (29%). For the counting range (6–8 items), the patients' accuracy scores ranged from 0% to 100% correct, with an average of 75.79% (*SD* = 30.2%). Counting performance for the controls ranged from 95.6% to 100% correct (mean = 98.1%, *SD* = 1.4%). In comparison with control performance, 27 patients (66%) are considered impaired (>3 *SD*s from the mean). There was a significant correlation between the patients' accuracy on subitizing and on counting ($r = .80$, $p < .001$; Figure 1, Top). For each patient, we also computed his or her average response per numerosity (Figure 1, Bottom). This provides a description of the relative accuracy and type of error made by each patient. For example, an average response of 2 for a five-dot display suggests the patient is undervaluing the number of items present. For descriptive purposes only, we assigned the patients to groups based on their accuracy performances relative to controls: nonimpaired, impaired in subitizing and counting, and impaired in counting only.[2] We note that, as the number of items increased, patients were more likely to undercount than overcount the number of dots per display. This suggests that patients missed items more than they recounted them. Recounting of an item, when it occurred, was more common at the subitizing range, especially for one-dot displays.

In a subset of 28 patients, we were also able to collect data on their performance on a standardized assessment of cognition, the BCoS (www.bcos.bham.ac.uk). We conducted correlations between various measures of accuracy (overall, subitization, and counting) and tests from BCoS measuring sustained attention, working memory, comprehension, general orienting in space and time, executive function and calculation abilities (see Table 1 and Humphreys, Samson, & Bickerton, 2011, for further descriptions of the tests). The time and space orientation and comprehension tests were chosen to control for general comprehension difficulties impeding on patients' performance. In addition, working memory measures were chosen, as this is likely to be involved in counting, when maintaining a running total and keeping track of already counted items (e.g., Tuholski, Engle, & Baylis, 2001). Finally, higher-level functional tests measuring executive function and calculation abilities were also chosen. Accuracy across the counting range (but not the subitization range) was correlated with a measure of executive function (the ability to find the rule by which a spatial pattern changes) and with a measure of calculation (including addition, subtraction, division, and

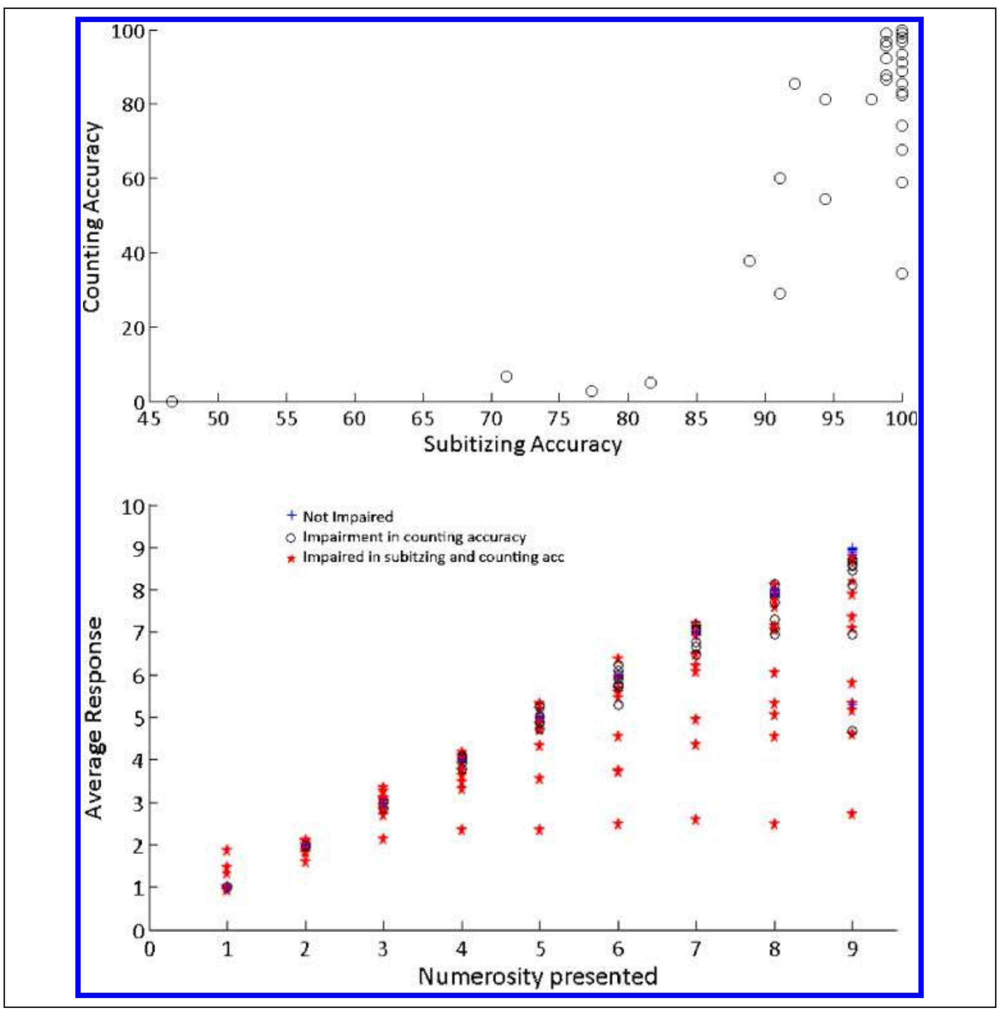

Figure 1. Top: Accuracy performance in the subitizing and counting range for all 41 patients. Bottom: Average response for each presented magnitude for all 41 patients.

Table 1. Correlations across between (i) Overall Accuracy (acc), Accuracy in the Subitization Range (subacc), Accuracy in the Counting Range (countacc), RT Slope in The Subitization Range (subRT), and RT Slope in the Counting Range (countRT) and (ii) Subtests from the BCoS (Humphreys et al., 2011)

BCoS Tasks/Enumeration Measures	*Overall acc*	*subacc*	*countacc*	*subRT*	*countRT*
Sustained attention	−0.03	−0.13	0.03	−0.02	−0.49
Working memory (practices)	−0.13	0.11	−0.20	−0.18	0.46*
General comprehension (~MMSE)	0.12	−0.01	0.16	−0.01	−0.18
Instruction comprehension	−0.03	−0.14	0.01	0.20	−0.19
Executive functioning	0.28	−0.10	0.38*	0.02	−0.20
Calculation	0.35	0.06	0.41*	−0.17	−0.21

The BCoS measures reported here reflect measures of sustained attention (the magnitude of drop across trial blocks in a task requiring the patient to respond to three target words and to refrain from responding to three related distractor words in an auditory list), working memory (the number of times the target words had to be repeated before they could be reported for the sustained attention task), general comprehension (performance on general orienting questions similar to the MMSE), instruction comprehension (the ability to comprehend the instructions during the BCoS), executive functioning (finding the rule guiding shifts of a visual pattern) and calculation (a conglomerate measure of addition, subtraction, multiplication and division).

*Significant correlation ($p < .05$).

multiplication). The full set of correlations is presented in Table 1.

Reaction Time Slopes

The traditional way of assessing the difference between efficient subitizing and less efficient counting with unlimited presentation durations has been to compare the RT slopes in the two ranges, as accuracy is normally at ceiling for both subitizing and counting. Neurologically healthy participants demonstrate a shallow slope for subitizing and a much steeper slope for counting. Steep slopes in the subitizing range suggest a counting strategy for these small numerosities and demonstrate impairment in efficient subitizing (cf. Ashkenazi et al., 2008; Halpern et al., 2007; Lemer et al., 2003).

We removed four outlier patients who scored <85% average correct in enumerating one to three items from the analysis.

Subitizing RT slopes for the patients ranged from 0.42 to 1125.6 msec/item, with an average of 194.90 msec/item (*SD* = 231.5 msec/item). For the controls, the average subitizing RT slope was 42.7 msec/item (*SD* = 21.2 msec/item), with a range from 8.2 to 73.2 msec/item. Nineteen patients (51%) fell more than 3 *SD*s from the control average and were considered impaired. For the counting range (6–8 items), the RT slopes for the patients ranged from 160.83 to 6583.4 msec/item, with an average of 942.15 msec/item (*SD* = 1134.0 msec/item). The range of slope values for the controls was from 196.9 to 456.8 msec/item (mean = 300.0 msec/item, *SD* = 77.9 msec/item). Nineteen patients (51%) fell outside the normal control range and were considered impaired. Note that the two groups of patients who were impaired on the RT measures relative to the controls did not overlap; hence, some patients showed subitizing speed impairments (e.g., because of counting in the subitizing range) whereas others showed deficits on counting when compared with healthy controls. There was no reliable correlation between the RT slopes for subitizing and counting for the group of 37 patients ($r = .24$, $p = .15$). A scatterplot of each patient's RT slope for both the subitizing and counting ranges can be found in Figure 2.

Similar analyses to those performed with the accuracy data were carried out on RT slopes across the subitization and counting parts of the number range. The only reliable correlation was between the RT slope in the counting range and a measure of working memory (Table 1).

Additional Behavioral Measures

Our sample of 41 patients contained nine patients who were reported to have a visual field deficit (two in the right visual field) in the clinical notes. Four of these nine participants had an additional attentional deficit, as well as 11 different patients who also demonstrated an attentional deficit (neglect or extinction; see Methods).

Voxel-based Morphometry Results

We used a voxel-based morphometry analysis based on general linear model statistics to test subitizing- and counting-specific impairments in relation to tissue abnormality in the patients. The analysis demonstrated a marked dissociation between the neuroanatomical substrates of subitizing and counting performance, along with some overlapping areas.

To establish which areas are generally involved in visual enumeration accuracy and given the behavioral correlation on the accuracy measure, we first present a conjunction voxel-based morphometry analysis, which tested for

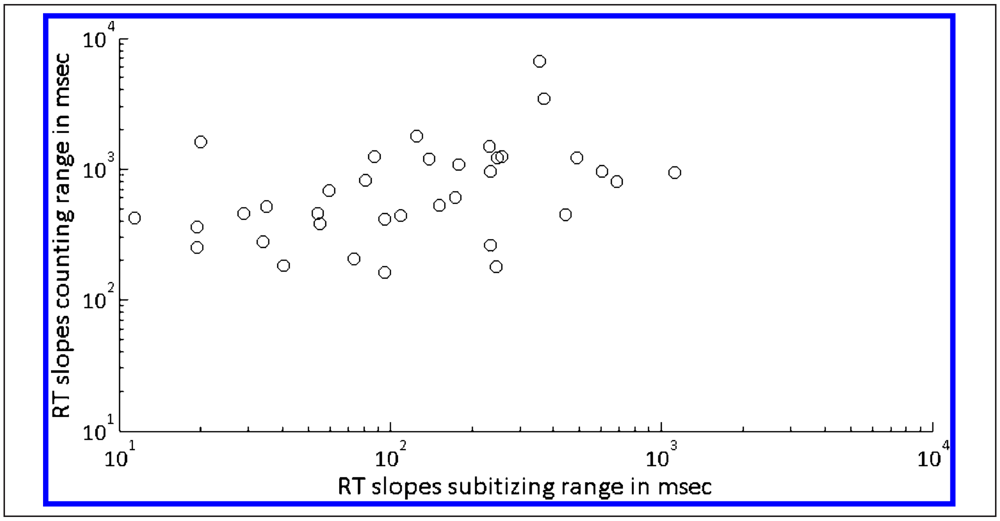

Figure 2. RT slopes in msec in the subitizing and counting range for 37 patients.

gray and white matter voxels associated with impairments in both subitizing and counting accuracy.

Accuracy—All Patients (n = 41)

Visual enumeration: Across the board conjunction (1–3 and 6–8). Gray matter: we found a network of lesions involving bilateral middle and superior occipital areas, parietal areas including the IPS and cuneus and also the anterior superior and medial frontal cortices, all associated with impaired enumeration. For the white matter analysis, we found lesions in bilateral regions comprising the posterior callosal body extending into the optic radiation. The resulting areas are depicted in Figure 3. All results can be found in full in Table 2.

Subitizing range. A failure to accurately enumerate even up to three items was associated with large lesions to the left occipital cortex. This comprised of early visual areas, the left middle occipital gyrus and the left superior occipital gyrus including the tentative visual object area LOC. These regions showed reduced gray matter with decreasing accuracy performance. In addition, there were smaller areas in the right occipital cortex, comprising the right cuneus and a small cluster in the right superior occipital gyrus (right LOC). In addition, a frontal region around the right superior medial gyrus and the right middle frontal gyrus was associated with poor subitizing accuracy. Importantly, all these foci were reliably more associated with performance in the subitizing range than the counting range, suggesting a neuroanatomical dissociation. The

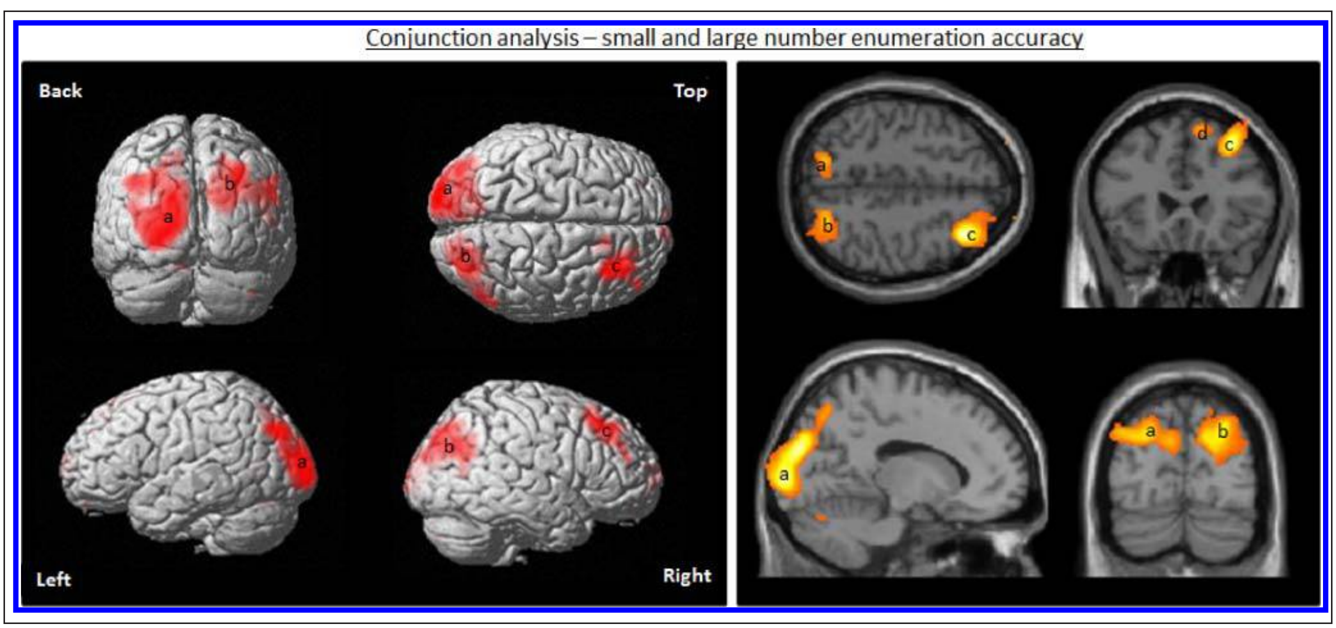

Figure 3. Left: SPM (p < .001, uncorrected) overlaid on a rendered brain, presenting the correlation between gray matter lesions and poor accuracy performance in enumerating elements both in the subitizing and in the counting range (conjunction analysis). Right: gray matter lesions correlating with poor accuracy performance on both subitizing and counting (conjunction). SPM overlaid on T1 weighted MR slices. See Table 2 for anatomical foci labels.

Table 2. The Results Reflect Voxel-based Correlations of Voxel Signal Intensities across the Entire Brains of 41 Patients in a Conjunction Analysis of Subitizing and Counting Accuracy

Contrast	*Cluster Size*	*Label in Figure 3*	*Z (Peak Vx)*	*x y z*	*Location (Brodmann's Area)*
Gray matter					
Enumeration (subitizing + counting conjunction)	4578	[a]	6.56*	−20 −98 0	Left middle occipital gyrus (BA 17/BA 18)
			6.14*	−14 −88 26	Left superior occipital gyrus (BA 18)
			4.9*	−24 −78 36	Left superior parietal lobe extending to the IPS (BA 19, 7)
	2737	[b]	5.13*	17 −84 24	Right cuneus extending to inferior parietal and the IPS (BA 19, 7)
			5.1*	28 −74 40	Right superior occipital gyrus (BA 7/BA 18)
			3.5	48 −66 26	Right middle occipital gyrus (BA 39)
	1607	[c]	6.35*	34 28 48	Right middle frontal gyrus (BA 9)
	141	[d]	3.97	10 64 2	Right superior medial frontal gyrus (BA 10)
White matter					
Enumeration (subitizing + counting conjunction)	1437		5.13*	−12 −60 28	Left optic radiation (near left cuneus and precuneus)
	150		3.42	24 −60 18	Right optic radiation (near right cuneus and precuneus)

x, *y*, and *z* refer to the stereotaxic MNI coordinates of the peak of the cluster. The threshold for significance of the clusters reported here was set at a voxel-wise uncorrected $p < .001$ (whole brain) and a spatial extent of 100 voxels.

*FWE corrected significant ($p < .05$) at peak voxel level.

resulting areas are depicted in Figure 4 (in red). All results can be found in full in Table 3. We note that the foci within the posterior occipital cortices partly overlapped with the lesions related to an overall enumeration problem, suggesting the latter results may have been driven primarily by performance in the subitizing range. The white matter analysis did not result in any suprathreshold clusters.

Counting. Impairments in enumerating large numbers of items (i.e., counting 6–8 items) were associated with lesions to a small area at the frontal pole (see Figure 4, blue areas). This region showed a small but reliable differential effect between subitizing and counting (see Table 3). This lesion site overlapped with the frontopolar region observed before for overall enumeration problems, suggesting that the link to overall problems mostly reflected enumeration impairments in the larger range. In addition, white matter damage to a part of the posterior callosal body was associated with poor enumeration accuracy specifically in the counting range.

The Reduced Group—37 Patients

It is not surprising that patients who cannot accurately enumerate even as few as three items also cannot enumerate large numbers of items, as was evident by the reliable correlation of enumerating accuracy of both ranges. For example, if these patients are impaired at applying FINSTs in the small number range (e.g., Trick & Pylyshyn, 1993), then they will also be poor at reapplying FINSTs in the larger number range. To test neural evidence for an opposite dissociation (an impairment in counting rather than subitizing), we removed the four poorest patients who could not reliably enumerate in the subitizing range

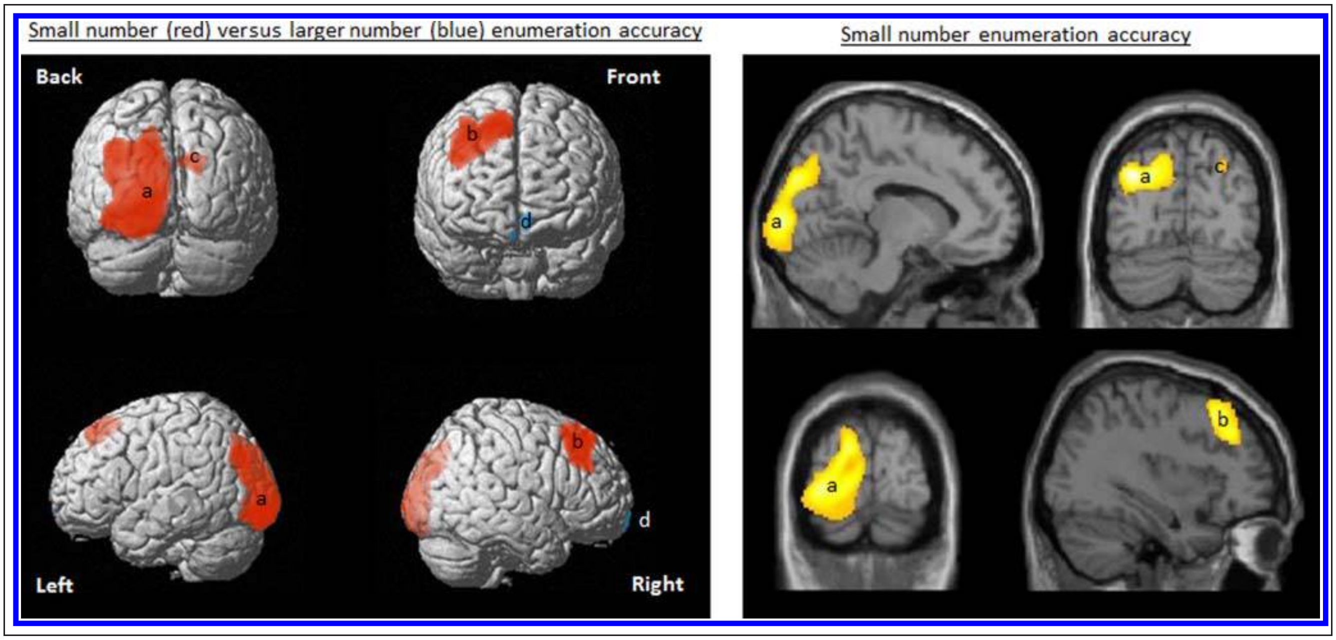

Figure 4. Accuracy results in the full group of patients ($n = 41$). On the left: SPM ($p < .001$) overlaid on a rendered brain, presenting the correlation between gray matter lesions and performance in enumerating small numbers (subitizing range; red) and counting larger numbers (blue). On the right: SPM ($p < .001$) overlaid on a T1 weighted MR saggital and coronal slices presenting regions where gray matter tissue morphometry correlated with accuracy performance on the subitizing range. See Table 3 for anatomical labeling of the reliable clusters.

(see Behavioral Results). Note that this leaves open the possibility that patients who succeed with small numbers may do so by serial counitng rather than some separate (parallel) subitizing process (see below).

When we assessed accuracy in the counting range for this reduced group, we found that reduced gray matter in the horizontal part of the IPS was associated with worsening performance. This focus also showed reliably larger gray matter reduction for counting when compared with subitizing (see Figure 5; Table 4). Although the clusters were relatively small, the peak survived multiple comparisons when we applied small volume corrections using a 10-mm sphere centered on an area previously linked to number-related activity in functional imaging studies (MNI: −31 −62 48, as reported by Piazza, Pinel, Le Bihan, & Dehaene, 2007). Furthermore, using a lower voxel threshold ($p < .01$),

Table 3. The Results Reflect Voxel-based Correlations of Voxel Signal Intensities for Gray Matter across the Entire Brains of 41 Patients with Contrasts Assessing Correlations Specific for Subitizing Accuracy and Counting Accuracy

Contrast	*Cluster Size*	*Label in Figure 4*	*Z (Peak Vx)*	*F(1, 40)*	*x y z*	*Location (Brodmann's Area)*
Subitizing	4806*	[a]	5.09**	31.73	−36 −74 34	Left middle occipital gyrus
			4.82**	22.68	−16 −98 0	(BA 19/BA 18)
			4.69**	23.66	−22 −78 34	Left superior occipital gyrus, left LOC (BA 18)
	1876*	[b]	4.87**	32.03	12 36 52	Right superior medial gyrus (BA 9)
			4.59	18.61	34 26 48	Right middle frontal gyrus (BA 9)
			4.33	21.46	40 36 32	Right superior medial gyrus (BA 46)
	117	[c]	3.49	9.8	14 −80 28	Right cuneus (BA 18)
Counting	187	[d]	3.64	4.53	−2 78 −10	frontal pole/middle orbital (BA 11)

x, *y*, and *z* refer to the stereotaxic MNI coordinates of the peak of the cluster. The threshold for significance of the clusters reported here was set at a voxel-wise uncorrected $p < .001$ (whole brain) and a spatial extent of 100 voxels. *F* scores reflects the effect size of the interaction testing for voxel correlations with subitizing accuracy vs. counting accuracy.

*Cluster significant at FWE corrected level ($p < .05$) for the cluster.

**FWE corrected significant ($p < .05$) at peak voxel level.

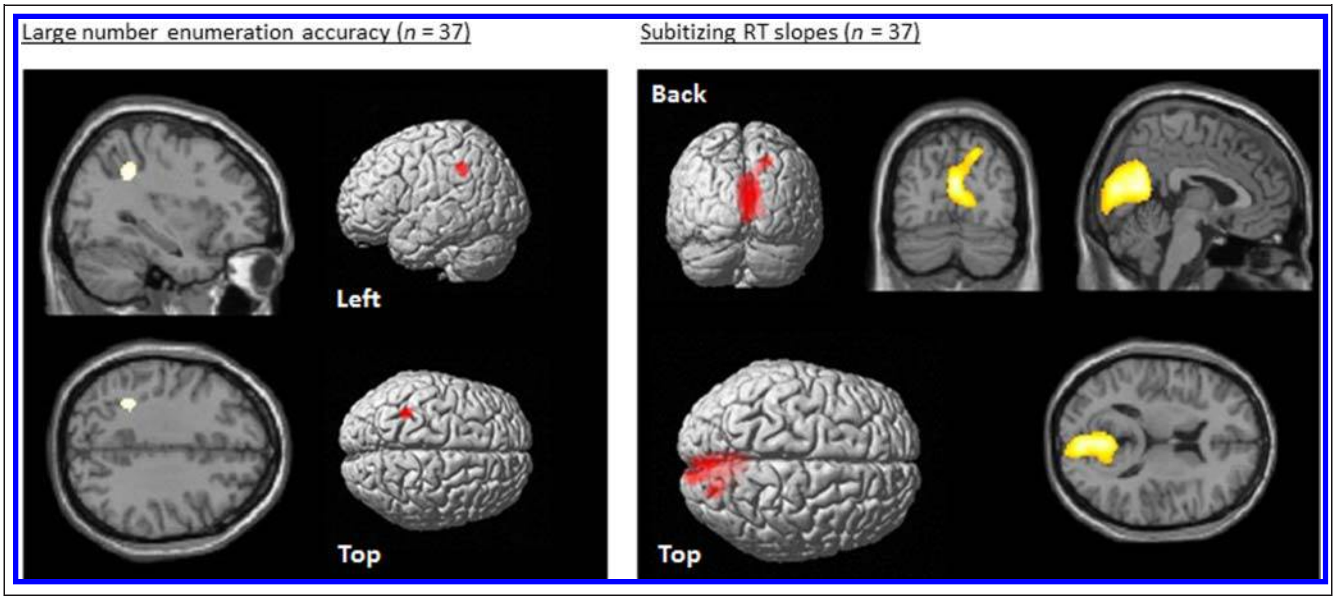

Figure 5. Accuracy and RT slope results in the reduced group ($n = 37$). Left: SPM results ($p < .001$, uncorrected) overlaid on a rendered brain and T1 weighted MR slices showing a correlation between large number enumeration (accuracy) and gray matter morphology. Right: SPM results ($p < .05$ FWE-corrected cluster level) presenting the correlation of gray matter and RT slopes for subitizing.

the cluster was significant with family-wise error (FWE) correction (cluster size = 2141, $P_{FWE} = .043$). No significant white matter areas were found. Not surprisingly, with this subset of patients, there were no suprathreshold clusters for either cortical gray or white matter associated with poor subitizing performance, as all patients performed almost at ceiling for subitizing accuracy. A full table of results is given in Table 4.

As mentioned in the Introduction, the most crucial test for intact subitizing is the efficiency of the enumeration process. For this, we next tested whether the slope of the RT functions correlated with changes in gray and white matter. Given that steeper slopes reflect serial counting rather than parallel subitization, we hypothesized that patients who suffer a lesion to regions involved in subitizing will show steeper slopes for enumerating small numbers.

The RT slopes for subitizing correlated with reduced gray matter in a large medial bilateral (though more pronounced on the right) occipital area comprising the calcarine gyrus

Table 4. The Results Reflect Voxel-based Correlations of Voxel Signal Intensities across the Entire Brains of 37 Patients with Contrasts Assessing Correlations Specific for Subitizing Accuracy, Counting Accuracy and Subitizing Speeds and Counting Speeds Separately

Contrast	*Cluster Size*	*Z (Peak Vx)*	*F(1, 36)*	*x y z*	*Location*
Accuracy					
Subitizing		No suprathreshold results			
Counting	125	3.16	*ns*	−32 −46 36	Left horizontal part of IPS (BA 40)
RT slopes					
Subitizing	3212*	4.97**	34.95	2 −62 20	Right precuneus (BA 23)
		4.7**	32.27	2 −80 14	Right cuneus (BA 18)
		3.93	20.72	20 −76 46	Bilateral calcarine gyrus (BA 19, BA 7)
Counting		No suprathreshold results			

x, y, and z refer to the stereotaxic MNI coordinates of the peak of the cluster. The threshold for significance of the clusters reported here was set at a voxel-wise uncorrected $p < .001$ (whole brain) and a spatial extent of 100 voxels.

*Cluster significant at FWE-corrected level for the cluster.

**FWE-corrected significant at peak voxel level.

as well as the cuneus and precuneus (see Figure 5). Lesions in these regions were reliably more associated with subitizing than counting slopes (Table 4). There were no suprathreshold white matter results. For enumerating in the counting range, no areas were found to be selectively associated with poor RT slopes (both in gray and white matter analyses).

In a final analysis, we removed patients with a visual field deficit. This was done because a visual field deficit may mean that patients have to take more time exploring and scanning a display. This may lead in turn to an incorrect representation of their RT slopes. After the five patients who had a visual field deficit were removed, the analysis included 32 patients only, which means it had a reduced power. We used a similar model as above, focusing on the RT slopes, but with the exception of one less covariate (no visual field deficit).

Despite removing the hemianopic patients, steeper RT slopes for subitizing correlated with damage to a large area around the left rolandic operculum and precentral gyrus (significant at FWE-cluster corrected, with cluster size of 873). In addition, we observed that reduced gray matter correlated with steeper subitizing RT slopes in an area around the right superior occipital gyrus and cuneus, as well as additional areas in the left thalamus, the left inferior temporal gyrus, middle cingulate and inferior frontal gyrus (see Figure 6 and Table 5). We speculate that removing the hemianopic patients may have reduced some of the variance, allowing weaker effects to become statistically reliable at peak level, although they do not survive cluster correction (see Table 5). Therefore, we will not discuss these smaller clusters in more detail.

There were no suprathreshold white matter results. For enumerating in the counting range, no areas were found to be selectively associated with poor RT slopes (both in gray and white matter analyses).

DISCUSSION

This article presents a lesion–symptom analysis of deficits in enumeration after brain lesion. We found that lesions to several parts of a network including bilateral visual areas, higher occipito-parietal areas, and frontal gyri were detrimental to accurate visual enumeration. This is in line with fMRI results, where visual enumeration tasks activate a large number of extrastriate and fronto-parietal regions, and the results likely reflect some common processes involved in subitizing and exact counting (e.g., Sathian et al., 1999). However, in contrast to most functional imaging studies, we were able to separate out areas that were uniquely associated with enumerating small and large numbers. We investigated both accuracy performance and RT slopes for the enumeration function to differentiate the neuroanatomical structures necessary for the different numerosity ranges (small: 1–3 and large: 6–8). The data point to a clear dissociation between the sites of damage associated with selective problems in each number range, when variance because of a deficit in the alternative range was extracted. Note that the correlations of the neural changes with deficits in enumeration occurred even with variance because of the presence of visual field defects and attentional problems (e.g., neglect) factored out.

The behavioral data demonstrate that patients who are poor in terms of their subitizing accuracy tend also to make errors when counting. Given that even subitization is inaccurate, these patients also do not have recourse to a compensatory process of counting small numbers of

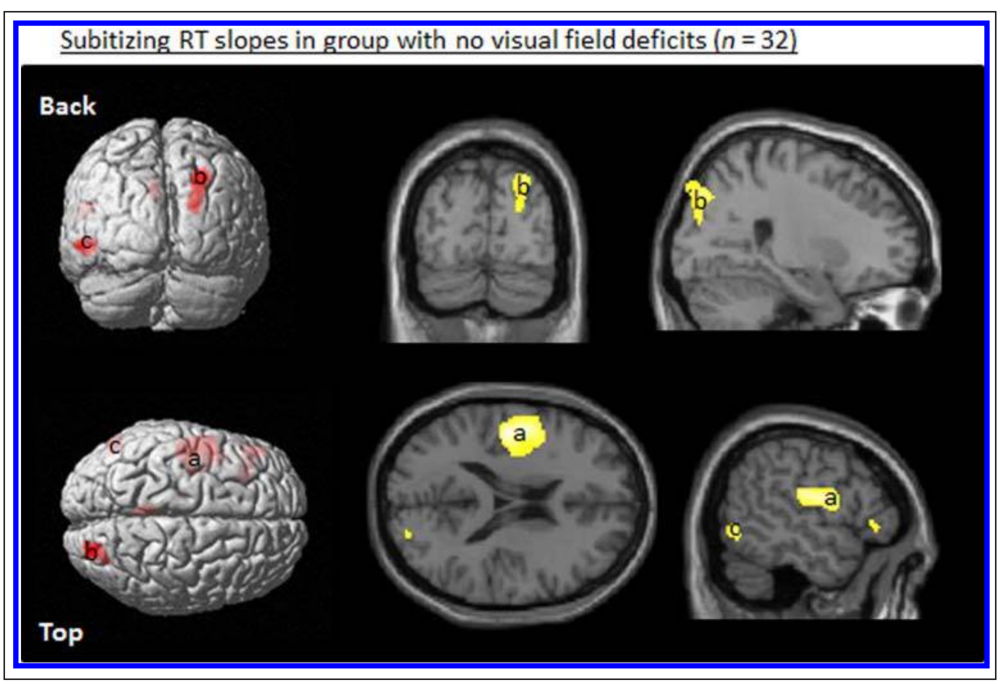

Figure 6. RT slope results in the group with no visual field deficits (n = 32). SPM results (p < .001, uncorrected) overlaid on a rendered brain and T1 weighted MR slices showing a correlation between subitizing speeds (RT slopes) and gray matter morphology. The anatomical labels and coordinates for the peaks can be found in Table 5.

Table 5. The Results Reflect Voxel-based Correlations of Voxel Signal Intensities for Gray Matter across the Entire Brains of 32 Patients (All Patients with Any Visual Field Deficits Removed) with Contrasts Assessing Correlations Specific for Subitizing Speeds and Counting Speeds Separately

Contrast	*Cluster size*	*Label in Figure 6*	*Z (Peak Vx)*	*x y z*	*Location (BA)*
Gray matter					
RT slopes	873*	[a]	4.12	−46 −16 20	Left rolandic operculum (BA 48)
Subitizing			3.92	−50 −4 20	Left precentral gyrus (BA 48)
	100		4.05	−14 −14 12	Left thalamus
	347	[b]	3.6	26 −82 42	Right superior occipital gyrus (BA 19)
			3.53	22 −86 22	extending to right cuneus (BA 18)
	133	[c]	3.58	−52 −68 −6	Left inferior temporal gyrus (BA 37)
	120		3.55	−6 −44 34	Left middle cingulate (BA 23)
	358		3.51	−48 32 −2	Left inferior frontal gyrus (BA 47)
			3.46	−32 28 6	Left insular lobule (BA 47)
Counting		No suprathreshold results			
White matter		No suprathreshold results			

x, *y*, and *z* refer to the stereotaxic MNI coordinates of the peak of the cluster. The threshold for significance of the clusters reported here was set at a voxel-wise uncorrected $p < .001$ (whole brain) and a spatial extent of 100 voxels.

*Cluster significant at FWE-corrected level ($p < .05$) for the cluster.

items individually. Interestingly, with the very inaccurate patients removed, RT slopes in the subitization and counting ranges did not correlate (Figure 2). We suggest that patients with a high subitization slope, but with accurate performance, resorted to serial counting of individual stimuli even in the subitization range (reflecting loss of parallel subitization but implementation of a compensatory strategy). Patients with intact RT slopes in the subitization range but impaired slopes for counting larger numbers may then have disturbance to other processes that are "weighted" more strongly for counting, including working memory and verbalisation. In this respect, it is interesting to note the results of the behavioral correlations between the RT slopes for counting and standard measures of cognition (from the BcoS; Humphreys et al., 2011), which revealed reliable correlations with a measure of working memory (Table 1).

In the first accuracy analysis, severely impaired enumeration in the small number range was linked to damage in a number of occipital regions bilaterally, although more strongly on the left, including the left middle occipital gyrus and the bilateral superior occipital gyrus, comprising LOC and the right cuneus. In addition, an area in the right superior medial gyrus was implicated. There was no associated white matter change. In contrast, accuracy impairments in the larger number range were linked to damage in the frontal pole. The damage to more frontal regions, associated with inaccurate counting, may reflect processes such as keeping a running count of the items and guiding visual attention, necessary to assimilate displays with large numbers of items. Again the correlations with the BCoS tests are informative, because accuracy in the counting range was linked with poor executive function (e.g., keeping a running account of shifts in a visual pattern) and in calculation, suggesting that these basic processes contribute to the accuracy of counting. The damage to the more posterior areas we consider in more detail below. One difficulty with this analysis is that it includes the patients who were impaired at counting both small and large numbers; this may obscure any dissociative pattern given that patients with poor accuracy on small numbers are also inaccurate with larger number displays. Interestingly, with the four most severe patients removed, the analysis of the accuracy scores did reveal a selective impairment for larger numbers associated with damage to the left horizontal part of the IPS.

Next, RT slopes were investigated. To dissociate true (fast and efficient) subitizing (parallel processing) from the slower, more effortful counting process, the slope of the RT function (the RT cost for every item added) was used as our dependent variable. In the small numerosity range, a shallow slope indicates efficient subitizing, whereas slower slopes point to a counting strategy even with a small set size. Damage to bilateral early occipital areas (calcarine gyrus), more heavily pronounced on the right and extending into right cuneus and precuneus, was associated with steep RT slopes in the subitization range. This suggests that, when these areas are damaged, a counting strategy, rather than efficient subitizing was used to enumerate these small sets of elements (1–3 items). Interestingly, even when removing patients with any visual field deficit, damage to higher occipital areas still correlated with impaired subitizing, confirming the idea that fast and parallel subitizing strongly weights early visual processes.

In addition to this, we found damage to the left rolandic operculum and precentral gyrus to be associated with steeper subitizing slopes. The posterior part of the precentral gyrus has been traditionally linked with hand–body representations in primary motor cortex (e.g., Sanes, Donoghue, Venkatesan, Edelman, & Warach, 1995). Although this finding was not predicted here, we can speculate that the occurrence of finger representations in a visual enumeration task might be related to the importance of finger-counting in number learning (e.g., Wiese, 2003). Its occurrence specifically in the subitizing range rather than the counting range remains unexpected, although one might again speculate it to be the embodiment of the FINST principle, with its maximum of four fingers of instantiation (Julesz, 1984).

Counting

Although the analysis across the full patient group revealed an association between impaired counting accuracy and damage to the frontal pole, it is possible that this was contributed to by patients with poor subitizing as well as counting, as this finding was also present in the conjunction analysis. Consistent with this, the analysis including only the less impaired cases revealed a single correlation with damage to the left IPS. Tasks involving symbolic numbers (such as mental arithmetic and number comparisons) have repeatedly indicated the involvement of bilateral IPS in number representation (for a review, see Dehaene, Piazza, Pinel, & Cohen, 2003). Interestingly, we also found that counting accuracy correlated with a calculation measure taken from the BCoS screening tool. More recently, studies have investigated how nonsymbolic number (e.g., dot displays such as the ones used in this study) relate to this "abstract number area" in the IPS. Although not universally found (Shuman & Kanwisher, 2004), several studies have revealed selective number-specific adaptation effects in the IPS (e.g., Ansari, Dhital, & Siong, 2006; Cantlon, Brannon, Carter, & Pelphrey, 2006). Piazza et al. (2007) found that neural adaptation occurred irrespective of whether the numbers were conveyed in a symbolic (Arabic numeral) or nonsymbolic (dot pattern) format, suggesting that the IPS may contain representations that respond to an abstract number irrespective of how it is presented. Our data indicate that the left IPS can support both accurate counting and subitizing, as revealed by its reliable emergence in the conjunction analysis. Where patients have inaccurate subitization and counting, although it is likely that a compensatory counting process cannot be recruited to support subitization, and this may mask evidence for selective involvement of the IPS in counting, When the patients with very impaired subitization accuracy were removed, then the IPS correlated selectively with the accuracy of counting. This is consistent with the IPS being necessary for counting, reflecting (e.g.) updating of number representation as the enumeration of larger numbers proceeds.

Subitizing

Severe impairments in the ability to enumerate even small numbers of items have been reported before in case studies of simultanagnosic patients (e.g., Demeyere & Humphreys, 2007; Humphreys, 1998). In our first analysis, linking accuracy of small enumeration to changes in gray matter, we found lesions to the left posterior occipital cortex, bilateral lateral occipital cortex, and the right superior frontal cortex to be detrimental for the ability to correctly enumerate small numbers of items. Given the factors controlled for in our model analysis, these deficits suggest a critical role for these brain regions in apprehending small number over and above loss of visual field and or the allocation of attention to space. For example, these regions may support a spatial indexing process (cf. Trick & Pylyshyn, 1994) necessary for the parallel subitization of small numbers. A deficit in spatial indexing would render it difficult to count large arrays too, if the same spatial indices are recruited. Interestingly, none of our patients had frank problems in the recognition of simple objects, making it unlikely that poor pattern recognition per se was a contributory factor (cf. Mandler & Shebo, 1982).

In normal participants, subitizing is not only accurate but also efficient. When investigating the RT slopes for the less severe cases, we found that damage to the right calcarine gyrus, extending into right cuneus and precuneus, was associated with steep RT slopes in the subitizing range. This suggests that when these areas were damaged, a counting strategy, rather than efficient subitizing, was used to enumerate these small sets of elements (1–3 items). That damage was associated with an abnormal slope on the subitization counting function suggests that these regions are necessary for the efficient, parallel apprehension of a small number of objects. We note that damage to the precuneus (along with underlying white matter) has been associated with simultanagnosia (Riddoch et al., 2010;

Raichle et al., 2001), and we might expect that a lesion that impairs the rapid apprehension of a small number of objects will lead to patients being aware only of a limited number of objects at a time. Other studies have also found simultanagnosia to be linked to poor subitizing ability (Demeyere & Humphreys, 2007; Humphreys, 1998; Dehaene & Cohen, 1994) as well as to a poor representation of global shape (e.g., Friedman-Hill, Robertson, & Treisman, 1995; Coslett & Saffran, 1991). It is therefore conceivable that similar mechanisms underly both detailed global perception and subitizing. Himmelbach, Erb, Klockgether, Moskau, and Karnath (2009), in an event-related fMRI study of a simultanagnosic patient, found bilateral activations for the primary intermediate sulcus and the precuneus when the patient correctly saw "the whole" global stimulus (a compound letter), compared with when she was not able to see the global level. It can be argued that this awareness of the whole is impaired in patients with simultanagnosia and linked to poor parallel apprehension of stimuli in sufficient detail to discriminate between small number displays. Where patients show implicit global processing (e.g., see Demeyere & Humphreys, 2007; Shalev, Humphreys, & Mevorach, 2005), this may depend on more approximate representations that do not support subitization.

Conclusions

We have demonstrated the necessary regions associated with impairments in subitizing and counting by using a voxel-by-voxel correlation method in a large sample of neuropsychological patients. Overall visual enumeration impairments were associated with damage to a network of areas comprising bilateral visual areas, higher occipito-parietal areas, and frontal gyri. This matches fMRI activations in counting tasks (Piazza et al., 2003; Sathian et al., 1999). The damage to more frontal regions, associated with poor counting, may reflect additional processes such as keeping a running count of the items and guiding visual attention. When the poorest patients were removed, damage to the left IPS was found to selectively disrupt the enumeration of larger numbers. In contrast, poor subitization was linked to damage to earlier visual regions and the precuneus. The data highlight that deficits to the enumeration of small and larger numbers follow different lesions, supporting the argument for the functional distinction between subitization and counting.

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Notes

1. Numerosity 5 was also omitted to enable us to compare an equal number of numerosities in the "small" and "large" ranges.
2. There were no patients who showed impaired accuracy on subitization but showed normal accuracy on counting.

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